Faunistical and ecological studies on the bark-dwelling spiders (*Araneae*) living on Black Pine (*Pinus nigra*) in urban and forest habitats

Doktori (PhD) értekezés

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Debrecen, 2004.

Contents

Study I – Horváth, R. & Szinetár, Cs. (1998): Study of the bark-dwelling spiders (*Araneae*) on black pine (*Pinus nigra*) I. *Miscellanea Zoologica Hungarica*, **12**: 77-83.

Study II – Horváth, R. & Szinetár, Cs. (2002): Ecofaunistical study of bark-dwelling spiders (*Araneae*) on black pine (*Pinus nigra*) in urban and forest habitats. *Acta Biologica Debrecina*, **24**: 87-101.

Study III – Horváth, R., Magura, T. & Szinetár, Cs. (2001): Effects of immission load on spider living on black pine. *Biodiversity and Conservation*, **10**: 1531-1542.

Study IV – Horváth, R., Lengyel, Sz., Szinetár, Cs. & 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. *Edited by* F. Samu and Cs. Szinetár. Plant Protection Institute and Berzsenyi College, Budapest. pp. 95-102.

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1. Introduction

1.1. State of the art

Trees represent well-defined and unique habitats for animals. On the one hand, trees are structurally complex and include several microhabitats (foliage, branch, trunk). Thus, they provide ample opportunity for niche-segregation (Lawton 1978). On the other hand, trees provide a stable food source for animals dwelling on them (Southwood 1978). These characters are coupled with a large geographical range in most tree species (Strong 1979). All these factors result in a high species richness and diversity of tree-living animal communities. It also follows that arthropod animal assemblages of characteristic species composition are found on trees (Moran & Southwood 1982). In animal assemblages dwelling on trees the arthropod groups represented by the highest number of species are (i) phytophagous organisms consuming the organic material (wood) of the tree, (ii) parasitoids, (iii) predatory arthropods, and (iv) the so-called tourists, i.e., insects that primarily fly and stay on trees only temporarily (Moran & Southwood 1982).

With respect to the proportions of the above groups, differences are found in the case of trees with different foliage or canopy structure. With respect to the number of individuals, phytophagous insects are obviously the dominant group, which comprise up to 68% of the total number of individuals according to some studies (Moran & Southwood 1982). With respect to biomass, this primary consumer group again is the dominant one (54%), but predatory insects also have a substantial share (26%) (Moran & Southwood 1982).

Tree trunks, as a distinctive microhabitat of the tree, are characterised by numerous unique biotic and abiotic environmental factors, which explains why we can also discern a separate, so-called bark-dwelling arthropod assemblage. Of the abiotic factors, the structure and colour of the bark and the microclimatic factors closely associated to them have a primary role. For example, in the deeper layers and below the bark temperature is consistently higher and more even than on the surface of the bark. The different and more even heat conditions of the bark as a potential hiding place well explain the long-lasting or temporary colonisation of numerous arthropods. Furthermore, in the part of the trunk exposed to the south, similarly to south-facing slopes of mountain ranges, the surface temperature is even higher than in those parts of the trunk that face other compass directions. Since the south-facing parts operate as a heat trap, arthropod communities are more speciose here (Putman & Wraten 1984) (Fig. 1.).

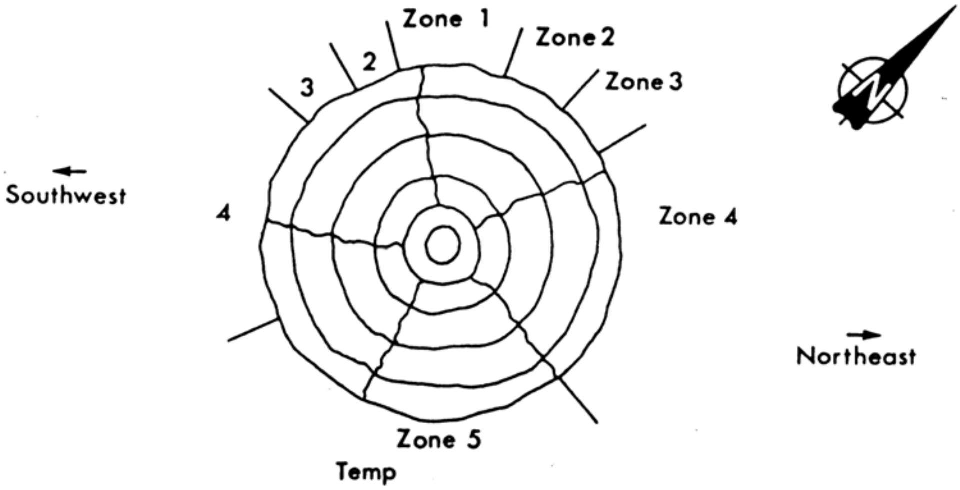


Figure 1. Microclimatic variation in a decaying tree trunk. Source: Schimitschek (1931).

On trees with darker bark we can experience substantial differences with respect to measured temperature compared to the bark of lighter colours (Nicolai 1986). Spiders represent a dominant taxon of bark-dwelling predatory arthropods. Well-recognisable adaptation phenomena, which can be observed in bark-dwelling spiders, provide evidence for the evolution of species living on or under the bark. This process is a sequential evolution, in which the relationship between the plant and the arthropod living on it is essentially asymmetric, i.e. not of a coevolutionary type, rather, the animals follow the evolution of the host plant without significantly affecting it (Jermy 1987). Adaptations of bark-dwelling spiders can be seen in morphology, phenology, and physiology.

One of the morphological adaptations is the typical body shape observable in many species (e.g. *Araneidae*: *Nuctenea umbratica* (Clerck, 1757), *Philodromidae*: *Philodromus margaritatus* (Clerck, 1757), *Philodromus fuscomarginatus* (De Geer, 1778), *Thomisidae*: *Coriarachne depressa* [C. L. Koch, 1837]). The body of these species is characteristically flattened, which well reflects an adaptation to modes of living between the bark layers or under the bark. This adaptation can be coupled with colour adaptations. *Philodromus fuscomarginatus*, for example, blends well with its reddish-brown coloration into the phloem layer of Scots Pine (*Pinus sylvestris*), which is the almost exclusive habitat of this philodromid spider. *Philodromus margaritatus* with its dark colours blends well into the surface of trees with darker bark, and can thus hide from predators, mainly birds, that consume it.

The most important of the phenological adaptations is that many exclusive bark-dwelling species are eurychron, i.e. adults and juveniles can be found year-round, or diplochron, i.e., the species has two reproductive periods annually. Reproduction throughout the entire year or throughout a substantial part of the year is made possible by the higher and more even temperature under the bark. Besides temperature, prey availability also can play a role in the phenological changes. Furthermore, in the case of the so-called facultative bark-dwelling species, i.e., species that use the bark only for overwintering, adaptation to the bark as an overwintering habitat can be observed.

The more even microclimate makes physiological adaptations possible in species living here, which is manifest in a prolonged activity periods. This means that these species occasionally can move, or even feed even during the coldest winter months (e.g. *Collembola*, *Aphidina*, *Diptera*). Besides, in many insect groups that overwinter in or under the bark (e.g. *Lygaeidae*, *Pyrrhocoridae*, *Coleoptera*), the phenomenon of late-winter sunbathing can be observed due to a more even microclimate.

We can find several examples of adaptation to the biotic factors of tree bark in spiders. Among these, we can first highlight the different structure of tree species. This means that we can experience rather strong differences with respect to the species spectrum in the case of tree species that have different bark structure. The more specific the bark structure of a tree, the more unique the spider species assemblage on the bark of the given tree species (Kovács 2002).

The other important biotic factor to which spiders adapt is the presence of prey animals. Because spiders are generalist predators, normally the quantitative conditions, rather than the quality composition of the prey influences them. This is because when the prey animals are present in suitable quantities in a given habitat, other factors can play a primary role in the formation of spider communities (Gunnarsson 1988, 1990).

The third biotic adaptation serves the purpose of defence against predators. One example is the adaptation in coloration to the colour of the tree bark, already mentioned above. Furthermore, the bark, due to its peculiar structure, can provide excellent protection to the spiders living under it because only a few bird species (e.g. nuthatch, tree-creepers) search for prey under the surface of the bark. Furthermore, the protection against predators is served also by the peculiar diurnal activity. This is because a large number of spider species showing nocturnal activity lives under the bark, thereby reducing the predation pressure caused by birds (Gunnarsson 1983, 1998).

Relatively few studies have been published on bark-dwelling spiders to date, and most of them are of a rather faunistical nature (Koslinska 1967; Albert 1976; Hansen 1992; Weiss 1995; Koponen 1996; Sebestyén 1996; Richman 2003), and only a few authors have studied the ecological-environmental factors affecting bark-dwelling spiders (Wunderlich 1982; Nicolai 1986; Bogya 1995; Simon, U. 1995; Kovács 2002). Koslinska (1967) conducted surveys concerning bark-dwelling arachnids by removing the bark, i.e., by hand catching in orchards in Poland (Kraków, Lódz). She found that web-building spider species were dominant over active hunters in both orchards. Albert (1976) mentioned only one species, *Drapetisca socialis* (Sundevall, 1833) as that living exclusively on the bark of European Beech (*Fagus sylvatica*) at the level of the trunk in the area of the Solling Project Ecosystem Research, although *Meioneta innotabilis* (O. P.-Cambridge, 1863) was also included in his collection. Based on our current knowledge, the latter species is considered a bark-dwelling species. Albert (1976) stated that 49 of the 85 species he studied occurred characteristically on the tree trunk and not at the ground-level. Hansen (1992) investigated the spider fauna, and particularly the biota of the bark, of a park tree species favoured in cities, the London Planetree (*Platanus hybrida*) in Venice, Italy between 1982 and 1985. In his studies, he found 68 spider species on the planetree bark, among which 22 was new to the fauna of Venice and three species (*Oonops domesticus* Dalmas, 1916; *Philodromus albidus* Kulczynski, 1911 and *Midia midas* [Simon, 1884]) were new even to the fauna of Italy. Furthermore, he came across a species (*Tuberta maerens* [O. P.-Cambridge, 1863]), which had not been found in Italy for 120 years before. Weiss (1995) collected spiders and harvestmen in forests at different altitudes above sea level in Bavarian Forest National Park, Germany, by using modified pitfall traps at different heights of the trunk of living and dead Norway Spruce (*Picea abies*). In the course of his studies he showed that the spider communities collected at the bottom of the trunk or from fallen trunks showed a great similarity to each other. In contrast, the community of traps installed at higher parts of the trunk differed considerably from the above communities. Koponen (1996) studied bark- and foliage-dwelling spiders on English Oak (*Quercus robur*) in north-western Finland, but could not find significant differences when he compared the collected material with communities of beech and pine species from other areas of Europe. In Hungary, such studies have been carried out since 1994. In connection with research by Hansen, a survey of the bark-dwelling spiders of planetree has been carried out (Sebestyén 1996). In her studies Sebestyén (1996) collected spiders using three sampling methods (belt traps, hand catching, and bark-sifting) and documented 45 species from the areas. Richman (2003) collected spiders living on the bark and on the branches using glue traps in pecan nut plantations in New Mexico, Texas and Arizona. During his studies he managed to detect 30 species among which the *Anyphaenidae* species *Hibana incursa* (Chamberlin, 1919) was represented by large numbers from the Mesilla Valley in New Mexico. This species can play a substantial role in the protection against pests because it consumes both the aphids living on pecan nuts and the moth *Acrobasis* *nuxvorella* Neunzig, 1970, belonging to the family of Pyralidae, which is one of the most important pests of this tree species.

In Central Europe, trunk-dwelling spider species were first listed by Wunderlich (1982), who also characterised their basic ecological properties. Nicolai (1986) has classified the tree species studied based on their bark structure into smooth surface bark, light surface bark, cracked bark and scaly bark categories. He also gave a description of the basic physical properties of the bark of every tree species. Furthermore, he collected spiders and other arthropod taxa from these tree species using hand catching and hand-held suction sampler. He concluded that *Drapetisca socialis*, which previously had been thought to live primarily on European Beech, was far more common on Silver Birch (*Betula pendula*). *Meioneta innotabilis* and *Moebelia penicillata* (Westring 1951) occurred in greatest numbers on trees with cracked or scaly bark surfaces. The highest number of species and individuals was found on Sessile Oak (*Quercus petraea*), which has the most structured bark of the trees studied. On trees with a more structured bark he found higher diversity and evenness than on trees with less structured bark. Bogya (1995) examined the role spiders play in orchard monocultures. He studied clubionid spiders on apple trees, which spiders are a potential means of biological control. During his experiments it was proven that spiders consume arthropod pests of apple trees (e.g. *Tortricidae* caterpillars, pear lace bug and aphids) in considerable amounts. Therefore, spiders can play an important role in the battle against pests. Simon U. (1995) conducted the most comprehensive study of spiders living on Scots Pine from the soil to the canopy in Germany, by which he was able to establish stratocoenoses or assemblages characteristic to a layer. First he considered those species that can be considered generalists from the perspective of above-ground height, i.e., that did not show any special attachment to any of the designated height levels. Besides these, he unambiguously separated three groups, comprising of species living (i) in the bottom, (ii) in the middle and (iii) in the upper trunk level (Fig. 2.). Kovács (2002) found that the bark structure of the tree species studied (*Pinus sylvestris*, *Quercus petraea*, *Fagus sylvatica*) has an important role in the formation of bark-dwelling species assemblages.

1.2. Aims of the study

My current work describes the results of a faunistical and ecological study of bark-dwelling spiders of Black Pine (*Pinus nigra subsp. nigra*). The study is the most comprehensive of its kind to date. I chose Black Pine because it is very wide-spread in Hungary even though it is not native, and the canopy-dwelling spiders have been surveyed previously in several locations in Hungary (Balogh 1935; Szinetár 1996). I conducted the study at seven sampling locations in two large landscape regions of Hungary (in Western Hungary: Szombathely – Millennium Park [formerly Gagarin Avenue], Csónakázó pond, Paragvári Street; Kőszeg Mountains – Bozsok, Hörman spring, and in the Great-Plain: Debrecen – Nagyerdő forest, Fancsika ponds).

In my dissertation, I aimed to study the following questions in detail:

1a. Which species and in which composition of hunting strategies occur on the bark?
1b. What are the typical species of Black Pine?
1c. What characteristic differences can be shown between urban and forest habitats? (Study I – V.)

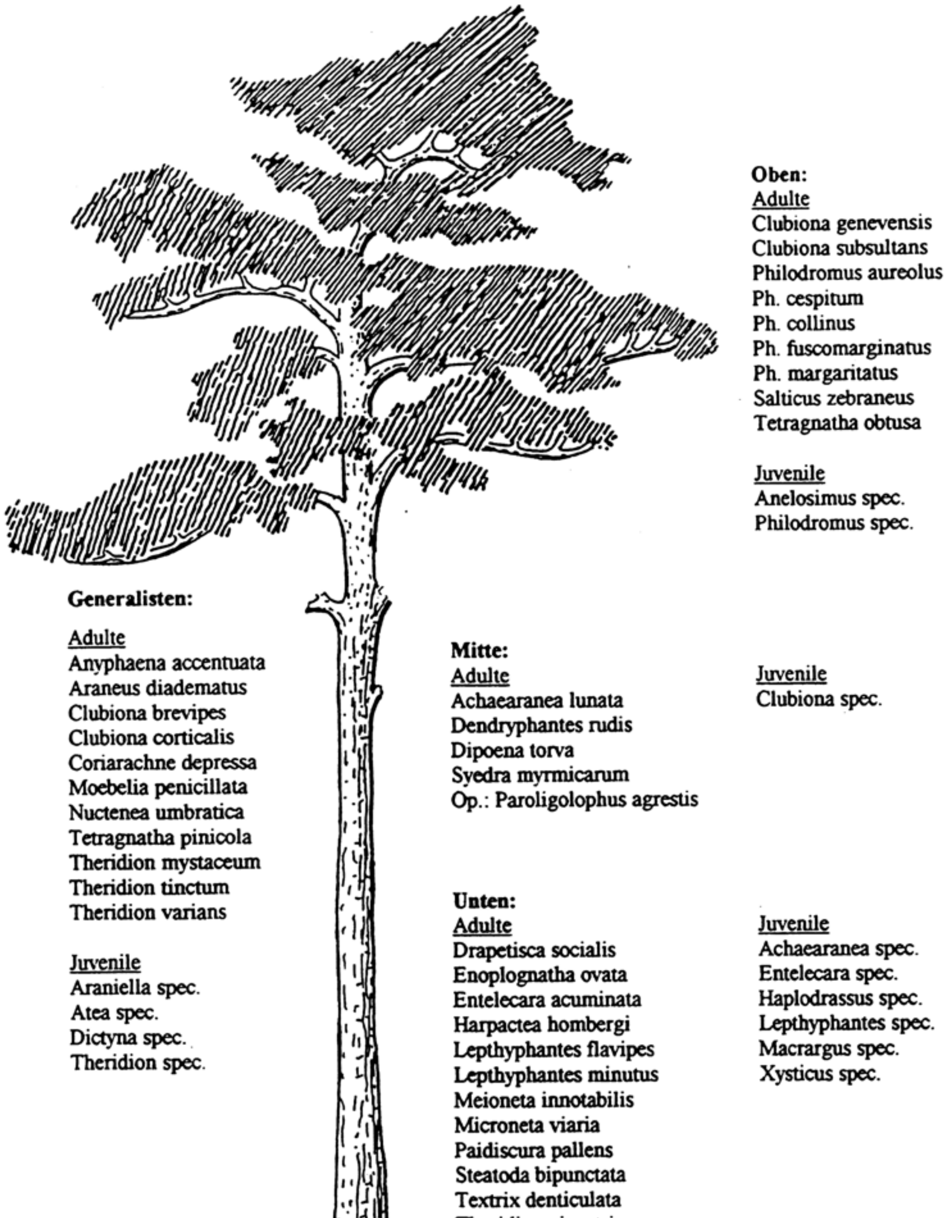


Figure 2. A classification of spiders and harvestmen on Scots Pine (*Pinus sylvestris*) based on their preferred above-ground height. Source: Simon, U. (1995).

2a. Are bark-dwelling spiders sensitive to air pollution?
2b. Can differences be detected in species richness and diversity between differently polluted areas in the city of Szombathely?
2c. Which species can be considered good indicators of air pollution? (Study II – III.)

3. Does trap exposition time or air temperature have a major role in the movement of spiders under the bark for overwintering? (Study IV)

4a. Are there differences in spider communities and their prey animals between urban and forest habitats in different seasons?
4b. Can correlations be detected between the number of individuals, species richness and diversity of spiders and the quantitative relations of prey in different areas?
4c. Is there a relationship between the number of individuals and species richness of spiders belonging to different guilds and the number of their prey?
4d. What correlation exists between the number of prey and the number of individuals of exclusive or facultative bark-dwelling spiders? (Study V)

2. Material and methods

2.1. Study areas and sampling methods

Spiders were collected by traps fixed on trunks of Black Pines in seven localities between 1996 and 2000. In 1996, spiders were collected at two sampling sites in the city of Szombathely (UTM coordinate XN23) and at one forest site (Hörman spring, Kőszeg Mountains XN14). From 1997 to 1999, spiders were collected at three sites in Szombathely and at three forest sites, one in W-Hungary (near the village of Bozsok, XN14) and two in E-Hungary (Debrecen: Nagyerdő forest: ET46, Fancsika ponds: ET56). In 1999, the potential prey of spiders were also collected using nylon traps fixed on the same trees. In 2000 only one E-Hungarian sampling site was used (Fig. 3.). In all of these sites, Black Pine plantations were planted during or shortly after the second World War. A short description of the sampling sites is given below.

(1) Szombathely, Millennium Park (formerly called Gagarin Avenue): This site was studied between 1996 and 1999. The site is in a park along the avenue, which is surrounded by residential areas. There is small traffic at the edge of the park, and immission load from air pollution is minimal (Photo 1.).

(2) Szombathely, Paragvári Street: This site was surveyed from 1996 to 1999. Black Pines are located along a main road, and because of heavy traffic, immission load is high (Photo 2).

(3) Szombathely, Csónakázó pond: This site, sampled from 1997 to 1999, is also in a park and pine trees are located along a small road between an artificial pond and an open-air swimming pool. Traffic is weak and the site is only moderately polluted (Photo 3).

(4) Kőszeg Mountains, Hörman spring: This site, studied in 1996 only, is situated in the southern part of the mountains 720 m above sea level. The

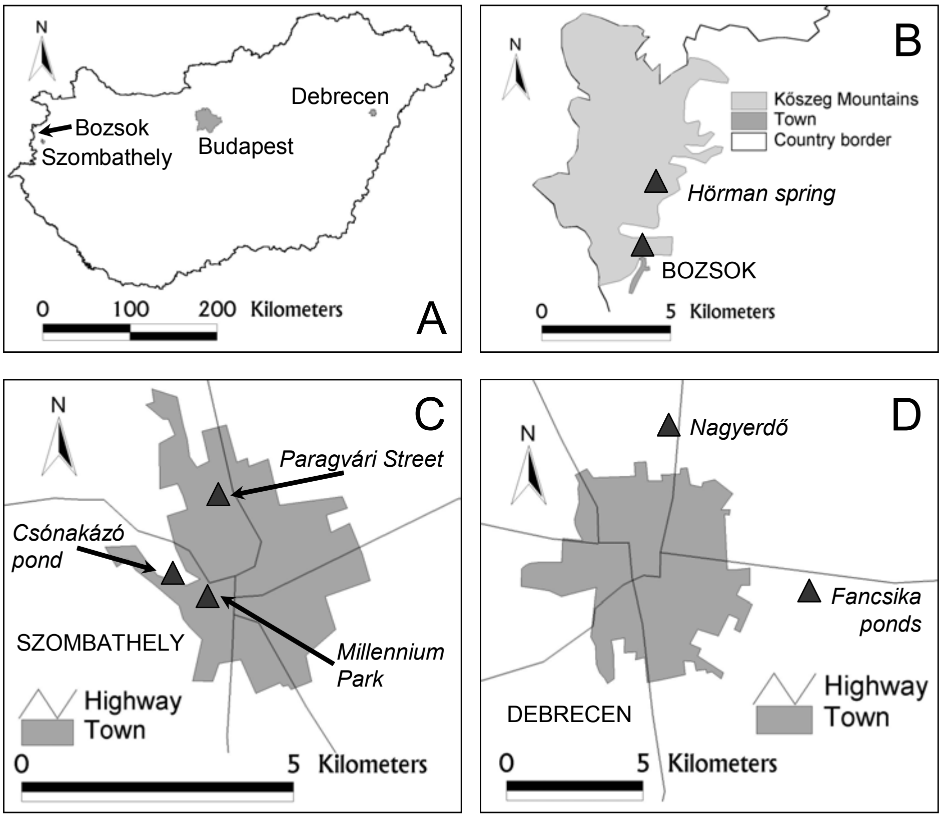


Figure 3. Geographical location of sampling localities in Hungary (A). Two forest localities were near Bozsok (B), three urban localities were in Szombathely (C), and two forest localities were near Debrecen (D). Sampling localities are indicated by triangles, and their names are italicized.

site is a large Black Pine forest stand, completely free from air pollution and other sorts of disturbances (Photo 4.).

(5) Kőszeg Mountains, Bozsok: This site was surveyed from 1997 to 1999. The 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 canopies is located higher in this forest than in the other sampling sites (Photo 5.).

(6) Debrecen, Nagyerdő forest: This site was sampled from 1997 to 1999. A large Black Pine plantation, surrounded by deciduous forests, can be found 200 m away from a highway with heavy traffic north of the city of Debrecen. Despite heavy traffic, immission load is moderate due to the filtering effect of the surrounding forest (Photo 6.).

(7) Debrecen, Fancsika ponds: This site, studied from 1997 to 2000, is surrounded by ponds located south-east from the city of Debrecen. Immission load is low because the site is far from highways and industrial plants (Photo 7.).

Spiders in each sampling site were collected by trunk-traps made of waved cardboard wrapped and fixed on the tree bark. This method is a standard way of collecting both exclusive and facultative bark-dwelling spider species (Wunderlich 1982). Traps were 15 cm wide and were placed 3 m above the ground on the trunk, with their waved surfaces facing the trunk and covering the entire diameter of the tree, as if a kind of artificial bark (Bogya 1995). Sampling times are given in Table 1.

Spiders were stored in 70% ethanol and identified to the species level using standard keys (Loksa 1969, 1972; Heimer & Nentwig 1991; Roberts 1995). Concerning the species, the nomenclature of Platnick (2004) was followed.

Prey were collected by 5-cm-wide trunk traps made of transparent nylon foil (0.2 mm thickness), which were positioned at a height of 2 m on the same trees where spider traps were installed. The outer surfaces of the traps were treated by Soveurode aerosol (Sovilo Co.). Spider and prey traps were taken off the trees simultaneously in late morning and early afternoon

Photo 1. The sampling locality in Millennium Park. (Photo by Csaba Szinetár)

Photo 2. The sampling locality at Paragvári Street. (Photo by Csaba Szinetár)

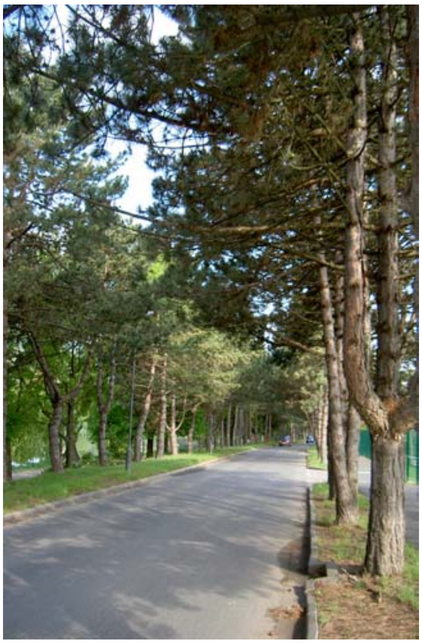


Photo 3. The sampling locality at Csónakázó pond. (Photo by Csaba Szinetár)

Photo 4. The sampling locality in the vicinity of Hörman spring, Kőszeg Mountains. (Photo by Csaba Szinetár)

Photo 5. The sampling locality in Bozsok, Kőszeg Mountains. (Photo by Csaba Szinetár)

Photo 6. The sampling locality in Nagyerdő forest (Debrecen). (Photo by Gábor Ruff)

Photo 7. The sampling locality near the Fancsika-ponds. (Photo by Gábor Ruff)

Table 1. The times of installation and collection of traps.

Sampling sites	Installation time	Collection times
Millennium Park	22.10.1995.	16.01.1996., 12.04.1996., 18.06.1996.
	31.10.1997.	28.12.1997., 30.01.1998., 27.02.1998., 27.03.1998., 01.05.1998.
	27.03.1998.	29.05.1998., 03.07.1998., 31.07.1998., 28.08.1998., 02.10.1998., 30.10.1998., 04.12.1998.
	02.07.1999	12.07.1999.
	22.10.1999	01.11.1999
Paragvári Street	22.10.1995	17.01.1996., 12.04.1996., 18.06.1996.
	31.10.1997.	28.12.1997., 30.01.1998., 27.02.1998., 27.03.1998., 01.05.1998.
	27.03.1998.	29.05.1998., 03.07.1998., 31.07.1998., 28.08.1998., 02.10.1998., 30.10.1998., 04.12.1998.
	02.07.1999	12.07.1999.
	22.10.1999	01.11.1999
Csónakázó pond	31.10.1997.	28.12.1997., 30.01.1998., 27.02.1998., 27.03.1998., 01.05.1998.

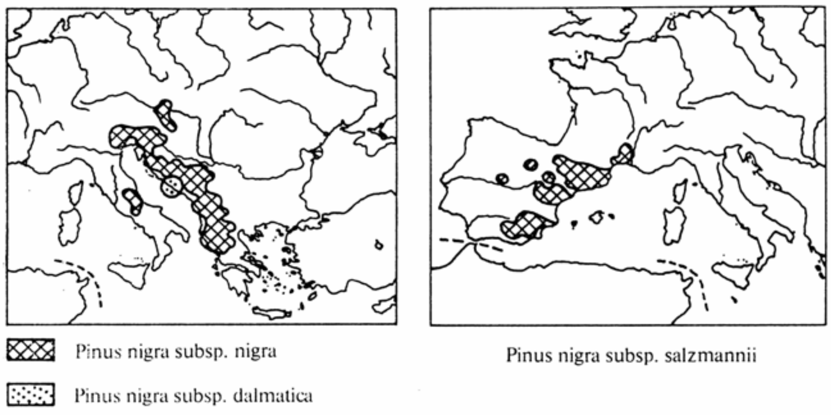
Table 1. Continued.

	27.03.1998.	29.05.1998., 03.07.1998., 31.07.1998., 28.08.1998., 02.10.1998., 30.10.1998., 04.12.1998.
	02.07.1999	12.07.1999.
	22.10.1999	01.11.1999
Hörman spring	23.10.1995.	18.01.1996., 13.04.1996., 19.06.1996.
Bozsok	01.11.1997.	28.12.1997., 31.01.1998., 28.02.1998., 28.03.1998., 02.05.1998
	28.03.1998.	30.05.1998., 04.07.1998., 01.08.1998., 29.08.1998., 03.10.1998., 31.10.1998., 05.12.1998.
	02.07.1999	12.07.1999.
	22.10.1999	01.11.1999
Nagyerdő forest	29.10.1997.	07.01.1998., 02.02.1998., 03.03.1998., 01.04.1998., 29.04.1998.
	01.04.1998.	25.05.1998., 01.07.1998., 29.07.1998., 26.08.1998., 30.09.1998., 09.11.1998., 02.12.1998.
	02.07.1999	12.07.1999.
	06.11.1999	16.11.1999.
Fancsika ponds	03.11.1997.	07.01.1998., 02.02.1998., 03.03.1998., 01.04.1998., 29.04.1998.
	01.04.1998.	25.05.1998., 01.07.1998., 29.07.1998., 26.08.1998., 30.09.1998., 09.11.1998., 02.12.1998.
	02.07.1999	12.07.1999.
	26.10.1999.	31.10.1999., 05.11.1999., 10.11.1999., 15.11.1999., 20.11.1999., 25.11.1999., 30.11.1999., 05.12.1999., 10.12.1999., 15.12.1999.
	06.11.1999	16.11.1999.
	17.10.2000.	22.10.2000., 27.10.2000., 01.11.2000., 06.11.2000., 11.11.2000., 16.11.2000., 21.11.2000., 26.11.2000., 01.12.2000., 06.12.2000.

under calm (no wind) conditions. Prey stuck on the nylon foil were identified to the order level using a microscope and standard keys (Móczár 1984; Steinmann 1970, 1974; Ujhelyi 1957, 1959; Mihályi 1972; Müller 1985). I followed the nomenclature of Papp (1996).

2.2. Pinus nigra Arnold

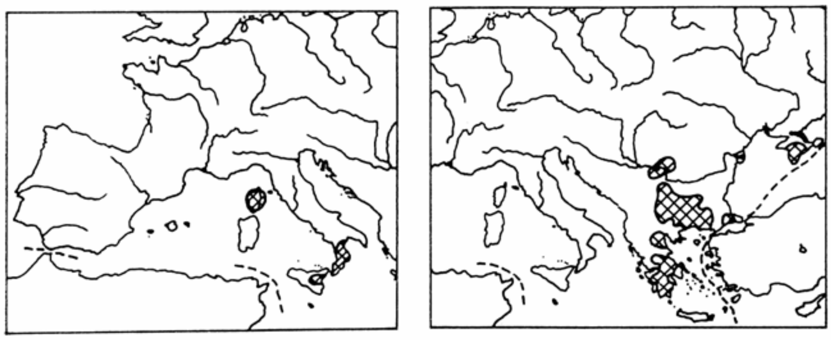
Black Pine is a xerothermic and heliophilous species that requires calcareous soils for its growth and is distributed in Southern Europe, Asia Minor and North Africa (Meusel 1965). Its range is disjunct and the species is separated into well-defined subspecies (*subsp. salzmannii*, *subsp. laricio*, *subsp. nigra*, *subsp. pallasiana*, *subsp. dalmatica*) (Terpó 1986) (Fig. 4.). Although its geographical range nearly reaches Hungary, contrary to previous suggestions, it is not native in Hungary (Simon, T. 1992). It occurs at the eastern margin of the eastern pre-Alps of Lower Austria, in the Vienna Basin, the Istrian peninsula, the northern areas of the former Yugoslavia and near Hercules Bath in Romania (Horvat et al. 1974). In Hungary, the subspecies *Pinus nigra subsp. nigra* has been planted on both dolomite and calcareous sandy soils. Its most important planted stands are in the Balaton-uplands, the Mecsek and Pilis hills and in the area between the Danube and Tisza rivers. Stands on sites with lower production are degraded and are damaged by many pests. At an early age, the bark of Black Pine is uniform brownish grey. The bark of younger trees is evenly covered by tiny scales, whereas that of older trees is covered by fissured larger flat tiles and is stratified by characteristic whitish and reddish-brown stripes. This tree well tolerates both air pollution and poor soils. Since it lives in both cities and nature-like habitats, it is suitable for detecting differences in spider assemblages between urban and forest habitats.



▩ Pinus nigra subsp. nigra

▨ Pinus nigra subsp. dalmatica

Pinus nigra subsp. salzmannii



Pinus nigra subsp. laricio

Pinus nigra subsp. pallasiana

Figure 4. Geographical distribution of subspecies of Black Pine (*Pinus nigra*) in Europe. Source: Terpó (1986).

2.3. Statistical analysis

I used both multivariate and univariate statistical methods to analyse data. Univariate parametric statistical methods were used only if the assumptions of the tests were met. Normality was checked by using the Kolmogorov-Smirnoff test and homoscedasticity was checked by the Levene-test. When the data did not meet these assumptions, hierarchical cluster analysis (Tóthmérész 1993) using the Matusita index of similarity and Ward-Orlóci fusion method was used to assess similarities of spider assemblages in different localities from 1997 to 1998 (Study II) and in 1999 (Study V).

To find indicator species and species assemblages characterising the different sampling sites, the IndVal (Indicator Value) approach was used (Dufrêne & Legendre 1997) (Study II and Study III). This method derives indicator species and species assemblages from hierarchical or non-hierarchical site classifications.

Unpaired *t*-tests (Sokal & Rohlf 1981) were used to detect differences in per trap species richness and Shannon diversity (Pielou 1975) between the two sampling sites (Millennium Park and Paragvári Street) in Study III.

Non-metric multidimensional scaling (NMDS) (Gordon 1981) using the Bray-Curtis index of percentage similarity (Ludwig & Reynolds 1988) was used for abundances to assess the similarity of spider assemblages among the traps (Study III).

In Study IV, average species richness, diversity and number of spiders in samples collected during different sampling times were analysed by one-way analyses of variance (ANOVA) or the non-parametric Kruskal-Wallis test (Barta et al. 2000; Kuehl 1994). I used multiple linear regression models to evaluate the effects of exposition time and temperature on combined species richness, diversity and number of individuals simultaneously (Barta et al. 2000).

In Study V, species richness, number of individuals and diversity of spiders were tested by two-way mixed model ANOVAs in which locality and season were the main effects. I used paired *t*-tests to compare the quantity of spiders in summer and autumn samples (Barta et al. 2000). Linear regression models were fitted to test the relationship between species richness, number of individuals and diversity of spiders and those measures of prey. These models also were used to test the correlation between spiders and prey within spider guilds and for frequent and exclusive bark-dwelling species (Barta et al. 2000).

Statistical analyses were carried out using NuCoSA 1.05, Statistica 5.1 for Windows, IndVal 2.0 and SPSS 9.0 for Windows.

3. Results

3.1. Faunistical results

In the study period between 1996 and 2000 a total of 7744 individuals were found which could be identified to the species-level in 59 taxa, to the genus-level in 22 taxa, to the subfamily-level in one case and to the family-level in 4 taxa. Of the species collected, *Clubiona leucaspis* Simon, 1932 was found to be new to the fauna of Hungary. This species belongs to the *compta* group, which is characterised by a surprisingly high morphological similarity (Mikhailov 1995). This is especially true for the *genevensis* subgroup into which two species belong: *Clubiona genevensis* L. Koch, 1866 and *Clubiona leucaspis*. I have collected the latter species only. Several authors pointed out that the very high similarity may lead to the occurrence of mis-identification (Malten 1984; Nentwig et al. 2003). However, the habitats of the two species differ greatly. *Clubiona genevensis* is a ground-dwelling species of dry, sandy areas, whereas *Clubiona leucaspis* is a typical bark-dwelling species, according to current views. Surprisingly, this species is not listed in the identification guide “Spinnen Mitteleuropas” (Heimer & Nentwig 1991), and can only be found in the most recent Internet data base (www.araneae.unibe,ch). Due to all these factors could it happen that in my previous papers (Horváth & Szinetár 1998, 2002; Horváth et al. 2001) this species was erroneously identified as *Clubiona genevensis*. Besides this, the species *Cheiracanthium mildei* L. Koch, 1864 is also worthy of mentioning, since it is a typical southern-European fauna element. In Hungary it occurs in larger numbers in cities which have a warmer climate than natural habitats and in orchards of the Great-Plain of Hungary. Most species were collected as juveniles and only a small proportion of them were adults. The data from the sampling localities are shown in Table 2. Only a small part of the species detected belonged to exclusive bark-dwellers, and most of them were facultative bark-dweller or species occurring on the bark only accidentally. The highest number of species occurs in moderately polluted urban areas (Millennium Park, Csónakázó pond). At the other localities, the number of species shows relatively small differences, with the exception of Hörman spring. The latter area had a low species richness, which can be explained by the fact that collections were made at this locality only in 1996 (Table 2.). From the spider guilds (Szinetár 1993), web-builders were represented by the highest number of species (29 species). They were followed by diurnal hunters (16 species) and nocturnal hunters (14 species) (Table 3.). Among the species, a number of species-pairs can be observed, one member of which occurs primarily in urban and Lowland forest sampling localities, and the other occurring exclusively in mountain forest areas (*Clubiona pallidula* (Clerck, 1757) – *Clubiona corticalis* (Walckenaer, 1802), *Segestria bavarica* C. L. Koch, 1843 – *Segestria senoculata* (Linnaeus, 1758), *Harpactea rubicunda* (C. L. Koch, 1838) – *Harpactea hombergi* [Scopoli, 1763]). In the series of studies I managed to detect many species characteristic to Black Pine (e.g. *Philodromus aureolus* species group (*Philodromus praedatus* O. P.-Cambridge, 1871), *Macaroeris nidicolens* (Walckenaer, 1802), *Clubiona* *leucaspis*, *Lathys humilis* (Blackwall, 1855), *Theridion mystaceum* L. Koch, 1870 etc.) (Table 3.) (Study I – V.).

Table 2. Faunistical data of spiders occurring at different sampling localities (S.: Sampling sites, N. s.: Number of species, N. g.: Number of genus, N. sf.: Number of subfamilies, N. f.: Number of families, N. i.: Number of individuals, N. F.: Number of females, N. M.: Number of males, N. J.:Number of juveniles)

S.	N. s.	N. g.	N. sf.	N. f.	N. i.	N. F.	N. M.	N. J.
Millennium Park	38	9	1	3	2462	263	94	2105
Paragvári Street	23	7	0	2	1212	85	54	1073
Csónakázó pond	29	5	0	3	1671	273	85	1313
Hörman spring	14	2	0	0	193	24	6	163
Bozsok	23	4	1	1	492	127	43	322
Nagyerdő forest	21	4	0	2	252	31	9	212
Fancsika ponds	24	5	0	2	1462	134	22	1306
Σ	59	22	1	4	7744	937	313	6494

3.2. Spatial differences in spider communities

In the winter, urban and forest samples separated clearly, which can be explained by a special species composition characteristic to the city habitat. Most species were collected in this period, which follows from the fact that canopy-dwelling species move to the bark for overwintering. Because canopy-dwellers retreat to the canopy in the spring, the species composition of urban and lowland areas becomes more even, and this explains the finding that the polluted urban locality showed the highest similarity with a Great-Plain forest, i.e. the Nagyerdő locality near Debrecen. In contrast, there was a relatively big difference between the mountain locality and the other site of the Great-Plain area (Fancsika ponds), which reflects the special climatic and topographic relations of the Kőszeg Mountains. The number of species decreases continuously from early April to late June due to the retreat of canopy-dwellers described above By late June, only exclusive bark-dwellers occur on the bark. In the summer, the Bozsok sampling site sharply separates from the other groups, which can be explained by the unique species composition of the Kőszeg Mountains. The Bozsok sampling locality substantially separates from the other localities also in the autumn, and the differences between urban and Lowland areas also increase in the autumn. The number of species increases continuously again until January.

Studies using character species analysis (IndVal) suggest that the detected species can be classified into seven big groups:

1) Habitat generalists, that occur in great numbers everywhere, except for Bozsok (*Philodromus margaritatus* (species group), *Scotophaeus scutulatus* L. Koch, 1866, *Nuctenea umbratica*),
2) Species characteristic to the mountain forest area (*Amaurobius fenestralis* (Stroem, 1768), *Clubiona corticalis*, *Harpactea hombergi*, *Segestria senoculata*),
3) Species characteristic to urban areas (*Clubiona leucaspis*, *Philodromus aureolus* (species group), *Keijia tincta* (syn. *Theridion tinctum*) [Walckenaer, 1802]),
4) Species characteristic to moderately polluted areas (*Clubiona pallidula*, *Moebelia penicillata*, *Nigma walckenaeri* [Roewer, 1951]),
5) Species characteristic to the heavily polluted areas (*Theridion mystaceum*, *Theridion blackwalli* O. P.-Cambridge, 1871),
6) Species characteristic to the Millennium Park sampling locality (*Steatoda bipunctata* (Linnaeus, 1758), *Cheiracanthium mildei*, *Lathys humilis*) and

7) Species characteristic to the Csónakázó pond sampling locality (*Philodromus rufus*, Walckenaer, 1826) (Study II).

3.3. The effect of air pollution on spider communities

I studied the effect of air pollution on spiders in two, differently polluted urban line of trees (moderately polluted: Millennium Park, heavily polluted: Paragvári Street) in three seasons (winter, spring, summer) in 1996 and in four seasons (winter, spring, summer and autumn) in 1997 and 1998. During the study it was found that in 1996 the species richness and Shannon diversity was significantly higher at the moderately polluted area in winter and spring, whereas there was no significant difference between the two locality in the summer. In 1998, I found similar patterns (winter – species richness: t=2,4137, df=1, 28 p=0,0226; diversity: t=2,1031, df=1, 28 p=0,0446; spring – species richness: t=2,1786, df=1, 28 p=0,0379; diversity: t=2,0708, df=1, 28 p=0,0477; summer – number of species: t=1,6414, df=1, 28, p=0,1119; diversity: t=1,3073, df=1, 28, p= 0,2017; Fig. 5A-C), but in contrast to the previous study period, the study was conducted also in the autumn, and the differences in the two studied variables were significant in this season (species richness: t=6,0871, df=1, 28 p<0,0001; diversity: t=5,6959, df=1, 28, p<0,0001; Fig. 5D). An ordination analysis (NMDS) in 1996 showed that the spider communities clearly separated in the first two study periods, whereas in the third period the communities of the two localities were completely similar. Using the IndVal statistical method, I managed to classify species into three main groups based on their reaction to air pollution (Table 4A-D): 1) habitat generalists, which occurred in high numbers at both localities and are not sensitive to air pollution (*Keijia tincta* (syn. *Theridion tinctum*), *Theridion mystaceum*, *Nuctenea umbratica*, *Lathys*

Table 3. The most important characteristics of the species sampled (Way of life: F – Facultative bark-dwelling species, E – Exclusive bark-dwelling species, A – Accidental species).

Species	Way of life	Hunting strategy	State of development A: adult J: juveniles	When on bark?	Habitat and occurrence
Segestriidae					
Segestria bavarica C. L. Koch, 1843	F	Web-builder (Space web spider)	A: All year J: All year	All year	forest, rock under tree bark, in fissures on rock walls
Segestria senoculata (Linnaeus, 1758)	F	Web-builder (Space web spider)	A: All year J: All year	All year	forest, rock under tree bark, in fissures on rock walls, under stones
Dysderidae					
Harpactea hombergi (Scopoli, 1763)	F	Nocturnal hunter	A: V-XI. J: IV-IX.	IV-IX.	forest under tree bark, under tones
Harpactea rubicunda (C. L. Koch, 1838)	F	Nocturnal hunter	A: II-X. J: All year	All year	open, forest under stones, in houses
Theridiidae					
Achaearanea riparia (Blackwall, 1834)	F	Web-builder (Space web spider)	A: V-VII. J: autumn, spring	VIII-X.	open, park on rock walls, on tree trunks
Anelosimus vittatus (C. L. Koch, 1836)	F	Web-builder (Space web spider)	A: V-VII. J: X-IV.	X-IV.	edge, park on bushes in orchards
Dipoena melanogaster (C. L. Koch, 1837)	F	Web-builder (Space web spider)	A: V-VIII. J: autumn, spring	IV.	forest on bushes, on trees (mainly in coniferous forests), on herbs
Keijia tincta (syn. *Theridion tinctum*) (Walckenaer, 1802)	F	Web-builder (Space web spider)	A: I-VI. J: All year	All year	open, forest on bushes and trees in various forest

Table 3. Continued.

Lasaeola tristis (syn. *Dipoena tristis*) (Hahn, 1833)	F	Web-builder (Space web spider)	A: V-VII. J: All year	VIII-X.	open on low vegetation
Steatoda bipunctata (Linnaeus, 1758)	F	Web-builder (Space web spider)	A: All year J: All year	All year	forest, buildings under tree bark, in hollow trees, in houses
Theridion blackwalli O. P.-Cambridge, 1871	F	Web-builder (Space web spider)	A: V-VII. J: All year	All year	floodplain edge, park – on tree trunks
Theridion impressum L. Koch, 1881	F	Web-builder (Space web spider)	A: V-VII. J: All year	I-IV.	open, park on vegetation in all open habitats
Theridion mystaceum L. Koch, 1870	E	Web-builder (Space web spider)	A: V-VII. J: All year	All year	forest on tree trunks (mainly in coniferous forests)
Theridion pinastri L. Koch, 1872	F	Web-builder (Space web spider)	A: VI-VII. J: All year	IX-XI.	open, forest on solitary trees (mainly on coniferous)
Linyphiidae					
Erigone atra Blackwall, 1833	A	Web-builder (Space web spider)	A: All year J: All year	A	open, edge, park wide range of open habitats
Linyphia triangularis (Clerck, 1757)	A	Web-builder (Space web spider)	A: VIII-XI. J: spring, summer	A	open, forest on vegetation in forest edge and in forests
Meioneta innotabilis (O. P.-Cambridge, 1863)	E	Web-builder (Space web spider)	A: VIII. J: All year	VIII.	forest on tree trunks
Moebelia penicillata (Westring, 1851)	E	Web-builder (Space web spider)	A: All year J: All year	All year	edge on tree trunks, on tree bark

Table 3. Continued.

Araneidae					
Araneus diadematus Clerck, 1757	A	Web-builder (Orb-weaver)	A: VIII-IX. J: spring, summer	VI-IX.	open, forest on herbs, bushes, trees
Gibbaranea bituberculata (Walckenaer, 1802)	A	Web-builder (Orb-weaver)	A: IV-VI. J: autumn, spring	XI-I.	edge, rock, steppes on vegetation
Larinioides ixobolus (Thorell, 1873)	A	Web-builder (Orb-weaver)	A: VII-X. J: spring, summer	VIII.	open on buildings, on trees near water
Mangora acalypha (Walckenaer, 1802)	A	Web-builder (Orb-weaver)	A: V-VII. J: autumn, spring	A	open, edge, park on vegetations in all open habitats and in forest edges
Nuctenea umbratica (Clerck, 1757)	E	Web-builder (Orb-weaver)	A: All year (females) VI-VIII. (males) J: All year	All year	forest, buildings under tree bark, on wooden constructions
Agelenidae					
Agelena labyrinthica (Clerck, 1757)	A	Web-builder (Space web spider)	A: VII-X. J: spring, summer	A	edge among herb vegetation on various forest edges
Tegenaria ferruginea (Panzer, 1804)	A	Web-builder (Space web-spider)	A: II-XI. J: All year	VII-I.	forest, building under tree bark, in hollow trees, in buildings
Dictynidae					
Dictyna civica (Lucas, 1850)	A	Web-builder (Space web spider)	A: VI-XI. J: All year	A	building on walls of houses, on tree trunks in town
Dictyna uncinata Thorell, 1856	A	Web-builder (Space web spider)	A: V-VIII. J: autumn, spring	A	edge, park on tree branches on forest edges

Table 3. Continued.

Lathys humilis (Blackwall, 1855)	F	Web-builder (Space web spider)	A: IV-VI. J: All year	IX-V.	forest, park on trees (mainly on coniferous)
Nigma walckenaeri (Roewer, 1951)	F	Web-builder (Space web spider)	A: VI-X. J: early summer	IX-I.	forest, park on trees, bushes and on walls of houses
Amaurobidae					
Amaurobius fenestralis (Stroem, 1768)	E	Web-builder (Space web spider)	A: IV-XI. J: IV-XI.	IV-XI.	forest, rock under tree bark, in hollow trees, in fissures on rock walls
Amaurobius jugorum L. Koch, 1868	E	Web-builder (Space web spider)	A: VI-IV. J: autumn, spring	IX.	forest steppe, edge under stones
Miturgidae					
Cheiracanthium mildei L. Koch, 1864	F	Nocturnal hunter	A: V-VI. J: autumn, spring	IX-IV.	open, edge, orchards on trees, on and in buildings
Anyphaenidae					
Anyphaena accentuata (Walckenaer, 1802)	F	Nocturnal hunter	A: V-VIII. J: IX-IV.	IX-IV.	forest on leaves and branches of trees (winter on and under bark)
Liocranidae					
Liocranum rupicola (Walckenaer, 1830)	A	Nocturnal hunter	A: III-XII. J: All year	A	scree, building on sun-exposed scree slopes, on floors of buildings
Clubionidae					
Clubiona brevipes Blackwall, 1841	F	Nocturnal hunter	A: IV-VII. J: autumn, spring	I.	forest, edge on tree bark, on bushes in sun-exposed forest

Table 3. Continued.

Clubiona comta C. L. Koch, 1839	F	Nocturnal hunter	A: IV-VII. J: autumn, spring	XII.	forest on trees (mainly in deciduous forests)
Clubiona corticalis (Walckenaer, 1802)	E	Nocturnal hunter	A: IV-IX. J: All year	All year	forest under tree bark
Clubiona leucaspis Simon, 1932	E	Nocturnal hunter	A: III-VII. J: All year	All year	forest, edge under tree bark, on tree trunks (mainly on coniferous)
Clubiona pallidula (Clerck, 1757)	F	Nocturnal hunter	A: IV-IX. J: All year	VIII-IV.	forest on tree trunks (mainly in deciduous forests)
Clubiona terrestris Westring, 1851	A	Nocturnal hunter	A: All year J: All year	A	forest among leaf litter and detritus
Corinnidae					
Phrurolithus festivus (C. L. Koch, 1835)	A	Nocturnal hunter	A: IV-X. J: spring	A	open, forest among grass and detritus
Gnaphosidae					
Micaria subopaca Westring, 1861	E	Nocturnal hunter	A: IV-X. J: spring	IV-X.	open, forest on solitary trees, on and under bark
Scotophaeus scutulatus (L. Koch, 1866)	E	Nocturnal hunter	A: All year J: All year	All year	forest, park, building under tree bark, in houses
Philodromidae					
Philodromus aureolus (Clerck, 1757)	F	Diurnal hunter (Runner)	A: IV-VII. J: autumn, spring	All year	forest, edge, park on vegetation in forest edges
Philodromus dispar Walckenaer, 1826	F	Diurnal hunter (Runner)	A: IV-VII. J: autumn, spring	I.	forest on vegetation in forest edges

Table 3. Continued.

Philodromus longipalpis Simon, 1870	F	Diurnal hunter (Runner)	A: IV-VII. J: autumn, spring	I.	forest, edge, park on trees (mainly on coniferous), shrubs and herbs
Philodromus margaritatus (Clerck, 1757)	F	Diurnal hunter (Runner)	A: V-VIII. J: autumn, spring	All year	forest on tree trunks and branches
Philodromus praedatus O. P.-Cambridge, 1871	F	Diurnal hunter (Runner)	A: IV-VII. J: autumn, spring	VI.	forest, edge, park on trees (mainly on coniferous), shrubs and herbs
Philodromus rufus Walckenaer, 1826	F	Diurnal hunter (Runner)	A: V-VI. J: autumn, spring	X-IV.	edge, park on vegetation in various habitats
Thomisidae					
Diaea dorsata (Fabricius, 1777)	F	Diurnal hunter (Crab spider)	A: IV-VI. J: autumn, spring	XI-IV.	forest on leaves of bushes and trees in forest habitats
Diaea livens (syn. *Diaea pictilis*) Simon, 1876	F	Diurnal hunter (Crab spider)	A: IV-VI. J: autumn, spring	II.	edge on branches of solitary trees (mainly oak)
Misumenops tricuspidatus (Fabricius, 1775)	F	Diurnal hunter (Crab spider)	A: V-VIII. J: autumn, spring	X-XII.	steppe, meadow, park on herbs and bushes
Synaema globosum (Fabricius, 1775)	A	Diurnal hunter (Crab spider)	A: V-VII. J: autumn, spring	A	open, edge on vegetation (mainly on flowers)
Salticidae					
Dendryphantes rudis (Sundevall, 1833)	F	Diurnal hunter (Jumping spider)	A: V-VIII. J: autumn, spring	IX-XI.	forest on branches in coniferous forest and their margins

Table 3. Continued.

Macaroeris nidicolens (Walckenaer, 1802)	F	Diurnal hunter (Jumping spider)	A: summer J: autumn, spring	VIII-IV.	forest, park on branches of trees (mainly coniferous) in xerothermic habitats
Marpissa muscosa (Clerck, 1757)	E	Diurnal hunter (Jumping spider)	A: IV-X. J: autumn, spring	IV-X.	open, edge, park under tree bark, on the trunks
Pseudeuophrys erratica (syn. *Euophrys erratica*) (Walckenaer, 1826)	F	Diurnal hunter (Jumping spider)	A: summer J: autumn, spring	VI-IX.	open, forest on bushes, on trees, on surface of rocks
Pseudicius encarpatus (Walckenaer, 1802)	E	Diurnal hunter (Jumping spider)	A: V-VIII. J: autumn, spring	X-IV.	forest, park on tree bark
Salticus zebraneus (C. L. Koch, 1837)	F	Diurnal hunter (Jumping spider)	A: V-VI. J: autumn, spring	All year	open, forest on trunks and lower branches of trees

Notes to the table:

1. The phenological characterisation of species was assembled using works by Loksa (1969, 1971), Heimer and Nentwig (1991) and Roberts (1995) as well as data from my own collections.

2. The occurrence on the bark is given based entirely on my own collections.

3. I primarily used Buchar and Ruzicka (2002) to give habitat and occurrence characterisation. When information from Hungary were available in addition to data from the Czech Republic, I added the habitat attachment of species according to this knowledge.

humilis, *Clubiona leucaspis*, *Scotophaeus scutulatus*, *Philodromus* (*aureolus)* species group); 2) species sensitive to air pollution, which occurred exclusively or in significant numbers only at the moderately polluted area (*Steatoda bipunctata*, *Moebelia penicillata*, *Gibbaranea bituberculata* (Walckenaer, 1802), *Anyphaena accentuata* (Walckenaer, 1802), *Cheiracanthium mildei*, *Clubiona pallidula*, *Philodromus* (*margaritatus*) species group, *Salticus zebraneus* [C. L. Koch, 1837]); (3) species that showed a higher density at the polluted area (*Theridion blackwalli*, *Micaria subopaca* Westring, 1861) (Study II – III.).

3.4. The effect of exposition time and temperature on the overwintering of spiders

I studied the effect of exposition time (i.e. time passed between the installation and collection of the traps) and temperature on the overwintering of spiders at the Fancsika ponds locality in 1999 and 2000. During the sampling, I did not find significant differences among the ten sampling times in either average number of species or the per-trap average diversity of spiders using the Kruskal-Wallis test. In 1999, there was no significant difference among sampling times in the per-trap average number of individuals, whereas I found a significant difference between the last sampling time and the previous times in this variable in 2000, which could be traced back to a substantial increase in the numbers of one species (*Philodromus margaritatus*). When data collected at any one sampling time were combined in 1999, using multiple regression analysis I found that the absolute number of species showed a marginally significant positive relationship with temperature, but there was no correlation with exposition time. However, the absolute diversity and number of individuals of spiders

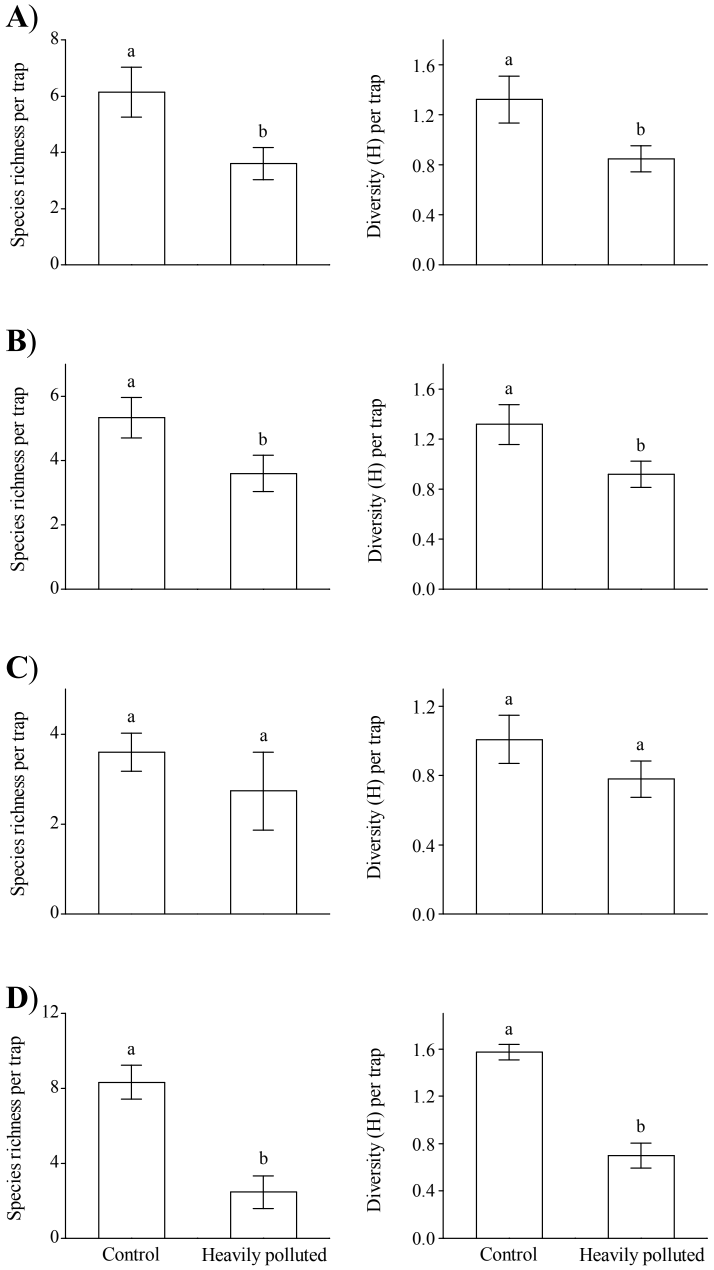


Figure 5. Species richness and Shannon diversity of spiders per trap in the differently affected areas in the winter (A), spring (B), summer (C) and autumn (D) sampling period in 1998. Means with different letters indicate a significant ($p<0.05$) difference by unpaired t-test.

Table 4. Two-way indicator table showing the species indicator power of the habitat clustering hierarchy for the species that were represented by more than ten individuals in the winter (A), spring (B), summer (C) and autumn (D) sampling period in 1996 and in 1998.[a]

	IndVal		Control area with low immission load	Area with high immission load
(A) Control area with low immission load				
Clubiona pallidula	76.00	*	373/19	0/0
Steatoda bipunctata	71.93	*	53/19	3/3
Anyphaena accentuata	63.65	*	181/16	1/1
Cheiracanthium mildei	40.00	*	25/10	0/0
Philodromus spp. (margaritatus)	37.50	*	25/12	7/4
Gibbaranea bituberculata	30.46	*	11/9	2/2
Both areas				
Philodromus spp. (aureolus)	80.00	ns	143/20	70/20
Keijia tincta	72.00	ns	108/21	144/15
Theridion mystaceum	42.00	ns	17/9	72/12
Clubiona leucaspis	36.00	ns	50/6	58/12
Nuctenea umbratica	36.00	ns	10/10	8/8
Lathys humilis	20.00	ns	15/5	5/5
(B) Control area with low immission load				
Clubiona pallidula	52.00	*	62/13	0/0
Moebelia penicillata	47.05	*	38/13	4/2
Steatoda bipunctata	42.16	*	26/15	11/6
Anyphaena accentuata	32.00	*	21/8	0/0
Cheiracanthium mildei	20.00	*	14/5	0/0
Both areas				
Clubiona leucaspis	74.00	ns	75/18	216/19
Theridion mystaceum	52.00	ns	20/11	91/15
Nuctenea umbratica	24.00	ns	6/6	10/6
Philodromus spp. (aureolus)	24.00	ns	13/8	5/4
Micaria subopaca	16.00	ns	3/3	10/5
Area with high immission load				
Theridion blackwalli	33.04	*	4/3	19/10
Keijia tincta	32.55	*	7/5	66/9
Scotophaeus scutulatus	30.59	*	4/3	13/10
(C) Control area with low immission load				
Moebelia penicillata	28.24	*	15/8	2/1
Nuctenea umbratica	26.35	*	14/8	3/3
Salticus zebraneus	24.00	*	19/6	0/0

Table 4. Continued.

Both areas				
Scotophaeus scutulatus	76.00	ns	54/16	82/22
Clubiona leucaspis	24.00	ns	13/6	10/6
Area with high immission load				
Micaria subopaca	17.65	ns	2/2	15/5
(D) Control area with low immission load				
Moebelia penicillata	80.00	*	30/12	0/0
Clubiona pallidula	46.67	*	140/7	0/0
Cheiracanthium mildei	46.67	*	49/7	0/0
Both areas				
Steatoda bipunctata	46.67	ns	19/9	10/5
Clubiona leucaspis	40.00	ns	23/7	6/5
Philodromus spp. (aureolus)	40.00	ns	21/8	8/4
Nuctenea umbratica	33.33	ns	15/6	6/4
Scotophaeus scutulatus	33.33	ns	9/5	18/5
Area with high immission load				
Keijia tincta	32.08	ns	5/2	11/7

[a] In the row for each species, the first number indicates the number of specimens present and the second number corresponds to the number of traps where the species is present, in this sample group. The IndVal column indicates the species indicator value for the corresponding clustering level, which is the maximum indicator value observed in all the clustering hierarchy. ns: not significant; * $p<0.05$.

showed a significant positive relationship only with exposition time and none of these variables was related to temperature. In this year, in periods of decreasing temperature (sampling time 1 to 7) absolute number of individuals continuously increased with the passing of time, and was significantly and positively related to both temperature and exposition time during this period of decreasing temperature. The absolute diversity of spiders showed a significant positive correlation only with exposition time within this period. In 2000, the absolute number of species and absolute diversity did not show significant relationships with either exposition time or temperature. In the case of absolute number of individuals, however, I found a significant positive correlation with exposition time, but I could not detect any relationship with temperature in this case. In this year, during the second “cold” period (between sampling times 5 to 9) I found a significant positive correlation between the absolute diversity of spiders and temperature and between exposition time. These results suggest that when temperature is constantly high, exposition time may be a limiting factor (Study IV).

3.5. The effect of prey availability on spider communities

I studied the effect of prey availability on spider communities in three urban localities (Millennium Park, Paragvári Street, Csónakázó pond), one mountain forest locality (Bozsok) and in two Great-Plain forest localities (Nagyerdő forest, Fancsika ponds) in the summer and autumn of 1999.

I examined spatial and temporal differences in spider communities using two-way ANOVAs. There were significant differences among sampling localities in species richness and Shannon-diversity of spiders, and I found no significant differences with respect to season or interaction between locality and season. There was a significant interaction between season and locality in the number of spider individuals, whereas the effects of sampling locality and season were not significant in this analysis.

The six sampling localities could be classified into four groups using hierarchical cluster analysis: 1) moderately polluted urban localities (Millennium Park and Csónakázó pond), 2) heavily polluted urban locality (Paragvári Street), 3) mountain forest locality (Bozsok) and 4) Great-Plain forest localities (Nagyerdő forest and Fancsika ponds). Further analyses were conducted based on this classification.

I used linear regression models to detect relationships between spider communities and their prey. Analysing the entire spider community I found that the number of species and number of individuals of spiders was positively related to number of prey taxa in Bozsok, although these correlations in the two variables were negative in the moderately polluted urban localities. Interestingly, the number of spider species showed a positive relationship with prey taxon diversity in the moderately polluted urban localities. There was a positive correlation between the number of spider and prey individuals in Bozsok, whereas this relationship was negative in the heavily polluted urban areas. Surprisingly, there was a positive correlation between the number of spider individuals and prey taxon diversity in the Great-Plain forest areas. Finally, there was a positive relationship between spider diversity and number of prey taxa at the mountain forest locality (Study V, Table 3.).

I also studied whether there are detectable correlations between the number of species and individuals of the different guilds and the number of prey individuals. After classifying spider species into guilds (based on Szinetár 1993), I found that nocturnal hunters occurred in the highest numbers, followed by web-builders and diurnal hunters were represented by the lowest number of species in the six sampling localities. Because nocturnal hunters do not consume *Diptera*, the number of prey was classified into two categories (all prey occurring on the bark minus *Diptera* and prey animals occurring exclusively on the bark).

This distinction was necessary because nocturnal hunters consume the so-called “tourists” in smaller proportions due to their differing daily activity, and mainly feed on exclusively bark-dwelling prey animals. The results showed that only there is a relationship with number of prey individuals only in the case of nocturnal hunters. The number of species belonging to this guild showed a positive correlation with number of prey individuals (using both measures of prey availability) in the moderately polluted urban localities and in Bozsok. However, I found a positive relationship between numbers of spider and prey individuals only in Bozsok (using both measures of prey availability).

Because exclusive bark-dwelling spiders can be found on the bark throughout the year, whereas facultative bark-dwellers can be found primarily between autumn and spring (in the summer, only in very small numbers), it was also useful to examine the species of the two groups separately. In the case of exclusive bark-dwellers I treated data from the two seasons combined, whereas I examined the summer and autumn periods separately for facultative bark-dwellers. In the case of exclusive bark-dwellers I found a positive correlation between the number of spiders and number of prey individuals in the Great-Plain forest areas. In contrast, there was a negative relationship between spider numbers and prey numbers in the case of the heavily polluted areas. I could not detect any correlation between number of spider and prey individuals in either the summer or the autumn study period (Study V).

4. Discussion

4.1. Spatial differences in spider communities

The species composition, species richness and diversity of spider communities living on the bark of Black Pine primarily can be influenced by the quantity of prey, climatic conditions, and the structural heterogeneity of the environment, height of the canopy and the density of pine leaves as well as air pollution (Horváth & Szinetár 2002; Horváth et al. 2001, 2004). The higher species richness and diversity of cities can be explained by higher quantities of prey, warmer climate characteristic to cities and denser foliage. In forest samples, both the quantity of prey and the density of foliage is considerably smaller than in the cities, and the canopy usually is located at least 10 m above the ground, and therefore, these conditions can explain the lower species richness and diversity. Lower predation, which can be an important selective force mainly from birds (Gunnarsson 1983), can also play a role in the higher abundance of spiders experienced in the cities. The number of individuals of many of the species found in high numbers in urban samples in the winter decreases dramatically in spring samples (*Steatoda bipunctata*, *Lathys humilis*, *Clubiona pallidula*, *Philodromus rufus*, *Philodromus (aureolus)* species group, *Philodromus (margaritatus)* species group), for which one reason is that the species using the bark only for overwintering migrate back to the canopy. I suppose that one reason for the rather low number of individuals in spring and summer samples was that these species hunt on the surface of the bark during the daytime. Therefore, they were not present in the belt traps collected during the day. However, two exclusive bark-dwelling species (*Scotophaeus scutulatus*, *Moebelia penicillata*) occur in the spring samples, which spent the winter under the deeper layers of the bark, and therefore these species could not be collected by using belts installed on the surface of the bark in the winter. *Scotophaeus scutulatus* can further be found in great quantities until the next winter, and hides back into the deeper layers of the bark due to the unfavourable climatic conditions. In contrast, the number of individuals of the species *Moebelia penicillata* decreases considerably by the summer, and occurs in high abundance only again in the autumn. It would also be worthwhile to study the reason for this later. Species that occurred in high numbers on the bark back in the spring (*Theridion mystaceum*, *Keijia tincta* (syn. *Theridion tinctum*), *Anyphaena accentuata*, *Clubiona pallidula*, *Steatoda bipunctata*) disappear completely from the summer samples. These five species are therefore those that are the last to migrate back to the canopy. As it shows from the results, only exclusive bark- or branch-dwellers can be found in greater numbers in the summer in all areas. However, it can be stated that in the Kőszeg Mountains four species can be found (*Segestria senoculata, Harpactea hombergi, Amaurobius fenestralis, Clubiona corticalis*), which occur exclusively here, which can be explained by the characteristic climatic conditions of the mountains and by the connectedness with natural forest associations of the neighbouring forests. The reason for the occurrence of these species in the summer also can be the fact that they spent the winter under the deeper layers of the bark. In the autumn, when unfavourable changes take place in the climatic conditions, the new migration of the species towards the bark begins, and therefore, species living in the canopy only during the summer (*Keijia tincta* (syn. *Theridion tinctum*)*, Clubiona pallidula, Anyphaena accentuata, and Steatoda bipunctata)* occur in greater numbers again. However, two species (*Cheiracanthium mildei, Nigma walckenaeri*) completely absent from the sample of the previous winter appear in autumn samples. The reason for this can be that these are the species which begin their downward migration to the bark at the earliest, as early as in September. Because I installed the traps only in late October in 1997, by that time these two species already had gone completely into hibernation, and therefore I did not manage to collect any individuals of them in the duration of winter. Although exclusive bark- and branch-dwellers can still be found in the samples, their numbers strongly decrease, which shows that the retreat of these species into the deeper layers of the bark also begins, parallel with the downward migration of foliage-dwellers.

4.2. The effect of air pollution on spider communities

In the study of the effect of air pollution on spiders I concluded that my results are in accordance with the results of numerous previous studies that demonstrated that the indirect effects of air pollution are the most important determinants of the composition, species richness and diversity of spider communities (Alstad et al 1982, Clausen 1986, Gunnarsson 1988). These indirect effects include changes in the structure of the habitat and in the environmental conditions. In the summer sampling period, there is no significant difference between the moderately polluted and heavily polluted areas in the composition, species richness and diversity of spider communities. This phenomenon can be explained by the fact that in this period species living exclusively on the bark or under the bark (e.g. *Scotophaeus scutulatus*, *Clubiona leucaspis*) occurred in the highest abundance because in this period facultative bark-dwelling spiders, that use the bark only for overwintering, returned to the canopy. These results allow to infer that air pollution affects spiders living exclusively on the bark or under the bark to a smaller extent. The bark is presumed to be a suitable hiding place, and thus, exclusive bark-dwelling spiders can be exposed to the direct effects of air pollution only moderately. Furthermore, the effect of air pollution exerts on the microhabitat-structure and microclimate of the bark, which can be envisioned as an indirect effect, is not substantial. On the other hand, in the other sampling periods canopy-dwelling spiders also got into the samples besides exclusive bark-dwellers. In these sampling periods, there were significant differences between the two Black Pine plantations in the composition, species richness and diversity of spider communities. These results can be explained by the finding that some species (e.g. *Anyphaena accentuata*, *Clubiona pallidula*, *Cheiracanthium mildei*) completely disappeared, or their abundance decreased considerably in the heavily polluted area. The mentioned species are facultative bark-dwellers, and the above-mentioned direct and, even more so, the indirect effects of air pollution presumably influenced their distribution. The results of the analyses of indicator species have proven the unambiguous classification of spiders based on their reaction to air pollution. In the winter sampling period, the species called *Keijia tincta* (syn. *Theridion tinctum*) was found to be a habitat generalist, whereas in the other sampling periods it occurred in higher numbers in the polluted area. In my opinion, however, this canopy-dwelling species is likely to be a habitat generalist, rather than a species typical of polluted areas and the differences found can be traced back to the errors of the sampling method. It is highly likely that in the moderately polluted area the individuals of this species returned earlier to the canopy after overwintering, and this contributes to the decrease of their abundance in this area. This assumption is corroborated by the fact that the indicator value of this species was not significant, and its presence could not be predicted unambiguously in the heavily polluted area. A similar case also can be observed in *Steatoda bipunctata*. In the winter sampling period this species was a significant indicator species of the moderately polluted area, whereas it showed as a habitat generalist in the spring and autumn sampling. This species is likely to be a canopy-dwelling animal sensitive to air pollution, and its individuals return to the canopy earlier in the spring in the moderately polluted area, which causes a substantial decrease of their abundance. During the autumn, however, they begin their downward migration to the bark for overwintering later, and therefore their abundance is also low in this period, and thus no significant difference shows between the two areas. Previous studies (Luczak 1984; Bengtsson & Rundgren 1984; Clausen 1984) demonstrated that species of the families *Linyphiidae* and

Clubionidae can be collected in higher numbers from polluted areas. My studies do not or only partially support the above. For example, only very few individuals could be collected in the urban area with heavily polluted air (Paragvári Street) of the species (*Moebelia penicillata*) that represented the family *Linyphiidae* in high numbers, whereas it occurred in high numbers in the moderately polluted sampling locality (Millennium Park). In the case of the family *Clubionidae* I received results contradicting with the above. Two common species of the family (*Cheiracanthium mildei, Clubiona pallidula*) occurred exclusively in the urban areas with moderate air pollution, whereas they were absent from the Paragvári Street that had heavy road traffic. *Clubiona leucaspis*, which occurred in high numbers in the heavily polluted area, was also abundant in the moderately polluted area, therefore, this also contradicts the earlier observations. Apart from all these, it can be concluded that two species of the family *Theridiidae* (*Theridion mystaceum, Theridion blackwalli*) and one species of the family *Gnaphosidae* (*Micaria subopaca*) occurred in highest numbers in the polluted area, which can indicate a higher tolerance to environmental load in these species. My results attested that spiders are suitable for studies of biological indication. Further manipulative and non-manipulative studies are necessary to formulate proposals on management and nature protection with the objective of eliminating or decreasing environmental damages.

4.3. The effect of exposition time and temperature on the overwintering of spiders

In the study of the effect of exposition time and temperature I concluded that in 1999 species richness increased as temperature decreased gradually, but because it increased slightly at the end of the sampling period, the relationship was only marginally significant. Because temperature was low in the middle of the sampling period, spiders appeared on the bark in higher numbers and in a higher diversity, which did not change even after the slight increase of temperature at the end of the sampling period. Therefore, I concluded that spiders that had migrated to the bark by the middle of the sampling period did not leave the bark because of the slight increase in temperature. This resulted in that the absolute number of individuals and diversity were influenced by exposition time but not by temperature. In periods when temperature was decreasing, the number of individuals increased with the progression of time. However, the effect of temperature on the diversity of spiders was not significant, in contrast to that of exposition time. The latter result indicates that although more spiders appeared on the bark during the cooling period, the increase can be attributed to the appearance of only a few species. This is supported by the fact that species richness did not change significantly with either temperature or time. The conclusion that average diversity and number of individuals did not change during the sampling period whereas absolute diversity and absolute number of individuals increased during the sampling period indicate that the use of the averaged variables masked the differences that can have biological relevance. In 2000, the difference in the average number of individuals among sampling times was caused by a sudden increase in spider numbers at the last sampling time. This was in turn a consequence of the appearance of the species *Philodromus margaritatus*. No differences showed in the average number of species and number of individuals. When the entire sampling period was considered, absolute species richness and absolute diversity did not show significant correlations with either time or temperature. In the second cooling period, however, diversity showed a significant relationship with both temperature and exposition time. The total number of individuals, however, showed a significant positive correlation with exposition time, but not with temperature. The increase in the number of individuals in this case also could be attributed to the sudden increase of *Philodromus margaritatus* at the last sampling period. The lack of the effect of exposition time and temperature can be explained by the fact that temperature was continuously high during the sampling period and that spiders did not migrate under the bark as it had happened in 1999. Temperature did not change much in this period and was higher than 10°C in eight of the ten sampling times. We know that spiders are active at temperatures above 5°C (Bogya 1995), therefore, it is not surprising that I did not find differences caused by temperature in 2000, when temperature was above 8°C in each sampling time. My results, therefore, show that the migration of spiders to the tree bark is a characteristic temporal process, which can be detected well by using belt traps. Results from 1999 show that the diversity and number of spiders increased continuously, i.e., when temperature increased only slightly, spiders kept on moving from the canopy to the bark. Results from 2000, however, indicate that this movement of spiders can be delayed if temperature is continuously high during the autumn.

4.4. The effect of prey availability on spider communities

In the study of the effect of prey availability on spider communities I concluded that there were significant differences in spider species richness among the areas because the number of species was low at the Nagyerdő forest sampling site. This area is isolated from other Black Pine plantations by deciduous forests, therefore, juvenile spiders that spread by wind can be found in lower proportions in this area than in the other sampling sites. The number of individuals increases from summer to autumn in urban areas due to the appearance of facultative bark-dwelling species, which migrate to the bark for overwintering (Wunderlich 1982; Horváth et al. 2004). In contrast, the number of individuals decreases or remains constant in the forest areas. This can be explained by the fact that the canopy is higher and the foliage is less dense in the forests and spiders are distributed evenly on different parts of the bark, which results in that density at the height of my belt traps was lower in forests than in the urban areas. However, predation by birds is stronger in forest areas, which can explain why the number of individuals does not increase from summer to autumn in the forest areas. The diversity of spiders was low in the Great-Plain sampling sites and in the heavily polluted urban locality, which is primarily a consequence of the fact that species richness and number of individuals are originally low in these areas, due to reasons mentioned above.

I found a significant positive relationship between spiders and prey communities in the moderately polluted urban areas and in Bozsok. This result indicates that spiders respond numerically to prey living on the bark of Black Pine and that prey abundance may be important in explaining spider abundance in certain areas. For example, in the Bozsok sampling site each parameter of spider communities showed positive correlations with the number of prey taxa and number of prey individuals. In contrast, prey diversity showed positive relationships with spider species richness and number of individuals only in the moderately polluted urban localities. These results suggest that there are several ways in which prey abundance can influence the occurrence of spiders and also that spiders can affect prey abundance to a different degree as a consequence of their hunting strategies.

In urban areas, the occurrence of spiders showed a negative correlation with prey abundance (number of prey taxa and/or number of prey individuals). These results appear to contradict my previous results that showed positive relationships between spiders and prey. This apparent contradiction arises from the fact that there was a negative correlation between the number of prey taxa and prey diversity in the moderately polluted urban areas. On some trees in these areas, high numbers of prey taxa coincided with high numbers of prey individuals, which prey (mainly *Diptera*) were consumed by spiders in smaller proportions. The dominance of such prey led to a lower prey diversity, which can in turn result in lower spider species richness. On other trees, prey taxa are distributed more evenly, which results in higher prey diversity and higher number of spider species and number of individuals. These results suggest that under some conditions the composition of prey communities can also be important in explaining the abundance of spiders.

I observed a negative correlation between the number of spiders and number of prey individuals in the heavily polluted urban area. In this area, air pollution damages the bark of several trees, which are thus more exposed to herbivore and pest species. This area provides unfavourable conditions to spiders due to air pollution, which can reduce their abundance especially on trees more exposed to air pollution. These two effects coupled can explain the negative correlation between the number of spiders and prey abundance in this area.

In the guild-level analysis I found a positive relationship between spiders and their prey only in the case of nocturnal hunters. This correlation could be detected in the moderately polluted urban areas and in Bozsok with respect to both ways of prey classification. In Bozsok, each of the four comparisons (spider numbers and species richness with number of prey categorised in two different ways) showed significant positive results, whereas in the moderately polluted urban areas only the number of spider species showed positive correlations with number of prey categorised in two ways. In contrast, I did not find relationships between the variables in the case of the other two guilds. One reason for this may be that diurnal hunters were active when collections were made (12:00 noon), and therefore, they were present in the traps in small numbers. The females of web-builders, in contrast, are highly sessile, therefore, they do not move much from the traps. However, most specimens of these species were collected as juveniles, and because such individuals actively hunt on the bark as diurnal hunters do, I could not detect a correlation with the number of prey individuals in this guild.

Finally, I found a positive relationship between the number of exclusive bark-dwelling individuals and number of prey individuals in the Great-Plain sampling localities. One reason for why such a correlation could be detected only in these areas is that the number of individuals of these species was highest here, which is a consequence of the massive presence of two species (*Marpissa muscosa*, *Nuctenea umbratica*). The effect of the number of exclusive bark-dwelling spiders in the entire relationship is likely to be less substantial in other areas due to the presence of several facultative species that occur in substantial numbers.

Although I found significant correlations between spiders and prey communities, the direction of causes and effects, i.e., whether spiders exploit the prey populations or whether prey influence spiders, remains to be unclear.

In summary, it can be concluded that the effect between prey abundance and spider communities is not general, correlations can be detected in certain areas. My study provides evidence that the trophic

relationships between spiders and their prey are important in the organisation and quantitative composition of arthropod communities even in a relatively constant and weakly structured habitat, such as the tree bark.

The results of my dissertation show that numerous factors play a role in the formation and distribution of bark-dwelling spider communities, such as the structural diversity of habitat (which includes the canopies of different quality and structure), the productivity of the habitat, climatic conditions, air pollution, the phenomena related to overwintering, the abundance of predators (primarily birds) of spiders, the abundance of prey and competition and predation among spider species.

My results also provided evidence that different species assemblages characterise the bark-dwelling fauna of Black Pine in different habitats, therefore, bark-dwelling spiders can be suitable subjects of studies of biological monitoring and indication.

5. Summary

In my dissertation, I presented and discussed the results of the faunistical and ecological surveys of spider communities living on the bark of Black Pine (*Pinus nigra subsp. nigra*). I conducted collections between 1996 and 2000 at seven sampling locations in two large landscape regions of Hungary (in Western Hungary: Szombathely – Millennium Park [formerly Gagarin Avenue], Csónakázó pond, Paragvári Street; Kőszeg Mountains – Bozsok, Hörman spring, and in the Great-Plain: Debrecen – Nagyerdő forest, Fancsika ponds). I collected bark-dwelling spiders using belt traps. Belts were made of waved cardboard, they were 15 cm wide and installed at a height of ca. 3 m on the trees with their waved surfaces facing the trunk, and operated as artificial bark. Prey were collected by traps made of 5-cm-wide nylon foil and positioned at a height of ca. 2 m on the trees and their outer surfaces were treated by the glue Soveurode aérosol (Sovilo Co.). The collection of both spiders and prey took place around 12:00 noon in calm weather. In the dissertation, I discussed the results of several different studies:

(i) Results of faunistical studies,
(ii) Results of the effects of air pollution on spider communities,
(iii) Results of the roles of exposition time and temperature in the overwintering of spiders,
(iv) Results of the correlations between spider communities and quantitative relations of prey.

In the five years of study, I collected 7744 individuals of which 59 spiders could be identified to the species-level, 22 to the genus-level, 1 to the subfamily-level and 4 to the family-level. Of the collected species, *Clubiona leucaspis* proved to be new to the fauna of Hungary. Besides this, the species *Cheiracanthium mildei* is also worthy of mentioning, since it is a typical southern-European fauna element. In Hungary it occurs in larger numbers in cities which have a warmer climate than natural habitats and in orchards iof the Great-Plain of Hungary.Only a small part of the species detected belong to exclusive bark-dwellers. Most of them belong to the facultative bark-dweller or to the species which occur on the bark only accidentally.

The highest number of species was observed in the moderately polluted urban areas (Millennium Park, Csónakázó pond). The number of species showed relatively small differences in the other sampling locations, except for Hörman spring. This area displayed a low number of species. The reason of which was probably that this area was studied only in 1996. In the series of studies, I managed to detect several species characteristic to Black Pine (e.g. *Macaroeris nidicolens*, *Clubiona leucaspis, Theridion mystaceum* etc.). Urban and forest areas separated from each other relatively well in all study periods and cities also proved to be more speciose. Reasons for this may be the warmer climate of cities, smaller predation pressure by birds, higher foliage density and higher availability of prey. At the same time, the Kőszeg Mountains sampling site (Bozsok) separates sharply from all other sampling sites in the summer and autumn, when exclusive bark-dwellers occur in the highest numbers on the trunk. The reason for this can be sought in the unique species composition of the mountain range, which can be explained by the characteristic topographic and climatic conditions of the mountain range.

I conducted the effect of air pollution on spiders in two, differently polluted urban line of trees (moderately polluted: Millennium Park, heavily polluted: Paragvári Street). In the studies, it was concluded that both the number of species and Shannon diversity were higher in the winter, spring and autumn in the moderately polluted area, whereas no substantial difference showed in the summer period between the two study sites.

The reason for the differences may be that facultative bark-dwellers react much more sensitively to direct and indirect (change in habitat structure and in environmental conditions) effects caused by air pollution, therefore their abundance is lower in the polluted area. I did not find a significant difference between the two sites in the summer because at this time, only the exclusive bark-dwelling species occur in higher numbers on the trunk. Because the bark is presumably a suitable hiding place, these species area only moderately exposed to the direct effects of air pollution, and, furthermore, the effect of air pollution on the microhabitat-structure and microclimate of the bark is also non-significant. The species detected could be classified into three big groups based on their reaction to air pollution:

1) habitat generalists, which occurred in high numbers in both areas and are not sensitive to air pollution (*Keijia tincta* (syn. *Theridion tinctum*), *Clubiona leucaspis* etc.),

2) species sensitive to air pollution, which occurred exclusively or in significant numbers only at the moderately polluted area (e.g. *Clubiona pallidula*, *Moebelia penicillata* etc.),

3) species that tend to show a significantly higher density at the polluted area (e.g. *Theridion mystaceum*, *Theridion blackwalli* etc.). This result demonstrates well that different species react to air pollution in different ways.

In the study of the effect of exposition time and temperature on the overwintering of spiders (at Fancsika ponds) I concluded that I experienced significant differences among sampling times with respect to the averaged variables (species richness, diversity and number of individuals) only in 2000 and even then only with respect to the number of individuals, which was caused by the increased number of individuals of one species (*Philodromus margaritatus*) of the last sampling time.

When collections of one sampling time were combined, then it can be concluded that in 1999 absolute species richness showed marginal significance with temperature, and absolute diversity and absolute number of individuals showed a significant positive relationship with exposition time, whereas I did not manage to find such correlations with temperature. In 2000, only the absolute number of individuals showed significant relationship with exposition time, and temperature did not have a detectable effect on the overwintering of spiders. The reason for this was the constantly high (≥ 8°C) temperature in 2000, in contrast to 1999, when I measured temperatures much lower than this.

My results thus suggest that the migration of spiders on the tree bark is a characteristic temporal process, which can be detected by using belt traps. Results from 1999 show that the diversity and number of spiders increased continuously, i.e., when temperature increased only slightly, spiders moved to the bark from the canopy even at this time. Results from 2000, however, indicate that the movement of the spiders may be delayed if temperature is constantly high during the autumn.

In the study of the effect of prey availability on spider communities I concluded that with respect to the entire species community in the case of the studied variables (species richness, diversity, and number of individuals) there are correlations of differing directions among the studied areas. I experienced a positive relationship between spider communities and prey, however, the direction of the correlation was negative in the heavily polluted area. In the latter area, air pollution damages the bark of more trees, which are thus more exposed to herbivorous and pest species. This area provides unfavourable conditions to spiders due to air pollution, which can decrease their abundance especially on trees more exposed to air pollution. In the moderately polluted urban areas both positive and negative relationships could be detected.

This arises from the fact that there was a negative correlation between number of prey taxa and prey diversity in these areas. On some trees in these areas high number of prey taxa resulted in high number of prey individuals, and spiders were likely to consume these taxa (mainly *Diptera*), and the dominance of these prey is followed by a lower prey diversity, which can result in a lower spider species richness. On other trees prey taxa are distributed more evenly, which results in a higher prey diversity and higher number of spider species and spider individuals.

These results suggest that under certain conditions the composition of prey communities can also be important in the explanation of spider abundance. I did not experience any correlation between spiders and prey in the Great-Plain forest areas. This fact can be explained by the low number of species and number of individuals. In the guild-level analysis I found a positive relationship between spiders and the number of their prey only in the case of nocturnal hunters in the moderately polluted urban areas and in Bozsok.

A correlation of such direction could be detected only in the case of this guild because the species belonging to this guild rest on the bark during the day and thus they can be collected in high numbers. In contrast, I did not find a relationship between the variables with respect to the other two guilds. One reason for this may be that juveniles (mostly individuals at this level of development were collected) of diurnal hunters and web-builders were active at the time of collecting (12:00 noon), and they were present in the traps only in small numbers.

Finally, I found a positive correlation between the number of individuals of exclusive bark-dwelling spiders and prey numbers at the Great-Plain sampling sites. The massive dominance of two such species (*Marpissa muscosa*, *Nuctenea umbratica*) is one of the reasons why this correlations could be detected only in these areas. The presence of the exclusive bark-dwelling spiders in the entire relationship is probably less substantial in other areas due to the presence of several facultative bark-dwellers that occur in high numbers in other areas.

In summary, it can be concluded that although the effect between the abundance of prey and spider communities is not general, correlations can be detected in certain areas. **My studies provided evidence that the trophic interactions between spiders and their prey is important in the organisation and quantitative composition of arthropod communities even in a habitat that is relatively stable and less structured, such as the tree bark.**

The results of my dissertation show that many factors are responsible in the formation and distribution of bark-dwelling spider communities, such as the structural diversity of habitat (including the canopies of different quality and structure), the productivity of the habitat, climatic conditions, air pollution, the phenomenon of overwintering, the abundance of predators of spiders (mainly birds), the abundance of prey, and the competition and predation among spiders species.

My results also have attested that different spider species assemblages characterise the bark-dwelling fauna of the Black Pine, therefore, bark-dwelling spiders may be ideal subjects for biological monitoring and indication studies.

6. Összefoglalás

Disszertációmban a feketefenyő (*Pinus nigra ssp. nigra*) kérgén élő pókközösségek faunisztikai és ökológiai vizsgálatainak eredményeit tárgyaltam. A gyűjtéseket 1996 és 2000 között végeztem Magyarország két nagy tájegységének (Nyugat-Magyarország, Alföld) hét mintavételi helyén (Szombathely: Ezredforduló park (korábban Gagarin sétány), Csónakázó-tó, Paragvári út; Kőszegi-hegység: Bozsok, Hörman forrás; Debrecen: Nagyerdő, Fancsikai-tavak). A kéreglakó pókokat övcsapdák segítségével gyűjtöttem. Az övek hullámos kartonpapírból készültek, amelyek szélessége 15 cm volt és kb. 3 m magasságban helyeztem fel a fákra úgy, hogy a hullámos felükkel befelé helyezkedtek el, így mesterséges kéregként működtek. A prédák gyűjtése pedig 5 cm széles nylon fóliából készült csapdákkal történt, amelyek pedig kb. 2 m magasságban helyezkedtek el a fákon és Soveurode aérosol (Sovilo cég) típusú ragasztóval volt lefújva a külső felületük. Mind a pókok, mind a prédák gyűjtése a déli órákban, szélcsendes időben történt. A dolgozatban több különböző vizsgálatsorozat eredményét tárgyaltam:

(i) a faunisztikai vizsgálatok eredményei;

(ii) a légszennyezés pókközösségekre gyakorolt hatásainak eredményei;

(iii) az expozíciós időnek illetve a hőmérsékletnek a pókok áttelelésében játszott szerepének eredményei;

(iv) a pókközösségek valamint a prédák mennyiségi viszonyai közötti kapcsolatok eredményei.

Az öt éves vizsgálatsorozat alatt összesen 59 faj, 22 genus, 1 alcsalád és 4 család szintig meghatározható pók 7744 egyede került elő. A begyűjtött fajok közül a *Clubiona leucaspis* hazánk faunájára újnak bizonyult. Ezen kívül említést érdemel még a *Cheiracanthium mildei* nevű faj is, amely egy tipikus dél-európai faunaelem, és hazánkban csak a természetes élőhelyeknél jóval melegebb klímájú városokban, valamint az Alföld gyümölcsöseiben fordul elő jelentősebb számban. Az előkerült fajoknak csak egy kis része tartozott a kizárólagos kéreglakók közé, nagyobb részük fakultatív kéreglakónak, illetve véletlenszerűen előforduló fajnak mutatkozott.

A legtöbb faj a mérsékelten szennyezett városi területeken (Ezredforduló park, Csónakázó-tó) fordult elő. A többi gyűjtőhelyen a fajok száma viszonylag kis különbségeket mutat a Hörman forrás kivételével. Ez a terület alacsony fajszámmal rendelkezett, aminek az oka, hogy ezen a helyen csak 1996-ban folytak vizsgálatok. A vizsgálatsorozat alatt több, a feketefenyőre jellemző fajt sikerült kimutatnom (pl. *Macaroeris nidicolens*, *Clubiona leucaspis, Theridion mystaceum* stb.). A városi és az erdei területek viszonylag jól elkülönültek egymástól valamennyi vizsgált időszakban és a városok fajgazdagabbnak is bizonyultak. Ennek oka lehet a városok melegebb klímája, a madarak részéről jelentkező kisebb predációs nyomás, a sűrűbb lombozat és a nagyobb prédakínálat. Ugyanakkor a kőszegi-hegységbeli mintavételi terület nyáron és ősszel, amikor a legnagyobb számban a valódi kéreglakó fajok találhatók a törzsön, élesen elkülönül az összes többi gyűjtőhelytől. Ennek oka a hegyvidék sajátos fajösszetételében keresendő, ami a hegyvidék jellegzetes domborzati és klimatikus viszonyaival magyarázható.

A légszennyezés pókokra gyakorolt hatását két, eltérő módon szennyezett (mérsékelten szennyezett: Ezredforduló park, erősen szennyezett: Paragvári út) városi fasorban végeztem. A vizsgálatok során megállapítást nyert, hogy a fajszám és a Shannon diverzitás egyaránt szignifikánsan magasabb volt télen, tavasszal és ősszel a mérsékelten szennyezett területen, de a nyári időszakban nem mutatkozott jelentős különbség a két vizsgált hely között.

A különbségek oka lehet, hogy a fakultatív kéreglakó fajok a légszennyezés okozta direkt és indirekt (változás az élőhely struktúrájában és a környezeti kondíciókban) hatásokra jóval érzékenyebben reagálnak, emiatt abundanciájuk alacsonyabb a szennyezett területen. A nyári időszakban azért nem találtam szignifikáns különbséget a két terület között, mivel ilyenkor nagyobb számban csak a kizárólag kérgen élő fajok fordulnak elő a törzsön. Mivel a kéreg feltehetően megfelelő búvóhely, így ezen fajok csak mérsékelten vannak kitéve a légszennyezés direkt hatásainak, ezen kívül a légszennyezésnek a kéreg mikrohabitat-struktúrájára és mikroklímájára gyakorolt hatása sem jelentős. Az előkerült fajokat a légszennyezésre adott válaszuk alapján három nagy csoportba lehetett besorolni:

1) habitat generalisták, amelyek mindkét területen nagy számban fordultak elő és nem érzékenyek a légszennyezésre (pl. *Keijia tincta* (syn. *Theridion tinctum*), *Clubiona leucaspis* stb.);

2) légszennyezésre érzékeny fajok, amelyek kizárólag, vagy jelentős számban csak a mérsékelten szennyezett területen fordulnak el (pl. *Clubiona pallidula*, *Moebelia penicillata* stb.);

3) olyan fajok, amelyek inkább a szennyezett területen mutatnak szignifikánsan nagyobb abundanciát (pl. *Theridion mystaceum*, *Theridion blackwalli* stb.). Ez az eredmény jól mutatja, hogy a különböző fajok eltérő módon reagálnak a légszennyezésre.

Az expozíciós időnek és a hőmérsékletnek a pókok áttelelésére gyakorolt hatásának vizsgálatakor (Fancsikai-tavak) megállapítottam, hogy az átlagolt változókat figyelembe véve (fajszám, diverzitás, egyedszám) csak 2000-ben és akkor is csak az egyedszám tekintetében tapasztaltam szignifikáns különbségeket az egyes gyűjtések között, aminek oka az utolsó gyűjtési időpont egy fajának (*Philodromus margaritatus*) megnövekedett egyedszáma.

Ha az egy időpont gyűjtéseit összesítettem, akkor megállapítható, hogy 1999-ben az abszolút fajszám marginális szignifikanciát mutatott a hőmérséklettel, míg az abszolút diverzitás és abszolút egyedszám az expozíciós idővel mutatott pozitív szignifikáns kapcsolatot, azonban a hőmérséklettel nem sikerült ilyen összefüggést kimutatni. 2000-ben pedig csak az abszolút egyedszám mutatott szignifikáns kapcsolatot az expozíciós idővel, és a hőmérsékletnek ebben az évben sem volt kimutatható hatása a pókok telelésére. Ennek oka a 2000-ben végig magas (≥ 8°C) hőmérséklet volt, ellentétben 1999-el, ahol jóval alacsonyabb hőmérsékleteket is mértem.

Eredményeim tehát azt mutatják, hogy a pókok fakéregre történő vándorlása egy jellegzetes időbeli folyamat, amelyeket övcsapdázással lehet kimutatni. Az 1999-ből származó eredmények azt mutatják, hogy a pókok diverzitása és száma folyamatosan növekedett, azaz amikor a hőmérséklet csak kismértékben emelkedett a pókok akkor is a lombozatból a fák kérgére mozogtak. A 2000-es eredmények azonban azt jelzik, hogy a pókok mozgása elmaradhat, ha a hőmérséklet folyamatosan magas az ősz folyamán.

A prédakínálat pókközösségekre gyakorolt hatásának vizsgálatakor megállapítottam, hogy a teljes fajközösséget tekintve a vizsgált változók esetében (fajszám, diverzitás, egyedszám) a különböző területek között különböző irányú összefüggések figyelhetők meg. Pozitív összefüggést tapasztaltam Bozsokon a pókközösségek és a prédák között, viszont az erősen szennyezett területen a kapcsolat iránya negatív volt. Ezen a területen a légszennyezés több fa kérgét is károsítja, amelyek jobban ki vannak téve a herbivor és kártevő fajoknak. Ez a terület a légszennyezés következtében kedvezőtlen feltételeket nyújt a pókoknak, amely csökkentheti az abundanciájukat különösen a légszennyezésnek jobban kitett fákon. A mérsékelten szennyezett városi területeken pozitív és negatív kapcsolat egyaránt kimutatható volt.

Ez abból a tényből adódik, hogy negatív korreláció volt a préda taxonszám és a prédadiverzitás között ezeken a területeken. Ezen területek néhány fáján a magas préda taxonszám magas préda egyedszámot eredményezett és valószínűleg a pókok kisebb arányban fogyasztották ezeket a taxonokat (főleg *Diptera*-kat) és ezeknek a prédáknak a dominanciáját egy alacsonyabb prédadiverzitás követi, amely alacsonyabb pók fajgazdagságot eredményezhet. Más fákon a préda taxonok egyenletesebben oszlanak meg, amely magasabb préda diverzitást és nagyobb pókfajszámot és pók egyedszámot eredményez.

Ezek az eredmények azt sugallják, hogy bizonyos körülmények között a préda közösségek összetétele is fontos lehet a pókok abundanciájának magyarázatában. Az alföldi erdei területek esetében nem tapasztaltam semmilyen kapcsolatot a pókok és a prédák között. Ez a tény ezen területek alacsony fajszámával és egyedszámával magyarázható. A guild szintű analízis során csak az éjszakai vadászok esetében találtam pozitív kapcsolatot a pókok és a prédáik egyedszáma között a mérsékelten szennyezett városi területeken és Bozsokon.

Az ilyen irányú kapcsolat azért csak ennek a guildnek az esetében volt kimutatható, mivel az ide tartozó fajok nappal a kérgen pihennek így nagy számban gyűjthetők. Ellenben a másik két guild tekintetében nem tapasztaltam kapcsolatot a változók között. Ennek egyik oka az lehet, hogy a nappali vadászok és a hálószövők fiataljai (főleg ezen fejlettségi szintű példányok kerültek begyűjtésre) aktívak voltak a gyűjtés időpontjában (déli 12 óra) és emiatt csak kis számban voltak jelen a csapdákban.

Végül pedig pozitív kapcsolatot tapasztaltam a valódi kéreglakó fajok egyedszáma és a prédák egyedszáma között az alföldi mintavételi területeken. Az egyik ok amiért csak ezeken a területeken sikerült kapcsolatot kimutatni az, hogy itt volt a legnagyobb ezen fajok egyedszáma, ami két faj (*Marpissa muscosa*, *Nuctenea umbratica*) tömeges jelenlétének a következménye. A valódi kéreglakó pókok egyedszámának hatása a teljes kapcsolatban valószínűleg kevésbé jelentős más területeken, több, nagy egyedszámban előforduló fakultatív kéreglakó faj jelenléte miatt.

Összességében megállapítható, hogy bár a prédák abundanciája és a pókközösségek között a hatás nem általános, mégis kimutatható kapcsolat bizonyos területeken. **A vizsgálataim bizonyítékot szolgáltattak arra, hogy a pókok és a prédáik közötti trofikus kapcsolatok jelentősek az ízeltlábú közösségek szerveződősében és mennyiségi összetételében még egy olyan viszonylag állandó és gyengébben strukturált élőhelyen is, mint amilyen a fakéreg.**

A disszertációm eredményei azt mutatják, hogy a kéreglakó pókközösségek kialakításában és megoszlásában számos tényező játszik szerepet, mint az élőhely strukturális diverzitása (ez magába foglalja a különböző minőségű és struktúrájú lombozatot), az élőhely produktivitása, a klimatikus viszonyok, a légszennyezés, az áttelelés jelensége, a pókok predátorainak (elsősorban madarak) abundanciája, a prédák abundanciája és a pókfajok közötti kompetíció és predáció.

Az eredményeim azt is igazolták, hogy a különböző habitatokban eltérő fajegyüttesek jellemzik a feketefenyő kéreglakó faunáját, ezért a kéreglakó pókok jó alanyai lehetnek a biológiai monitoring és indikációs vizsgálatoknak is.

7. Acknowledgements

I first thank my advisors, Dr. Csaba Szinetár and Prof. Dr. Zoltán Varga who helped my work with useful advice throughout the entire data collection and writing period, and were always available when necessary.

I thank my co-authors, Szabolcs Honti, László Jakab, Dr. Szabolcs Lengyel and Dr. Tibor Magura without whom this dissertation would not be possible. Szabolcs Lengyel revised the English text of parts of this dissertation.

I am grateful to Prof. Dr. Béla Tóthmérész for help during the statistical analysis of the data and to Dr. István Grigorszki for useful comments.

Thanks are also due to János Eichardt, Roland Györke, my mother Katalin Horváthné, László Kolman, Péter Kozma, Dr. Zoltán Müller, Attila Sándor Nagy and Gábor Ruff for their help during field-work.

I would like to thank Dr. Béla Kiss for help in the preparation of maps, Gábor Németh for making weather data available to me and for Dr. Tibor Várkonyi for providing the data on air pollution.

Last but not least I would like to thank Dr. István Rácz for providing a stimulating yet calm atmosphere for my work during the entire period.

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9. Appendices

Study I

Study II

Study III

Study IV

Study V

Study I

Study of the bark-dwelling spiders (*Araneae*) on black pine (*Pinus nigra*) I

Horváth, Roland & Szinetár, Csaba

Miscellanea Zoologica Hungarica (1998), 12: 77-83

MISCELLANEA ZOOLOGICA HUNGARICA

Tomus 12. 1998 p. 77-83

Study of the bark-dwelling spiders (Araneae) on black pine (Pinus nigra) I.

by

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(Received May **28,1998)**

Abstract: Spiders were collected in two lines of planted trees in a town called Szombathely (Hungary) and in a black pine plantation in the Kőszeg Mountains. The study was carried out in 1995 and 1996. Samples were collected three times with trunk-traps placed on the trunks at two meters height. During our study 1603 specimens belonging to 42 species were trapped. Both the number of species and specimens collected in the town exceeded those in the Kőszeg Mountains. The structure of the spider fauna also differed among the three sampling sites.

Key words: bark-dwelling spiders, black pine, town

Introduction

Some of the tree-dwelling spiders temporarily or seasonally stay under the bark or on its surface. Special microclimatic and structural conditions develope in the cracks of the bark and in the hollows. Furthermore, a certain number of insects live on the bark, which serve as prey for the predators living on or under the bark and thus offer the possibility of constant colonization. This might explain the fact that some of the spiders are adapted to this special habitat so perfectly that bark might be the only adequate habitat for them. Only a small number of authors have been engaged in studying bark-dwelling spiders so far (Koslinska 1967, Albert, 1976, Wunderlich 1982, Hansen 1992, Simon 1995, Bogya 1995, Koponen 1996, Szinetár 1996a). Koslinska (1967) studied bark-dwelling Arachnids in orchards in Poland (He got his samples by pearling the bark). Albert (1976) investigated the bark-dwelling spiders in the beech forest of Solling. According to him 49 species out of the 85 he collected seemed to appear characteristically on the bark and not on the ground level. Wunderlich (1982) carried out a summary on the bark-dwelling fauna of Central Europe on the basis of his own and other researchers' collections. Besides having described the most frequent bark-dwelling species he also tipified them as exclusive and facultative bark-dwellers. Hansen (1992) performed an investigation on the bark-dwelling Arachnids of *Platanus* trees in Venice. There have also been some similar studies in Hungary since 1994. First the study of the bark-dwelling spider fauna of Platan trees was carried out repeating the studies of Hansen (Szinetár 1996a).

Bogya placed trunk-traps on apple and pear trees in order to collect *Clubiona* spiders in orchards of the Netherlands and in Hungary (Bogya 1995). We began to apply this method in the autumn of 1995 to study the bark-dwelling spiders on black pine. Balogh (1935) studied the foliage-dwelling spiders of black pine in the 30's, and Szinetár (1996b) has been studying it since the middle of the 90's.

There were studies on pine with liquid trunk-trap and branch-trap method in Germany (Simon 1995) (samples were taken from the top to ground level). In South-West Finland near the north forest border Koponen (1996) studied the spider species living on the bark and on the branches of turkey oakes. He made a comparison between his data and other studies carried out on the spider fauna of beech and pine species in other countries of Europe, but he could not prove significant differences in the species structure.

The aim of our study was to observe the black pine adapted spider fauna and their frequency. Studying paralelly a town habitat in Szombathely and a forest habitat in Kőszeg Mountains we would answer the following questions:

1. Which species and which guilds can be found on the trunk of the black pine?
2. Which are the most typical species accompanying black pine?
3. Is there any difference in the quantity and quality of the spider fauna of the black pine:
   a) between the two different habitat in the city in Szombathely?
   b) between biotopes in the town and in the forest?
   c) compared to other studies on different tree species?

Material and methods

Samples were taken with trunk-traps made of waved cardboard. Traps were 15 centimeters wide and placed at 2 meters above the ground on the trunk. Belts were put around the trunk, their waved surfaces facing the trunks and covering the whole outline of the tree as if a kind of artificial bark. We provided each of the sampling sites with 30 trunk-traps in the October of 1995. We checked the traps 3 times during 1996, in January, April, and in June, collecting 10-10 samples on an occasion. The samples were collected at around noon or early in the afternoon in calm weather. Bogya (1995) applied similar methods in orchards in the Netherlands. He is using the same methods in Hungary as well.

We sorted out the samples in the laboratory and the specimens were stored in 70% ethanol.

Some juveniles were kept at 20-22 C° temperature fed with fruit-flies *(Drosophila melanogaster)* until they completely developed and we could identify them. We used the books of Loksa (1969, 1972), Heimer & Nentwig (1991) and that of Roberts (1995) for identification and the nomenclature of Platnick (1997) was followed.

We carried out our studies at the following sampling sites:

1. Szombathely, Gagarin avenue (G; Traps were installed: 22.10.1995.; Collecting time: 16.01.1996., 12.04.1996., 18.06.1996.)

This avenue is surrounded by detached houses. There is only a small road along it therefore the air pollution is not significant here.

2. Szombathely, Paragvári street (P; Traps were installed: 22.10.1995.; Collecting time: 17.01.1996., 12.04.1996., 18.06.1996.)

This site is situated next to a main road, which leads the traffic partly to Kőszeg and partly to Gencsapáti. Because of the heavy traffic the air is heavily polluted in this part of the town.

3. Kőszeg Mountain, Hörman spring (K; Traps were installed: 23.10.1995.; Collecting time: 18.01.1996.; 13.04.1996.;19.06.1996.)

This site is situated in the southern part of the mountain 720 meters above the sea level. There is a quite large black pine forest stand here, which was planted during the second World War. This area is completely free from air pollution and from other sorts of disturbances.

Results

During our study we found altogether 1603 specimens (Gagarin avenue: 26 species, 10 genus, 966 specimens; Paragvári street: 13 species, 6 genus, 444 specimens; Kőszeg Mountains 14 species, 2 genus, 193 specimens) belonging to 37 species and to another 13

Table 1. Bark-dwelling spider families on black pine (female/male (juvenile)) in Szombathely (G: Gagarin avenue, P: Paragvári street) and in Kőszeg Mountains (K)

Species	G	P	K	Σ
Segestriidae				
Segestria bavarica C.L.Koch,1843	2/2(1)	-/-(-)	-/-(-)	2/2(1)
Segestria senoculata (Linnaeus, 1758)	-/-(-)	-/-(-)	7/1(26)	7/1(26)
Dysderidae				
Harpactea hombergi (Scopoli, 1763)	-/-(-)	-/-(-)	2/-(15)	2/-(15)
Harpactea rubicunda (C.L.Koch,1838)	4/1 (-)	-/-(-)	-/-(-)	4/1(-)
Harpactea sp.	-/-(1)	-/-(-)	-/-(-)	-/-(1)
Theridiidae				
Anelosimus vittatus (C.L.Koch,1836)	-/-(3)	-/-(-)	-/-(-)	-/-(3)
Dipoena melanogaster (C.L.Koch,I837)	-/-(-)	-/-(1)	-/-(-)	-/-(1)
Dipoena sp.	-/-(2)	-/-(-)	-/-(-)	-/-(2)
Stealoda bipunctata (Linnaeus,1758)	23/9(1)	7/2(3)	-/-(-)	30/11(4)
Theridion blackwalli O. P.-Cambridge,!87]	3/-(2)	1/-(5)	-/-(-)	4/-(7)
Theridion impressum L.Koch, 1881	-/-(-)	-/-(1)	-/-(2)	-/-(3)
Theridion mystaceum L.Koch,1870	-/-(20)	-/-(79)	-/-(1)	-/-(100)
Theridion sp.	-/-(1)	-/-(-)	-/-(-)	-/-(1)
Theridion tinctum (Walckenaer,1802)	-/-(88)	4/-(107)	-/-(-)	4/-(195)
Linyphiidae				
Linyphiidae sp.	-/-(1)	-/-(-)	-/-(-)	-/-(1)
Moebelia penicillata (Westring, 1951)	3/1(-)	-/-(-)	-/-(-)	3/1(-)
Linyphiidae sp.	-/-(1)	-/-(-)	-/-(-)	-/-(1)
Tetragnathidae				
Tetragnatha sp.	-/-(-)	-/-(1)	-/-(-)	-/-(1)
Zygiella sp.	-/-(1)	-/-(1)	-/-(-)	-/-(2)
Araneidae				
Araneus diadematus Clerck,1757	-/-(-)	-/-(-)	-/-(1)	-/-(1)
Araneus sp.	-/-(-)	-/-(1)	-/-(-)	-/-(1)
Gibbaranea bituberculata (Walckenaer, 1802)	-/-(8)	-/-(2)	-/1(19)	-/1(29)
Nuctenea umbratica (Clerck.1757)	2/-(8)	5/1(6)	-/-(-)	7/1(14)
Agelenidae				
Tegenaria ferruginea (Panzer,1804)	-/-(2)	-/-(-)	-/-(-)	-/-(2)
Dictynidae				
Lathys humilis (Blackwall,1855)	2/-(3)	-/-(3)	-/-(I)	2/-(7)
Nigma walckenaeri (Roewer,1951)	2/-(-)	-/-(-)	-/-(-)	2/-(-)
Amaurobiidae				
Amaurobius fenestralis (Stroem, 1768)	-/-(-)	-/-(-)	4/-(8)	4/-(8)
Anyphaenidae				
Anyphaena accentuata (Walckenaer,1802)	-/-(167)	-/-(-)	-/-(-)	-/-(167)
Liocranidae				
Liocranum rupicola (Walckenaer, 1830)	1/-(-)	-/-(-)	-/-(-)	1/-(-)
Clubionidae				
Cheiracanthium mildei L.Koch,1864	1/3(34)	-/-(-)	-/-(-)	1/3(34)

Species	G	P	K	Σ
Clubiona brevipes Blackwall, 1841	-/-(1)	-/-(-)	-/-(-)	-/-(1)
Clubiona corticalis (Walckenaer, 1802)	-/-(-)	-/-(-)	7/4(24)	7/4(24)
Clubiona genevensis L.Koch,1866	1/-(23)	1/-(128)	-/-(-)	2/-(151)
Clubiona pallidula (Clerck,1757)	10/12(362)	-/-(-)	-/-(-)	10/12(362)
Clubiona sp.	-/-(-)	-/-(1)	-/-(-)	-/-(1)
Gnaphosidae				
Micaria subopaca Westring,1862	1/-(-)	-/-(3)	-/-(-)	1/-(3)
Scotophaeus scutulatus (L.Koch,1866)	2/1(37)	-/-(37)	-/-(-)	2/1(74)
Scotophaeus sp.	-/-(1)	-/-(-)	-/-(-)	-/-(1)
Philodromidae				
Philodromus dispar Walckenaer, 1826	-/-(1)	-/-(-)	-/-(1)	-/-(2)
Philodromus longipalpis Simon,]870	-/-(-)	-/-(-)	-/-(-)	-/5(-)
Philodromus margaritatus (Clerck,1757)	1/-(4)	-/-(-)	-/-(-)	1/-(4)
Philodromus praedatus O.P-Cambridge,1871	1/-(-)	-/-(-)	-/-(-)	1/-(-)
Philodromus rufus Walckenaer, 1826	1/-(1)	-/-(7)	-/-(-)	1/-(8)
Philodromus spp. (aureolus)	-/-(91)	-/-(36)	-/-(53)	-/-(180)
Philodromus spp. (margaritatus)	-/-(8)	-/-(1)	-/-(8)	-/-(17)
Thomisidae				
Diaea dorsata (Fabricius,1777)	-/-(-)	-/-(-)	-/-(1)	-/-(1)
Salticidae				
Euophrys erratica (Walckenaer, 1826)	-/-(-)	-/-(-)	4/-(-)	4/-(-)
Macaroeris nidicolens (Walckenaer, 1802)	-/-(3)	-/-(-)	-/-(1)	-/-(4)
Marpissa muscosa (Clerck,I757)	-/-(-)	-/-(-)	-/-(2)	-/-(2)
Pseudicius encarpatus (Walckenaer, 1802)	-/-(1)	-/-(-)	-/-(-)	-/-(1)
	60/29/(877)	18/3(423)	24/6(163)	102/38(1463)

Table 2. Guild composition of spiders on the bark of black pine in Szombathely (G: Gagarin avenue, P: Paragvári street) and in Kőszeg Mountains (K)
(Crab spiders include *Thomisidae* and *Philodromidae*)

Guilds	G	P	K
WEB BUILDERS			
Space web spiders	18.43%	47.97%	34.71%
Orb weavers	1.97%	3.83%	10.88%
Σ WEB BUILDERS	20.40%	51.80%	45.59%
HUNTERS			
Runners			
Nocturnal hunters	68.01%	38.29%	18.13%
Σ Runners	68.01%	38.29%	18.13%
Ambushers			
Crab spiders	11.18%	9.91%	32.12%
Jumping spiders	0.41%	0.00%	4.16%
Σ *Ambushers*	11.59%	9.91%	36.28%
Σ HUNTERS	79.60%	48.20%	51.41%
	100.00%	100.00%	100.00%

Table 3. The most frequent bark-dwelling spiders on black pine concerning collecting places and dates (G: Gagarin avenue, P: Paragvári street, K: Hörman spring, Kőszeg Mountains) (1 = the most frequent species, – = missing from the 10 most frequent species):

	January				April		
	G	P	K		G	P	K
Clubiona pallidula	1	–	–	*Clubiona pallidula*	1	–	–
Anyphaena accentuata	2	–	–	*Clubiona genevensis*	2	1	–
Theridion tinctum	3	1	–	*Theridion mystaceum*	3	2	–
Philodromus spp.(aureolus)	4	2	1	*Theridion tinctum*	–	3	–
Clubiona genevensis	–	3	–	*Clubiona corticalis*	–	–	1
Gibbaranea bituberculata	–	–	2	*Segestria senoculata*	–	–	2
Clubiona corticalis	–	–	3	*Philodromus spp.(aur)*	–	–	3

	June		
	G	P	K
Scotophaeus scutulatus	1	1	–
Theridion blackwalli	2	6	–
Nuctenea umbratica	3	5	–
Micaria subopaca	–	2	–
Theridion tinctum	–	3	–
Segestria senoculata	–	–	1
Harpactea hombergi	–	–	2
Amaurobius fenestralis	–	–	3

taxa determined on the level of genera. 7.87 percent of the trapped spiders that is 115 individuals were mature when they were collected. 89 of them were females (77.39%) and 26 of them were males (22.61%).

We sum up the data of the collected taxa in Table 1. The distribution of data sorted by hunting strategies is shown in Table 2., while in Table 3. we can see the data of the most frequent species sorted by sampling sites and times.

Discussion

Beside frequent bark-dwelling spiders we also found some rare species. In spite of their low numbers some of the rare species seem to be characteristic ones *(Entelecara penicillata, Amaurobius fenestralis, Harpactea hombergi, Micaria subopaca, Marpissa muscosa).* It is also important to point out that we found a species characteristic of the South-European fauna *(Cheiracanthium mildei).*

The following species can be regarded as species accompanying black pine forests: *Philodromus (aureolus)* species-group *(longipalpis, praedatus), Macaroeris nidicolens, Clubiona genevensis, Lathys humilis, Theridion mystaceum, Theridion tinctum, Dipoena melanogaster.*

As Table 3 shows there are significant differences between not only the spider fauna of the town and that of the mountains, but also between the two sampling sites of the town.

Many of the collected species were found on the trunks of various trees in Europe, thus indicating that this trunk fauna generally lives on trees, not especially on black pine. Of the collected species Wunderlich (1982) listed *Entelecara penicillata, Amaurobius fenestralis, Micaria subopaca, Philodromus margaritatus, Marpissa muscosa, Harpactea hombergi* as exclusive dwellers on or under bark of living trees in Central Europe; and *Segestria senoculata, Segestria bavarica, Steatoda bipunctata, Nuctenea umbratica, Scotophaeus scutulatus,* and *Clubiona corticalis* as facultative bark-dwellers.

18 of the 42 species found have been reported on the trunk of pine (Simon 1995) and 12 species occur on the trunk of turkey oak (Koponen 1996). These facts prove that the distribution of the majority of bark-dwellers species were not affected by climatic and different structural factors. Of the abundant or other interesting black pine species in Hungary, only the following were not listed in the above-mentioned Wunderlich (1982) lists: *Clubiona pallidula, Anyphaena accentuata, Theridion tinctum, Gibbaranea bituberculata, Lathys humilis, Euophrys erratica, Cheiracanthium mildei, Diaea dorsata, Dipoena melanogaster, Pseudicius encarpatus.* Out of the above mentioned species only *Pseudicius encarpatus* can be regarded as a real bark-dwelling spider as the other nine species appear on the barks only during winter when they use the bark for overwintering. If we compare the three different collecting sites with each other we may state that, there might be significant differences between the sampling sites even in one microregion.

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Study II

Ecofaunistical study of bark-dwelling spiders (*Araneae*) on black pine (*Pinus nigra*) in urban and forest habitats

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Acta Biologica Debrecina (2002), 24: 87-101

Acta Biologica Debrecina (2002) **24**: 87-101

Ecofaunistical study of bark-dwelling spiders *(Araneae)* on black pine *(Pinus nigra)* in urban and forest habitats

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Abstract The study of the bark-dwelling spiders on black pine was carried out from the winter of 1997 to the autumn of 1998 in two different regions of the country (Western-Hungary, Great Hungarian Plain) in six sampling sites in urban habitats and pine plantages. Five samples from each site monthly were taken by trunk-traps placed at 3 meters height. We compared the forest and urban habitats, and the areas with different geographical and climatic conditions. There was an essential difference between the urban and forest sampling sites, as well as the two different sites of the country. The similarity of the spider communities of the sampling sites also shows specific seasonal changes. That the mountain forest biotope had a characteristic species structure, which is typical only of the forests of the western borderland in Hungary, which was reinforced by the IndVal statistical method. The higher species richness of the moderately polluted urban samples in relation to the forest samples and the higher abundance values can be effected by the following factors: (i) the significantly higher prey density of towns, (ii) the warmer climate of towns, which enables Southern-European species to settle down (iii) the weaker predation in towns, which can originate partly from the lower number of predators (mainly birds), partly from the more dense foliage of pines in towns as it can offer a better hiding place for spiders.

Keywords Bark-dwelling spiders, Black pine, Town, Forest, Indicator species.

Introduction

With the accelerating development of industry and transport, special climatic conditions have been developed which allowed a lot of creatures to settle down. There are several among them which find their living conditions exclusively in or near human settlements today (Braun 1956, Beer 1978, Schäfer and Kock, 1979, Pisarski and Kukesza 1982, Salz 1992, Szinetár 1993). Among them, there are some species settled down in towns with warmer climate as well, which species are found exclusively in natural habitats in the mediterranean areas (Szinetár 1992a, Horváth and Szinetár 1998). During our study the spider fauna of a town (Szombathely) was investigated in comparison with spiders occurring in pine plantages in natural circumstances. For our studies black pine *(Pinus nigra)* was chosen which is a frequent species both in towns and pine plantages. We concentrated on the study of bark-dwelling spiders because this topic has been studied by only a few auctors both in Hungary and abroad (Albert 1976, Wunderlich, 1982, Hansen 1992, Bogya 1995, Koponen 1996, Szinetár 1996, Horváth and Szinetár 1998, Schulz and Schmidt 1998). Because the bark has special microclimatic and structural conditions, it is an exclusive habitat for many spider species (Wunderlich 1982). The ecology of spiders is relatively well-known, which allows to use them as the subjects of ecological studies (Tretzel 1952, Braun and Rabeler 1969). Our studies were carried out in three urban and three forest habitats. One of the forest habitats is situated in the Kőszeg Mountains while the other two are found in areas surrounding Debrecen. Despite spiders are mobile and relatively short lived, they are suitable for indicating abiotic and biotic environmental changes.

In the present study we carried out a comparative ecological study between the forest and urban habitats. We studied the differences in species composition, species richness and diversity of spiders between urban biotopes and pine plantages.

Material and Methods

Study area and sampling

Samples were taken with trunk-traps made of waved cardboard. Using trunk-traps, one can sample and study not only the exclusive dwellers on or under the bark of black pine, but also the foliage-dwelling spiders, because a part of the foliage-dwelling spider overwinter under the bark (Wunderlich 1982). Traps were 15 centimetres wide and placed at 3 meters above the ground on the trunk. Belts were put around the trunk, with their waved surfaces facing the trunks and covering the whole outline of the tree as if a kind of artificial bark. 30-30 trunk-traps were installed to the six sampling sites, first in October of 1997 then in April of 1998. We collected 5 trunk-traps from the six sampling sites in every month. The samples were collected at around noon or early in the afternoon in calm weather. Bogya (1995) applied similar methods in orchards in the Netherlands and in Hungary.

We sorted out the samples in the laboratory and the specimens were stored in 70% ethanol. Some juveniles were kept at 20-22°C temperature and fed with fruit-flies *(Drosophila melanogaster)* until they completely developed and we could identify them. We used Loksa (1969, 1972), Heimer and Nentwig (1991) and that of Roberts (1995) for identification and the nomenclature of Platnick (1997) was followed.

We carried out our studies at the following sampling sites:

(1) Szombathely, Gagarin avenue (G): This avenue is surrounded by family houses. There is only a small traffic road along it, therefore, the air pollution is not significant there.

(2) Szombathely, Paragvari street (P): This site is next to a main road, which leads the traffic partly to Kőszeg and partly to Gencsapáti. Because of the heavy traffic the air is heavily polluted in this part of the town.

(3) Szombathely, Csónakazó pond (Cs): This is a green belt area with two artificial ponds and an open-air swimming pool. The studied row of trees is situated along a road without heavy traffic between the two artificial ponds and the open-air pool, therefore this site is only moderately polluted.

(4) Kőszeg Mountain, Bozsok (B): This site is situated in the southern part of the mountain 200 meters above the sea level near Bozsok. We can find a quite large black pine forest here, which was planted during the second World War. This area is completely free from air pollution and from other sorts of disturbances.

(5) Debrecen, Nagyerdő forest (N): A large black pine plantation can be found here. This area is situated 200 m away from the highway No 4. Despite the heavy traffic, this area is only moderately polluted due to the filtering effect of the forest.

(6) Debrecen-Kondoros, Fancsika ponds (F): This sampling site is surrounded with ponds and is located beyond the suburbs of the town. The air pollution is not significant here, because it is far from both the highway and the industrial plants.

Data analyses

Hierarchical cluster analysis using the Matusita index of similarity was used for abundances to assess similarities in spider assemblages among the traps in the four studying periods (Tóthmérész 1993b).

To find indicator species and species assemblages characterising the sites with different air pollution the IndVal (Indicator Value) approach was used (Dufrêne and Legendre 1997). This method derives indicator species from site classification. We obtained the site classification from hierarchical cluster analysis using Matusita similarity for abundances. Based on this site classification IndVal identifies the indicator species corresponding to the various groups. Indicator species are defined as the most characteristic species of each group, found mostly in a single group of the classification and present in the majority of the sites belonging to that group. The method is robust to differences in the absolute abundances of different taxa. Furthermore, by using a Monte Carlo permutation test it is possible to assess the statistical significance of the species indicator values (Legendre and Legendre 1998, McGeoch and Chown 1998). This method has been applied successfully in studies on other arthropods (Magura *et al.* 2000).

We examined whether there were any seasonal changes in the diversity and species composition of spiders, therefore, 4 seasonal periods were distinguished: A – winter period (December, January, February); B – spring period (March, April, May); C – summer period (June, July, August); D – autumn period (September, October, November).

During our analysis the pooled samples of the 3 months representing the given seasonal period were used.

	species	genus	subfamily	family	counts	diversity
Gagarin avenue	27	9	1	2	1111	2.666
Csónakázó pond	23	12	1	2	1227	2.618
Paragvári street	16	9	1	2	613	2.217
Bozsok	18	6	0	1	311	2.167
Fancsika ponds	19	10	0	1	393	2.418
Nagyerdő forest	15	6	0	1	184	2.312

Tab. 1: Studied characteristics of the spider assemblages.

Results

During the study a total of 3839 individuals belonging to 49 species, 17 taxa, 1 subfamilia and 4 familia were trapped. Tab. 1 shows a few characteristics of the spiders in the given habitat. 18.26% of the trapped spiders (701 individuals) were mature when they were collected. 560 of them were females

(79.88%) and 141 of them were males (20.12%).

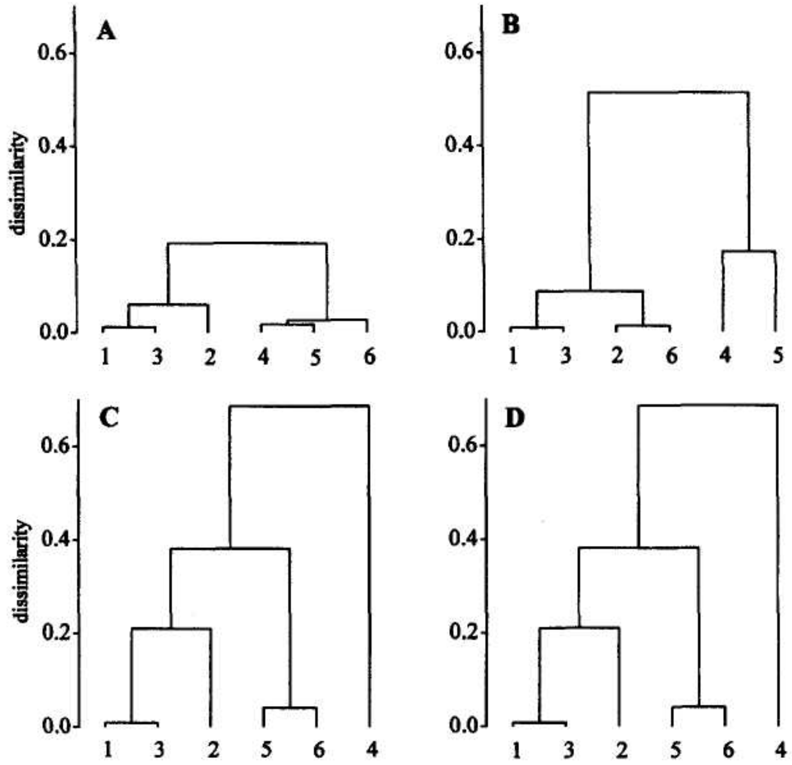

Fig. 1: Tree-diagrams of the spider assemblages during the seasons in 1998. A – winter, B – spring, C – summer, D – autumn. 1: Gagarin avenue, 2: Paragvári street, 3: Csónakázó pond, 4: Bozsok, 5: Fancsika ponds, 6: Nagyerdő forest.

The results obtained with the cluster analysis demonstrate the seasonal differences (Fig. 1 A-D). During the winter period urban and forest samples are segregated well, which can be interpreted by the special species composition characteristic of towns, although because of the many similar species (which occur in small number in the lowlands) even the largest difference does not reach 20%. In spring, because the foliage-dwelling spiders begin to move back, the species composition becomes more balanced. This explains why the polluted town area shows larger similarity to the Nagyerdő forest sampling site, and there is a relatively large difference between the mountain and plain (Fancsika ponds) areas. In summer, the sampling site of Bozsok stands out in sharp contrast to the other groups. The reason for this is the special species composition that originates from the climatic and relief

	IndVal	G	P	Cs	B	F	N
Gagarin avenue							
Steatoda bipunctata	54.6*	30/9	0/0	8/6	0/0	2/2	2/2
Anyphaena accentuata	35.3*	28/6	1/1	2/1	6/5	2/1	1/1
Lathys humilis	22.0*	13/4	2/2	2/1	0/0	1/1	0/0
Gagarin avenue and Csónakázó pond							
Clubiona pallidula	53.3*	53/9	0/0	57/7	0/0	0/0	0/0
Csónakázó pond							
Nuctenea umbratica	54.8*	4/4	3/3	37/13	3/2	11/8	4/4
Philodromus rufus	21.3*	3/2	0/0	12/4	0/0	0/0	0/0
Szombathely							
Philodromus sp.	63.2*	62/10	38/11	67/10	2/2	12/7	1/1
Theridion tinctum	62.9*	24/11	57/7	79/11	1/1	1/1	2/2
Clubiona genevensis	29.1*	49/5	49/5	26/5	2/1	0/0	16/3
Paragvári street							
Theridion mystaceum	64.2*	12/6	71/11	3/3	1/1	4/4	3/3
All sites							
Philodromus sp.	56.7ns	17/7	7/4	12/7	15/8	27/11	33/14

Tab. 2: The indicator table showing the species indicator power for the habitat clustering hierarchy for the species which were present by more than ten individuals during the first studied period.

conditions of the Kőszeg Mountains, where there are exclusive bark-dwelling spiders found only on the western borderline of Hungary. The sample from Bozsok is separated from the other sites in the autumn, as well. As a result of the wandering back of the foliage-dwelling spiders, the differences are increasing between the town and lowland areas.

The collected spider species can be divided into seven groups by characterisation of habitats by indicator species (Tab. 2-5): (1) habitat generalists that occurred numerously in all habitats *(Philodromus (margaritatus)* species group, *Scotophaeus scutulatus, Nuctenea umbratica),* (2) species occurring only in the Kőszeg Mountains (Bozsok) *(Amaurobius fenestralis, Clubiona corticalis, Harpactea hombergi, Segestria senoculata),* (3) species occurring in large numbers only in Szombathely *(Clubiona genevensis, Philodromus (aureolus)* species group, *Theridion tinctum),* (4) species that were abundant only in heavily polluted urban areas (Paragvári street) (*Theridion mystaceum, Theridion blackwalli),* (5) species that were abundant only in moderately

	IndVal	G	P	Cs	B	P	N
Szombathely							
Clubiona genevensis	61.1*	52/9	97/9	40/11	1/1	0/0	29/8
Gagarin avenue							
Steatoda bipunctata	50.8*	16/10	2/2	1/1	0/0	2/1	0/0
Gagarin avenue and Csónakázó pond							
Clubiona pallidula	22.6*	22/6	0/0	16/5	0/0	1/1	0/0
Moebelia penicillata	56.8*	14/7	3/1	44/12	0/0	0/0	1/1
Paragvári street							
Theridion mystaceum	22.2ns	5/4	13/5	5/3	0/0	8/4	7/4
Theridion tinctum	21.1*	3/3	44/4	11/5	1/1	5/4	3/2
Theridion blackwalli	32.9*	2/2	14/6	0/0	0/0	0/0	1/1
Bozsok and Fancsika ponds							
Anyphaena accentuata	25.3*	7/3	0/0	0/0	13/5	6/4	0/0

Tab. 3: The indicator table showing the species indicator power for the habitat clustering hierarchy for the species which were present by more than ten individuals during the second studied period.

	IndVal	G	P	Cs	B	F	N
All sites without Bozsok							
Scotophaeus scutulatus	45.0*	50/9	48/15	48/11	0/0	67/9	19/4
Nuctenea umbratica	45.3*	12/7	2/2	17/9	0/0	10/8	10/8
Bozsok							
Clubiona corticalis	86.7*	0/0	0/0	0/0	63/13	0/0	0/0
Amaurobius fenestralis	80.0*	0/0	0/0	0/0	33/12	0/0	0/0
Segestria senoculata	66.7*	0/0	0/0	0/0	27/10	0/0	0/0
Harpactea hombergi	46.7*	0/0	0/0	0/0	17/7	0/0	0/0

Tab. 4: The indicator table showing the species indicator power for the habitat clustering hierarchy for the species which were present by more than ten individuals during the third studied period.

polluted areas (Gagarin avenue, Csónakázó pond) *(Clubiona pallidula, Moebelia penicillata, Nigma walckenaeri),* (6) species occurring in large numbers only at the sampling site of Csónakázó pond *(Philodromus rufus),* (7) 3 species occurring in only at the sampling site of Gagarin avenue *(Steatoda bipunctata, Lathys humilis, Cheiracanthium mildei).*

	IndVal	G	P	Cs	B	F	N
Szombathely							
Theridion tinctum	45.6*	11/4	34/9	38/9	0/0	4/3	0/0
Clubiona genevensis	35.6*	22/6	4/3	13/7	0/0	0/0	0/0
Scotophaeus scutulatus	30.6*	8/5	18/5	7/5	0/0	2/2	0/0
Gagarin avenue and Csónakázó pond							
Moebelia penicillata	61.6*	18/10	0/0	35/14	0/0	0/0	0/0
Clubiona pallidula	32.8*	236/9	0/0	233/9	0/0	11/5	0/0
Philodromus sp.	40.4*	20/8	5/3	62/9	0/0	3/2	2/2
Nigma walckenaeri	31.3*	5/4	0/0	18/6	0/0	0/0	0/0
Gagarin avenue							
Cheiracanthium mildei	56.0*	56/9	0/0	4/4	0/0	0/0	0/0
Steatoda bipunctata	39.4*	23/9	7/4	3/3	0/0	1/1	1/1
Anyphaena accentuata	18.6*	23/4	2/1	6/2	2/2	0/0	0/0
Fancsika ponds							
Philodromus sp.	48.8*	7/6	1/1	6/3	0/0	91/9	7/3
All sites without Bozsok							
Nuctenea umbratica	41.3*	18/8	4/2	24/11	0/0	8/4	7/6
Bozsok							
Amaurobius fenestralis	44.9*	0/0	0/0	0/0	38/10	0/0	0/0

Tab. 5: The indicator table showing the species indicator power for the habitat clustering hierarchy for the species which were present by more than ten individuals during the fourth studied period.

Discussion

Earlier studies (Wunderlich 1982) have shown that only some bark-dwelling spiders live constantly on the bark or under the bark, while the others visit the bark only temporarily (mainly for the purpose of overwintering). For this reason, bark-dwelling spiders can be divided into two large groups: (1) the group of exclusive bark-dwelling spiders which live exclusively on bark and can be collected from there during the whole year and (2) the group of facultative bark-dwelling spiders which live also in another places besides bark and use the bark of the tree as a habitat temporarily (for example, for overwintering).

The species found during our study can be included in the above-mentioned categories in the following way: Exclusively bark-dwelling species: *Theridion mystaceum, Moebelia penicillata, Nuctenea umbratica, Amaurobius fenestralis, Amaurobius jugorum, Micana* *subopaca, Scotophaeus scutulatus, Marpissa muscosa, Pseudicius encarpatus.*

Facultative bark-dwelling species: *Segestria bavarica, Segestria senoculata, Harpactea rubicunda, Harpactea hombergi, Achaearanea riparia, Steatoda bipunctata, Theridion tinctum, Theridion blackwalli, Lathys humilis, Nigma walckenaeri, Anyphaena accentuata, Cheiracanthium mildei, Clubiona corticalis, Clubiona genevensis, Clubiona pallidula, Philodromus aureolus, Philodromus margaritatus, Philodromus praedatus, Philodromus rufus, Diaea dorsata, Diaea pictilis, Misumenops tricuspidatus, Macaroeris nidicolens, Salticus zebraneus, Dendryphantes rudis.*

The occurrence of the other species considered as occasional because of the low number of species and various habitat-selection: *Anelosimus vittatus, Dipoena tristis, Steatoda triangulosa, Erigone atra, Linyphia triangularis, Araneus diadematus, Gibbaranea bituberculata, Mangora acalypha, Agelena labyrinthica, Tegenaria ferruginea, Dictyna civica, Dictyna uncinata, Phrurolithus festivus, Clubiona comta, Clubiona terrestris, Synaema globosum.*

Further research, including studies on other tree species, are required in order to be sure which species can be regarded as facultative bark-dwellers and which are the ones that occur only accidentally.

In comparison with our earlier study (Horváth and Szinetár 1998), the following species are found:

Achaearanea riparia (Blackwall 1834): This species occurs both on ground level and in vegetation. It prepares its web and specific hiding-place in crevices (under stones or bark). Its sparse and rare occurrence is due to its hidden way of life. In Hungary, it is found mainly on the bark of platan (Szinetár 1996).

Dipoena tristis (Hahn 1833): This is an European species with sparse occurrence. In Hungary, only a few data are known (Samu and Szinetár 1999). It lives generally in low vegetation near the ground and often on low branches of Scotch fir (Heimer and Nentwig 1991).

Steatoda triangulosa (Walckenaer 1802): The species is known from central and Northern Europe, the Turkestan and North America (it does not occur in England). This is a typical synantrop species in Central-Europe. In inhabited areas it can occur accidentally outdoors, and near buildings, as well (Szinetár 1992b).

Erigone atra (Blackwall 1841): Holarctic species. Stenotopic species, photobiont, hygrobiont; it lives on damp meadows, in detritus, grass, on shrubs and on bark.

Linyphia triangularis (Clerck 1757): The species with Palearctic distribution. It lives in various biotopes, on shrubs and smaller plants. It is common in the alder carr, occurring in all above-ground layers, especially in the herb layer. Because of this, its turn-up on bark can be regarded as occasional.

Mangora acalypha (Walckenaer 1802): This species is wide spread in whole Europe, in the temperate zone of Asia, in Asia Minor, in North-Africa and in several islands. In Hungary, it is very frequent both in lowlands and in hilly areas (Loksa 1972). It is thermophilous, avoiding cool forests, so its occurrence in a stand of black pine above Bozsok can be regarded as occasional.

Agelena labyrinthica (Clerck 1757): It often makes its web in dense bushes or hedges of parks and gardens (Loksa 1969). It occurs accidentally on the bark of trees, for example at knags or at cracked parts of the bark where there are appropriate conditions for preparing its large funnel web.

Dictyna civica (Lucas 1849): It prepares its web mainly on walls of houses. It is frequent in Europe, in North-America and in a lot of atlantic islands. In Hungary, this species is wide-spread in towns and smaller habitat, so its occurrence in the sample from Paragvári street is occasional and it is due to the closeness of houses (Loksa 1969).

Dictyna uncinata Thorell 1856: An European, Eastern-Asian species. It is very frequent in Hungary, it can be found both in damp and dry areas. It prepares its web in vegetation, on tree-trunks and on the walls of buildings, so its occurrence is likely with low number of species in other areas, as well (Loksa 1969).

Amaurobius jugorum (L. Koch 1868): A Central-European, mountain species. It is common in the Mecsek, Kőszeg and Sopron Mountains. It is occurrence in the sample from Bozsok is typical (Loksa 1969).

Phrurolithus festivus (C. L. Koch 1835): The species is known from all over Europe, the Caucasus and Northern Africa. Mesic species, hemiombrophil, hemihygophil; it mostly occurs on sandbanks, in moss and pine woods. This forest species may occur at other sites, as well.

Clubiona comta C. L. Koch 1839: European species; it lives in stands, on shrubs and stalks, in moss, litter and under rind of trees. Only one individual has been found so far. It is a species living mainly on deciduous trees in Hungary.

Clubiona terrestris Westring 1862: European species. It lives among high stalks and shrubs, under rind of trees and in grass on meadows. Only one individual has been found so far, as well. It is a species living mainly in the leaf-litter layer. Its occurrence in large numbers is unlikely.

Diaea pictilis (Banks 1896): The species occurs in Nearctic and Palearctic Region too. It has been known in Europe from Switzerland, Austria, Czech Republic and Turkey (Buchar and Thaler 1984) and has also occurred in Hungary since 1996 (Szinetár 1996). It lives in oak forest on shrubs and lower branches of trees (Maurer and Hänggi 1990).

Misumenops tricuspidatus (Fabricius 1775): The species with Palearctic distribution; it occurs in masses on leafy trees and green plants in sunny sites. This foliage-dweller species may appear on the barks during the winter period.

Synaema globosum (Fabricius 1775): Palearctic species with southern distribution. Poland is considered its northern boundary. It lives on blooms and leaves of smaller plants in warm and dry biotopes. Likewise the previous species, small numbers of this species can be detected during the winter-period.

Dendryphantes rudis (Sundevall 1833): A forest species, frequent on gymnosperms, especially on Scotch pine and on spruce (Roberts 1995, Heimer and Nentwig 1991). In this country as well, it lives mainly in forests. In urbanized areas, on planted pines, *Macaroeris nidicolens* is much more common than this species (Szinetár 1995).

Salticus zebraneus (C. L. Koch 1837): European species known also from the Near East; it lives on trunk of trees. In Hungary, it is known to occur in the foliage of both spruce and black pine, for this reason, its occurrence were expected (Szinetár 1992b, 1996).

Species composition, species richness and diversity of bark-dwelling spider communities can be mainly influenced by the mass of prey, the climatic conditions, the structural heterogenity of the environment and the needle-density of the foliage. The higher species richness and diversity in towns can be interpreted by the warmer climate characteristic of towns and the much more dense foliage. In samples from forests, both the mass of prey and the density of the foliage are much lower than in towns, so this can account for the lower species richness and diversity. In the higher abundance of spiders found in towns, the lower predation may have a share, which can be a significant selective effect made by birds (Gunnarsson 1983). The number of individuals of many spiders which can be found in samples during the winter period is reduced is samples taken in spring *(Steatoda bipunctata, Lathys humilis, Clubiona pallidula, Philodromus rufus, Philodromus (aureolus)* species group, *Philodromus* *(margaritatus)* species group). One of the reasons for it is that the species using the bark only for an overwintering habitat returned to the foliage (Tab. 2). The strong reduction in the number of individuals of some species in spring and summer samples may also result from the fact that according to the favourable changes in climatic conditions they get prey running about by day, therefore they are absent in belt traps collecting in daytime. This supposition must be studied later, by using part of the day-traps. In spring samples two bark-dwelling spiders occurs *(Scotophaeus scutulatus* and *Moebelia penicillata),* which spend the winter under the deeper parts of the bark, for this reason, these species can't be trapped with the aid of belts posited on the surface of the bark in the winter period (Tab. 3). The *S. scutulatus* can be found in large numbers until the next winter when it slips back to the deeper layers of bark because of the unfavourable climatic conditions. On the contrary, the number of individuals of a *M. penicillata* decreases heavily by the summer and it turns up again with large numbers only in the autumn. The reason for it would be worth studying later. In samples which are taken during the summer the species occurring in large numbers in spring on bark disappear *(Theridion mystaceum, Theridion tinctum, Anyphaena accentuata, Clubiona genevensis, Clubiona pallidula, Steatoda bipunctata).* Hence, those six species are to move back to the foliage the latest. It is obvious from the data (Tab. 4), that in summer only the real bark-dwelling or branch-dwellers are found in large numbers in every area. However, it is also visible that the four species found in Kőszeg Mountains *(Segestria senoculata, Harpactea hombergi, Amaurobius fenestralis, Clubiona corticalis)* are exclusively found there, which can be explained by the special climatic conditions of the mountain area as well as the relationship with the natural communities of the surrounding forests. The reason for the occurrence of these species can also be that they spend the winter under the deeper layers of the bark. In autumn (Tab. 5), when there are unfavourable changes in climatic conditions, the species begin to migrate again towards the bark, therefore species living in the foliage only in summer turn up in larger numbers again (*Theridion tinctum, Clubiona genevensis, Clubiona pallidula, Anyphaena accentuata, Steatoda bipunctata).* However, in the autumn samples there are two species *(Cheiracanthium mildei, Nigma walckenaeri)* present which are absent in the previous winter sample. This may result from the fact that those are the species which begin to migrate the earliest, even in September, towards the bark. As we took out the traps only at the end of October, in 1997, by that time those two species were

having a rest. That is why we could not catch even an individual of them. Although the exclusive bark-dwellers and branch-dwellers can be found in the samples, their number of individuals decreased considerably. It shows that when the foliage-dwelling species begin to migrate, at the same time these species start to slip back to the deeper layers of the bark.

Previous studies (Luczak 1984, Bengtsson and Rundgren 1984, Clausen 1984) have shown that the species of the *Linyphiidae* and *Clubionidae* families can be sampled in large numbers from areas with air pollution. Our study has not confirmed the results mentioned above. We collected very few of the species *(Moebelia penicillata)* representing the familia *Linyphiidae* from the air polluted area (Paragvári street), but they were present in large numbers in samples from green belts. In the case of the familia *Clubionidae* we also had contradictory results. The two frequent species of the familia *(Cheiracanthium mildei, Clubiona pallidula)* occur exclusively in the moderately polluted town areas and they are absent in the Paragvári street with the biggest traffic. *Clubiona genevensis* occurring in large numbers in Paragvári street is frequent in the two other sites of the town as well, therefore, it has not supported the earlier studies. It can be considered that the two species of familia *Theridiidae* (*Theridion mystaceum, Theridion blackwalli)* occurred with the larger number of individuals in the polluted area which shows their higher tolerance to environmental pollution.

The foregoing studies verified that different species compositions are characteristic of the fauna of the bark of black pine. For this reason, bark-dwelling spiders can be suitable subjects for biological monitoring and indicative research. To find out which factors are responsible for the differences the factual measurement of environmental parameters, manipulative and non-manipulative investigations are needed.

Acknowledgements The authors would like to express their thanks to László Jakab for technical assistance, and to Prof. Dr. Varga Zoltán and Prof. Dr. Tóthmérész Béla for their constructive comments on the manuscript. The study was supported by PFP grant 2235/1998. Csaba Szinetár was a Bolyai Fellow of the Hungarian Academy of Sciences.

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Study III

Effects of immission load on spiders living on black pine

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Biodiversity and Conservation (2001), 10: 1531-1542

Biodiversity and Conservation 10: 1531-1542, 2001.

Effects of immission load on spiders living on black pine

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Received 14 January 2000; accepted in revised form 20 October 2000

Abstract. The effects of immission load on spiders living on black pine *(Pinus nigra* Arnold) were studied in a town in Western Hungary. In three sampling periods, trunk-trap catches of spiders from black pine trees planted in a control urban area were compared with those from black pines planted in an area with high immission load. In the first two sampling periods – when apart from the exclusive dwellers on or under bark of the black pine, foliage-dwelling spiders overwintering under the bark (facultative bark-dwellers) could also be trapped – the species richness and the Shannon diversity were significantly higher in the control area than in the area highly affected by immission. In these sampling periods, the composition of spider assemblages also significantly differed in the studied areas. In the third sampling period – when only the exclusive bark-dwellers could be trapped because facultative bark-dwelling spiders returned to the foliage after the overwintering – the species richness, Shannon diversity and the composition of spider assemblages were similar in the differently affected areas. Our results suggest that spiders living exclusively on or under the bark are not significantly influenced by immission load, while foliage-dwellers are sensitive to immission. Indicator species analysis also proved the clear classification of the responses of spiders to immission load. The probable direct and indirect effects of immission, causing differences in the species richness, diversity and the composition of spider assemblages, are also discussed.

Key words: bark, black pine *(Pinus nigra),* diversity, immission, species richness, spiders

Introduction

With the exponential increase of human activities and technical progress, many procedures and equipment are developed that alter and damage the natural environment. Intense industrial production and traffic increasing quantities of sulphur dioxid (SO_2), nitrogen oxide (NO_x), cyclic hydrocarbons and heavy metals (e.g. lead, zinc, cadmium, etc.) in the air also threaten species directly and indirectly through destruction and change in their habitats. In this respect, primarily the towns are regarded as especially dangerous areas.

The town called Szombathely, located in West-Hungary, is also affected by gas (SO_2, NO_x) and dust (including heavy metals) pollutants emitted by local events (heat and power generating plants, car traffic, etc). The goal of our study was an analysis of the spider assemblages in two lines of black pine trees planted in areas differently affected by immission. Spiders are favourable subjects for comparative ecological studies, because they are diverse and abundant, and their ecology and systematics are relatively well-known. Moreover, spiders can be found almost everywhere, and being mobile and relatively short-lived, they may adjust rapidly to changes in abiotic and biotic environmental factors. Since they are predaceous, there is the potential for biological concentration of toxic matter such as air pollutants (e.g. heavy metals). Previous studies have also indicated that spiders are sensitive to air pollution, therefore they are useful as an indicator group to assess human influence on natural habitats (Clausen 1986; Szinetár 1993). Our paper was also motivated by the fact that there have been relatively few investigations concerning the effect of immission load on arthropods, especially on spiders (Freitag and Hastings 1973; André 1977; André et al. 1982; Clausen 1984b).

In this paper, we have presented a comparative ecological analysis of spiders living on black pine in areas differently affected by immission. We examined whether there were any differences in structure, species richness or diversity of spider assemblages in scarcely and highly affected areas. Furthermore, we have also analysed the responses of spiders living on different parts of the pine concerning immission load.

Materials and methods

Study area and sampling

The sampling sites were located in the town of Szombathely in West-Hungary (see Horváth and Szinetár 1998). Two lines of planted black pine *(Pinus nigra* Arnold) trees were selected for the analysis, according to the extent of immission load (Table 1):

1. Control urban area: Gagarin Avenue. This avenue is surrounded by free-standing houses. There is only a small road near it, therefore the immission load is low.
2. Highly affected area: Paragvári Street. This sampling site is situated next to a main road.

Due to heavy traffic, the immission load is high in this part of the town. The difference in the amount of SO_2 and dust was not significant between the two areas, either in a heating period or in a period without heating. The amount of NO_x appears to be the crucial factor regarding the immission load of the localities (Table 1).

Samples were taken with trunk-traps made of waved cardboard. Not only the exclusive dwellers on or under the bark of black pine, but also the foliage-dwelling spiders can be sampled and studied by using trunk-traps, because foliage-dwelling spiders overwinter under bark (Wunderlich 1982). Traps were 15 cm wide and placed 2 m above the ground on the trunk. Belts were placed around the trunk, their waved surfaces facing the trunk and covering the whole outline of the tree, as if a kind of

Table 1. Mean quantities of the air pollutant in areas with different immission loads in the studied town. The heating period covered the months from November to March, while the period without heating includes the months from April to June.

	Heating period in 1995-1996			Period without heating in 1996		
	SO_2 (μgm^{-3})	NO_x (μgm^{-3})	Dust (g m^{-2} per 30 days)	SO_2 (μgm^{-3})	NO_x (μgm^{-3})	Dust (g m^{-2} per 30 days)
Control area with low immission load	10.45	37.07	2.41	1.90	16.77	6.11
Area with high immission load	13.05	46.64	2.75	2.44	31.71	6.23

artificial bark (Bogya 1995). In October 1995, 30 trunk-traps were placed in each sampling site on different trees. Traps were checked three times, in January, April and June of 1996, in order to study the seasonal activities of spiders. In each period 10 samples were collected from each site. Trapped spiders were identified by species using standard keys (Loksa 1969, 1972; Heimer and Nentwig 1991; Roberts 1995). Some juveniles were kept at 20-22 °C and fed fruit-flies *(Drosophila melanogaster)* until they completely developed and we could identify them. Concerning the species, the nomenclature of Platnick (1997) was followed.

Data analyses

To test effects of immission load on spiders living on black pine, the species richness and Shannon diversity (e.g. Pielou 1975) was analysed per trap. The unpaired *t*-test was used to detect differences in the spider species richness and the diversity per trap, between the two sampling sites in the three sampling periods (Sokal and Rohlf 1981).

Non-metric multidimensional scaling (NMDS) (Gordon 1981) using the Bray-Curtis index of percentage similarity (Ludwig and Reynolds 1988) was used for abundances to assess similarities in spider assemblages among the traps, in the three sampling periods.

To find indicator species and species assemblages characterising the sites with different immission load, the IndVal (Indicator Value) approach was used (Dufrêne and Legendre 1997). This method derives indicator species and species assemblages from hierarchical or non-hierarchical site classification. We obtained the site classification from the NMDS using the Bray-Curtis similarity for abundances. Based on this site classification, IndVal identifies the indicator species corresponding to the various groups. Indicator species are defined as the most characteristic species of each group, found mostly in a single group of the classification and present in the majority of the sampling points belonging to that group. The method is robust to differences in the absolute abundances of different taxa. Furthermore, by using a

Monté Carlo permutation test, it is possible to assess the statistical significance of the species indicator values (Legendre and Legendre 1998; McGeoch and Chown 1998). In the three sampling periods samples were analysed separately, because in each period the 10 traps were collected from different black pines in both habitats. Therefore, the pooling of samples for the entire sampling period is not acceptable in respect to data analysis.

Results

During the study, all together, 1382 individuals belonging to 26 species and to another 12 taxa determined on the level of genera were trapped (Table 2).

Species richness of spiders was significantly higher in the control sampling site with low immission load (Gagarin Avenue) than in the highly affected site (Paragvári Street) during the first two sampling periods (t = 5.4187, df = 1, 18, $P < 0.0001$; t = 2.2361, df = 1, 18, P = 0.0383, respectively; see Figures 1A,B), while in the third period, the difference in species richness between the sampling sites was not significant (t = 0.2182, df = 1, 18, P = 0.8297; Figure 1C).

The same basic pattern was obtained regarding the Shannon diversity. Spider diversity was significantly higher on Gagarin Avenue (control area with low affection) than on Paragvári Street (high immission load) during the first two sampling periods (t =4.1691, df = 1, 18, P = 0.0006; t = 3.6631, df = 1, 18, P =0.0018, respectively; see Figures 1A,B), while in the third period the difference in diversity between the above two sites was not significant (t = 0.0483, df = 1, 18, P = 0.9620; Figure 1C).

The results of the ordination (NMDS) show that in the first two sampling periods the spider assemblages of areas with low and high immission load separated from each other. These facts suggest that sampling sites with a different extent of immission load have different species assemblages (Figures 2A,B). In the third sampling period, however, the spider assemblages of differently affected areas were similar to each other (Figure 2C).

The collected spider species can be divided into three groups by characterisation of habitats by indicator species (Table 3A-C): (1) habitat generalists that existed numerously in all habitats, suggesting that they are not sensitive to immission load (e.g. *Philodromus (aureolus)* species group, *Nuctenea umbratica* (Clerck 1757); *Clubiona genevensis* L. Koch 1866; *Theridion mystaceum* L. Koch 1870; *Scotophaeus scutulatus* L. Koch 1866), (2) species that are sensitive to immission were recorded exclusively, or were the most abundant in the control sampling site with low immission load (e.g. *Anyphaena accentuata* (Walckenaer 1802); *C. pallidula* (Clerck 1757); *Cheiracanthium mildei* L. Koch 1864) and (3) in the second sampling period, one species *(T. tinctum* [Walckenaer 1802]) seems to have preferred the area with high immission load, although its indicator value was not significant.

Table 2. Nuraber of individual spiders (female/male [juvenile]) collected in the differently affected areas.

Species	Control area with low immission load	Area with high immission load	Σ
Segestriidae			
Segestria bavarica C.L. Koch, 1843	2/2(1)	0/0(0)	2/2(1)
Dysderidae			
Harpactea rubicunda (C.L. Koch, 1838)	4/1(0)	0/0(0)	4/1(0)
Harpactea sp.	0/0(1)	0/0(0)	0/0(1)
Theridiidae			
Anelosimus vittatus (C.L. Koch, 1836)	0/0(3)	0/0(0)	0/0(3)
Dipoena melanogaster (C.L. Koch, 1837)	0/0(0)	0/0(1)	0/0(1)
Dipoena sp.	0/0(2)	0/0(0)	0/0(2)
Steatoda bipunctata (Linnaeus, 1758)	23/9(1)	7/2(3)	30/11(4)
Theridion blackwalli O.P.-Cambridge, 1871	3/0(2)	1/0(5)	4/0(7)
T. impressum L. Koch, 1881	0/0(0)	0/0(1)	0/0(1)
T. mystaceum L. Koch, 1870	0/0(20)	0/0(79)	0/0(99)
Theridion sp.	0/0(1)	0/0(0)	0/0(1)
T. tinctum (Walckenaer, 1802)	0/0(88)	4/0(107)	4/0(195)
Linyphiidae			
Linyphiidae sp.	0/0(1)	0/0(0)	0/0(1)
Moebelia penicillata (Westring, 1951)	3/1(0)	0/0(0)	3/1(0)
Tetragnathidae			
Tetragnatha sp.	0/0/(0)	0/0(1)	0/0(1)
Zygiella sp.	0/0(1)	0/0(1)	0/0(2)
Araneidae			
Araneus sp.	0/0(0)	0/0(1)	0/0(1)
Gibbaranea sp.	0/0(8)	0/0(2)	0/0(10)
Nuctenea umbratica (Clerck, 1757)	2/0(8)	5/1(6)	7/1(14)
Agelenidae			
Tegenaria ferruginea (Panzer, 1804)	0/0(2)	0/0(0)	0/0(2)
Dictynidae			
Lathys humilis (Blackwall, 1855)	1/0(3)	0/0(3)	1/0(6)
Nigma walckenaeri (Roewer, 1951)	2/0(0)	0/0(0)	2/0(0)
Anyphaenidae			
Anyphaena accentuata (Walckenaer, 1802)	0/0(167)	0/0(0)	0/0(167)
Clubionidae			
Cheiracanthium mildei L. Koch, 1864	1/3(34)	0/0(0)	1/3(34)
Clubiona brevipes Blackwall, 1841	0/0(1)	0/0(0)	0/0(1)
C. genevensis L. Koch, 1866	1/0(23)	1/0(128)	2/0(151)
C. pallidula (Clerck, 1757)	0/0(362)	0/0(0)	0/0(362)
Clubiona sp.	0/0(0)	0/0(1)	0/0(1)
Gnaphosidae			
Micaria subopaca (Westring, 1862)	1/0(0)	0/0(3)	1/0(3)
Scotophaeus scutulatus (L. Koch, 1866)	2/1(37)	0/0(37)	2/1(74)
Scotophaeus sp.	0/0(1)	0/0(0)	0/0(1)
Philodromidae			
Philodromus dispar (Walckenaer, 1826)	0/0(1)	0/0(0)	0/0(1)
P. margaritatus (Clerck, 1757)	1/0(4)	0/0(0)	1/0(4)
P. rujus (Walckenaer, 1826)	0/0(1)	0/0(7)	0/0(8)
Philodromus spp. *(aureolus)*	0/0(90)	0/0(35)	0/0(125)
Philodromus spp. *(margaritatus)*	0/0(9)	0/0(1)	0/0(10)

Table 2. Continued.

Species	Control area with low immission load	Area with high immission load	Σ
Salticidae			
Macaroeris nidicolens (Walckenaer,	0/0(3)	0/0(0)	0/0(3)
Pseudicius encarpatus (Walckenaer,	0/0(1)	0/0(0)	0/0(1)
Σ	46/17(876)	18/3(422)	64/20(1298)

Discussion

Previous studies on effects of immission have shown that composition, species richness and diversity of spiders are related to the extent of immission load. Gunnarsson (1988) pointed out that pollution has an impact on the composition of spider assemblages. Clausen (1984b), studying the number of spider species, also reported that there is a very strong, significant negative correlation between the species richness of spiders and the SO_2 concentration in the air; e.g. when increasing the SO_2 level, the number of spider species decreases. However, Gilbert (1971) did not find that the species richness of spiders significantly correlated to SO_2 concentration, but the number of individuals as well as species was surprisingly small, although he applied only visual detection as a 'sampling method'. Apart from SO_2 concentration, spiders were studied in relation to the level of heavy metals. Effects of heavy metals on spider assemblages were mentioned only in cases of extremely high pollutant concentration (Strojan 1978; Bengtsson and Rundgren 1984; Clausen 1984b). Clausen (1984b, 1986), analysing the impact of immission on spiders, showed that there are no significant relationships between the Shannon and Simpson diversity and the extent of immission load. Therefore, he argued that diversity indices should be used with caution, if used at all in studies analysing effect of immission load. Clausen (1986) reasoned that results of Lebrun (1976) and André (1977) are contradictory; they found a positive and a negative correlation, respectively, between the Shannon diversity and the pollution level. However, our results proved that immission load has a significant effect on the composition, species richness and the diversity of spider assemblages (Figures 1 and 2).

Arthropods living in vegetation in polluted areas may be affected directly and/or indirectly by immission load. Direct effects of pollutants comprise their toxic influences on animals, whereas indirect effects may be a result of changed habitat structure and environmental conditions. Both types of effects are described in terrestrial arthropod populations (Alstad et al. 1982). Earlier studies (Williamson and Evans 1972; Price et al. 1974; Wade et al. 1980; Bengtsson and Rundgren 1984; Clausen 1984a) noted that heavy metal concentrations in spiders have elevated values in areas highly affected by immission and may cause toxic effects on spiders. Heavy metals in

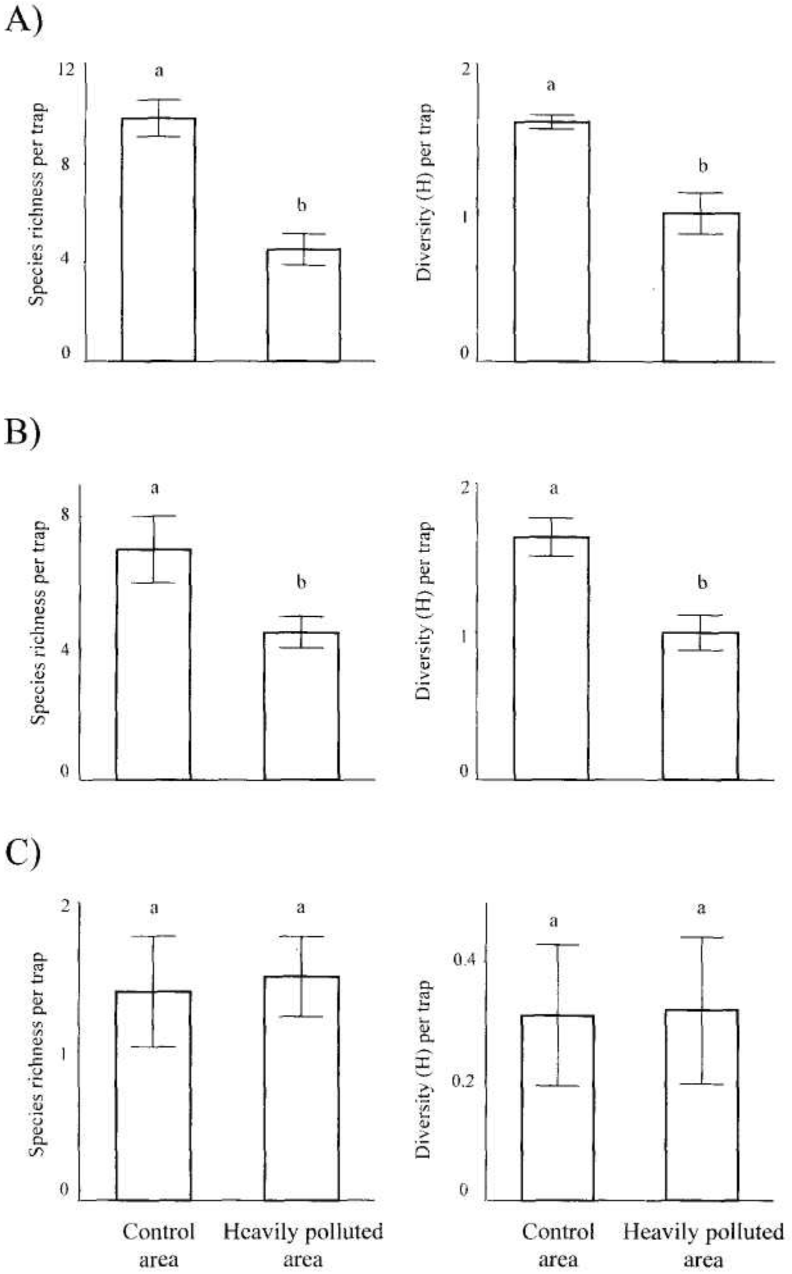

Figure 1. Species richness and Shannon diversity of spiders per trap in the differently affected areas in the first (A), second (B) and third (C) sampling period. Means with different letters indicate a significant ($P < 0.05$) difference by unpaired *t*-test.

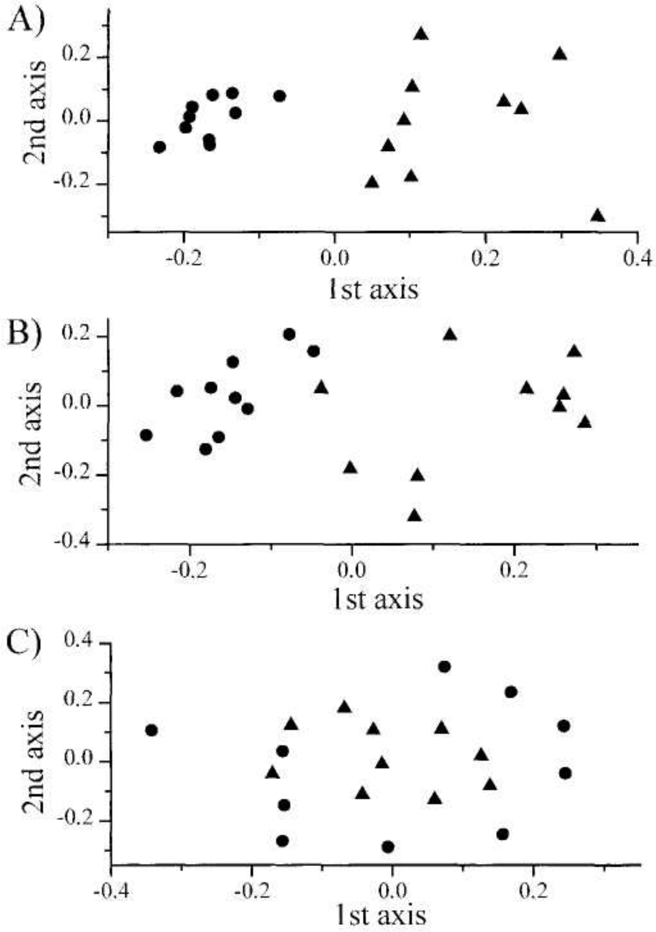

Figure 2. Ordination plot (NMDS by Bray-Curtis index of percentage similarity) of the traps of the differently affected areas in the first (A), second (B) and third (C) sampling period. (•: Control area with low immission load, and ▲: Area with high immission load).

spiders originate directly from the air and from particles deposited on the surface, but indirectly they may arise from consumed prey as well (Clausen 1986). Acid rain may be regarded as a direct effect of pollution on spiders. Gunnarsson and Johnsson (1989), analysing the effects of acid rain on the growth rate of spruce-living spiders in laboratory experiments, pointed out that significant growth reduction occurred only at high acid pH value, so there is weak evidence for the infiuence of acid rain on spiders. The indirect effects of immission load causing changes in microhabitat structure and environmental conditions probably have a more important infiuence on structure, species richness and diversity of spider assemblages than direct toxic effects (Clausen 1986; Gunnarsson 1988). Pollution is presumed to cause needle-loss in spruce in Nordic Europe (Andersson 1986), with a consequent change in habitat

Table 3. Two-way indicator table showing the species indicator power of the habitat clustering hierarchy for the species that were represented by more than ten individuals in the first (A), second (B) and third (C) sampling period.[a]

	IndVal		Control area with low immission load	Area with high immission load
(A) Control area with low immission load				
Anyphaena accentuata	100.00		153/10	0/0
Clubiona pallidula	100.00	*	320/10	0/0
Cheiracanthium mildei	90.00	*	24/9	0/0
Steatoda bipunctata	88.46	*	23/10	3/3
Both areas				
Philodromus spp. *(aureolus)*	95.00	ns	81/10	32/9
Theridion tinctum	90.00	ns	84/10	87/8
Nuctenea umbratica	55.00	ns	6/6	5/5
(B) Control area with low immission load				
Clubiona pallidula	70.00	*	40/7	0/0
Anyphaena accentuata	50.00		14/5	0/0
Cheiracanthium mildei	50.00	*	14/5	0/0
Both areas				
Clubiona genevensis	95.00	ns	23/9	119/10
Theridion mystaceum	85.00	ns	15/7	78/10
Steatoda bipunctata	45.00	ns	10/5	9/4
Philodromus spp. *(aureolus)*	40.00	ns	9/5	3/3
(C) Area with high immission load				
Theridion tinctum	42.31	ns	4/2	22/5
Both areas				
Scotophaeus scutulatus	70.00	ns	38/7	34/7

[a] In the row for each species, the first number indicates the number of specimens present and the second number corresponds to the number of traps where the species is present, in this sample group. The IndVal column indicates the species indicator value for the corresponding clustering level, which is the maximum indicator value observed in all the clustering hierarchy. ns: not significant; * $P < 0.05$.

structure for spruce-living spiders and other arthropods. Gunnarsson (1988) studying the composition of spiders in two close spruce stands, having relatively high and low percentages of needle-loss, respectively, demonstrated that needle-loss in spruce may have an impact on the composition of spider assemblages. He revealed that raptorial spiders are associated with needle-dense branches, since these branches offer good hiding-places for the spiders between the needles. Another explanation for the differences in spider composition may be bird predation, which is known to cause high mortality among spruce-living spiders (Askenmo et al. 1977; Gunnarsson 1983). In the stand with high percentages of needle-loss, spiders might be more vulnerable to bird predation, since they should be easier to detect on branches with few needles (Gunnarsson 1988). An alternative explanation for the differences in spider composition is the microclimate, which may be favourable (wetter and colder) for spiders in the sheltered stand, having low percentages of needle-loss, than in the exposed stand (high percentages of needle-loss) (Gunnarsson 1988). Although we did not study the direct and indirect effects of immission load, presumably the above discussed impacts are also significant in Central Europe.

Our results seem to be in accordance with several previous findings, which have shown that the indirect effects of immission load (changes in habitat structure and environmental variables) are the most important determinants in the composition, species richness and diversity of spider assemblages. In the third sampling period, we detected that the composition, species richness and the diversity of spider assemblages in the control and highly affected areas were not significantly different (Figures 1C and 2C). This can be explained by the fact that in this period the most abundant spiders were those living exclusively on or under the bark of the black pine (e.g. *S. scutulatus* L. Koch 1866), in both areas. Since, in this period, foliage-dwelling spiders that use the bark only for overwintering (facultative bark-dwellers) returned to the foliage (see Table 3C). These results suggest that spiders living exclusively on or under the bark are not significantly influenced by immission load. The bark is presumably a suitable hiding-place, therefore the exclusively bark-dwelling spiders are only moderately exposed to the direct effects of immission. Moreover, the influences of immission load on the microhabitat structure and microclimate (indirect effects) of the bark may not be considerable. On the other hand, in addition to the exclusive bark-dwelling spiders, foliage-dwellers were also sampled in the first two sampling periods. In these periods, differences in the composition, species richness and diversity of the spider assemblages between the two studied black pine stands were significant (Figures 1 A,B and 2A,B). These findings can be explained by the fact that some species (e.g. *A. accentuata* (Walckenaer 1802); *C. pallidula* (Clerck 1757); *C. mildei* L. Koch 1864) completely disappeared or their abundance considerably decreased in the highly affected area (Table 3). The mentioned species are facultative bark-dwelling, so it is presumable that the above-discussed direct and rather indirect effects of immission load influenced their distribution.

The results of the indicator species analysis proved a clear classification of the responses of spiders to immission (Table 3). In the first sampling period, *Theridion tinctum* (Walckenaer 1802) was identified as habitat generalist (Table 3A), while in the second period it seemed to prefer the area with high immission load (Table 3B). This contradiction may derive from biased sampling. In our opinion, this foliage-dwelling species is probably a habitat generalist. However, in the black pines located in the control area (Gagarin Avenue), the individuals of *T. tinctum* (Walckenaer 1802) may have returned earlier to the foliage after the overwintering, and this return contributed to the decrease of its abundance in this area. Our assumption was verified by the fact that the indicator value of this species was statistically insignificant (Table 3B), and that is its presence cannot be unambiguously predicted in the area with high immission load. An analogous case can be observed concerning the species *Steatoda bipunctata* (Linnaeus 1758). In the first sampling period it was a significant indicator species in the control area (Table 3A), while in the second period it was regarded as a habitat generalist (Table 3B). *S. bipunctata* (Linnaeus 1758) is probably a foliage-dwelling species that is sensitive to immission load, but in the area with low immission load (control area) its individuals also returned to the foliage earlier following the overwintering, which resulted in a decrease of its abundance. Earlier studies (Luczak 1984; Bengtsson and Rundgren 1984; Clausen 1984b) indicated that spider species of families Linyphiidae and Clubionidae are more common in areas with high immission load. Regarding species of the family Linyphiidae, our results could not confirm this finding because of the limited number of individuals in the samples (Tables 2 and 3). However, concerning the species of the Clubionidae family, we obtained an opposite result, since certain species of this family *(C. mildei* L. Koch 1864; *C. pallidula* (Clerck 1757)) responded the most sensitively to the immission load (see Tables 2 and 3).

Our results proved that spiders are a suitable group for biological monitoring and indication, and for assessment of biodiversity. However, further manipulative and non-manipulative studies are needed to identify factors that are responsible for changes in structure, species richness and diversity of spider assemblages in areas affected by immission. Only with the full knowledge of these facts can we prepare management and conservation plans in the affected areas that stop or reduce environmental damage.

Acknowledgements

We thank Prof. Z. Varga for proposing the research problem and for many suggestions. Financial support was received from the Pro Regione Hungariae Fund and the Pro Renovanda Cultura Hungariae Fund. Cs. Szinetár was Bolyai Fellows of HAS.

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Study IV

The effect of exposition time and temperature on spiders (*Araneae*) overwintering on the bark of black pine (*Pinus nigra*)

Horváth, Roland; Lengyel, Szabolcs; Szinetár, Csaba & Honti, Szabolcs

European Arachnology 2002 (2004): 95-102

European Arachnology 2002 (F. Samu & Cs. Szinetár eds.), pp. 95-102.
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(Proceedings of the 20th European Colloquium of Arachnology, Szombathely 22-26 July 2002)

The effect of exposition time and temperature on spiders (Araneae) overwintering on the bark of black pine *(Pinus nigra)*

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Abstract
The effect of exposition time (time between the installation of traps and the collection of spiders) and autumn air temperature on spiders overwintering on tree bark was studied in a planted black pine *(Pinus nigra)* forest, near Debrecen (east Hungary). We collected spiders from traps fixed 2 m high on tree trunks once every five days for 50 days in 1999 and 2000. We collected 957 spiders belonging to 15 species and I species determined to the genus level in the two years combined. In 1999, the diversity and number of spiders increased with exposition time but were not influenced by temperature when data were combined for each sampling time. This was because temperature was low in the middle of the sampling period, but increased again at the end, which weakened its effect. However, the diversity and number of individuals continued to increase even when temperature increased at the end of the sampling period. In 2000, the number of individuals increased by exposition time because we found individuals of *Philodromus margaritatus* in very high numbers on the last sampling occasion. There were no other differences in 2000 because temperature was constantly high during the sampling period. Our results suggest that the movement of spiders to the bark is a characteristic process and that the diversity and number of spiders continue to increase in the autumn even when temperature slightly increases. This process, however, can be delayed if temperature is constantly high during the study period.

Key words: bark-dwelling spiders, species richness, diversity, number of individuals

INTRODUCTION

In temperate zones, poikilotherm animals are faced with the challenge of surviving extreme cold periods. Invertebrate species have evolved a number of ways to tackle this problem. Spiders, for example, can use hibernacula (shelters for overwintering), develop cold resistance or adapt their metabolism to a lower level to reduce the effect of cold (Kirchner 1987). Spiders living in the vegetation or on the soil use various hibernacula, such as leaf litter, grass tussocks, rocks, caves or houses, bird nests, upper vegetation, or crevices on the bark of trees (Engelhardt 1964; Schaefer 1977; Balkenhol & Zucchi 1989; Gajdoš et al. 1991). The microclimate of these microhabitats can be milder than that of the general habitat, which enable spiders to survive the winter.

Spiders can overwinter either as eggs, juveniles or adults. Adult and juvenile spiders can use a silken sac to enhance the insulation of the hibernacula or just simply stay immobile at the hibernacula. Species that use silken sacs can stay there throughout the winter, whereas others can leave the sac during favourable conditions to feed. Under favourable conditions juveniles can even speed up their development to reach adulthood earlier (Kiss & Samu 2002).

The bark of trees is one of the most important overwintering microhabitats of spiders. Exclusive bark-dwelling spiders use the bark throughout the year and occur only on the bark, whereas facultative bark-dwelling species use the bark only for certain periods (e.g. for overwintering) but spend most of the year in the foliage or on the branches (Wunderlich 1982). Facultative bark-dwelling spiders are usually found on the bark only between November and April (Horváth et al. 2001). These species use the bark only for overwintering and move to the bark only when air temperature drops substantially (Horváth & Szinetár 1998). The movement of spiders to and from the bark is a characteristic process of overwintering. The movement can occur rapidly if the conditions change quickly, in contrast, it can happen over a longer period if the conditions deteriorate less rapidly. In spite of the importance of the movement of spiders to the bark, there are no data available on how (i.e. at what temperatures and how fast) the movement occurs.

The aim of our study was to determine how exposition time (between the installation and collection of traps) and changes in air temperature in the autumn affect the movement of spiders to the bark before overwintering. Specifically, first we were interested in whether there is a correlation between air temperature and species richness, number of individuals and diversity of spiders. Second, our aim was to determine the temporal characteristics of the movement, i.e. to find out whether time affects the species richness, number of individuals and diversity of spiders.

MATERIAL AND METHODS

Study area and sampling

We collected spiders using belt traps fixed on trunks of black pine *(Pinus ragra)* at the Fancsika water reservoir near Debrecen, eastern Hungary (UTM: ET 56 A4). The forest is a 3-ha planted stand of black pine (70%) and black locust *(Robinia pseudoacacia)* (30%) (Fig. 1).

Trunk-traps were made of waved cardboard (15 x 120 cm) and were fixed 2 m above the ground on the trunk by tape. Belts were placed around the trunk with their waved surfaces facing the trunk and covering the whole perimeter of the tree, as a kind of artificial bark with the real bark under the traps (Horváth et al. 2001). There were two trapping periods. In the first collection period we installed 100 trunk-traps on 26 October, 1999, out of which we removed 10 every five days. The last 10 traps were collected on 15 December, 1999. Because in 1999 every spider species could be collected by using 50 traps (Honti 2002), in the second period we installed 50 trunk-traps on 19 October, 2000 and removed them by five traps every five days, and the last traps were collected on 8 December, 2000. Traps were installed on trees other than those used in 1999. We aimed to conduct the study for 50 days in both years, and to end the study by mid-December because spiders usually move to the bark by this time.

Traps were removed at 12:00 noon on each occasion. Spiders were identified by species using standard keys (Loksa 1969, 1972; Heimer & Nentwig 1991; Roberts 1995). We used the nomenclature of Platnick (1997) during the identification.

Air temperature was measured at a permanent meteorological station ca. 2 km from the study site by the Department of Meteorology

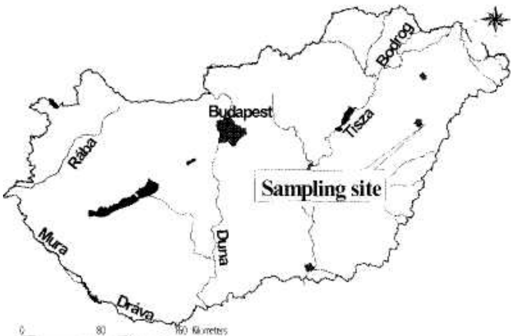

Fig. I. Geographical location of the sampling site.

at the University of Debrecen, and we used the values measured at 12:00 noon on each collection day.

Data analyses

Data from the two years were treated separately. We first checked for the normality of average species richness, diversity and number of individuals using Kolmogorov-Smirnoff tests. If data showed normal distribution, we analysed samples collected during different sampling times using one-way analyses of variance (ANOVA). When the data did not meet parametric assumptions, we used nonparametric tests, i.e. Kruskal-Wallis tests (Barta et al. 2000; Kuehl 1994). We used multiple regression models to evaluate the effects of exposition time and temperature on combined species richness, diversity and number of individuals at the same time (Barta et al. 2000). In these analyses, data were combined so that all spiders collected at any one sampling day were considered as one set and species richness, diversity and number of individuals were calculated for each sampling day. This way one data point represented one sampling time in each year, thus we had ten data points for each multiple regression model for each year. Exposition time was considered a continuous, quantitative variable in both ANOVA-type and regression-type analyses (Kuehl 1994). Statistical analyses were carried out by using Statistica 5.1 for Windows (StatSoft Inc. 1995) and NuCoSA 1.05 (Tóthmérész 1993) software packages.

RESULTS AND DISCUSSION

During the study a total of 957 individuals belonging to 15 species and 1 species determined to the genus level were trapped (Table 1.). Temperature varied between 1.0 and 14.6° C in 1999 and between 8.2 and 20.6°C in 2000 (Fig. 2).

When data from each trap collected at one sampling time were considered separately in 1999, there was no difference in average species richness among collection times (Kruskal-Wallis test: H_9=5.59, N=100, NS; Fig. 3A). There were also no differences among sampling times in either average diversity (ANOVA, $F_{9,99}$=1.20, NS; Fig. 3B) or average number of individuals ($F_{9,99}$=1.63, NS; Fig. 3C).

However, when data were combined for each sampling time in 1999, combined species richness was marginally significantly influenced by temperature but not by sampling time (multiple regression, R^2=0.44, $F_{2,7}$=2.73, NS; temperature: t_7=2.33, P=0.053; exposition time: t_7=1.02, NS; Fig. 4A). However, the combined diversity of spiders was influenced by exposition time but not by temperature (R^2=0.73, $F_{2,7}$=9.38, P<0.011; exposition time: t_7=3.33, P=0.010; Fig. 4B; temperature: t_7=0.71, NS). Exposition time alsó affected the combined number of individuals, whereas temperature did not (R^2=0.64, $F_{2,7}$=6.17, P<0.028; exposition time: t_7=3.43, P=0.011; Fig.4C; temperature: t_7=1.06, NS).

These results suggest that combined species richness increased as temperature decreased, but because temperature increased slightly toward the end of the sampling period (Fig. 2), its effect was only marginally significant. However, because temperature was low in the middle of the sampling period, spiders appeared on the bark in higher numbers and higher diversity at this time, and the increased combined diversity and number of individuals did not change even after the slight increase of temperature at the end of the sampling period. In other words, spiders that moved to the bark during the middle of the sampling period did not move back from the bark at the slight increase of temperature, which may have resulted in our observation that combined diversity and number of individuals were affected by exposition time but not by temperature. During the period when temperature decreased (sampling time 1 to 7, Fig. 2), the number of individuals increased as time passed and temperature decreased (R^2=0.85, $F_{2,4}$=11.14, P=0.023; exposition time: t_4=4.21, P=0.014; temperature: t_4=3.22, P=0.032). However, the effect of temperature on the diversity of spiders was

Table I. Number of individual spiders [female/male/(juvenile)] collected in 1999 and in 2000. Facultative bark-dwellers are marked with a letter "F" after the species name and exclusive bark-dwellers are marked with an "E".

FAMILY/Species	1999	2000
DYSDERIDAE		
Harpactea rubicunda "F" (C. L. Koch, 1838)	0/0/(0)	0/0/(1)
THERIDIIDAE		
Anelosimus vittatus "F" (C. L. Koch, 1836)	0/0/(4)	0/0/(0)
Steatoda bipunctata "F" (Linnaeus, 1758)	13/2/(1)	3/0/(1)
Theridion blackwalli "F" O. P.-Cambridge, 1871	0/0/(1)	0/0/(0)
T. mystaceum "E" L. Koch, 1870	0/0/(3)	0/0/(0)
T. tinctum "F" (Walckenaer, 1802)	0/0/(4)	0/0/(0)
ARANEIDAE		
Gibbaranea bituberculata "F" (Walckenaer, 1802)	0/0/(2)	0/0/(0)
Nuctenea umbratica "E" (Clerck, 1757)	46/0/(10)	6/0/(1)
DICTYNIDAE		
Dictyna sp.	0/0/(2)	0/0/(0)
ANYPHAENIDAE		
Anyphaena accentuata "F" (Walckenaer, 1802)	0/0/(38)	1/0/(0)
CLUBIONIDAE		
Clubiona pallidula "F" (Clerck, 1757)	0/0/(92)	0/0/(3)
GNAPHOSIDAE		
Scotophaeus scutulatus "E" (L. Koch, 1866)	0/0/(0)	0/0/(1)
PHILODROMIDAE		
Philodromus spp. (aureolus) "F"	0/0/(77)	0/0/(17)
Philodromus spp. (margaritatus) "F"	0/0/(519)	0/0/(100)
THOMISIDAE		
Misumenops tricuspidatus "F" (Fabricius, 1775)	0/4/(4)	0/0/(0)
SALTICIDAE		
Marpissa muscosa "E" (Clerck, 1757)	0/0/(0)	0/0/(1)
Σ	59/6/(757)	10/0/(125)

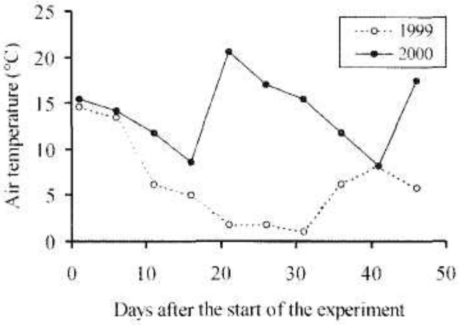

Fig. 2. Air temperature measured at 12:00 noon at a meteorological station 2 km from the study site on each sampling day during the sampling period in 1999 and in 2000.

not significant, unlike that of exposition time (R^2=0.85, $F_{2,4}$=10.99, P=0.024; exposition time: t_4=3.15, P=0.035). The latter result indicates that although more spiders appeared on the bark during the cooling period, the increase can be attributed to the appearance of individuals of only a few species. This was supported by the finding that species richness did not change with time or temperature during the cooling period (R^2=0.39, $F_{2,4}$=1.27, NS).

The findings that average diversity and number of individuals did not differ among sampling times, whereas combined diversity and number of individuals increased during the sampling period also suggest that the use

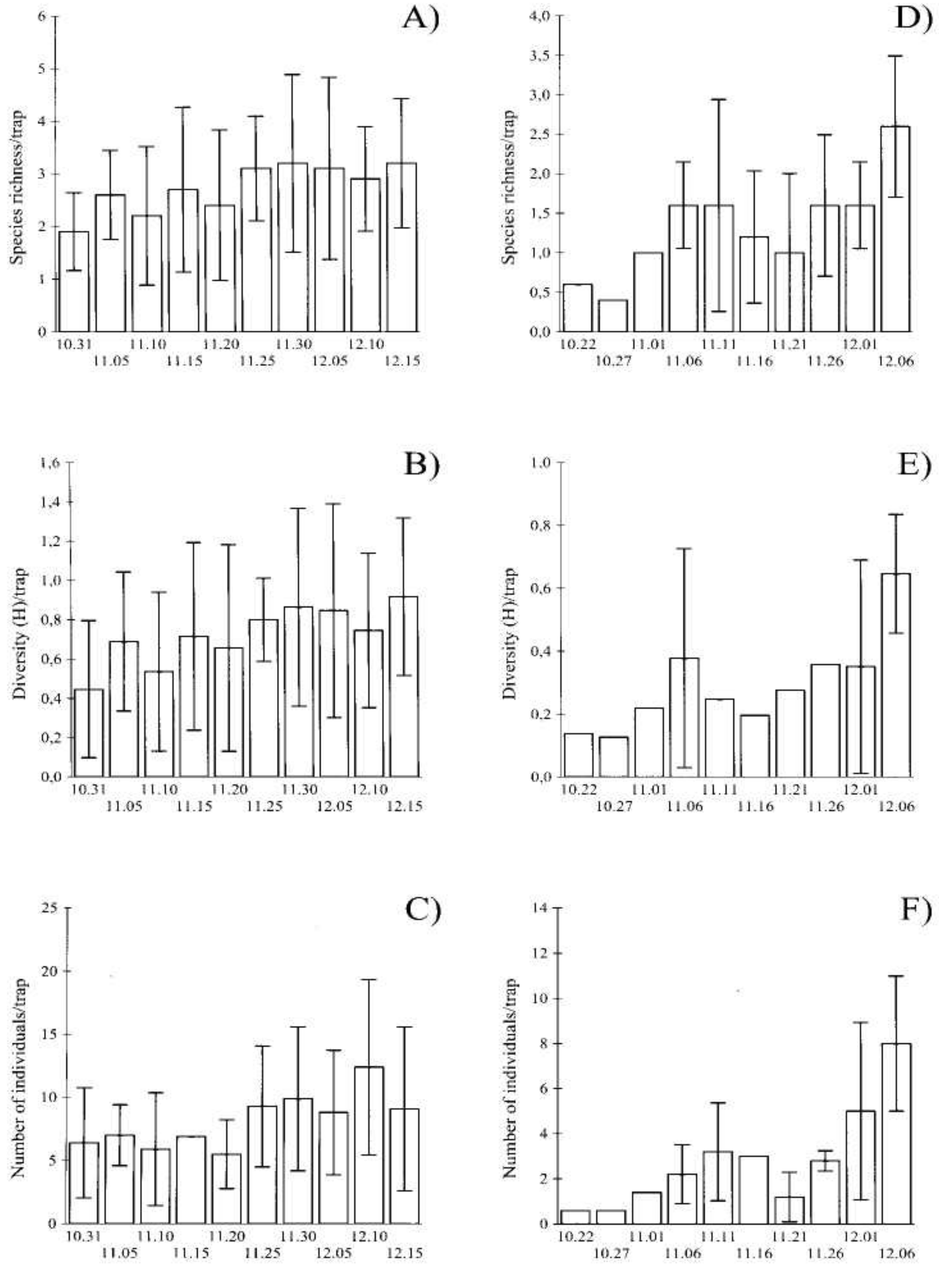

Fig. 3. Mean ± SD species richness (**A, D**), diversity (**B, E**) and number of spiders (**C, F**) collected at each sampling time in 1999 (**A-C**) and in 2000 (**D-F**). Dates are given in mm.dd format.

of the averaged variables obscured the differences that may have had biological relevance. It is also possible that the size of the traps was too small for the type of patchiness observed. However, we chose 15-cm-wide traps because our previous experience suggested that this size is adequate to detect differences, and because we used this traps in a previous study (Horváth et al. 2001).

When data from each trap were treated separately in 2000, average species richness was not different among sampling times (H_9=12.23; NS; Fig. 3D). Similarly, average diversity did not differ among sampling times (H_9=12.23, NS; Fig. 3E). However, the average number of individuals differed among sampling times (H_9=19.16, P=0.024), mostly because we found more spiders in the last sampling time than on the previous occasions (Fig. 3F). This was caused by a sudden increase in the numbers of a single species, *Philodromus margaritatus,* in the last sampling time.

When data from each trap were combined for each sampling time in 2000, combined species richness was not influenced by either sampling time or temperature (R^2=0.10, $F_{2,7}$=0.40, NS; exposition time: t_7=0.18, NS; temperature: t_7=0.88, NS). The combined diversity of spiders was also not significantly affected by either exposition time or temperature (R^2=0.17, $F_{2,7}$=0.71, NS; exposition time: t_7=0.45, NS; temperature: t_7=1.12, NS). However, diversity was influenced by both exposition time and temperature during the second cooling period in 2000 (from sampling time 5 to 9, Fig. 2) (R^2=0.98, $F_{2,2}$=41.99, P=0.023; exposition time: t_2=9.10, P=0.012; temperature: t_2=9.16, P=0.012). The combined number of individuals, however, was significantly influenced by exposition time but not by temperature during the entire sampling period (R^2=0.68, $F_{2,7}$=7.56, P<0.020; exposition time: t_7=3.86, P=0.006; Fig. 4D; temperature: t_7=0.64, NS). In this case, too, the increase in the number of individuals

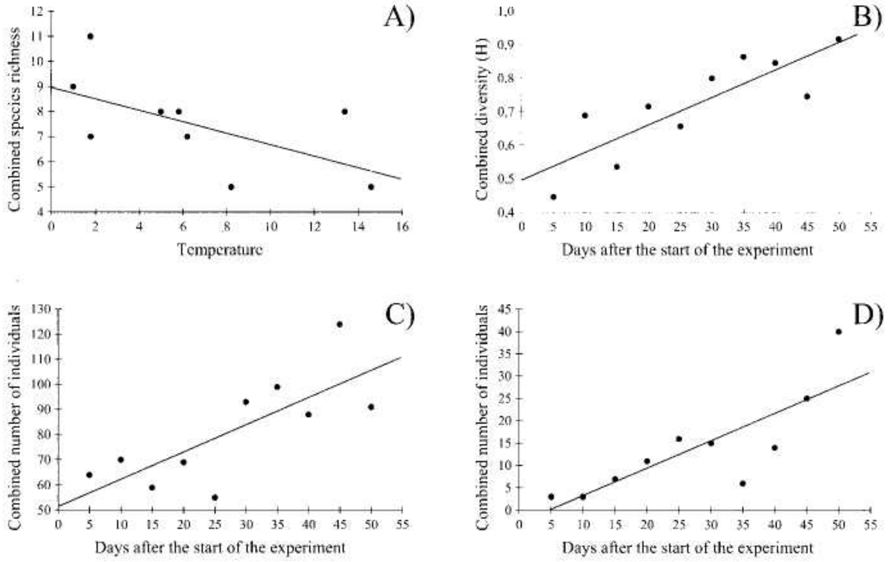

Fig. 4. The relationship between temperature and combined species richness (**A**), exposition time and combined diversity (**B**), exposition time and combined number of individuals (**C**) in 1999, and between exposition time and combined number of individuals in 2000 (**D**). Lines shown were obtained by multiple linear regression models (see Material and methods for definition of variables and Results and discussion for statistics).

could be attributed to the sudden increase of one species, *P. margaritatus,* on the bark in the last sampling time. The appearance of this species on the bark was distributed more evenly in 1999.

The lack of the effect of exposition time and temperature can be explained by the fact that temperature was constantly high during the sampling period (Fig. 2) and spiders did not move to the bark as they did in 1999. Temperature did not vary much during this period, and was above 10°C in eight of the ten sampling times. Spiders are known to be active at temperatures as low as 5°C (Bogya 1995), thus it is not surprising that we did not find differences by temperature in 2000, when temperature was above 8°C at each collection time.

In summary, our results suggest that the movement of spiders to the bark of trees is a characteristic temporal process, which can be detected by using trunk-traps. The results from 1999 show that spiders continued to increase in diversity and in number, i.e. they moved to the bark of trees from the canopy, even when temperature slightly increased. The results from 2000, however, indicate that the movement of spiders can be delayed if temperature is constantly high during the autumn.

ACKNOWLEDGEMENTS

We wish to thank Prof. Zoltán Varga for many suggestions during the research. Péter Kozma helped with field logistics. Dr. Béla Kiss helped with the preparation of the maps and Gábor Németh provided us with temperature data. Szabolcs Lengyel was supported by an OTKA grant (F30403) and a Békésy Postdoctoral Fellowship and Csaba Szinetár was a Bolyai Fellow of the Hungarian Academy of Sciences during the preparation of the manuscript.

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Study V

The effect of prey availability on spider assemblages on Black Pine (*Pinus nigra*) bark: spatial patterns and guild structure

Horváth, Roland; Lengyel, Szabolcs; Szinetár, Csaba & Jakab, László

Canadian Journal of Zoology (submitted 2004)

The effect of prey availability on spider assemblages on Black Pine (*Pinus nigra*) bark: spatial patterns and guild structure

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Abstract: Spider assemblages are influenced primarily by habitat structural complexity and secondarily by prey availability. We studied whether prey availability affects spiders in a structurally poor habitat, the bark of Black Pine (*Pinus nigra*), 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. Spider species richness (SR), number (N), and diversity were positively related to number of prey taxa (NPT) and prey individuals (NP) in a forest in W-Hungary and SR and N were negatively related to NPT or NP in the urban localities. Nocturnal hunters but not diurnal hunters or web-builders showed positive relationships to the number of their respective prey in the forest in W-Hungary and in the moderately polluted urban localities. Exclusive bark-dwelling spiders were positively associated with prey numbers in forests in E-Hungary and negatively in the polluted urban locality. We suggest that patterns in spider assemblages can be influenced by prey availability in several ways and that other factors (e.g. habitat structural diversity and air pollution) also need to be considered in explaining these patterns.

Introduction

Trophic relationships are one of the most important factors determining the composition of communities. This is because populations mainly interact through their feeding relationships (Ricklefs and Miller 1999), for example, the availability of prey largely affects the distribution of their predators. The amount of prey present can lead to variation in the number of predators (numerical response), whereas predators can switch to alternative prey when their primary prey decreases below a certain threshold (functional response) (Holling 1959; Wise 1993). Understanding the response of predators to prey availability is crucial in an understanding how the interaction between predators and prey influences 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 the strength of these interactions depends on other factors, e.g. habitat structure, disturbance etc.

Spiders (Araneae) are ubiquitously important generalist predators in most terrestrial ecosystems. Spider assemblages are thought to be primarily influenced by habitat structural diversity and secondarily by prey availability and abundance (Halaj et al. 1998, 2000; Nyffeler and Sunderland 2003). Several empirical studies appear to corroborate this hypothesis. 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 may be *per se* important for spider assemblages. Floristically more diverse Scots pine (*Pinus sylvestris*) plantations hosted more spider species than did structurally less complex lodgepole pine (*Pinus contorta*) plantations both at the ground level and at the canopy level (Docherty and Leather 1997). Large-scale patterns in agricultural land use can also explain the abundance of spiders based on habitat diversity. For example, farm sizes are considerably smaller in Europe than in North America, which corresponds to higher habitat diversity in agroecosystems and higher densities of small web-building spiders in northern Europe (Nyffeler and Sunderland 2003). Spiders of different guilds may react to changes in habitat structural diversity in different ways because of differences in their habitat use. However, all arboreal spiders were shown to be limited by strong bottom-up forces in Douglas-fir (*Pseudotsuga menziesii*) canopies (Halaj et al. 2000). Although habitat structural diversity was of primary importance in determining arboreal spiders, prey availability also explained significant part of the variation in spider species richness (Halaj et al. 2000). The strong relationship between habitat structural diversity and spider assemblages 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 prey availability, besides habitat complexity, can also play a role in the occurrence and numbers of spiders within a habitat. For example, in a review of spiders and various pests of coniferous forests, mostly the availability of moths (Tortricidae, Lymantridae, Lasiocampidae) was found to influence 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 proportion of the total variance in spider numbers and diversity than did habitat structure (Halaj et al. 1998).

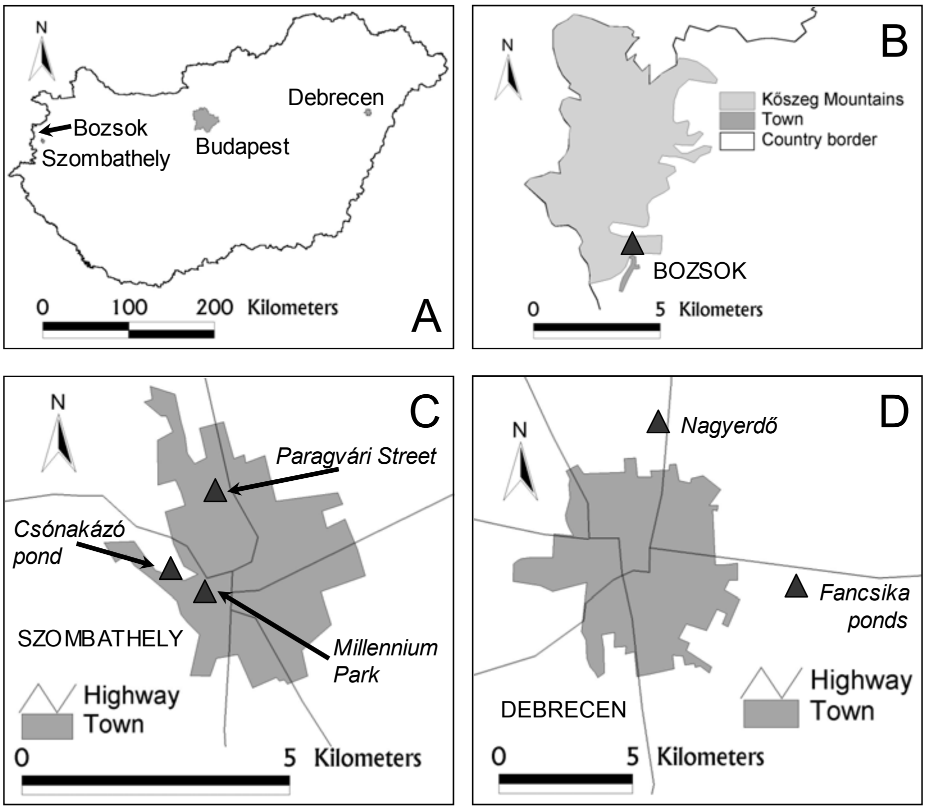
Spiders are usually considered generalist predators, and their potential prey encompasses most invertebrate taxa of similar or smaller size and present in the habitat (Nentwig 1987). However, the prey spectra of spiders differ by their way of hunting and habitat. For example, ground-dwelling spiders consume more Collembola and Hymenoptera but less Diptera and Hemiptera than do species that hunt on the 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 to certain prey taxa or prey type has been well demonstrated by laboratory studies (Li et al. 1996; Li and Jackson 1996; Lang and Klarenberg 1997; Li et al. 1997; Riechert and Lawrence 1997; Jackson and Li 1998; Jackson et al. 1998; Li et al. 1999; Bilde and Toft 2000; Clark and Jackson 2000; Harland and Jackson 2000; Jackson 2000; Li 2000; Jackson and Li 2001). 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 spider habitat choice (e.g. Nentwig 1987; Bardwell and Averill 1997; Crouch and Lubin 2000; Harwood et al. 2001) rather than what spiders consume under controlled conditions.

Although plenty of evidence suggest that habitat structural diversity greatly influences spider assemblages, only a few studies found a direct link between the variation in prey availability and variation in spider assemblages (e.g. Halaj et al. 1998; Harwood et al. 2001, 2003; Ibarra-Nunez et al. 2001). These studies either found that the effect of prey abundance on spiders is of secondary importance to that of habitat structural diversity (Halaj et al. 1998) or detected a link between spiders and potential prey in structurally poor agroecosystem habitats (Harwood et al. 2001; Ibarra-Nunez et al. 2001). To our knowledge, there is no published study on the relationship between spiders and their prey from structurally complex natural habitat or in natural habitats where habitat diversity is low.

The aim of this study was to determine the spatial and temporal (seasonal) variation in spider species assemblages and to 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 Black Pine (*Pinus nigra*) among localities in forests (E-Hungary and W-Hungary) and a city (W-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?, (iii) 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?, and (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 for both spiders and their potential prey. In general, the bark is structurally less complex than the canopy of the trees, thus, the bark provides an opportunity to investigate the relationship between spiders and their prey in a natural habitat where structural diversity is low, and habitat complexity theoretically is expected to play a minor role in influencing spider

Fig. 1. Geographical location of sampling localities 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.



assemblages. Studies of bark-dwelling spiders are rare (e.g. Albert 1976; Nicolai 1986; Hansen 1992; Simon 1995; Koponen 1996), even though many species live on the tree bark due to the existence of special microhabitats (Wunderlich 1982; Szinetár 1992). Most spiders use tree bark only temporarily, e.g. for overwintering (facultative bark-dwelling species), whereas others are exclusive bark-dwellers (Wunderlich 1982). Special microclimatic and structural conditions make it possible that the bark of pine trees holds populations of various prey taxa. Many insect taxa also use tree bark as their exclusive habitat (e.g. taxa from Pseudoscorpiones, Acari, Dermaptera, Psocoptera, Thysanoptera, Heteroptera, Auchenorrhyncha, Sternorrhcyncha, Coleoptera etc.). The 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 at three urban sites in the city of Szombathely (UTM coordinate XN23) and three forest sites, one in W-Hungary (near the village of Bozsok, XN14) and two in E-Hungary (Nagyerdő: ET46, Fancsika: ET56), in 1999 (Fig. 1.). In all of these sites, Black Pines were planted between 1940 and 1950.

(1) Szombathely, Millennium Park (formerly named as Gagarin Avenue): The sampling site is in a park along the avenue, which is surrounded by residential areas. There is small traffic at the edge of the park, and immission load from air pollution is minimal (see Horváth et al. 2001).

(2) Szombathely, Paragvári Street: Black Pines are located along a main road, and because of heavy traffic, immission load is high.

(3) Szombathely, Csónakázó pond: This site is also in a park area and pine trees are located along a small road along between an artificial pond and an open-air swimming pool. Traffic is weak and the site is only moderately polluted.

(4) Kőszeg 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 foliage in this forest is located higher than in the other sampling sites.

(5) Debrecen, Nagyerdő forest: A large Black Pine plantation, surrounded by deciduous forests, can be found 200 m away from a highway with heavy traffic north of the city of Debrecen. Despite the heavy traffic, immission load is moderate due to the filtering effect of the forest.

(6) Debrecen, Fancsika ponds: This sampling site is located east from the city of Debrecen and is surrounded by ponds. Immission load is low because the site is far from highways and industrial plants.

Spiders were collected by trunk-traps made of waved cardboard wrapped and fixed on the tree bark. This method is a standard way of collecting both exclusive and facultative bark-dwelling spider species (Wunderlich 1982). Traps were 15 cm wide and were placed 3 m above the ground on the trunk, with their waved surfaces facing the trunk and covering the entire diameter of the tree, as if a kind of artificial bark (Bogya 1995). One trunk-trap was placed on ten different trees each and traps were on the bark for 10 days in each sampling site. Samples were collected twice, summer samples were taken between 2 and 12 July and fall samples were taken between 22 October and 1 November in sampling sites in W-Hungary and between 2 and 12 July and between 6 and 16 November in sampling sites in E-Hungary. Spiders were stored in 70% ethanol and identified to the species level using standard keys (Loksa 1969, 1972; Heimer and Nentwig 1991; Roberts 1995). Concerning the species, the nomenclature of Platnick (2004) was followed. For guild-level analyses, spider species were classified into either of three groups: nocturnal hunters, diurnal hunters and web-builders (Wise 1993).

Prey were collected by 5-cm-wide trunk traps made of transparent nylon foil (0.2 mm thickness), which were positioned at a height of 2 m on the same trees where spider traps were installed. The outer surfaces of the traps were treated by Soveurode aerosol (Sovilo Co.). 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 (Móczár 1984; Steinmann 1970, 1974; Ujhelyi 1957, 1959; Mihályi 1972; Müller 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) flying "tourists" that visit the bark temporarily (Nentwig 1987). 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 can also catch bark-dwelling arthropods to a smaller extent (Nentwig 1987). Spiders occurring accidentally on the study trees (n = 36 individuals of n = 9 species) were excluded from all analyses.

Statistical analysis

Tree trunk diameter was similar in traps collecting prey and spiders because they were positioned ca. 30 cm away, and trunks of Black Pine does not change much in this range. Therefore, we considered the unweighted number of individuals collected in all analyses. Species richness, number of individuals and diversity of spiders was tested by two-way, mixed model ANOVAs in which locality and season were the main effects. Full models, including the locality*season interaction, were fitted first, and the model was re-fitted without the interaction term ('reduced model') if the interaction was not significant. Locality was a random factor, which is appropriate if the sampling localities are a random sample of all localities possible for study (McKone and Lively 1993; Beck 1997). We used t-tests to compare the quantity of spiders in summer and fall samples and corrected for non-equal variances where appropriate by adjusting degrees of freedom based on the SPSS algorithm. A hierarchical cluster analysis (Tóthmérész 1993) was used to compare the similarity of spider species assemblages among localities. Linear regression models were fitted to test the relationship between species richness, number of individuals and diversity of spiders and 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 due to the low number of spiders in some localities, which would lead 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 ± S.E.s, F-values and significance values are given. Means ± S.D.s and two-tailed probabilities are reported throughout the text.

Results

1. Spatial and seasonal variation in spider assemblages

We collected a total of 1290 spider individuals belonging to 28 species and 24,186 prey individuals belonging to five 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 average number of spiders per trap was 10.8 ± 17.27 (range 0 – 150, n = 120 traps) and 11 traps contained no spiders. The average number of prey per

Table 1. Mean ± S.D. species richness, number of individuals and Shannon diversity of spiders collected on the bark of Black Pine (*Pinus nigra*). Millennium Park, Paragvári Street and Csónakázó pond are in the city of Szombathely, whereas Bozsok is a forest in Kőszeg Mountains (W-Hungary) and the Nagyerdő and Fancsika ponds localities are lowland forests in E-Hungary (see Figure 1.). Twenty traps were used at each locality (N = 10 in both summer and fall).

Season	Locality	Species richness	Number of individuals	Shannon diversity
Summer	Millennium Park	3.8 ± 1.75	10.0 ± 4.76	1.11 ± 0.47
	Paragvári Street	2.7 ± 1.42	4.5 ± 2.01	0.77 ± 0.54
	Csónakázó pond	4.0 ± 1.15	10.4 ± 3.75	1.17 + 0.31
	Bozsok	4.0 ± 1.15	11.1 ± 4.25	1.24 + 0.31
	Nagyerdő	1.5 ± 0.85	2.6 ± 2.37	0.35 ± 0.40
	Fancsika ponds	2.6 ± 1.26	4.0 ± 1.94	0.75 ± 0.52
Fall	Millenium Park	5.7 ± 1.49	26.9 ± 24.64	1.24 ± 0.47
	Paragvári Street	3.0 ± 3.02	10.8 ± 16.2	0.71 ± 0.63
	Csónakázó pond	6.1 ± 2.33	33.5 ± 42.48	1.26 ± 0.29
	Bozsok	3.3 ± 2.63	6.9 ± 5.13	0.93 ± 0.69
	Nagyerdő	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

trap was 201.6 ± 130.68 (range 31 – 615, n = 120).

Spider species richness differed among localities (two-way mixed-model ANOVA, reduced model, $F_{5,113} = 10.64$, $p < 0.001$), whereas the effect of season and the interaction term were not significant (season: $F_{1,113} = 3.26$, $p = 0.074$; interaction, full model: $F_{5,108} = 1.95$, $p = 0.091$). This was because species richness was low in Nagyerdő and higher in other localities (Table 1.).

There was a significant interaction between locality and season in the number of spider individuals (two-way ANOVA on log-transformed data, locality*season interaction $F_{5,108} = 2.51$, $p = 0.034$), whereas locality and season were not significant (locality: $F_{5,108} = 4.31$, $p = 0.067$; season: $F_{1,108} = 0.14$, $p = 0.720$). The reason for the interaction was that the number of individuals increased significantly 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), decreased marginally significantly in Bozsok (summer: 11.1 ± 4.25, fall: 6.9 ± 5.13, t = 1.99, $df_{corrected} = 17.4$, p = 0.062) and did not change in localities in E-Hungary (summer: 3.3 ± 2.23, fall: 4.15 ± 3.60, df = 38, p = 0.375) (see also Table 1.).

The Shannon diversity of spiders differed significantly among localities (two-way ANOVA, reduced model, $F_{5,113} = 8.69$, $p < 0.001$), whereas the effect of season and the interaction were not significant (season: $F_{1,113} = 0.05$, $p = 0.831$; interaction, full model: $F_{5,108} = 0.66$, $p = 0.651$). 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 E-Hungary (Table 1.).

The species composition of the localities corresponded well with the above results, because the unpolluted localities in Szombathely were highly similar and closer to each other than to the polluted locality, whereas Bozsok was distantly similar to the forest sites in E-Hungary that were similar to each other (Fig. 2.).

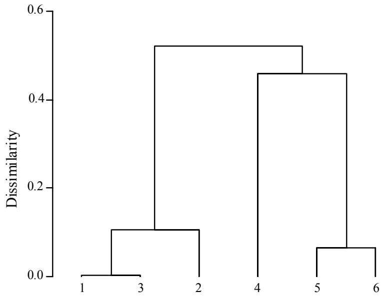
Based on the spatial and temporal differences as well as the species set of the localities, we classified the localities into four groups in further analyses. The unpolluted urban localities (Millennium Park and Csónakázó pond) formed the first group (referred to as UnpCity thereafter), the polluted urban locality (Paragvári Street, PCity) and the forest locality in W-Hungary (Bozsok, B) were treated separately, whereas the two forest localities in E-Hungary (Nagyerdő and Fancsika ponds, NF) formed the fourth group.

2. The relationship between spider and prey assemblages

Spider species richness was positively related to number of prey taxa in locality B (B = 0.46 ± 0.197, R^2 = 0.230, $F_{1,18}$ = 5.365, p = 0.033), and it was also positively related to prey diversity in the UnpCity localities (B = 3.19 ± 0.990, R^2 = 0.214, $F_{1,38}$ = 10.374, p = 0.003, Fig. 3A). However, spider species richness was negatively related to the number of prey taxa in the UnpCity localities (B = –0.69 ± 0.220, R^2 = 0.206, $F_{1,38}$ = 9.871, p = 0.003, 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 spider individuals was positively related to the number of prey taxa in locality B (B = 1.11 ± 0.502, R^2 = 0.214, $F_{1,18}$ = 4.905, p = 0.040). Although the number of spiders was negatively related to the number of prey taxa in the UnpCity localities (log-transformed number of spider individuals, B = –0.11 ± 0.041, R^2 = 0.159, $F_{1,38}$ = 7.201, p = 0.011), the number of spiders was positively related to prey diversity in these localities (log-transformed number of spider individuals, B = 0.47 ± 0.187, R^2 = 0.142, $F_{1,38}$ = 6.314, p = 0.016). The reason for the opposing trends is explained by a negative correlation between the number of prey taxa and prey diversity at these localities (Pearson r = –0.377, df = 40, p = 0.016). There was a positive relationship between the number of spiders and number of prey individuals in locality B (B = 0.05 ± 0.017, R^2 = 0.362, $F_{1,18}$ = 10.194, p = 0.005, Fig. 3C), whereas this relationship was negative in the PCity locality (log-transformed number of spider individuals, B = –0.001 ± 0.001, R^2 = 0.199, $F_{1,18}$ = 4.477, p = 0.049). There were no significant relationships between spider numbers and prey abundance in other localities.

Fig. 2. Dendrogram obtained by a hierarchical cluster analysis of the localities based on the similarity of their spider fauna. Summer and fall samples were pooled for this analysis. The Matusita index of similarity and the Ward-Orlóci fusion method was used. 1 – Millennium Park, 2 – Paragvári Street, 3 – Csónakázó pond, 4 – Bozsok, 5- Nagyerdő forest, 6 – Fancsika ponds.



The diversity of spiders was positively related to the number of prey taxa and the number of prey individuals in locality B (number of prey taxa: B = 0.139 ± 0.051, R^2

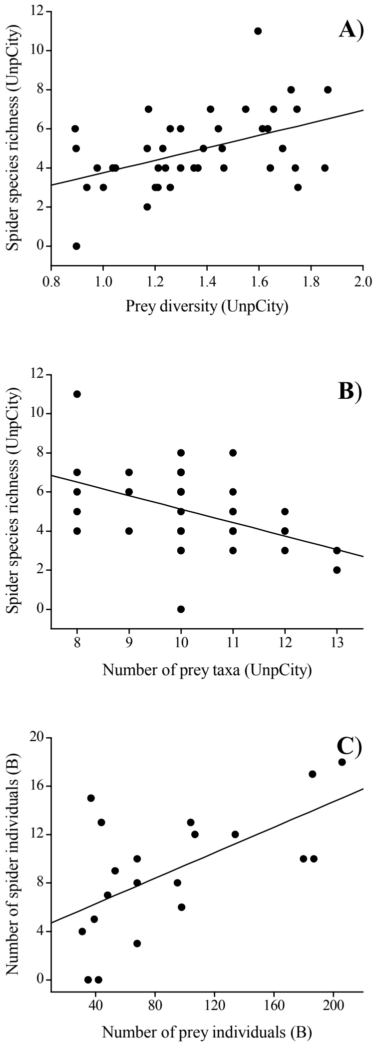
= 0.291, $F_{1,18}$ = 7.391, p = 0.014; number of prey individuals, with log-transformed diversity of spiders, B = 0.001 ± 0.000, R^2 = 0.205, $F_{1,18}$ = 4.655, p = 0.045). None of the other relationships between spider diversity and prey abundance were significant in the other locations.

3. The relationship between spider and prey assemblages within spider guilds

Nocturnal hunters were the dominant guild in most sampling localities; their proportion was 59% when sites were combined. The proportion of web-builders was lower (32%), whereas only 9% of the spiders collected belonged to the diurnal hunter guild (Table 2.).

The relationship between spiders and number of their respective prey were statistically significant in the dominant nocturnal hunter guild. Within this guild, spider species richness was positively related to number of prey individuals in the UnpCity localities combined (B = 1.248 ± 0.261, R^2 = 0.108, $F_{1,38}$ = 4.622, p = 0.038; Fig. 4A) and both species richness and number of individuals were positively related to number of prey individuals in locality B (species richness: B = 1.111 ± 0.681, R^2 = 0.253, $F_{1,18}$ = 6.103, p = 0.024; Fig. 4B; number of individuals: B = 0.898 ± 2.060, R^2 = 0.337, $F_{1,18}$ = 9.154, p = 0.007; Fig. 4C), but not in the other localities. These patterns were similar both when all prey without the diurnally active Diptera were used (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; Fig. 4D; locality B, species richness: B = 1.440 ± 0.637, R^2 = 0.201, $F_{1,18}$ = 4.519, p =0.048; Fig. 4E; number of individuals: B = 2.097 ± 1.954, R^2 = 0.270, $F_{1,18}$ = 6.643, p =

Fig. 3. The relationship between spider species richness and prey diversity (A), between spider species and number of prey taxa (B) in the unpolluted urban (UnpCity) localities and between the number of spider individuals and number of prey individuals in locality B (forest, W-Hungary, C). See text for details of statistical tests.



0.019; Fig. 4F). 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.

4. The relationship between exclusive and facultative bark-dwelling spiders and their respective prey

Because exclusive and facultative bark-dwelling spiders use the bark in different ways, we also tested the relationship between spiders and their prey separately for exclusive and facultative bark-dwellers. Exclusive bark-dwellers live on the tree trunk throughout the year, whereas facultative bark-dwellers use the trunk temporarily, mostly for overwintering. Therefore, in the analysis we combined data on exclusive bark-dwelling spiders from the two seasons, and data from the two seasons were treated separately for facultative bark-dwellers.

For exclusive bark-dwelling spiders, a negative relationship was found between spider numbers and number of prey individuals in the PCity locality (log-transformed number of spider individuals, B = –0.002 ± 0.001, R^2 = 0.336, $F_{1,18}$ = 9.092, p = 0.007, Fig. 5A). However, there was a positive relationship between the number of spiders and number of prey individuals in the NF localities combined (log-transformed number of spider individuals, B = 0.001 ± 0.000, R^2 = 0.180, $F_{1,38}$ = 8.351, p = 0.006, Fig. 5B).

There were no statistically significant relationships between the number of facultative bark-dwelling spiders and the number of prey individuals in the other localities or in the summer and fall samples.

Discussion

Spider species richness differed significantly among the localities, because of the low number of species in one forest locality in E-Hungary. This locality is isolated from other Black Pine plantations by deciduous forests and smaller spiders that disperse by air may reach the site in smaller proportions than the other localities. This may explain why we found a smaller number of species at this locality.

The number of individuals increased in the urban localities from summer to fall, probably due to the appearance of facultative bark-dwelling spiders coming down on the trunk for overwintering (Wunderlich 1982; Horváth et al. 2004). However, the number of spiders decreased or remained stable in the forest localities. This may be explained by the fact that foliage is usually higher and less dense in the forests than in urban localities. Spiders can thus be spaced out more on the tree trunks in forests, resulting in lower spider densities at the height of the trunk traps used in this study (3 m) in the forest than in the urban localities. Alternatively, predation, mostly by birds, may be more intense in the forest localities, which may explain why the number of individuals did not increase in the forest localities from summer to fall (c.f. Gunnarsson 1998).

The diversity of spiders was low in the E-Hungary locations (see also species richness and diversity in Table 1.), and in the PCity location, which is mostly due to the fact that species richness and the number of individuals were originally low in these localities, probably for reasons discussed above.

We found statistically significant positive relationships between spider and prey assemblages in the UnpCity and B localities(Table 3.). This result indicates that

Fig. 4. Positive relationships between species richness and numbers of nocturnal hunting spiders and their potential respective prey items, in the unpolluted urban localities (UnpCity: A, B) and in the forest in W-Hungary (locality B: C, D, E, F). Two measures of potential respective prey were used, number of prey individuals without Diptera (A, C, E) and number of exclusive bark-dwelling prey (B, D, F). See text for details of statistical tests.

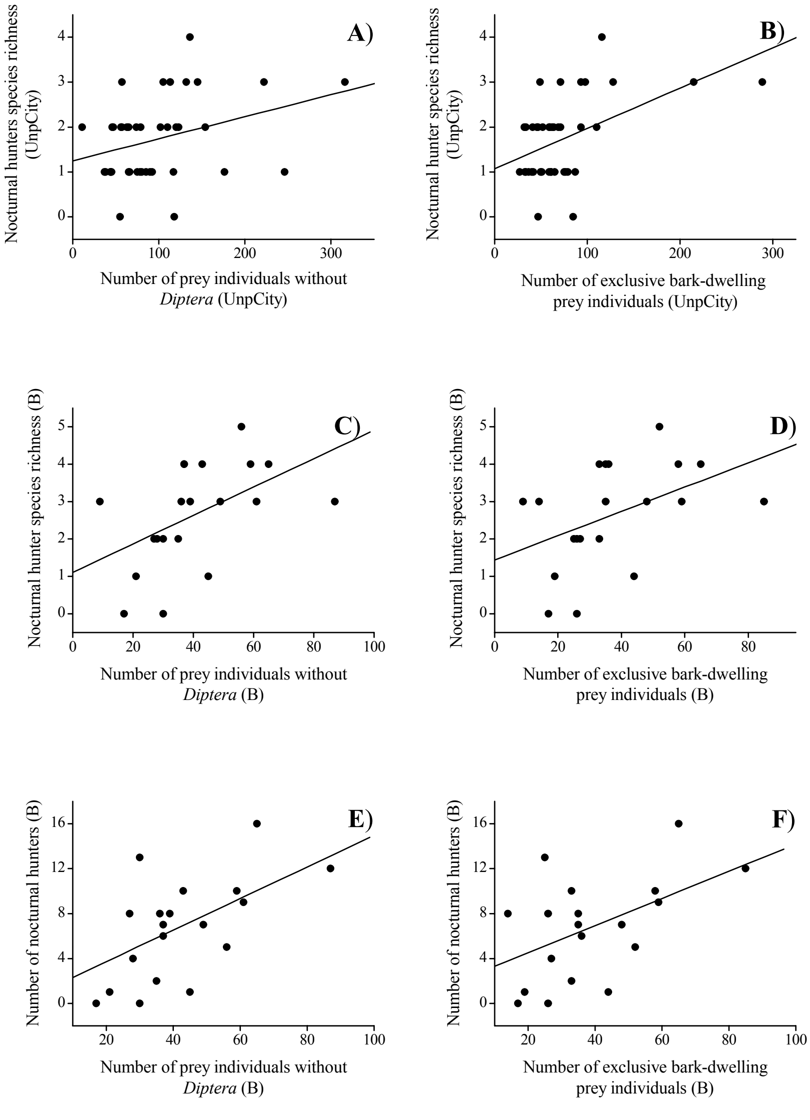
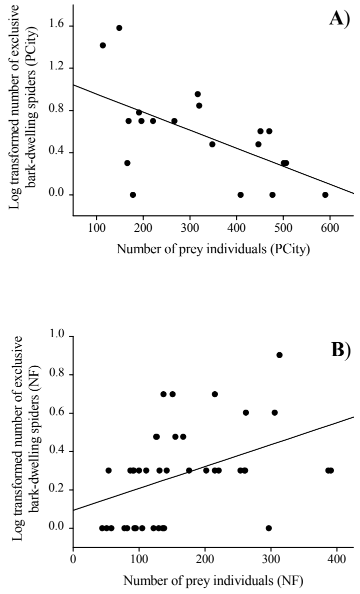


Fig. 5. The relationship between the number of exclusive bark-dwelling spiders and number of prey individuals in the polluted urban locality (PCity, A) and in the forest localities in E-Hungary (NF, B). See text for details of statistical tests.



spiders may respond numerically to prey on the bark of Black Pines and that prey abundance may be important in explaining the abundance of spiders in some localities. For example, in locality B, each measure of spider abundance was positively related to either the number of prey taxa or the number of prey individuals (Table 3.). Prey diversity, however, was positively related to spider species richness and number of individuals only in the UnpCity localities. These results suggest that there may be several ways in which prey abundance influences spider occurrence and that spiders may "react" to different measures of prey abundance depending on their way of hunting. Several field studies, conducted in a variety of habitats, also found evidence of a numerical response between spiders and their prey (Wise 1993). For example, the population size of the space web-builder *Achaearanea tepidariorum* increased with an increase of potential prey in a Canadian grassland (Turnbull 1964). The density of potential prey significantly and positively influenced spider density on three out of five tree species studied in western Oregon (Halaj et al. 1998). The frequency of predation by spiders was positively related to prey availability in the case of seven web-building spiders and their prey characteristic to coffee plantations (Ibarra-Nunez et al. 2001). In a study of Linyphiidae on fields of winter wheat prey availability was significantly higher at actual web microsites than at non-web sites (Harwood et al. 2001). At the level of individuals, active hunter wolf spiders *Rabidosa rapida* were found to respond to both spatial and temporal variation in prey availability in choice experiments (Riechert et al. 1999), which can theoretically lead to the numerical responses observed at the population level. Our study attests that, under some circumstances, prey availability can have a major role in structuring spider assemblages when the effect of habitat complexity on spiders is relatively smaller than that in other studies (e.g. 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 3.). These results appear to contradict our previous finding that spiders can be positively affected by prey abundance. The apparent contradiction arises from the fact that 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

Table 3. Summary of the results of linear regression models testing the relationship between the species richness, number of individuals and diversity of spiders and the number of prey taxa, number of prey individuals and prey diversity. Statistically significant positive relationships are indicated by (+), and negative relationships by (–).

Spider variable	Locality	Number of prey taxa	Number of prey individuals	Prey diversity
Species richness	UnpCity	(–) **	n.s.	(+) **
	PCity	n.s.	n.s.	n.s.
	B	(+) *	n.s.	n.s.
	NF	n.s.	n.s.	n.s.
Number of individuals	UnpCity	(–) *	n.s.	(+) *
	PCity	n.s.	(–) *	n.s.
	B	(+) *	(+) **	n.s.
	NF	n.s.	n.s.	n.s.
Spider diversity	UnpCity	n.s.	n.s.	n.s.
	PCity	n.s.	n.s.	n.s.
	B	(+) *	(+) *	n.s.
	NF	n.s.	n.s.	n.s.

* $p < 0.05$, ** $p < 0.01$

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 distributed by taxa more evenly, resulting in a higher prey diversity and higher number of spiders and spider species. These results suggest that, under some circumstances, the composition of prey assemblages may also be important in explaining the abundance of spiders. Spiders are known to exert different effects on different prey taxa (e.g. Riechert and Lawrence 1997; Denno et al. 2003), and thus, prey assemblages of different composition can affect spider assemblages. The actual prey taken by spiders is known to fluctuate with the relative abundance and availability of certain prey items (Bardwell and Averill 1997) and the prey preference detected in the lab does not necessarily correspond to what spiders actually eat in the wild (Herberstein 1996), which suggest that functional response by spiders to changes in prey composition is weaker than the numerical response to prey (Wise 1993).

We found a negative relationship between spider numbers and the number of prey individuals at the PCity location. At this locality, air pollution has damaged the bark of many trees, which are thus more exposed to herbivorous insects and pests. This locality also is suboptimal for spiders due to air pollution (Horváth 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 (Figure 5A), which also biased the relationship between prey abundance and the entire spider assemblage at this locality.

In guild-level analyses, we found positive relationships between spiders and the abundance of their respective prey only in the case of nocturnal hunters. Such relationships were found in the UnpCity and B localities (Fig. 4A-F), both when all prey without Diptera and when bark-dwelling prey were used. In locality B, each of the four comparisons (number of spiders and spider species with two sets of prey) resulted in statistically 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 were less likely to stay under the bark traps at the time of collection of the trunk traps (12:00 noon), and that the females of web-builders are more or less sessile, and are less likely to move during the sampling period. Our sample (Table 2.) contained mostly juvenile web-builders, which hunt on the bark during the day, similarly to active hunters, and this may be a reason why we did not detect a relationship between web-builder spiders and their respective prey.

Finally, we found 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 relationship was found only at localities with the smallest number of species but not at the other localities may be that two (*Marpissa muscosa*, *Nuctenea umbratica*) 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 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 influences the populations of spiders, 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 *Prokelisia* sap-feeders (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 community may be affected in different ways by predatory spiders (Denno et al. 2003). Indirect effects of spiders may also play a role in community structure. For example, although predation by spiders did not lead to a change in grasshopper densities in an old-field interaction web, predation risk by spiders led to a change in the diet of grasshoppers, which did have an effect on the interaction web (Schmitz 1998). An understanding of the relative strength of bottom-up and top-down forces influencing spider assemblages would require experimental manipulation of either spiders or prey and the knowledge of the prey actually consumed. However, such information is difficult to gather from a number of spiders (active hunters) due to the small body size of prey and quick consumption of prey by hunters (Nyffeler 1999). Even in the group of web-building spiders, where prey falling into the webs can be studied in the field with relative ease, the prey caught does not necessarily reflect the actual prey taken because spiders select among prey based on toxicity, quality and nutrition value (Toft 1999). Furthermore, spiders may require special prey, and broad categories of prey, such as that used in this study, may not be adequate to detect variation at such a small level (Halaj et al. 1998). It is also possible that prey was overabundant in the systems studied, which might have obscured the numerical responses of spiders to prey abundance.

Spiders are capable of recognising sites of higher prey availability. For example, the sit-and-wait predator *Misumenops argenteus* generally occupies sites with high prey frequency (Romero and Vascencellos-Neto 2004), whereas Linyphiidae 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 based on common microhabitat preferences, e.g. between two species of dwarf spider and their spring-tail prey in coastal sand dunes (Bonte and Mertens 2003). Although such a scenario is plausible with a small number of predators and prey, it is rather unlikely in our study, because the wide range 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, although the effect of prey abundance on spider assemblages was not general, we detected relationships at certain localities. It is possible that several factors influence spider assemblages, and that prey abundance is only one of them. Other factors that play a role in the composition and distribution of spider assemblages can be habitat structural diversity (Halaj et al. 1998; Nyffeler and Sunderland 2003; Langellotto and Denno 2004), including foliages of different composition and structure, the productivity of habitat (Shochat et al. 2004), competition between two or more species of predatory spiders (Shochat et al. 2004), air pollution (Horváth et al. 2001), and predator abundance (Gunnarsson 1998). Our study provides evidence 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 poor habitat, the tree bark.

Acknowledgements

We wish to thank Prof. Zoltán Varga for stimulating discussions during the research and to Szabolcs Honti and Péter Kozma for help in the field. Sz.L. was supported by an OTKA grant (F30403) and a Békésy Postdoctoral Fellowship and Csaba Szinetár was a Bolyai Fellow of the Hungarian Academy of Sciences during the preparation of the manuscript.

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