Szent István University

ARBOREAL HUNTING SPIDERS IN APPLE ORCHARDS: TAXONOMIC COMPOSITION, NATURAL PREY AND CIRCADIAN BIOLOGY

Ph.D. Dissertation

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The candidate has fulfilled all the conditions prescribed by the doctoral school of Szent István University, and the thesis is accepted for the defense process.

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Supervisors

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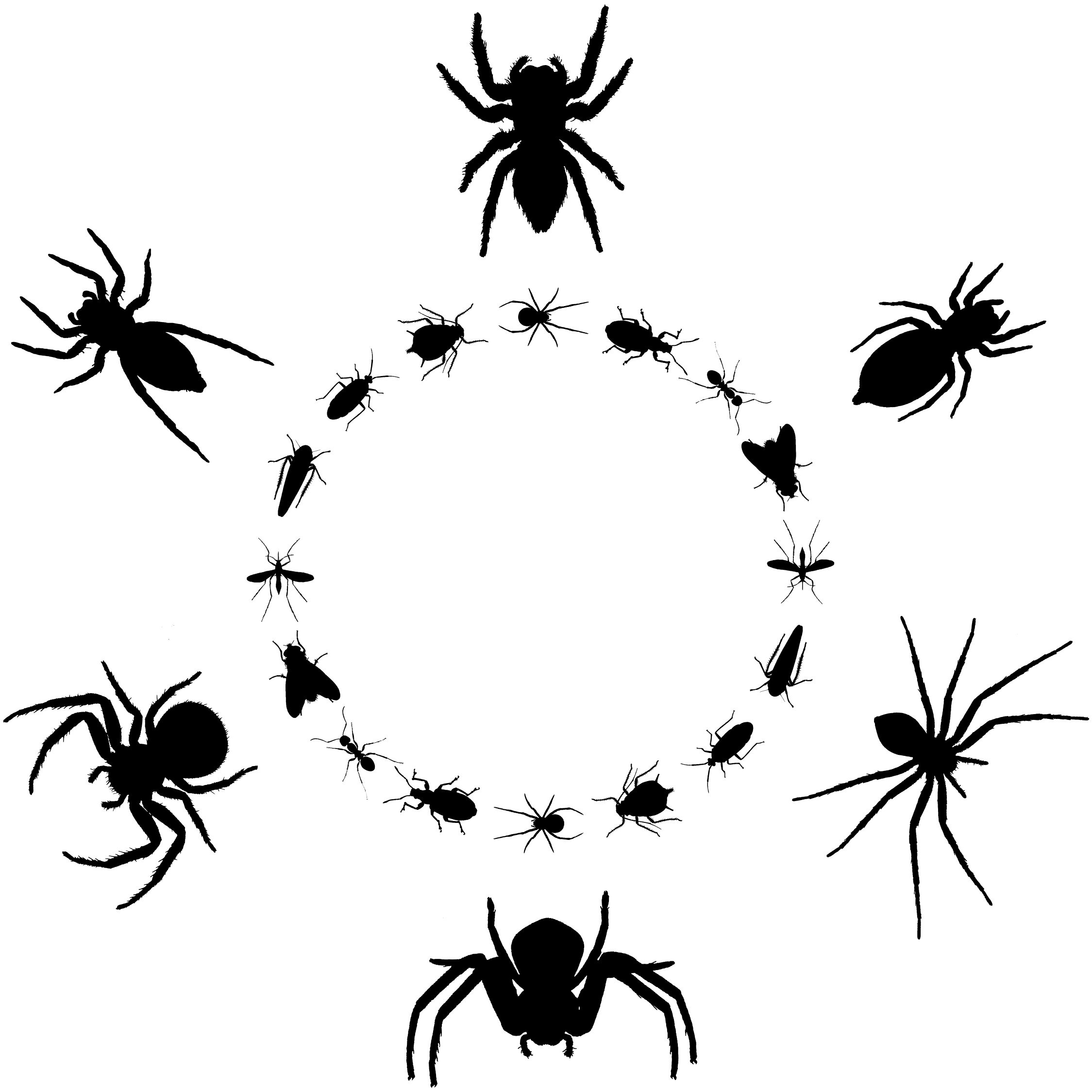
If you wish to live and thrive
Let a spider run alive.

Popular wisdom



INTRODUCTION

It seems that in the second half of the 20th century mankind has nearly overcome world hunger thus now, for the first time in human history, much more people are overweighted or obese than the number of those who are suffering from the symptoms of starvation or undernourishment (*Harari, 2016; FAO et al., 2019*). This is partly due to some innovative processes for intensifying agricultural production which took place mainly between the years 1960 and 1970 and later became known as 'Green Revolution'. Adoption of a series of new inventions and technologies such as high-yielding crop varieties, fertilization, irrigation, and modern pesticides increased worldwide agricultural production satisfying the nutritional needs of humanity, and resulting in a steep growth in human population (*Kush, 2001; Evenson & Gollin, 2003; Pingali, 2012*). However, it has now become clear that this system is unsustainable (*Goodland, 1997; Hoekstra & Wiedmann, 2014*). Furthermore, in exchange for the glut of agricultural products never seen before, humanity has to face ecological crises which require immediate global action. Several studies link features and consequences of modern agricultural practice such as intensive use of pesticides or loss and fragmentation of native habitats to honeybee colony collapse disorder (*Sluijs et al., 2013; Sánchez-Bayo et al., 2016; Lu et al., 2020*) or to arthropod decline and extinction (*Sánchez-Bayo & Wyckhuys, 2019; Seibold et al., 2019; Cardoso et al., 2020; Nyffeler & Bonte, 2020*). So, there is an urgent need to implement fundamental changes in the current practice (*Ripple et al., 2017*), which includes e.g., the invention and introduction of greener and more sustainable agricultural practices, conservation of biodiversity and maximisation of ecosystem services from conservation biological control (*Altieri, 2018; Samways et al., 2020*). Spiders are promising biological control agents as they form abundant and diverse assemblages in agroecosystems and consume a remarkable amount of arthropod prey (*Wise, 1993; Marc et al., 1999; Nyffeler & Birkhofer, 2017*). Although they may play a major role in conservation biological control, their ecology and function in agricultural systems is little known and require much more study. The more information we have about spiders inhabiting agroecosystems, the better we could conserve them and utilise their ability to control pests.

Taxonomic diversity of spiders

Currently, the World Spider Catalog lists 48,409 valid species of spiders from 120 families, worldwide (*WSC, 2020*). In Hungary, more than 800 species are present (*Mezőfi & Markó, 2018a; Nentwig et al., 2020*) and the possible number of species that occure here can be estimated at more than 850 as further species new to the fauna of Hungary are reported almost every year (e.g., *Mezőfi & Markó, 2018b; Szabó & Szinetár, 2018*), and there are specimens possibly represent new records but their identification is currently in progress (e.g., *Mezőfi et al., 2018*). In agricultural areas spiders form nearly as diverse and abundant assemblages as they do in natural habitats (*Samu & Szinetár, 2002; Szita et al., 2004*). More than 165 species were recorded from pome fruit orchards in Hungary which is approximately one fifth of the total spider fauna of Hungary (*Bogya et al., 1999a; Markó, 2017; Mezőfi & Markó, 2018a*). The species richness in Hungarian apple orchards is varying between 22 and 117 (*Markó, 2017*), and up to 62 species can occur just in the canopy level of one orchard at a time (*Markó & Keresztes, 2014*). Thus, spiders can make up to 57% of the species and 65% of the individuals of the predaceous macro-arthropods inhabiting apple orchards canopy (*Markó & Keresztes, 2014*). Here, the most widely occurring or dominant taxa are Araneidae: *Araneus* spp., *Araniella* spp., *Larinioides* spp.; Cheiracanthiidae: *Cheiracanthium* spp. (*C. mildei*); Oxyopidae: *Oxyopes* spp.; Philodromidae: *Philodromus* spp. (*Ph. cespitum*); Salticidae: *Carrhotus xanthogramma*, *Macaroeris nidicolens*; Theridiidae: *Theridion* spp. s. lat. and Thomisidae: *Ebrechtella tricuspidata*, *Xysticus* spp. s. lat. (*Bogya et al., 1999a, 1999b; Markó & Keresztes, 2014*).

What do the spiders eat?

A short answer to the question: almost everything. Spiders mainly feed on Diptera and Hemiptera prey, but besides these, their diet can comprise a wide variety of other arthropods such as Amphipoda, Arachnida, Blattodea, Collembola, Coleoptera, Hymenoptera, Lepidoptera (including caterpillars), Phasmatodea or Thysanoptera etc., but certain ground dwelling spiders catch earthworms or even snails occasionally (*Nentwig, 1990; Nyffeler et al., 1990a, 2001, 2017; Morse, 1997; Samish & Rehacek, 1999; Nyffeler & Symondson, 2001; Maloney et al., 2003; Michalko & Pekár, 2016*). Spiders prefer live prey primarily, but scavenging, although uncommon, has been found e.g., in Lycosidae, Salticidae or Sicariidae families (*Sandidge, 2003; Vetter, 2011; Vickers et al., 2014*), moreover, certain spiders exhibit kleptoparasitic behavior (*Martišová et al., 2009; Uetz et al., 2010*). Oophagy is also known in spiders: they consume sometimes eggs of various insects (*Pfannenstiel, 2008a, 2008b*) or even eggs of other spiders (*Willey & Adler, 1989; Nyffeler et al., 1990b*). Surprisingly, vertebrata consumption is not uncommon: mainly bigger hunting spiders catch smaller reptilians (*Maffei et al., 2010; Hernández & Rodríguez-Cabrera, 2014*), amphibians (*Menin et al., 2005; Barej et al., 2009; Calzada-Arciniega, 2014*), birds or rodents (*McCormick & Polis, 1982; Nyffeler & Vetter, 2018*), and bigger orb-weaver species (mainly from Nephilidae or Araneidae families) can even prey on bats (*Nyffeler & Knörnschild, 2013*). Spiders associated with wetland habitats (e.g., *Dolomedes* spp., Pisauridae) feed often on smaller fishes (*Nyffeler & Pusey, 2014*).

Freshly molted spiders sometimes suck out the remained fluid from their exuviae (*Dondale, 1965*), others consume their aged webs utilising pollens and spores stuck to the spider silk (*Smith & Mommsen, 1984; del Fiol et al., 2007; Pfannenstiel, 2012; Eggs & Sanders, 2013*). Even floral or extrafloral nectare of various plants or honeydew can serve as alternative food sources for certain (mainly arboreal) spiders (*Jackson et al., 2001; Taylor & Pfannenstiel, 2008; Nyffeler et al., 2016*) providing faster development (*Taylor, 2004; Taylor & Pfannenstiel, 2009*), longer lifespan (*Pollard et al.,1995; Pfannenstiel & Patt, 2012*) or increased fecundity (*Wu et al., 2011*). Moreover, juveniles of a jumping spider species (*Toxeus magnus*) feed on a special 'spider milk' provided by their mother (*Chen et al., 2018*).

Though, spiders are polyphagous (euryphagous) predators in general, many species show stenophagy (e.g., araneophagy, myrmecophagy) (*Harland & Jackson, 2000; Pekár et al., 2012*), and some extreme examples can also be found: e.g., *Evarcha culicivora* (Salticidae) consumes mainly vertebrate blood via preying on mosquitoes carrying blood (*Nelson & Jackson, 2012*) while *Bagheera kiplingi* (Salticidae), a quasi phytophagous spider, feeds almost exclusively on Beltian bodies of certain acacia trees (*Meehan et al., 2009*). Summing up, spiders can utilise an extremely wide variety of resources.

Hunting strategy dilemma

Possibly, almost every arachnologist agrees that within spiders, two major groups can be separated regarding their hunting strategy: spiders that use their web for hunting and spiders that do not. Former group is usually called as 'web-builders' while the latter as 'hunting spiders' or simply just 'hunters'. Some ecologists distinguish spiders from another point of view and separate them into sedentary or sit-and-wait, and active hunters (see e.g., *Mestre et al., 2020*). Different terminologies create ambiguous situations: e.g., thomisids can be classified either as hunting spiders (like salticids), or as sit-and-wait hunters (like araneids) as well. And there are other terms, like 'cursorial spider' and 'wandering or wanderer spider' used rather inconsistently, sometimes in conjunction with hunting spiders or active hunters. Moreover, there are other classification systems with a finer and more complicated division, see for example *Marc et al. (1999)* or *Uetz et al. (1999)*. Finally, let us not forget about some taxa with specialized hunting strategies such as net casting (Deinopidae, *Austin & Blest, 1979*), bolas (Araneidae, *Eberhard, 1980*) or spitting spiders (Scytodidae, *Suter & Stratton, 2009*). So, great diversity of spider species and life forms makes it difficult to form homogeneous groups regarding the hunting strategies of spiders.

In community ecology it is practical to group species according to their ecological or life-history traits, to make general statements on their possible role in the ecosystems. The guild concept (*Blondel, 2003*) is a popular and productive approach of this problem. Not surprisingly, arachnologists elaborated several guild classification systems (e.g., *Uetz et al., 1999; Höfer & Brescovit, 2001; Dias et al., 2010; Cardoso et al., 2011*) mainly based on a variety of traits related to foraging mode of various spider groups. These sometimes are called as hunting guilds or ambiguously just hunting strategies (e.g., *Michalko & Pekár, 2016*). Some studies use hybrid guild categories (e.g., *Rodrigues & Mendonça, 2012*) while others use simple and specific hunting strategies (e.g., *Schmitz & Suttle, 2001; Schmitz, 2008; Sanders et al., 2015*) independent from other traits. So, as the guild is a composite category it can not be equivalent with the hunting strategy. For example, the temporal niche of a predator alone can greatly affect predator-prey interactions (*Herberstein & Elgar, 1994; Kronfeld-Schor & Dayan, 2003; Welch & Harwood, 2014*), while guild classification systems take it into account just as one of the many traits considered (*Uetz et al., 1999; Höfer & Brescovit, 2001; Cardoso et al., 2011*). Nevertheless, use of both the guild concept (*Michalko & Pekár, 2016*) and simple hunting strategy categories (*Miller et al., 2014; Liu et al., 2015; Sanders et al., 2015*) shows that there are trophic differences between the guilds or hunting strategies. Which is the better approach and which system can predict more properly e.g., the prey of spiders (i.e., their trophic characteristics)? It is difficult to answer, but maybe it depends on the investigated ecological context as well.

Spiders in ecological webs

Spiders play an important role as natural predators of arthropods in various ecosystems. They hunt prey to fulfill their nutritional needs, but usually both web-builders and hunting spiders kill much more prey than would be necessary (wasteful killing) especially at high prey densities (*Samu & Bíró, 1993; Riechert & Maupin, 1998*). Thus, hundreds of million tons of prey are annually killed by the global spider community (*Nyffeler & Birkhofer, 2017*). At increasing prey densities, spiders usually exhibit Type II functional response: they increase prey consumption at a decreasing rate resulting in a saturation curve. However, certain spiders show a sigmoid, Type III functional response to prey densities, and in case of dangerous prey a dome-shaped, Type IV functional response have also been observed in spiders (*Maloney et al., 2003; Líznarová & Pekár, 2013*). In contrast to their high functional response, due to their limited dispersal abilities and moderate population increase, the numerical response of spiders usually lags behind the fast-growing populations of pests (*Riechert, 1999*). Though spiders have limited abilities to exhibit density-dependent tracking of their prey, besides their direct predation, they have several non-consumptive effects on herbivore populations (*Mansour et al., 1981; Beleznai et al., 2015; Tholt et al., 2018*). These non-consumptive effects on herbivore populations can be as strong as the consumptive effects (*Schmitz et al., 1997*). Due to their consumptive and non-consumptive effects on herbivores, spiders can mediate trophic cascades thus improving producers performance indirectly (*Schmitz et al., 1997; Schmitz & Suttle, 2001; Schmitz, 2008; Bucher et al., 2015*).

Many studies concluded that the spiders are promising biological control agents in various agroecosystems and can effectively suppress numbers of various pests (*Riechert & Lockley, 1984; Marc et al., 1999; Nyffeler & Sunderland, 2003; Michalko et al., 2019a*). Several studies reported that spiders inhabiting the canopy of pome fruit orchards prey on pome fruit pests and effectively reduce their numbers (e.g., *Mansour et al., 1980; Wyss et al., 1995; Isaia et al., 2010; Michalko & Pekár, 2015; Lefebvre et al., 2017*). But enhancing the abundance and diversity of arboreal spiders not necessarily has an impact on pests (e.g., *Markó & Keresztes, 2014*). Spiders form diverse assemblages in apple orchards' canopy (*Bogya et al., 1999a*) and different species possess different hunting strategies, associate with different microhabitats, forage in different temporal windows or have different prey preferences etc. (*Marc et al., 1999; Michalko et al., 2019b*). Due to these specific differences in trophic ecology, the actual taxonomic composition of spider assemblages also matters. And there are many other factors that influence the biological control provided by these assemblages (*Jonsson et al., 2017; Michalko et al., 2019b*). *Michalko et al. (2019b)* reviewed the factors potentially affect the pest suppression ability (and trophic niches) of spiders. For example, at the community level, intraguild predation or the presence of alternative prey can disrupt or reduce the biocontrol potential of generalist natural enemies (*Hodge, 1999; Finke & Denno, 2003; Madsen et al., 2004; Birkhofer et al., 2008*). Furthermore, the outcome of multi enemy interactions depends on the number or the identity of the natural enemies in the given multi enemy system (*Khudr et al., 2020*). Thus, in complex agroecosystems such as apple orchards, with multiple pest, natural enemy and neutral species, it may be extremely difficult to predict the effect of an arboreal spider assemblage, comprising many species with different trophic characteristics, on pest populations. The effectiveness of spiders in biological control in the mentioned ecosystems is rather context dependent. Thus, to better understand such systems, it is necessary to study the taxonomic composition and natural prey of their spider assemblages and the biology of the key spider species.

General objectives of the thesis

This thesis comprises three studies already published. Their aims were as follows: (1) to better explore the arachnofauna of apple orchards in Hungary; (2) to characterize and analyse the natural prey and the role of arboreal hunting spiders inhabiting apple orchards in pest suppression and in the food web dynamics, taking into account their hunting guild; (3) and finally, to get more information on the biology of the two most abundant arboreal hunting spider species in apple orchards in Hungary, especially on their temporal activity.

In the first study, I report and characterize some spider species collected during our faunal survey mainly in the canopy of apple trees in orchards in Hungary. In the second study, I characterize the arboreal hunting spider assemblage inhabiting apple orchards and analyse their natural prey, compare the most abundant species regarding their trophic characteristics and discuss their role in trophic webs and in conservation biological control. Last, I also describe the circadian biology of *Carrhotus xanthogramma* and *Philodromus cespitum*, with special attention to the possible sexual differences regarding their locomotor activity rhythms.

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STUDY1: SOME RARE AND REMARKABLE SPIDER SPECIES FROM HUNGARY (ARACHNIDA: ARANEAE)

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Abstract

This study reports the first records of two spider species for Hungary: *Cyclosa sierrae* Simon, 1870 (Araneidae) and *Porrhomma oblitum* (O. P.-Cambridge, 1871) (Linyphiidae). *Cyclosa sierrae* also represents the first record of this species from Central Europe. Furthermore, we provide evidence about the occurrence of *Dysdera lata* Reuss, 1834 and *Philodromus marmoratus* Kulczyński, 1891 in Hungary and we report new data for six further species: *Brigittea vicina* (Simon, 1873) (Dictynidae), *Iberina microphthalma* (Snazell & Duffey, 1980) (Hahniidae), *Mermessus trilobatus* (Emerton, 1882) (Linyphiidae), *Pulchellodromus ruficapillus* (Simon, 1885) (Philodromidae), *Lasaeola prona* (Menge, 1868) (Theridiidae) and *Diaea livens* Simon, 1876 (Thomisidae). Comments on the distribution, biology and taxonomy of the ten mentioned spider species are provided.

Introduction

In the early twentieth century *Chyzer & Kulczyński (1918)* published the first comprehensive checklist of the spiders from Hungary, and already listed 742 species. More than 80 years later *Samu & Szinetár (1999)* updated the list according to the present borders of Hungary, thus their list contains 725 species. Since then many new additions have been reported for the fauna (e.g., *Szűts et al., 2003; Pfliegler et al., 2012; Szinetár & Kovács, 2013; Pfliegler, 2014; Szinetár et al., 2014, 2015; Korányi et al., 2017*) and several new species from the country were described (*Szinetár & Samu, 2003; Szinetár & Kancsal, 2007; Szinetár et al., 2009; Kovács et al., 2015a*). Presently, the Spiders of Europe database lists 800 spider taxa for Hungary (*Nentwig et al., 2017*), although the list is still far from complete. In this paper we report two further spider species which are new to the fauna of Hungary. We also provide a new data on the occurrence and biology of some rare and interesting spider species.

Material and methods

The spiders were collected sporadically in various parts of Hungary, mainly in apple orchards (Bács-Kiskun, Pest, Szabolcs-Szatmár-Bereg and Tolna counties) and city parks (Budapest, Gödöllő) from 2013 to 2016. Exact locations are indicated with some comments in the Results. A variety of collecting methods were used, including hand collecting, beating, cardboard bands and litter sampling. For collecting overwintering spiders from apple trees, we used corrugated cardboard stripes (height 20 cm), which were placed around the tree trunks, at about 20 cm above ground usually in September. The bands and litter samples were collected during winter months, and for processing the litter samples we used Winkler extractors (*Sakchoowong et al., 2007*). Juvenile specimens of *Philodromus marmoratus* Kulczyński, 1891 and *Pulchellodromus ruficapillus* (Simon, 1885) were kept alive and fed with *Drosophila hydei* Sturtevant, 1921, until its final moult. The collected and reared specimens were stored in 70 % ethanol. Individuals were examined in the laboratory of the Department of Entomology, Szent István University. Identification was made under a binocular stereo microscope (Leica MZ6). In case of female specimens, the genitalia were dissected from the specimens, and the epigynes/vulvas were cleared with 20 % KOH. The specimens were identified using various keys (see in the Results section) and were deposited in the first author’s private collection. *Philodromus marmoratus* and *P. ruficapillus* habitus pictures were taken with a Nikon D3300 camera equipped with a Sigma 50mm 1:2.8 DG Macro lens. *Iberina microphthalma* (Snazell & Duffey, 1980), *Porrhomma oblitum* (O. P.-Cambridge, 1871) and *P. ruficapillus* epigynes/vulvas were photographed with a Zeiss Imager A2 light microscope equipped with AxioCam MRc5, and in other cases the photographs were taken with a Sony XCDSX90CR digital interface connected to a Zeiss Stemi 2000 stereomicroscope. The specimens’ parameters were measured with an ocular micrometer calibrated with a stage micrometer, and for post-processing work on the photographs, and for the preparation of the scale bars we used Adobe Photoshop CS3 software. Taxonomic names follow the nomenclature of the *WSC (2017)*.

Results and discussion

As a result of our study the following ten new or rare spider species were recorded from Hungary:

Araneidae Clerck, 1757

***Cyclosa sierrae* Simon, 1870** (Fig. 1.1)

Determination. *Levy, 1997; Nentwig et al., 2017*

Material examined. 1♂, Sükösd: 17.05.2016 – (46°17′59″N, 19°00′21″E, 100 m a.s.l., organic apple orchard). The specimen (leg. & det. L. Mezőfi) was collected by beating from the canopy of an apple tree.

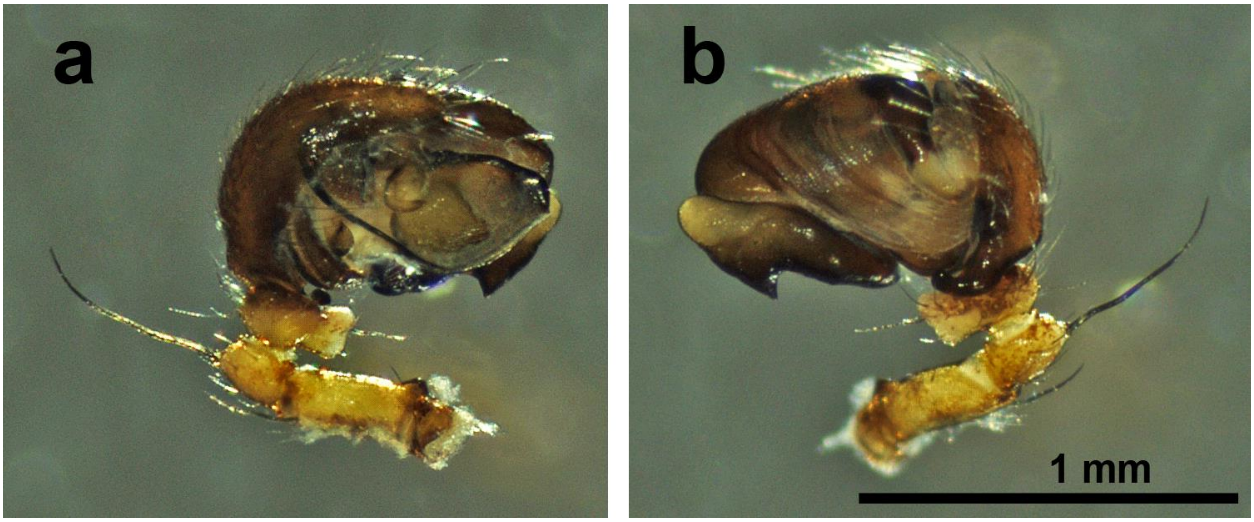

Figure 1.1: Left palp of *Cyclosa sierrae* male from Hungary; (**a**) prolateral view; (**b**) retrolateral view

Distribution. Europe to Georgia (*WSC, 2017*). In Europe it occurs in Albania, Bulgaria, Cyprus, France (exclusively Corsica), Greece (including North Aegean Islands and Crete), Italy (including Sardinia), Macedonia, Portugal, Russia (southern European part), Spain, Turkey (European part) and Ukraine (*van Helsdingen, 2017*). It is also present in, e.g., Azerbaijan, Georgia, Iran, Israel, Lebanon, Syria and Turkey (Asian part) (*Levy, 1997; Kashefi et al., 2013; Komnenov, 2013; Uyar et al., 2014*).

Remarks. Until now, two representatives of the genus *Cyclosa* were known from Hungary: *C. conica* (Pallas, 1772) and *C. oculata* (Walckenaer, 1802) (*Samu & Szinetár, 1999*). Here we report *C. sierrae* as the third member of this genus in Hungary. This Mediterranean species usually occurs in steppe-like or shrub vegetations, but also occurs in *Pinus* forests (*Komnenov, 2013; Polchaninova & Prokopenko, 2013; Ijland & van Helsdingen, 2014; Uyar et al., 2014*). *Cyclosa* spiders are easy to recognise by their habit of placing their prey remains and egg sacs in a vertical line crossing the center of their orb webs (*Levy, 1997*). Furthermore, *Cyclosa* species can usually be easily distinguished from their relatives by, among other features, the posterior-dorsal extended opisthosoma which bears various humps (*Levy, 1997*), but the identification of some species within the genus is difficult. In physical characteristics *C. sierrae* strongly resembles *C. conica,* but according to *Mcheidze (2014)* these two species can be distinguished on the basis of the sternum colouration: in case of *C. sierra* the sternum is black (or dark brown) with yellow marks on the edge (one anterior transversal, one apical and two lateral marks), while in *C. conica* the sternum is entirely black, without yellow marks. Presumably the small-sized male specimen of this typically southern species reached the sampling site by ballooning. Spreading of this species in a northern direction has not been detected before in Europe.

Dictynidae O. P.-Cambridge, 1871

***Brigittea vicina* (Simon, 1873)** (syn. *Dictyna vicina*) (Fig. 1.2)

Determination. *Loksa, 1969*

Material examined. 8♀♀, Budapest: 1♀ 26.05.2016, 3♀♀ 23.06.2016 – Haller park (47°28′29″N, 19°04′48″E, 107 m a.s.l., urban green area); 1♀ 23.06.2016 – Róbert Károly körút (47°32′09″N, 19°03′48″E, 106 m a.s.l., urban green area); 1♀ 19.07.2016, 1♀ 13.09.2016 – Margit Island (47°31′19″N, 19°02′43″E, 103 m a.s.l., urban green area with floodplain-like forest vegetation); 1♀ 19.07.2016 – Vérmező (47°29′60″N, 19°01′43″E, 127 m a.s.l., urban green area). All the specimens (leg. D. Korányi, det. L. Mezőfi) were collected by beating mainly in urban environments, from canopies of *Acer campestre* trees.

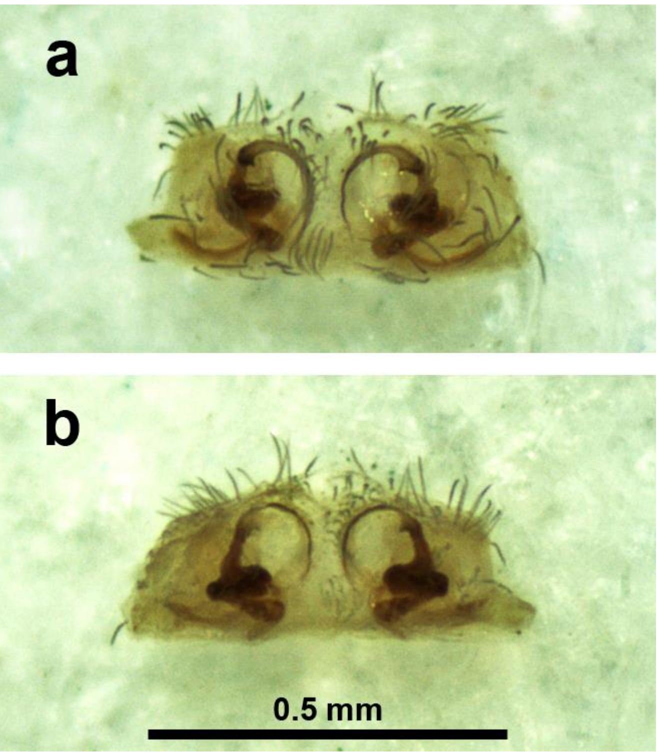

Figure 1.2: Cleared, dissected epigyne/vulva of *Brigittea vicina* female from Hungary; (**a**) epigyne, ventral view; (**b**) epigyne/vulva, dorsal view

Distribution. Mediterranean to Central Asia (*WSC, 2017*). In Europe it is present in Bulgaria, Croatia, Czech Republic, France (including Corsica), Greece (including Crete), Hungary, Italy, Macedonia, Moldova, Romania, probably in Russia (north-western European part), Slovakia, Ukraine and former Yugoslavia (*van Helsdingen, 2017*).

Remarks. A very rare mesophilic species (*Havranek & Molnár, 1965; Bryja et al., 2005b*), which is critically endangered in, for example, the Czech Republic (*Řezáč et al., 2015*). However, *B. vicina* is not considered to be very rare in Hungary and it can be characterised as a species with a rather sporadic occurrence (*Szinetár pers. comm.*). It occurs in the herb layer of downy oak forests (*Bryja et al., 2005b*) or at forest edges (*Havranek & Molnár 1965*), although *B. vicina* was reported from urban areas (from *Picea abies* trees) as well (*Szinetár, 1992*). In spite of the limited data on this species our results indicate that urban green ecosystems can provide appropriate habitats for *B. vicina*.

Dysderidae C. L. Koch, 1837

***Dysdera lata* Reuss, 1834** (Fig. 1.3)

Determination. *Kovblyuk et al., 2008; Le Peru, 2011; Bosmans et al., 2017*

Material examined. 1♂, Budapest: 27.07.2016 – Budai Arborétum (47°28′49″N, 19°02′24″E, 120 m a.s.l., urban green area). The specimen (leg. & det. L. Mezőfi) was collected by hand on a pavement near a rockery in the Botanical Garden of the Szent István University.

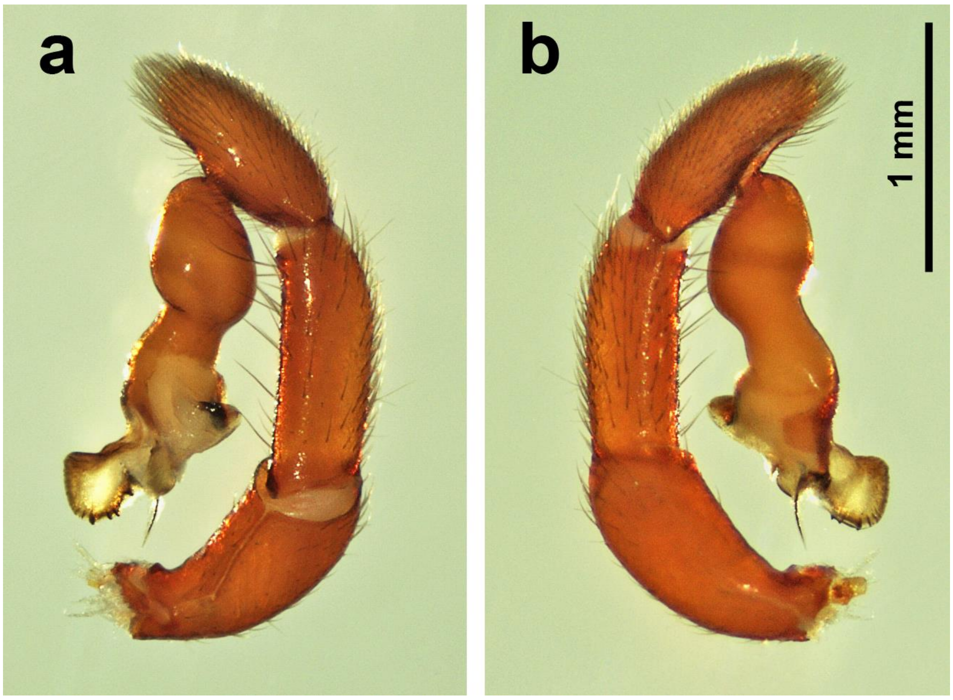

Figure 1.3: Left palp of *Dysdera lata* male from Hungary; (**a**) retrolateral view; (**b**) prolateral view

Distribution. Mediterranean to Georgia (*WSC, 2017*). In Europe this species occurs in Bulgaria, Cyprus, France (exclusively on Corsica), Greece (including North Aegean Islands, Cyclades and

Crete), Moldova, Portugal, Romania, Russia (southern European part), Slovakia, Spain (exclusively on the Balearic Islands) and Ukraine (*Otto, 2015; Bosmans et al., 2017; van Helsdingen, 2017; Lissner, 2017*).

Remarks. *Deeleman-Reinhold & Deeleman (1988)* and *Řezáč et al. (2008)* suggested that *Chyzer & Kulczyński* (*1897*: p. 267, plate 10, fig. 39) and *Loksa* (*1969*: pp. 75, 76 and 79, fig. 52 A–B) misidentified *Dysdera westringi* O. P.-Cambridge, 1872 and the species which they actually had was *Dysdera taurica* Charitonov, 1956. *Řezáč et al. (2008)* also examined some *D. taurica* specimens from Hungary to prove its presence in this country. Nevertheless, in the next year *D. taurica* was established as a junior synonym of *D. lata* by *Kovblyuk et al. (2008)*. The main difference between males of *D. westringi* and *D. lata* is that the former one has no teeth while the latter one has 3–7 teeth on the apical lobe of the bulbus (*Kovblyuk et al., 2008*). In this paper we confirm the occurrence of *D. lata* in Hungary. *Dysdera westringi* is rare in Hungary (*Szinetár et al., 2012*), and in the light of the above-mentioned problems in identification, all records need to be re-checked because they probably all belong to *D. lata*.

Hahniidae Bertkau, 1878

***Iberina microphthalma* (Snazell & Duffey, 1980)** (syn. *Hahnia microphthalma*) (Fig. 1.4)

Determination. *Snazell & Duffey, 1980; Szita et al., 1998*

Material examined. 2♀♀, Madocsa: 27.09.2016 – (46°40′50″N, 18°58′32″E, 92 m a.s.l., commercial apple orchard treated with pesticides). The specimens (leg. L. Mezőfi, det. É. Szita) were collected by beating from canopies of apple trees.

Distribution. Only known from Czech Republic, Germany, Great Britain, Hungary and Switzerland (*WSC, 2017*).

Remarks. Little is known about the biology of this rare species. Only a few records are available (*Řůžička & Dolanský, 2016*) and the male is still unknown. According to *Snazell & Duffey (1980)* the posterior median eyes are reduced, but various stages of eye reduction are possible and there may be differences in the form of the translucent copulatory ducts as well (*Szita et al., 1998; Hänggi & Stäubli, 2012*). *Růžička & Dolanský (2016)* summarised earlier records and found that all previous specimens were collected on the ground surface or in the grass layer by various methods (e.g., by pitfall traps, sweeping), except some specimens that were collected using pipe traps which were designed to catch subterranean invertebrates. *Snazell & Duffey (1980)* propose that some of the characteristics of the spider suggest subterranean habitat use and *Růžička & Dolanský (2016)* consider *I. microphthalma* as a ‘soil spider’. Nonetheless, its occurrence in the canopy of apple trees (at a height of approximately 1.5 m above the ground) suggest that besides the soil layer or the ground level *I. microphthalma* can sometimes also occur on plants.

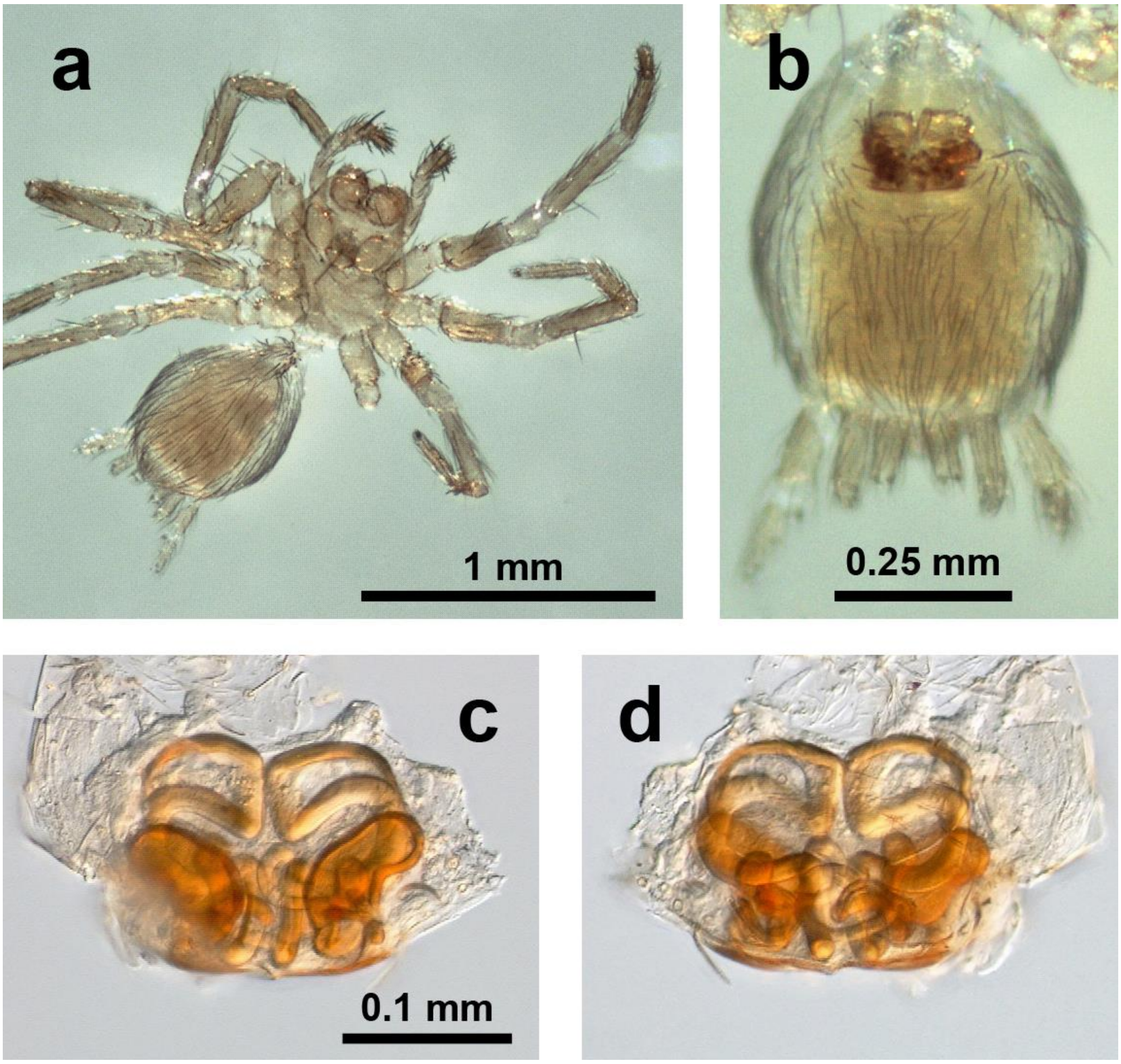

Figure 1.4: *Iberina microphthalma* female from Hungary; (**a**) general appearance, dorsal view; (**b**) opisthosoma with epigyne, ventral view; (**c**) epigyne/vulva, dorsal view; (**d**) epigyne, ventral view

Linyphiidae Blackwall, 1859

Mermessus trilobatus (Emerton, 1882)

Determination. *Nentwig et al., 2017; Šestáková et al., 2017*

Material examined. 2♂♂, 3♀♀: 2♀♀ 15.12.2015 – Monorierdő (47°19′13″N, 19°31′12″E, 158 m a.s.l,, organic apple orchard); 1♂ 05.02.2016 – Újfehértó (47°49′13″N, 21°39′58″E, 121 m a.s.l., organic apple orchard); 1♂, 1♀ 09.12.2016 – Sükösd (46°17′59″N, 19°00′21″E, 100 m a.s.l., organic apple orchard). The specimens (leg. & det. L. Mezőfi) were collected by litter sampling.

Distribution. North America. Introduced to Azores, Europe (*WSC, 2017*). In Europe it is present in Austria, Belgium, Croatia, Czech Republic, France, Germany, Great Britain, Hungary, Italy, Netherlands, Poland, Portugal (exclusively on Azores), Slovakia, Slovenia, Switzerland and Ukraine (*Dolanský et al., 2009; Katušić, 2009; Kovács et al., 2015b; Szinetár et al., 2015; van Helsdingen, 2017; Hirna, 2017*).

Remarks. This North American linyphiid spider was first found in Germany in the early 1980s and *M. trilobatus* is probably now the most frequently occurring alien spider in Europe (*Nentwig & Kobelt, 2010*). This invasive ground-living species is probably spreading primarily by ballooning (*Košulić et al., 2013; Blandenier et al., 2014*) and its high colonization ability may relate to this, although the exact reasons for the success of *M. trilobatus* are still unclear (*Eichenberger et al., 2009*). In Hungary the first specimen was collected in 2012 (*Kovács et al., 2015b*), and since then it was found in several locations, especially in the western part of the country (e.g., *Kovács & Szinetár, 2015; Kovács et al., 2015b; Szinetár et al., 2015*). Our results indicate that in recent years this species colonized almost the entire country, the central (Monorierdő), the southern (Sükösd) and the eastern (Újfehértó) parts equally. The species can also be expected to reach Serbia and Romania in the near future.

***Porrhomma oblitum* (O. P.-Cambridge, 1871)** (Fig. 1.5)

Determination. *Merrett, 1994; Russell-Smith, 2009*

Material examined. 1♀, Nagykálló: 05.02.2016 – (47°53′17″N, 21°48′57″E, 116 m a.s.l., organic apple orchard). The specimen (leg. & det. L. Mezőfi) was collected from a cardboard band.

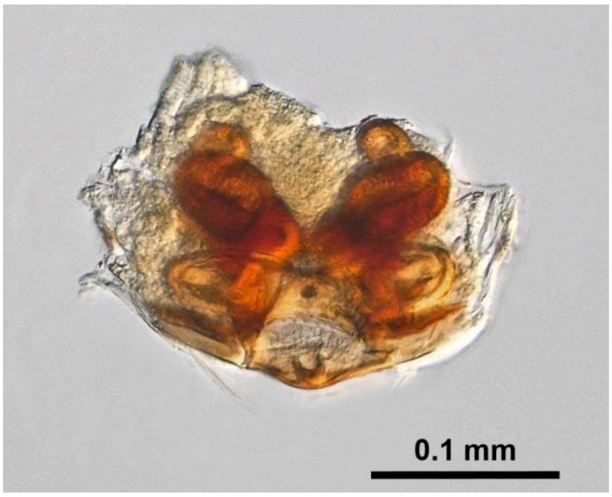

Figure 1.5: Cleared, dissected epigyne/vulva of *Porrhomma oblitum* female from Hungary; dorsal view

Distribution. Europe (*WSC, 2017*): Austria, Belgium, Czech Republic, Denmark, Finland, France, Germany, Great Britain, Greece, Iceland, Ireland, Italy, Lithuania, Netherlands, Norway, Poland, Romania, Russia (Eastern European part), Slovakia and Switzerland (*van Helsdingen, 2017*).

Remarks. *Samu & Szinetár (1999)* listed seven *Porrhomma* species from Hungary: *P. convexum* (Westring, 1851), *P. errans* (Blackwall, 1841), *P. microphthalmum* (O. P.-Cambridge, 1871), *P. montanum* Jackson, 1913, *P. profundum* Dahl, 1939, *P. pygmaeum* (Blackwall, 1834) and *P. rosenhaueri* (L. Koch, 1872), however the presence of *P. errans* and *P. rosenhaueri*, are uncertain (*Samu & Szinetár, 1999*). *Szinetár & Horváth (2006)* cited the unpublished M.Sc. thesis of *Kovács (2002)* for *P. oblitum*, suggesting that the species also occurs in Hungary, but in this thesis *P. oblitum* was not mentioned. Consequently, to the best of our knowledge we report *P. oblitum* for the first time in Hungary, making it the eighth member of its genus in the country.

This species is a facultative bark-dweller and it may occur in arable lands or various open and forest habitats, especially in semi-humid and humid ones (*Blick et al., 2000; Szinetár & Horváth, 2006*). Identification of *Porrhomma* species is quite difficult. Both *P. oblitum* and *P. montanum* belong to the *Porrhomma* group, where the metatarsi are spineless, femur I has only one prolateral spine and the dorsal spines are lacking, and tibia I has a prolateral spine. *Porrhomma oblitum* and *P. montanum* can be distinguished from each other only by small details of the dissected and cleared genitalia (*Russell-Smith, 2009; Šestáková, 2011*).

Philodromidae Thorell, 1870

***Philodromus marmoratus* Kulczyński, 1891** (syn. *Ph. buddenbrocki* Braun, 1965) (Fig. 1.6)

Determination. *Kubcová, 2004; Muster & Thaler, 2004*

Material examined. 2♂♂, 2♀♀ Budapest: 1♀ (leg. V. Hoffmann, det. L. Mezőfi) 20.04.2016, 1♀, 1♂ (leg. D. Gyóni, det. L. Mezőfi) 29.07.2016 – Margit Island (47°31′19″N, 19°02′43″E, 103 m a.s.l., urban green area with floodplain-like forest vegetation) (The male is a reared specimen, reached maturity after the ninth moult on 29.05.2017.). All specimens were collected by beating from shrubs. 1♂ (det. L. Mezőfi) an additional individual, an offspring of the female collected on 29.07.2016 was also examined. This reared specimen emerged from the egg on 10.08.2016 and reached maturity after the ninth moult on 19.05.2017.

Distribution. Only in Austria, Bulgaria, Czech Republic, Hungary, Slovakia, Ukraine and former Yugoslavia (with newer data from Serbia) (*Grbić & Savić, 2010; van Helsdingen, 2017*).

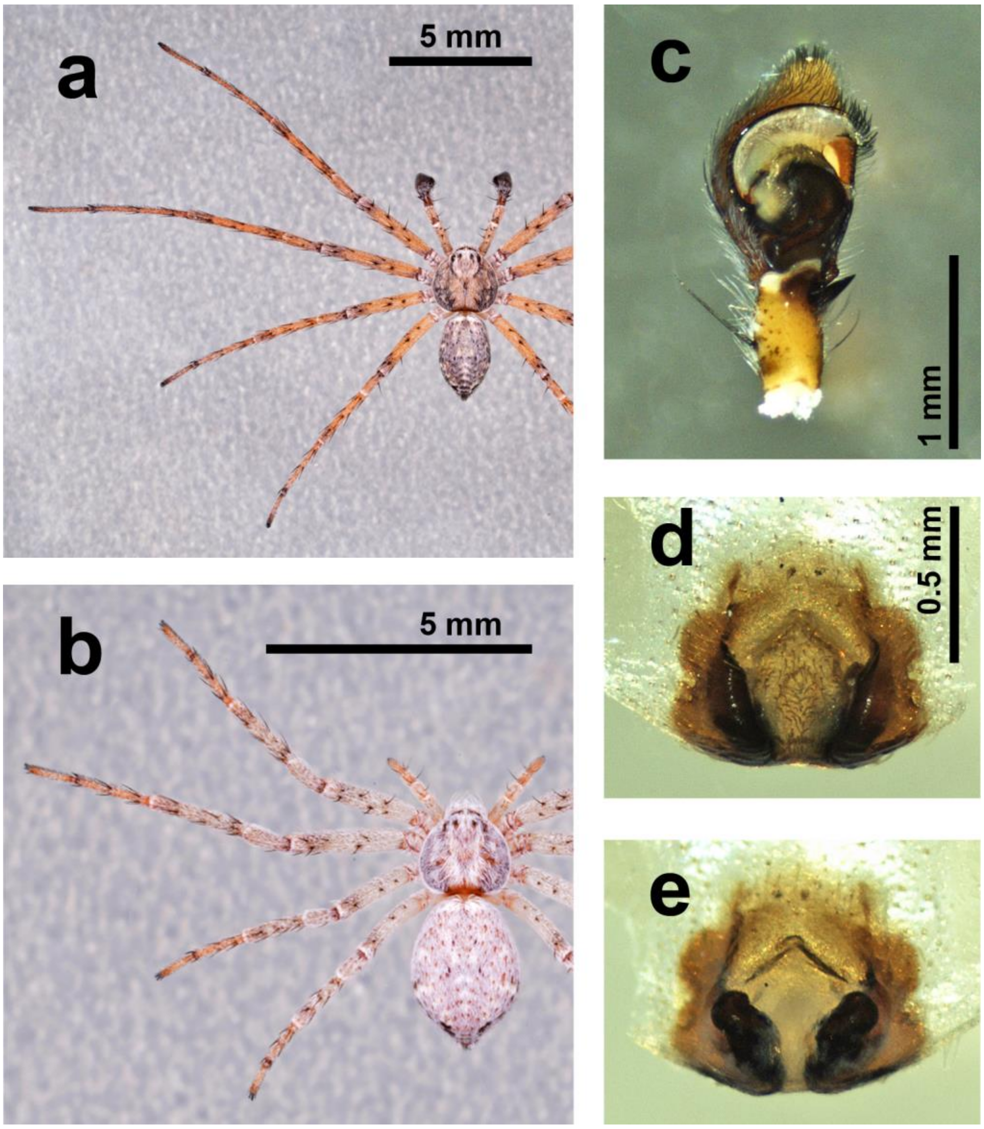

Figure 1.6: *Philodromus marmoratus* specimens from Hungary; (**a**) male, general appearance, dorsal view; (**b**) female, general appearance, dorsal view; (**c**) male's left palp, ventral view; (**d**) epigyne, ventral view; (**e**) epigyne/vulva, dorsal view

Remarks. A very rare species (*Bryja et al., 2005a, 2005b*), which is endangered in, e.g., the Czech Republic (*Řezáč et al., 2015*) and occurs near wetlands or floodplain forests (*Jäger, 1995; Bryja et al., 2005b*). This species belongs to the *Philodromus aureolus* group (*Segers, 1992*) and was originally described as *Ph. aureolus* ssp. *marmoratus* (in *Chyzer & Kulczyński, 1891*). *Segers (1992)* firstly mentioned that *Ph. buddenbrocki* is possibly a synonym of *Ph. aureolus marmoratus* and later *Kubcová (2004)* clarified the situation and established *Ph. buddenbrocki* as a junior synonym of *Ph. marmoratus*. Although *Chyzer & Kulczyński (1918)*, in their spider checklist reported several *Ph. aureolus marmoratus* records from the present territory of Hungary, surprisingly *Ph. marmoratus* was not included in the Hungarian checklist of spiders (*Samu & Szinetár, 1999*), probably because of its uncertain taxonomic status. Our data provide further evidence for the occurrence of *Ph. marmoratus* in Hungary. Furthermore, one individual (♂) was successfully reared from the egg. After the spider had emerged, it moulted nine times until maturity was reached. The other reared specimen (♂) which had been collected as a small nymph also moulted nine times until it reached adult stage. These observations indicate that *Ph. marmoratus* may have nine or more instars before maturity.

***Pulchellodromus ruficapillus* (Simon, 1885)** (syn. *Philodromus ruficapillus*) (Fig. 1.7)

Determination. *Muster et al., 2007; Kastrygina & Kovblyuk, 2014*

Material examined. 2♀♀, Nagykálló: 09.05.2016 – (47°53′17″N, 21°48′57″E, 116 m a.s.l., organic apple orchard) (reared specimens, final moulting reached on 25.07.2016). The specimens (leg. & det. L. Mezőfi) were collected by beating method from canopy of apple trees.

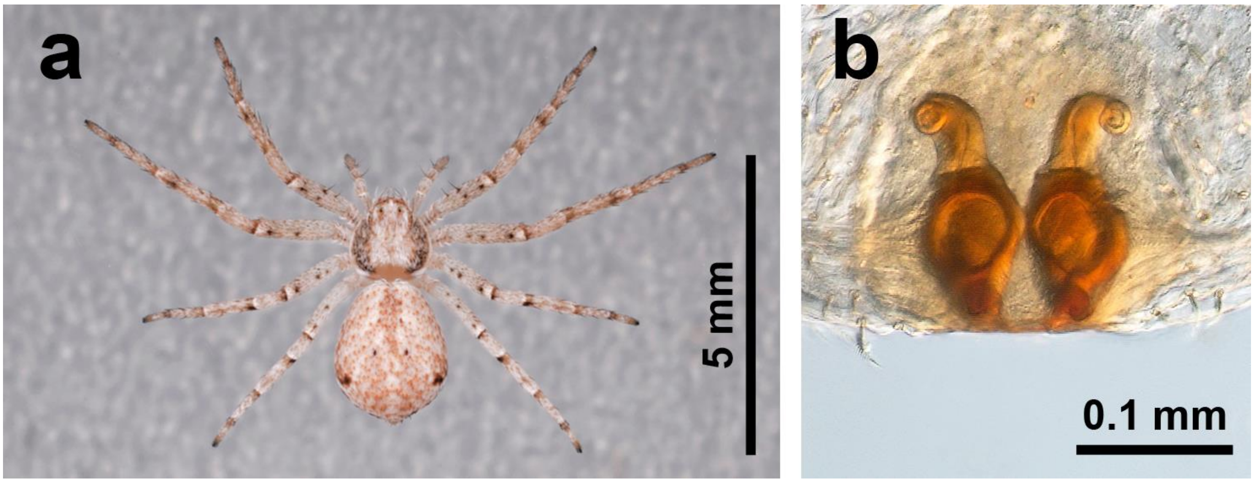

Figure 1.7: *Pulchellodromus ruficapillus* female from Hungary; (**a**) general appearance, dorsal view; (**b**) epigyne/vulva, dorsal view

Distribution. Mediterranean to Kazakhstan (*WSC, 2017*). In Europe it was found in Albania, Austria, France, Greece (including North Aegean Islands and Crete), Hungary, Italy, Portugal, Romania, Spain and Ukraine (*van Helsdingen, 2017*).

Remarks. In 2012 the genus *Pulchellodromus* was separated from the genus *Philodromus* by *Wunderlich (2012),* and the genus now contains 13 cryptic species (*WSC, 2017*), mostly from the Mediterranean region (*Muster et al., 2007; Wunderlich, 2012*). Two of them have data from Hungary: *P. pulchellus* (Lucas, 1846) (*Déri et al., 2007; Kancsal et al., 2010*) and *P. ruficapillus*, the latter of which seems to have the largest distribution area among the other species of the genus (*Duma, 2008*). Until now, in Hungary *P. ruficapillus* has been found in Fertő-Hanság (Northwestern Hungary) (*Muster et al., 2007*) and in the Balaton Upland (*Szinetár et al., 2016*), but our data (Nagykálló, Northeastern Hungary) suggest that it is widespread throughout Hungary. Furthermore, all the records of *P. pulchellus* from Hungary need to be re-checked, because they probably all belong to *P. ruficapillus* (*Szinetár et al., 2016*). *Pulchellodromus ruficapillus* occurs usually in wetlands or along riverbanks and also on seashores (*Muster et al., 2007; Duma, 2008; Szinetár et al., 2016*).

Theridiidae Sundevall, 1833

***Lasaeola prona* (Menge, 1868)** (syn. *Dipoena prona*)

Determination. *Roberts, 1985; Le Peru, 2011*

Material examined. 1♂, 2♀♀, 3 sub ♂♂, 4 sub ♀♀, 1 nymph: 2♀♀ (leg. C. Nagy, det. L. Mezőfi) 28.04.2014 (The specimens were collected from their webs, at the base of apple trees.), 1♂ (leg. & det. L. Mezőfi) 09.07.2014 [This specimen was consumed by a *Carrhotus xanthogramma* (Latreille, 1819) nymph (det. L. Mezőfi) on an apple tree.] – Újfehértó (47°49′13″N, 21°39′58″E, 121 m a.s.l., organic apple orchard). The spiders were collected by hand. 1 sub ♂ 01.12.2013 – Zsurk (48°24′54″N, 22°12′45″E, 103 m a.s.l., commercial apple orchard); 1 sub ♀ 01.12.2013 – Zsurk (48°23′30″N, 22°12′52″E, 105 m a.s.l., commercial apple orchard). These specimens (leg. M. Paróczai, det. L. Mezőfi) were collected by the cardboard band method. 1 nymph 22.09.2015 – Nyírcsaholy (47°55′17″N, 22°18′43″E, 126 m a.s.l., organic apple orchard); 1 sub ♂ 05.02.2016 – Újfehértó (47°49′13″N, 21°39′58″E, 121 m a.s.l., organic apple orchard). These specimens (leg. & det. L. Mezőfi) were collected by the cardboard band method. 1 sub ♂, 3 sub ♀♀ 05.02.2016 – Újfehértó (47°49′13″N, 21°39′58″E, 121 m a.s.l., organic apple orchard). The specimens (leg. & det. L. Mezőfi) were collected by litter sampling.

Distribution. North America, Europe, Caucasus, Japan (*WSC, 2017*). In Europe it is widely distributed: Albania, Austria, Belgium, Bulgaria, Czech Republic, Denmark, Estonia, Finland, France, Germany, Great Britain, Greece, Hungary, Italy, Latvia, Lithuania, Netherlands, Norway, Poland, Russia (eastern European, northern European and Kaliningrad Region), Slovakia, Slovenia, Spain, Sweden, Switzerland and Ukraine (*van Helsdingen, 2017*).

Remarks. Although widely distributed in Europe, this is quite a rare species and its biology is partly unknown (*Nentwig et al., 2017*). *Lasaeola prona* was classified as near threatened in the Carpathian Red List (*Gajdoš et al., 2014*), while in the Czech Republic it is critically endangered (*Řezáč et al., 2015*). Although much of its biology was previously unknown, more is known about it today. This thermophilous species usually occurs in open xerothermic habitats (*Bryja et al., 2005b; Franc & Korenko, 2008*) and is often found at ground level, e.g., under stones (*Roberts, 1985*). Adult individuals appear mostly from early June to the end of August (*Szinetár, 1995; Franc & Korenko, 2008; Kovblyuk et al., 2012; Kostanjšek & Gorjan, 2013; Aakra et al., 2016*), and our data indicates that the mentioned species overwinters mainly in the subadult stage under bark or in the litter. Therefore, it seems that *L. prona* is a stenochronous species with a summer reproductive and dispersing period. Furthermore, we have observed the two collected female individuals (see above) preying on ants [*Lasius niger* (Linnaeus, 1758), det. C. Nagy]. In *Dipoena* sensu lato myrmecophagy is a known phenomenon (*Roberts, 1985; Le Peru, 2011*), therefore *L. prona* is probably also a myrmecophagous species.

Thomisidae Sundevall, 1833

***Diaea livens* Simon, 1876** [syn. *D. pictilis* (Banks, 1896)]

Determination. *Buchar & Thaler, 1984; Nentwig et al., 2017*

Material examined. 2♂♂, 1♀, 2 sub ♂♂, 1 sub ♀, 3 nymphs: 1♀ 30.05.2015 – Gödöllő (47°35′35″N, 19°21′38″E, 222 m a.s.l., urban green area). The spider (leg. V. Hoffmann, det. L. Mezőfi) was collected by hand from a shrub. 1♂ 27.04.2016, 1 sub ♂ 14.10.2016 – Budapest, Normara (47°30′24″N, 18°57′43″E, 463 m a.s.l., urban green area with deciduous forest vegetation); 1♂ 26.05.2016, 1 nymph 14.09.2016, 1 sub ♂ 14.10.2016 – Budapest, Széchenyi-hegy (47°29′43″N, 18°58′31″E, 462 m a.s.l. urban green area); 1 sub ♀ 14.09.2016, 1 nymph 14.10.2016 – Budapest, Hűvösvölgy (47°32′31″N, 18°57′46″E, 228 m a.s.l. urban green area with deciduous forest vegetation); 1 nymph 14.09.2016 – Budapest, Zugligeti út (47°31′04″N, 18°59′08″E, 180 m a.s.l., urban green area). These specimens (leg. D. Korányi, det. L. Mezőfi) were collected by beating mainly in urban forest areas from canopies of *Acer campestre* trees.

Distribution. Southern and Central Europe, Turkey, Caucasus. Introduced to USA (*WSC, 2017*). In Europe it is present in Albania, Austria, Bulgaria, Czech Republic, France, Germany, Greece, Hungary, Italy, Serbia, Slovakia, Slovenia, Spain, Switzerland, Turkey (European part) and Ukraine (*Tomić & Grbic, 2008; van Helsdingen, 2017*).

Remarks. Throughout Europe this is a very rare species (*Nentwig et al., 2017*) which was classified as vulnerable in the Carpathian Red List (*Gajdoš et al., 2014*) while in the Czech Republic it is endangered (*Rezáč et al., 2015*). In Hungary it was firstly detected by *Szinetár (1995)* and since then the spider was found at several locations within the country (*Bogya et al., 1999; Horváth & Szinetár, 2002; Szita et al., 2002; Horváth et al., 2009; Kovács et al., 2009; Szinetár et al., 2011; Keresztes, 2013; Szita et al., 2014*), although *D. livens* is still a quite rare species here. This species is a facultative bark-dweller (*Szinetár & Horváth, 2006*) and occurs almost exclusively in oak forests on shrubs and lower branches of trees (*Szinetár, 1995; Szinetár et al., 2011; Nentwig et al., 2017*). Although it has several records from other habitats/plants: e.g., from apple (*Keresztes, 2013*) and pear (*Bogya et al., 1999*) orchards, from *Pinus nigra*, *Platanus hybrida* (*Szinetár & Horváth, 2006*), *Tilia* spp. and from *Acer* spp. trees (*Stenchly et al., 2007; Keresztes, 2013*). We collected several specimens from *A. campestre* trees as well, which suggests that *D. livens* might be less tightly bounded to the oak forests. The specimen collected in Gödöllő was consuming a *Smaragdina aurita* (Linnaeus, 1767) (Chrysomelidae) (det. L. Mezőfi) adult on a shrub.

Conclusions

Given their presence in neighbouring countries and distribution in Europe, the occurrence of the new records (*C. sierrae* and *P. oblitum*) for Hungary is not surprising. Probably the two above mentioned species have naturally spread to Hungary, because human-mediated dispersal is less typical for Araneidae and Linyphiidae species (*Nentwig, 2015*). At the moment, the Spiders of Europe database lists 800 spider taxa for Hungary (*Nentwig et al., 2017*), but the spiders reported here, and the many other recently described and first recorded species, indicate that the list is still far from complete. Therefore, in Hungary the number of spider species can be estimated to be much higher than 800. According to *Nentwig (2015)* international trade and climate change are the major factors that facilitate the spread and establishment of alien spider species. Currently one alien spider species per year is introduced to Europe, but this rate will surely increase in future. Therefore, it is important to continue the arachnological exploration of Hungary because, as in the case of Europe in general, many new species are expected to emerge in this country and also not all species that supposedly occur in Hungary have been found and listed yet.

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STUDY2: BEYOND POLYPHAGY AND OPPORTUNISM: NATURAL PREY OF HUNTING SPIDERS IN THE CANOPY OF APPLE TREES

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Abstract

Spiders (Araneae) form abundant and diverse assemblages in agroecosystems such as fruit orchards, and thus might have an important role as natural enemies of orchard pests. Although spiders are polyphagous and opportunistic predators in general, limited information exists on their natural prey at both species and community levels. Thus, the aim of this study was to assess the natural prey (realized trophic niche) of arboreal hunting spiders, their role in trophic webs and their biological control potential with direct observation of predation events in apple orchards. Hunting spiders with prey in their chelicerae were collected in the canopy of apple trees in organic apple orchards in Hungary during the growing seasons between 2013 and 2019 and both spiders and their prey were identified and measured. Among others, the composition of the actual (captured by spiders) and the potential (available in the canopy) prey was compared, trophic niche and food web metrics were calculated, and some morphological, dimensional data of the spider-prey pairs were analysed. Species-specific differences in prey composition or pest control ability were also discussed.

By analysing a total of 878 prey items captured by spiders we concluded that arboreal hunting spiders forage selectively and consume a large number of apple pests; however, spiders' beneficial effects are greatly reduced by their high levels of intraguild predation and by a propensity to switch from pests to alternative prey. In this study, arboreal hunting spiders showed negative selectivity for pests, no selectivity for natural enemies and positive selectivity for neutral species. In the trophic web, the dominant hunting spider taxa/groups (*Carrhotus xanthogramma, Philodromus cespitum*, *Clubiona* spp., *Ebrechtella tricuspidata*, *Xysticus* spp. and 'Other salticids') exhibit different levels of predation on different prey groups and the trophic web's structure changes depending on the time of year. Hunting spiders show a high functional redundancy in their predation, but contrary to their polyphagous nature, the examined spider taxa showed differences in their natural diet, exhibited a certain degree of prey specialisation and selected prey by size and taxonomic identity. Guilds (such as stalkers, ambushers and foliage

runners) did not consistently predict either prey composition or predation selectivity of arboreal hunting spider species. From the economic standpoint, *Ph. cespitum* and *Clubiona* spp. were found to be the most effective natural enemies of apple pests, especially of aphids. Finally, the trophic niche width of *C. xanthogramma* and *Ph. cespitum* increased during ontogeny, resulting in a shift in their predation. These results demonstrate how specific generalist predators can differ from each other in aspects of their predation ecology even within a relatively narrow taxonomic group.

Introduction

Spiders play an important role in ecosystems as predators of various invertebrate groups. In certain habitats, according to the highest realistic estimates, spiders might kill up to approximately 200 kg prey ha^{-1} year^{-1} (*Nyffeler, 2000*), which by extrapolation suggests that the global spider community might consume up to 400–800 million tons of prey annually (*Nyffeler & Birkhofer, 2017*). Generally, spiders are regarded as polyphagous (preying on a wide variety of prey) and opportunistic (taking their prey as a function of each prey species' availability), although some degree of selectivity in foraging is often observed (e.g., *Nentwig, 1980; Whitney et al., 2018; Eitzinger et al., 2019*). Moreover, stenophagy has evolved in certain groups of spiders, e.g. myrmecophagy in Zodariidae or araneophagy in Salticidae (*Pekár et al., 2012; Pekár & Toft, 2015*). Spiders mainly prey on insects, of which the preferred size is primarily ~50–80% of the spiders' size (*Nentwig & Wissel, 1986; Foelix, 2011*), but they can also feed on other invertebrates (*Nyffeler & Symondson, 2001; Nyffeler et al., 2017a*) or vertebrates (*Nyffeler & Knörnschild, 2013; Nyffeler & Pusey, 2014; Nyffeler et al., 2017b*), eggs of various arthropods (*Nyffeler et al., 1990; Ahmed et al., 2018*) or even on plant nectar and pollen (*Nyffeler, 2016; Nyffeler et al., 2016*).

In agroecosystems, spiders can contribute significantly to pest control by consuming a large number of various insect pests (e.g., *Nyffeler & Benz, 1988; Young & Edwards, 1990; Marc et al., 1999; Nyffeler & Sunderland, 2003; Birkhofer et al., 2008; Liu et al., 2015; Suenaga & Hamamura, 2015; Lefebvre et al., 2017*). A recent meta-analysis (*Michalko et al., 2019a*) of 58 studies found that spiders suppressed agricultural insect pests in 79% of the cases, although their efficacy varied among crops. From an economic point of view, hunting spiders have special importance, as they collect their prey directly from the surface of the crop and thus they more frequently consume less mobile stages (e.g., eggs, larvae, nymphs) of various arthropods than web-building spiders (*Marc et al., 1999; Nyffeler, 1999*). Also, hunting spiders have a wider trophic niche compared to web-builders (*Nyffeler, 1999; Michalko & Pekár, 2016*). Furthermore, besides direct predation, hunting spiders have several other non-consumptive effects on pests/herbivores (*Mansour et al., 1981; Sunderland, 1999; Beleznai et al., 2015; Bucher et al., 2015; Tholt et al.,* *2018*) and due to the consumptive and non-consumptive effects, hunting spiders can also improve crop performance indirectly (*Schmitz et al., 1997; Schmitz & Suttle, 2001; Schmitz, 2008*).

Trophic niche width (or diet breadth) of spider species varies along a continuum from extremely narrow (feeding on a single prey taxon) to extremely wide (feeding on all available prey taxa) diet range, although some differences may exist even at the more polyphagic end of the continuum (*Pekár et al., 2012; Pekár & Toft, 2015*). Although these generalist predators can effectively reduce pest numbers (*Symondson et al., 2002; Nyffeler & Sunderland, 2003*), many factors can influence their role in pest suppression and food-web dynamics at both community and individual levels (*Michalko et al., 2019b*). Several environmental factors and functional traits can be directly or indirectly involved, including the presence or absence of alternative prey (*Madsen et al., 2004; Kuusk & Ekbom, 2010*), the intensity of intraguild predation or predator interference (*Snyder & Wise, 1999; Wise, 2006; Petráková et al., 2016; Michalko et al., 2017*), the season of the year (*Snyder & Wise, 2001*), hunting strategy or guild (*Schmitz, 2008; Miller et al., 2014; Liu et al., 2015; Michalko et Pekár, 2016*), or ontogenetic differences (*Bartos, 2011*).

It is hard to assess what spiders' diets consist of or what role various species play in food webs or trophic cascades. In laboratory experiments, spiders might accept more prey types than in their natural environment (*Líznarová & Pekár, 2019*) and thus, these studies provide only limited insight into the natural diet of spiders (*Greenstone, 1999*). In the field, there are many methods to obtain information about the realized trophic niche of invertebrate predators (*Sunderland, 1988; Symondson, 2002; Birkhofer et al., 2017; Macías-Hernández et al., 2018*). Although they are labour-intensive, direct *in situ* observations can provide the most reliable data about the natural diet of a focal predator species (*Greenstone, 1999; Birkhofer et al., 2017; Pekár et al., 2017*), so it is not surprising that this method is widely used to assess diet concerning different species of spiders (*Yeargan, 1975; Lockley & Young, 1987; Morse, 1981; Nyffeler et al., 1992; Huseynov, 2005, 2007*). Many studies on the natural diet of spiders have focused on web-building spiders because the observation of sedentary species is easier than tracking mobile hunters, and in case of web-builders there is an opportunity to collect prey carcasses from their web. In many studies investigating hunting spiders, the diet of only one species or species-pair was examined without comparing the composition of potential and actual prey (see the references in *Pekár et al., 2012, 2017; Michalko & Pekár, 2016*). Thus, very little is known about the field diet of hunting spider assemblages, especially in the canopy layer, and limited information is available on how actual prey relates to potential prey, and how one species' diet relates to another.

Spiders form abundant and diverse assemblages in apple orchards and can contribute to the suppression of various apple pests (*Bogya et al., 1999a, 2000; Michalko & Pekár, 2015; Lefebvre* *et al., 2017*), although their function in biological control has been less studied in orchards (*Michalko et al., 2019a*). In the light of the above, the aim of this study was to assess the natural prey (realized trophic niche) of arboreal hunting spiders, their role in trophic webs, and their biological control potential using direct observation of predation events in apple orchards. More specifically, our objectives were (1) to evaluate the natural prey and (2) predation selectivity of the hunting spider assemblage in the canopy of apple trees, (3) to compare the preferred prey of the most abundant hunting spider species or groups (4) concerning their hunting guild. We also aimed to determine how (5) size and (6) the life stage of hunting spiders affect the composition and size of their prey.

Material and Methods

Data collection

Data on the natural diet (actual prey) of the arboreal hunting spider assemblage was collected between 2013 and 2019 in apple orchards in Hungary. For this, apple trees were visually inspected regularly in organic orchards, and hunting spiders with prey in their chelicerae were collected during the growing season (from the beginning of April to the end of October). The vast majority of the observations (N = 788, almost 90% of the data) came from one organic apple orchard located at Újfehértó (an experimental orchard of the Research Institute for Fruitgrowing and Ornamentals, National Agricultural Research and Innovation Centre), in Szabolcs-Szatmár-Bereg County, eastern Hungary. A further 37, 31 and 22 observations on the hunting spiders' natural prey (for a total of 878 observations) were collected in apple orchards of the Szent István University in the vicinity of Újfehértó (Szabolcs-Szatmár-Bereg County), in Pest County and Bács-Kiskun County, respectively. The orchard located in Újfehértó (~3.3 ha, 47°49'11.5"N, 21°39'56.9"E) was planted on flat land, on a fine sandy soil in autumn 2002 and contained the cultivars 'Florina', 'Prima', 'Rajka', 'Releika', 'Rewena', 'Rubinola' and 'Topaz' on 'M9', and 'Remo' and 'Resi' on 'M26' rootstocks. It had 32 rows, each consisting of ~90-135 trees. Rows were spaced 5 m apart and apple trees were spaced 1.5 and 2.25 m apart within rows. The orchard was surrounded by other orchards (cherry, apple) as well as other agricultural areas.

Our *in situ* observations were conducted both day and night (approximate ratio 7:3) to get information not only on the prey of the diurnal hunting spiders but also on the nocturnal ones. Apple trees were examined mainly between 9:00 and 12:00, between 14:00 and 18:00 and between 20:00 and 23:00 (after sunset). Spiders with prey in their chelicerae were collected (with a glass vial) and the prey was taken from the spiders to prevent any further degradation. In some cases, just the prey was collected because the spider escaped or because we did not want to influence other trials conducted in the orchard. After collecting the spiders with their prey, the material was taken to the laboratory of the Department of Entomology, Szent István University (Budapest, Hungary), and both the spider and the prey were identified (with a binocular stereo microscope, Leica MZ6) to the lowest taxonomic level possible. Moreover, in spiders, the width of the prosoma and in case of the preys (if their conditions allowed) the width of the thorax were measured with 0.1 mm accuracy using an ocular micrometer calibrated with a stage micrometer. In juvenile spiders where the species-level identification was not possible (e.g., in *Philodromus* species), spiders were raised to the adult stage (on *Drosophila hydei* Sturtevant) in the laboratory. Spiders were identified after *Nentwig et al. (2019)* and the taxonomic names follow the nomenclature of the *WSC (2019)*. The spiders were stored in 70% ethanol, while the prey items were stored mainly dry in glass vials. Approximately 4-5% of the prey items collected were unidentifiable due to the high level of degradation and were excluded from the analyses. The dataset [see Data S1 (can be found as an online supplement to the published paper)] contains only the cases where both the spider and its prey were identifiable (878 observations).

To obtain information on the potential prey community of arboreal hunting spiders, a D-VAC sampler was used. In the organic apple orchard located at Újfehértó, suction samples were taken at monthly intervals between April and October in 2016 and 2017 (on 14 sampling dates). On each sampling date, five samples were taken. Each sample consisted of suction samples collected from one (left or right) side of the canopy of four randomly selected apple trees in a randomly selected row. For the samplings, a ~25 cm long, tapering gauze bag (mesh < 0.5 mm) was inserted into the 12 cm diameter intake nozzle of the D-VAC sampler. Suction sampling was carried out during dry weather, approximately between 9:00 and 14:00. The collected material was sorted and identified (mainly to order, suborder, family or genus level) in the laboratory.

Preparation of data for analysis

For most analyses, the spiders were classified into six groups: (1) *Carrhotus xanthogramma* (Latreille), (2) Other salticids, (3) *Philodromus cespitum* (Walckenaer), (4) *Ebrechtella tricuspidata* (Fabricius), (5) *Xysticus* spp. s. lat., and (6) *Clubiona* spp. The main criterion for group formation was that the number of records in a particular group should exceed 5% of the total sample (i.e., a group must contain at least 44 observations) at the lowest possible taxonomic level. Thus, while *C. xanthogramma*, *Ph. cespitum* and *E. tricuspidata* were collected in sufficiently large numbers (44 < n) for analyses, the other species had to be placed in genus- (*Xysticus* spp. and *Clubiona* spp.) or family-level (Other salticids) groups. The group ‘Other salticids’ comprises the data on other spider species belonging to the family Salticidae, mainly three species: (1) *Heliophanus auratus* C. L. Koch, (2) *H. cupreus* (Walckenaer), (3) *Salticus scenicus* (Clerck), but not including *C. xanthogramma*. The group '*Xysticus* spp. s. lat. (hereafter *Xysticus* spp.)' comprises the following seven species: (1) *Xysticus acerbus* Thorell, (2) *X. cristatus* (Clerck), (3) *X. kochi* Thorell, (4) *X. lanio* C. L. Koch, (5) *X. striatipes* L. Koch (currently *Spiracme striatipes*, see *Breitling, 2019*), (6) *X. ulmi* (Hahn), and (7) unidentified juveniles of *Xysticus* spp. Finally, the group '*Clubiona* spp.' consists of *C. frutetorum* L. Koch and unidentified juveniles of *Clubiona* spp. (Table S2.1-S2.2). To compare the hunting strategies of the species collected, they were classified using two different guild classification systems (*Uetz et al., 1999; Cardoso et al., 2011*). According to *Uetz et al. (1999)*, hunting spider guilds included (1) stalkers (*C. xanthogramma* and Other salticids), (2) ambushers (*Ph. cespitum*, *E. tricuspidata* and *Xysticus* spp.) and (3) foliage runners (*Clubiona* spp.). Based on a more recent guild classification by *Cardoso et al. (2011)* our hunting spider groups could be grouped into just two guilds: ambush hunters (*E. tricuspidata* and *Xysticus* spp.) and other hunters (*C. xanthogramma*, Other salticids, *Ph. cespitum* and *Clubiona* spp.).

Using the slightly modified prey classification system of *Michalko & Pekár (2015)*, prey items retrieved from spiders or collected by D-VAC sampling were classified into the following 16 taxonomic groups: Acari, Araneae, Coleoptera, Lepidoptera, Formicidae, Other (non-formicid) Hymenoptera, Brachycera, Nematocera (i.e., all non-Brachycera dipterans), Auchenorrhyncha, Heteroptera, Sternorrhyncha, Ephemeroptera, Neuroptera, Psocoptera, Thysanoptera, and Trichoptera. The prey categories that had relative abundances of less than 1% in the total actual prey of the whole arboreal hunting spider assemblage, namely Acari, Ephemeroptera, Neuroptera, Psocoptera, Thysanoptera and Trichoptera, were pooled into the group of 'Other prey' in certain statistical analyses.

To evaluate the biological control potential of the hunting spiders, the prey items were categorized according to their economic status in apple orchards in Central Europe as pests, natural enemies and neutral arthropod groups. A prey species was considered to be a pest if at least one of its life stages is known to feed on any parts of the apple tree. The pest category included some beetles (mainly weevils), some moths (both adult and larva of e.g., leaf miners, tortrix moths), some leafhoppers and planthoppers, lace bugs, and all aphid and psyllid (Sternorrhyncha) species. Natural enemies are defined as species that can feed (at least in one of their life stages) on any stage of arthropods that were previously categorized as pests. This category includes red velvet mites (Trombidiidae), spiders, predatory beetles (e.g., coccinellids, carabids), parasitoid wasps, hoverflies, zoophagous bugs (e.g., some mirids and anthocorids), and lacewings. Finally, the neutral category was comprised of other (non-pest and non-natural enemy) prey species. For prey that could be identified only to suborder, such as Nematocera, the classification was made according to the dominant characteristics of the taxon [i.e., the vast majority of Nematocera occurring in apple orchard are neutral species (*Alford, 2014*)].

Only a few species of Diptera cause damage on apple in Europe [*Dasineura mali* (Keifer), *Resseliella oculiperda* (Rübsaamen) (Nematocera) and *Phytomyza heringiana* Hendel (Brachycera)] and they are of minor importance (*Alford, 2014*). None of these species or their damage were found in the orchard (Újfehértó). *Drosophila suzukii* (Matsumura) (and other *Drosophila* species, Brachycera) can breed exclusively on overripe, bruised and rotten apples, and usually infests fallen fruits. Therefore, in apple orchards, this species considered to be as a decomposer (*Alford, 2014*). Based on these considerations, Nematocera and Brachycera dipterans (excluding hoverflies) were classified as neutral species. The role of ants could change seasonally depending on the size of the aphid colonies. In apple orchards, ants act as mutualists in the early phase of the aphid population development (*Nagy et al., 2015*). However, later when the aphid abundance is already high, ants follow rather than drive aphid abundances (*Markó et al., 2013*). Because of the above criteria, and because of vast majority of ants captured by spiders were dispersing males or workers at the peak of aphid abundance, ants were also classified as neutral prey. Economic classification can be seen in Data S1 (can be found as an online supplement to the published paper) in more detail.

Data analysis

All statistical analyses were performed within the R (v.3.5.3.) statistical environment (*R Core Team, 2019*). For all analyses, the natural prey data were pooled across orchards and years (see later), except for the comparison of actual and potential prey where only the data collected at the same place (Újfehértó) and in the same years (2016-2017) were analysed.

(1) Comparison of actual versus potential prey: Generalised Linear Mixed Models with binomial error structure (GLMM-b) (*Pekár & Brabec, 2016*) were used to compare the relative frequency of prey taxa or economic groups between the actual and potential prey. For these analyses, abundance data in each prey category were pooled for each season (spring, summer and fall) regarding the given year (2016 or 2017). In the model, the response variable was a matrix (*Pekár & Brabec, 2016*) containing the abovementioned seasonal counts of a given prey category, and the difference of these seasonal counts and the seasonal sums of all actual or potential prey counts for the given year. Prey taxa, their economic status, prey type (actual vs. potential), season, and year were entered in the model as fixed factors and the interactions were calculated (Prey taxa/Economic status × Prey type, Prey taxa/Economic status × Season and Prey taxa/Economic status × Year). The model included an observation level random effect to avoid overdispersion. Significant interaction (e.g., between Prey taxa and Prey type) implies that hunting spiders select

prey disproportionately. Model contrasts for the prey types within each prey categories were computed separately using the R package 'emmeans' (*Lenth et al., 2020*). For the raw data of the previous analyses, see Data S2 (can be found as an online supplement to the published paper).

To assess the degree of selectivity shown by spiders, Ivlev's electivity indices (IE) were computed based on the relative abundances of the actual and potential prey categories (collected in Újfehértó 2016-2017). To filter out the effect of year, first, the index values were calculated for each year and prey category (taxonomic or economic), and then mean index values were calculated. For economic categories, the abundances were calculated as sums of all prey items belonging to the given category. The IE values range between -1 and +1, where negative and positive values indicate negative and positive prey selection relative to prey availability in the environment, respectively (*Cock, 1978*).

(2) Comparison of spider and prey composition on temporal and spatial scale: The accuracy of our hand sampling method was evaluated and the selectivity in spider predation was examined from another perspective as well. For this, a Mantel test based on Morisita dissimilarity distance was performed to calculate the correlation between the matrices of monthly abundance of the six spider groups in hand-collected versus suction samples (Újfehértó, 2016/2017, see Table S2.3) and between the matrices of monthly abundance of actual versus potential prey groups (Újfehértó, 2016/2017, see Table S2.4) using the 'vegdist' function of the R package 'vegan' (*Oksanen et al., 2019*) and the 'mantel' function of the R package 'ecodist' (*Goslee & Urban, 2019*). The same method was used to compare the abundances of the actual prey groups for the six most abundant spider taxa in Újfehértó, 2016/2017 with those from other sites or years (see Table S2.5). For further statistics, the data from Újfehértó 2016/2017 were pooled with the rest of the observations (as noted in Results).

(3) Food web metrics, niche width and niche overlap: To compare the trophic characteristics of the six most abundant spider taxa, specialisation metrics (a measure of stenophagy), trophic niche width, and degree of niche overlap were calculated based on the taxonomic composition of the spiders' prey (see the upper part of the Table S2.6). Food web specialization was calculated at both the network and species level (*Blüthgen et al., 2006*). Web specialization (H_2') was calculated using 'H2fun' function, while species-level specialization (d') was calculated for the six spider taxa using the 'dfun' function of the R package 'bipartite' (*Dormann et al., 2020*). The values of these quantitative, frequency-based specialization metrics range from 0 to 1, where 0 corresponds to total generalization and 1 corresponds to extreme specialization (*Blüthgen et al., 2006*). To estimate the trophic niche breadth Levins' index (B) (*Krebs, 1999*) was calculated using the R package 'spaa' (*Zhang, 2016*). Niche overlap indices

(*NOs*) between the six spider taxa based on prey taxonomic composition (categorical data) and prey size (log-transformed continuous data) were calculated using the script provided by *Geange et al. (2011)*. Null models with 10 000 permutations were used for each niche dimension (taxonomic, size and overall) to test the possible differences between the occupied niches of the hunting spider groups (*Geange et al., 2011*). Bonferroni correction was used to avoid the errors of multiple comparisons. 1– *NOs* as a distance measures were used to visualise differences among spider groups in their niches with multidimensional scaling (MDS) (*Geange et al., 2011*) using 'monoMDS' function of the R package 'vegan' (*Oksanen et al., 2019*). Levins' *B* ranges from 1 to *n*, where *n* is the total number of resource states and 1 corresponds with maximum specialization, while *NO* ranges from 0 to 1 where 1 corresponds with complete overlap (*Krebs, 1999; Geange et al., 2011*). As prey availability data were not available for every year and orchard, they were not involved in the above-mentioned measures.

(4) Comparison of prey composition of spider groups using fourth-corner analysis: The 'fourth-corner analysis' is an adequate multivariate technique for testing relationships between abundance data and species or other environmental trait matrices (*Dray & Legendre, 2008; Brown et al., 2014; Comay & Dayan, 2018*). The analysis provides coefficients indicating the strength of the association between each pair of traits and tests for significance using a permutation test (*Dray & Legendre, 2008; Brown et al., 2014*). In the analyses, the response variable was the abundance of the observed prey taxa, while the environmental components included species composition of the predators (i.e., spider groups) and seasonality (i.e., spring, summer, and fall). To calculate these coefficients, a LASSO-penalised regression model assuming a negative binomial distribution for model errors was applied by the 'mvabund' R package (*Wang et al., 2012*). The size of a coefficient reflects the relative importance of the given interaction, i.e., how a coefficient changes the slope of the relationship between abundance and a given environmental variable. A spider group (or season) and a prey taxon was considered as either negatively or positively associated if the absolute value of the coefficient was greater than 0.03.

(5) Analyses of the predator-prey size relationship and the variation in body size: To analyse the spider-prey size relationship, GLMs with gamma error structure and log-link (GLM-g) were used due to the Gamma distribution of the prey thorax widths (*Michalko & Pekár, 2015; Pekár & Brabec, 2016*). As a new variable, the thorax-prosoma (i.e., prey-predator) size ratio (prey thorax width divided by spider prosoma width) was computed in each possible spider-prey pair (if data was available). After that, the variation of the taxa-specific body traits, the predator prosoma width, prey thorax width and thorax-prosoma ratio were analysed separately by Linear Models (LMs). In all models, the body trait was the response variable, while the spider group, season and

prey taxa were entered as predictor variables. The body size variables were log-transformed to approach normal distribution. Special attention was paid to the life-stage-specific differences in two spider species (*C. xanthogramma* and *Ph. cespitum*), given both species were collected in large numbers. Within both species, the individuals were grouped into two life-stages, juveniles and adults (i.e., adult and subadult individuals). In adults, the data of different sexes were pooled for both species, because there were no sex-specific differences in the investigated morphological traits (i.e., prey thorax width: *C. xanthogramma*: $t = -0.315$, df = 75.406, $P = 0.753$; *Ph. cespitum*: $t = 1.646$, df = 45.803, $P = 0.107$; thorax-prosoma ratio: *C. xanthogramma*: $t = -0.878$, df = 65.904, $P = 0.383$; *Ph. cespitum*: $t = 0.973$, df = 39.225, $P = 0.337$). The following model structure was run in both species, separately: the log-transformed thorax-prosoma ratio was the response variable, while the Life-stage (i.e., juvenile and adult), Prey taxa and Season (spring, summer and fall) were the predictor variables (as factors). For testing the post-hoc contrasts, Welch's t-test with the Holm's correction (to avoid the errors of multiple comparisons) was used.

To compare the widths of the niches with respect to prey size between the different arboreal hunting spider groups or between the life stages of *C. xanthogramma* and *Ph. cespitum*, the variances (S^2) in prey-predator size ratios were computed (as *Michalko & Pekár, 2015*). To compare variances, Levene's test was used. This test tolerates a slight deviation from a normal distribution (*Reiczigel et al., 2018*), and thus, the data were not transformed to avoid the false interpretation of the results, because transformation might have affected the variability of our data (*Feng et al., 2014*). In the case of multiple comparisons, the *P*-values of Levene's test were adjusted using Holm's correction.

Results

A total of 878 hunting spider individuals, belonging to 29 species and seven families, were collected with identifiable prey in their chelicerae from the canopy of apple trees between 2013 and 2019 (Table S2.1). The most abundant spider taxa/groups in decreasing order were *C. xanthogramma*, *Ph. cespitum*, *Clubiona* spp., Other salticids, *E. tricuspidata* and *Xysticus* spp., which accounted for 89% of all spiders in the dataset (Table S2.2). Approximately 0.8–1.2 spiders with a prey item in the chelicerae were collected per person-hour, and 34, 46 and 20% of the individuals were collected in the morning, afternoon and after sunset, respectively. Species of Sternorrhyncha, Brachycera and Nematocera together accounted for 66.5% of the total prey of the hunting spider assemblage, and spiders most frequently (54%) preyed upon arthropods that were irrelevant to pest management (neutral prey) (Fig. 2.1, Table S2.7). Aphids and spiders were preyed upon to the greatest extent within the pest and natural enemy groups, respectively (Table S2.8-S2.9). In contrast, none of the hunting spiders collected in this study preyed on larvae or adults of codling moth [*Cydia pomonella* (L.)], the key pest of apple in Europe. Two salticid individuals (one each of *C. xanthogramma* and *Heliophanus* sp.) were observed to feed on lacewing eggs. For the monthly abundance count of spider and prey groups see Table S2.3 and S2.4. For the total hunting spider assemblage, prey size was significantly related to spider size (GLM-g, $F_{1,647} = 235.74$, $P < 0.001$, $R^2 = 0.23$), with the average prey thorax width and spider prosoma width being 1.13 and 1.72 mm, respectively, while the average prey-predator size ratio was 0.67 (SD: 0.34) (see Fig. S2.1).

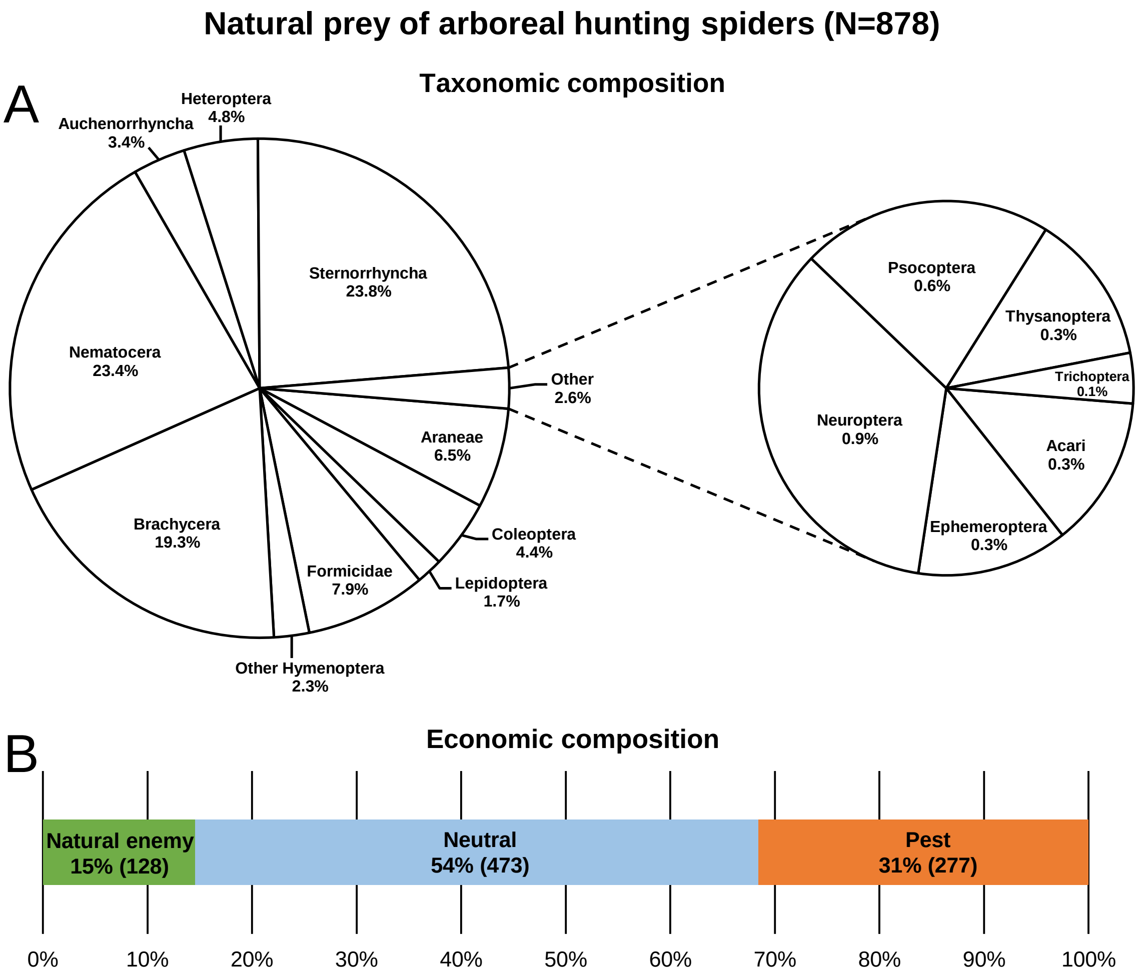

Figure 2.1: Natural prey (N=878) of arboreal hunting spiders collected in apple orchards. Taxonomic (**A**) and economic (**B**) composition.

Comparison of actual and potential prey

In the apple orchard located in Újfehértó in 2016 and 2017 the seasonal composition of hand-collected spiders (with prey) and suction-sampled spiders correlated (Mantel's r = 0.605, P = 0.004), which showed that our hand-collected sample represented well the total hunting spider assemblage in the canopy. However, the Mantel test showed no correlation between the seasonal composition of actual (held in the chelicerae) and potential (suction-sampled) prey groups (r = 0.013, P = 0.957) (for the raw matrices, see Table S2.3-S2.4). This suggests that the composition of actual prey was not strongly driven by the composition of potential prey. In accordance with this finding, the relative frequencies of actual prey groups differed significantly from those of potential prey [GLMM-b, Prey taxa vs. Prey type (actual vs. potential) interaction: LRT_{10} = 37.680, $P < 0.001$], demonstrating that hunting spiders, as a community, showed selectivity in their diet. Brachycera and Nematocera were captured significantly more (GLMM-b, contrasts, $P = 0.002$ and $P = 0.025$, respectively), while Coleoptera was captured significantly less (GLMM-b, contrast, $P < 0.001$) frequently than their abundance would suggest (Fig. 2.2-2.3, Table S2.10).

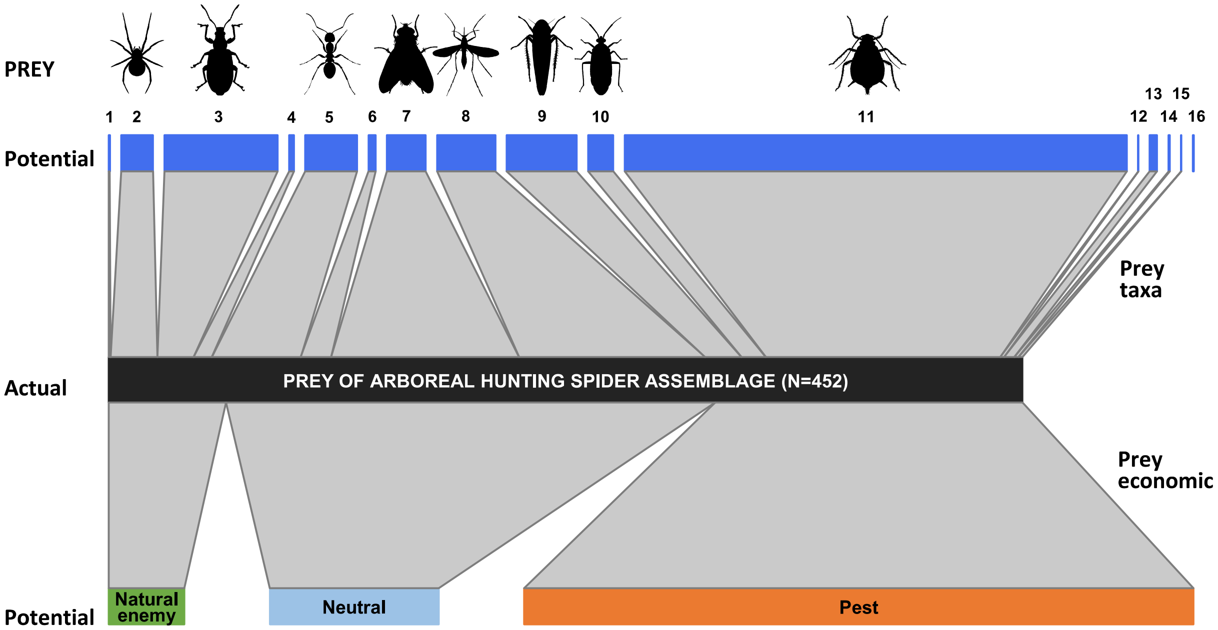

Figure 2.2: Trophic link structure for the arboreal hunting spider assemblage (middle bar) and its prey (upper and lower bars) at Újfehértó, Hungary, 2016-2017. Trapezoids connecting the bars show the frequency of prey categories in the natural diet of the spider assemblage (actual prey, N=452; center of connector) and in the canopy of apple trees (potential prey, N=11421; upper and lower end of connectors). Non-parallel sides in a trapezoid suggest selectivity in spiders predation on the focal prey category, with an outward tapering trapezoid suggesting an overrepresentation and an outward widening trapezoid suggesting underrepresentation of the given taxon or economic group in the diet of spiders. Note that the figure based on the two years sum of actual and potential prey items. Numbers refer to following prey taxa: **1** Acari, **2** Araneae, **3** Coleoptera, **4** Lepidoptera, **5** Formicidae, **6** Other Hymenoptera, **7** Brachycera, **8** Nematocera, **9** Auchenorrhyncha, **10** Heteroptera, **11** Sternorrhyncha, **12** Ephemeroptera, **13** Neuroptera, **14** Psocoptera, **15** Thysanoptera, **16** Other prey items.

Lepidoptera, Other Hymenoptera and Sternorrhyncha were marginally significantly, positively selected and Auchenorrhyncha was marginally significantly, negatively selected by spiders, while Araneae, Formicidae, Heteroptera and Other prey taxa were preyed proportionally to their availability (Fig. 2.2-2.3, for GLMM-b contrasts, see Table S2.10). Brachycera had the highest Ivlev's index value, while Coleoptera had the lowest value of the Ivlev's index being our measure of selective predation (Fig. 2.3, Table S2.10). The relative frequencies of prey groups differed significantly among seasons (GLMM-b, Prey taxa × Season interaction: $\text{LRT}_{20} = 83.765$, $P < 0.001$), but not among years (GLMM-b, Prey taxa × Year interaction: $\text{LRT}_{10} = 12.846$, $P = 0.232$).

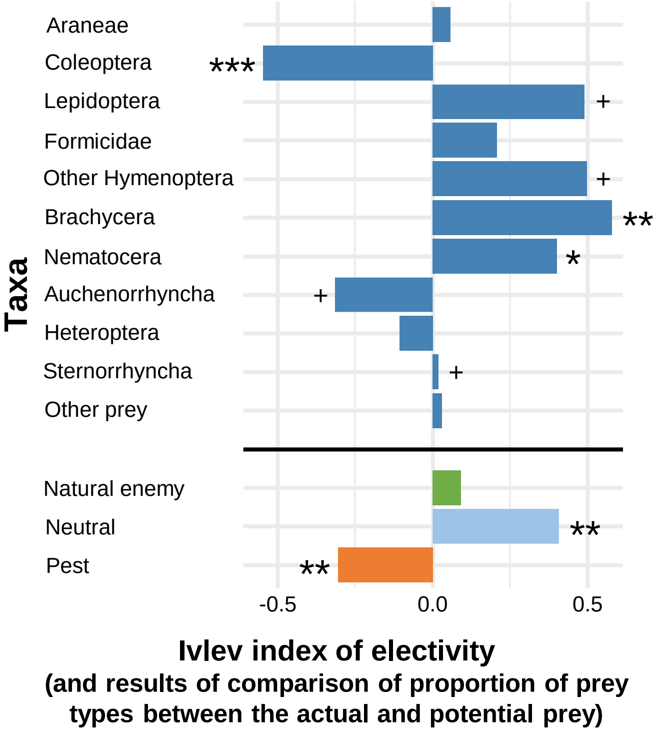

Figure 2.3: Ivlev's electivity index for the arboreal hunting spider assemblage, Újfehértó, Hungary, 2016-2017. Two-year means of the index values. In the given group asterisks indicate significant (* = P <0.05, ** = P <0.01, *** = P <0.001) or marginally significant ($^{+}$ = P <0.1) deviation between spider diet and relative abundance of potential prey based on model contrasts. For the indices and P values see Table S2.10.

Considering the economic status of prey species, the proportions of the categories in the actual prey differed significantly from the potential prey [GLMM-b, Prey status × Prey type (actual vs. potential) interaction: $\text{LRT}_{2} = 15.286$, $P < 0.001$, Fig. 2.2-2.3, Table S2.10]. We found that the actual prey of arboreal hunting spiders consisted of proportionally more neutral prey, and fewer pest individuals (GLMM-b, both contrast $P = 0.002$), as compared with the relative abundance of potential prey (Fig. 2.3, Table S2.10). Natural enemies were preyed proportionally to their availability (Fig. 2.3, Table S2.10). The diets of all hunting spider groups show a similar pattern (Fig. 2.4). Based on the Ivlev's index, four out of the six spider taxa selected natural enemies positively (Fig. 2.4). The proportions of the economic categories differed marginally between seasons (GLMM-b, Prey status × Season interaction: $\text{LRT}_{4} = 9.427$, $P = 0.051$) without difference between years (GLMM-b, Prey status × Year interaction: $\text{LRT}_{2} = 3.284$, $P = 0.194$).

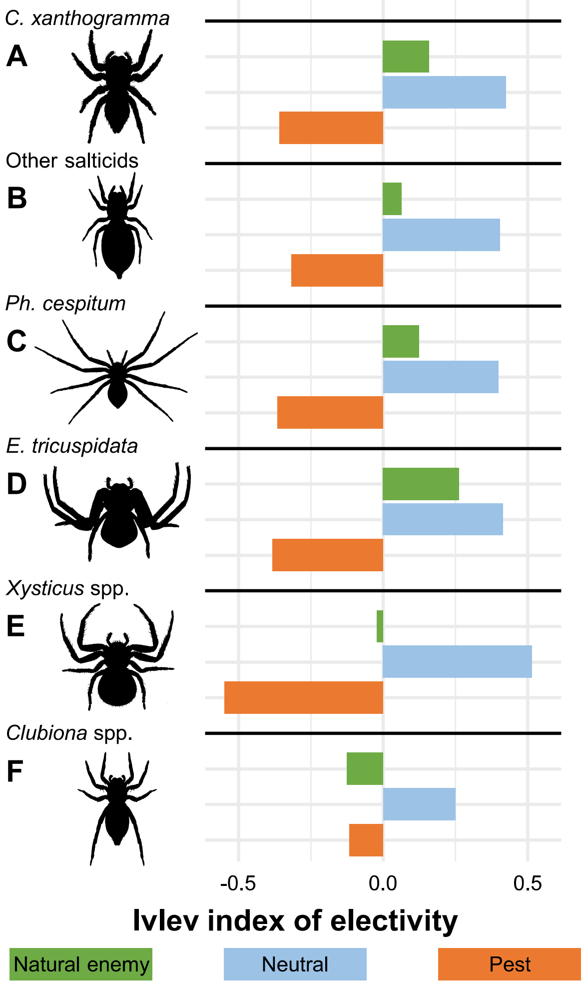

Figure 2.4: Ivlev's electivity index for arboreal hunting spider groups, Újfehértó, Hungary, 2016-2017. Two-year means of the index values. N = 214, 26, 73, 24, 22 and 57 for (**A**) *C. xanthogramma*, (**B**) Other salticids, (**C**) *Ph. cespitum*, (**D**) *E. tricuspidata*, (**E**) *Xysticus* spp. and (**F**) *Clubiona* spp., respectively.

Food web metrics, niche width and niche overlap

For further analyses, we focused only on the most abundant hunting spider groups. As the abundances of the actual prey groups for the six most abundant spider taxa at Újfehértó, 2016/2017 were correlated (Mantel's r = 0.515, P = 0.003) with those from other sites or years (see Table S2.5), the data were pooled across all sites and years. Figure 2.5 shows the trophic interactions between the spider groups and the canopy-dwelling arthropod community for the whole growing season. Overall, considering each group's abundance, the highest predation pressure for most prey groups (Araneae, Formicidae, Other Hymenoptera, Brachycera, Auchenorrhyncha, Heteroptera and Sternorrhyncha) was imposed by *C. xanthogramma*. Most nematoceran prey were consumed by *Ph. cespitum*, while coleopterans were preyed on mainly by *Xysticus* spp. In addition, *Ph. cespitum* and *Clubiona* spp. exerted a high predation pressure on Sternorrhyncha, and *Xysticus* spp. did so on Formicidae (Fig. 2.5). The majority of natural enemies were consumed by *C.*

xanthogramma, and the diets of *Ph. cespitum* and *Clubiona* spp. had the highest number of pests relative to the number of captured natural enemies (Fig. 2.5, for the raw data of the food-web, see Table S2.6). The seasonal abundance of the spider and potential prey groups, and therefore the food web structure, showed significant seasonal change (Fig. S2.2-S2.4). While *Ph. cespitum* was the most abundant hunting spider species in spring, *C. xanthogramma* dominated in summer and fall. Brachycera, Nematocera, and Sternorrhyncha were the most abundant prey groups in spring, summer, and fall, respectively (Fig. S2.2-S2.4).

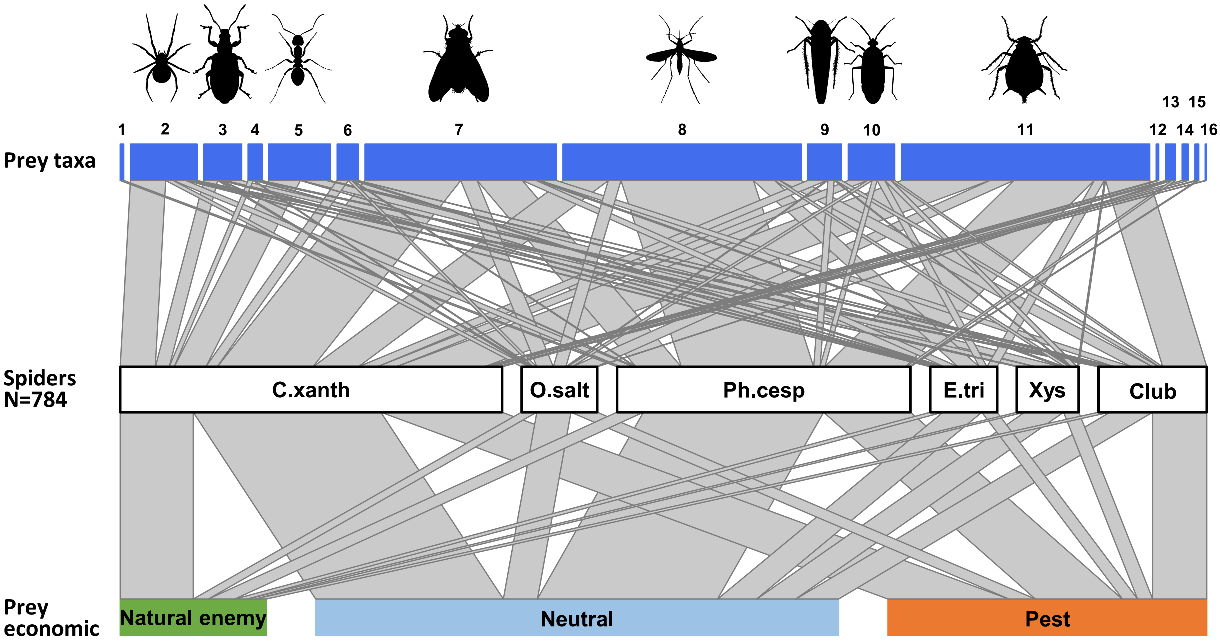

Figure 2.5: Trophic interactions between the most abundant hunting spider groups and the arthropod community in the canopy of apple trees. Whole growing season, N=784. The middle bars represent spider groups and upper and bottom bars represent the spiders' prey divided taxonomically and according their economic status. The width of the links between the trophic levels depict the frequency of interactions and bar widths indicate the relative abundance of each category. Numbers refer to following prey taxa: **1** Acari, **2** Araneae, **3** Coleoptera, **4** Lepidoptera, **5** Formicidae, **6** Other Hymenoptera, **7** Brachycera, **8** Nematocera, **9** Auchenorrhyncha, **10** Heteroptera, **11** Sternorrhyncha, **12** Ephemeroptera, **13** Neuroptera, **14** Psocoptera, **15** Thysanoptera, **16** Trichoptera; Spiders: **C.xanth** = *Carrhotus xanthogramma*, **O.salt** = Other salticids, **Ph.cesp** = *Philodromus cespitum*, **E.tri** = *Ebrechtella tricuspidata*, **Xys** = *Xysticus* spp., **Club** = *Clubiona* spp.

Food web specialization (H_2') was the highest in spring and the lowest in summer (Table 2.1). In general, hunting spiders were found to be generalists as their species-level specialization (d') was low (values are mostly close to 0) and their trophic niche breadth (B) was wide. *Xysticus* spp., followed by *Ph. cespitum,* was the most specialised (most stenophagous) group and, in accordance with this, had the narrowest niche breadth (Table 2.1).

Table 2.1. Trophic niche width (*B*) and specialization metrics (*d'* and *H_2'*) for hunting spider groups.

	Carrhotus xanthogramma	Other salticids	*Philodromus cespitum*	*Ebrechtella tricuspidata*	*Xysticus* spp.	*Clubiona* spp.
Levins' niche breadth (B)						
Whole season	6.512	5.158	3.275	5.231	3.842	4.183
Predator specialization (d')*						
Whole season	0.074	0.045	0.186	0.065	0.397	0.066
Spring	0.262	0.075	0.211	0.048	0.582	0.186
Summer	0.043	0.157	0.139	0.094	0.326	0.060
Fall	0.142	0.161	0.200	0.212	0.449	0.097
Food web specialization (H_2')*						
Whole season			0.142			
Spring			0.256			
Summer			0.130			
Fall			0.190			

*Specialization indices range from 0 for extreme generalization to 1 for extreme specialization.

Considering the taxonomic composition of their prey, spider groups exhibited a relatively high level of trophic niche overlap ($0.61 < NO$ in all comparisons), except for *Xysticus* spp., which had a relatively distinct prey composition ($NO < 0.39$ in all comparisons) (Fig. 2.6A, Table S2.11). The highest levels of niche overlap ($0.73 \leq NO$) were observed between the following group pairs: *C. xanthogramma* and Other salticids, *Clubiona* spp. and Other salticids, and *E. tricuspidata* and Other salticids (Fig. 2.6A, Table S2.11). Spider groups displayed significant clustering in their distribution across niche space with respect to taxonomic composition of their prey (null model: 10 000 permutations, $P < 0.001$, Fig. 2.6A, Table S2.11). In contrast, spider groups exhibited a high level of niche overlap ($0.72 \leq NO$ in all comparisons) without significant clustering across niche space with respect to size of their prey (null model: 10 000 permutations, $P = 0.135$, Table S2.11). When we considered both niche dimensions combined (taxonomic identity and prey size), the realized niches of the spider groups clustered in niche space (null model: 10 000 permutations, $P < 0.001$, Fig. 2.6C, Table S2.11). Although the overall niche overlap between spider groups remained relatively high (between 0.51 and 0.85, Table S2.11), we found significant differences in 11 out of 15 pairwise comparisons (Fig. 2.6C). For the detailed niche overlap indices and pairwise comparisons see Table S2.11 and S2.12.

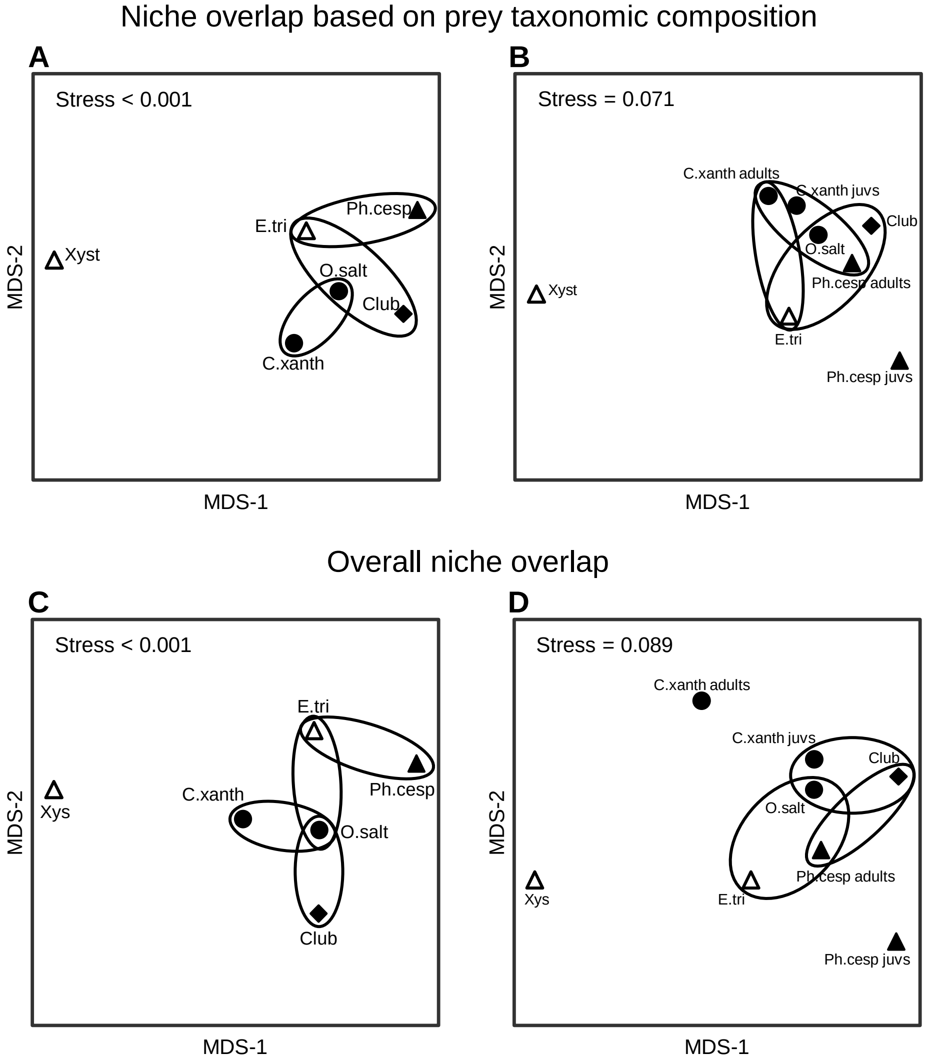

Figure 2.6: Trophic niche overlap between the most abundant arboreal hunting spider groups in apple orchards. Interspecific similarities in niche overlap based on taxonomic composition of spiders' natural prey (**A** and **B**) and on two functional traits (**C** and **D**): (1) taxonomic composition of natural prey and (2) prey size. (**A**, **C**) the six most abundant spider groups; (**B**, **D**) the same but *C. xanthogramma* and *Ph. cespitum* were split to juveniles (all juvenile stages) and adults (subadults and adults). Similarities are represented graphically as multi-dimensional scaling. Ellipses encircle species occupying niches that were not identified as significantly different using null model tests. Different marks and fill indicate different guilds: circle - stalkers, triangle - ambushers, square - foliage runners (based on guild classification by *Uetz et al., 1999*); empty marks - ambush hunters, solid marks - other hunters (based on guild classification by *Cardoso et al., 2011*). Spiders: **C.xanth** = *Carrhotus xanthogramma*, **O.salt** = Other salticids, **Ph.cesp** = *Philodromus cespitum*, **E.tri** = *Ebrechtella tricuspidata*, **Xys** = *Xysticus* spp., **Club** = *Clubiona* spp.

Fourth-corner analysis of spider-prey associations

Fourth-corner analysis revealed that the variables Spider groups (GLM-nb, $Dev_{12,5}$= 148.95, P = 0.01) and Season (GLM-nb, $Dev_{10,2}$= 82.01, P = 0.005) significantly contributed to the prey selection by spiders. Furthermore, the interaction between Spider groups and Season also explained a significant amount of variance in prey abundance (GLM-nb, $\mathrm{Dev}_{0,10}$= 216.97, P = 0.001). Coefficients for the significant predictors of prey abundance are depicted in Fig. 2.7 and the exact values are shown in Table S2.13.

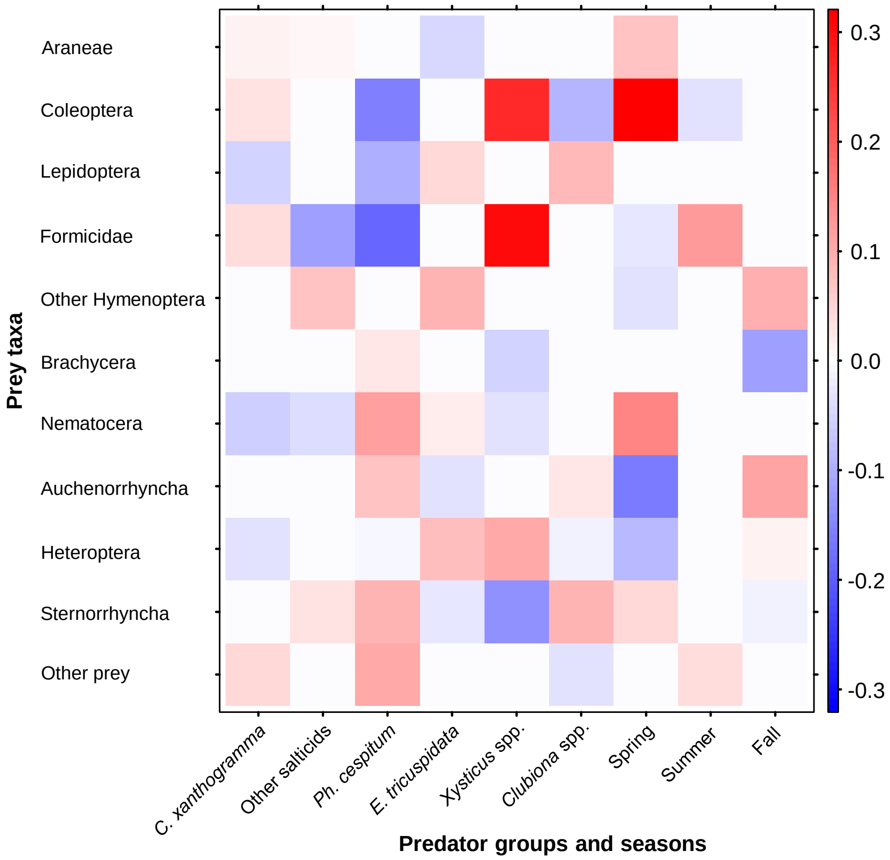

Figure 2.7: Fourth-corner analysis, including standardised coefficients of prey taxa vs. spider groups and seasonal predictors (GLM model-based approach with LASSO penalty). Darker colors indicate stronger associations than paler ones; positive associations are indicated by red, negative associations are indicated by blue color. For the coefficients see Table S2.13.

Prey taxa varied in their abundance across spider groups and within the growing season. Taking into account the differences in total and seasonal abundances we found that, as compared to the other spiders, *C. xanthogramma* was positively associated (PA) with the prey groups Formicidae (almost exclusively winged males) and Coleoptera and negatively associated (NA) with Nematocera, Lepidoptera, and Heteroptera. Similar selectivity was observed in other spider groups as well: Other salticids (PA: Other Hymenoptera, Sternorrhyncha; NA: Formicidae, Nematocera), *Ph. cespitum* (PA: Nematocera, Sternorrhyncha, Auchenorrhyncha; NA: Formicidae, Coleoptera, Lepidoptera), *E. tricuspidata* (PA: Other Hymenoptera, Heteroptera, Lepidoptera; NA: Araneae, Auchenorrhyncha), *Xysticus* spp. (PA: Formicidae, Coleoptera, Heteroptera; NA: Sternorrhyncha, Brachycera, Nematocera), *Clubiona* spp. (PA: Sternorrhyncha, Lepidoptera; NA: Coleoptera) (Fig. 2.7). The coefficient matrix also indicates significant seasonal variation in predation of certain prey taxa (e.g., Araneae, Coleoptera, Nematocera, Auchenorrhyncha) throughout the season (Fig. 2.7).

Intraguild differences and interguild similarities

Based on the guild classification of *Uetz et al. (1999)*, marked intraguild differences [*Ph. cespitum* vs. *Xysticus* spp. and *E. tricuspidata* vs. *Xysticus* spp. (null model: 10 000 permutations, $P < 0.001$ in both comparisons)] and high interguild similarities (*E. tricuspidata* vs. Other salticids, Other salticids vs. *Clubiona* spp. and *E. tricuspidata* vs. *Clubiona* spp.) were found in the composition (taxonomic or taxonomic + size) of natural prey (Fig. 2.5-2.6, Table S2.11). Prey preferences could also differ within a guild [e.g., in ambushers (*Ph. cespitum* vs. *E. tricuspidata* vs. *Xysticus* spp.), Fig. 2.7]. Based on the guild classification of *Cardoso et al. (2011)*, certain species also showed significant differences in their diet [*Ph. cespitum* vs. *Clubiona* spp., *C. xanthogramma* vs. *Ph. cespitum*, *C. xanthogramma* vs. *Clubiona* spp. and *E. tricuspidata* vs. *Xysticus* spp. (null model: 10 000 permutations, $P < 0.001$ in all comparisons, Fig. 2.6, Table S2.11)] or preferences (e.g., *C. xanthogramma* vs. *Ph. cespitum* or *E. tricuspidata* vs. *Xysticus* spp., respectively, Fig. 2.7) within the guilds of other hunters or ambush hunters. Furthermore, despite belonging to different guilds, *E. tricuspidata* and Other salticids or *E. tricuspidata* and *Ph. cespitum* showed no difference in trophic niche occupancy (Fig. 2.6, Table S2.11).

Predator–prey size relationships

A moderately strong exponential relationship was found between the spider and prey size for all six hunting spider groups (Fig. 2.8). Spider size differed between spider groups ($F_{5,553} = 31.543$, $P < 0.001$), seasons ($F_{2,553} = 67.337$, $P < 0.001$), and also between prey taxa ($F_{10,553} = 8.703$, $P < 0.001$). On average, *C. xanthogramma* and *Xysticus* spp. had the widest, while *Clubiona* spp. had the narrowest prosoma (Table 2.2). Prey size differed between spider groups ($F_{5,553} = 8.499$, $P < 0.001$), seasons ($F_{2,553} = 20.554$, $P < 0.001$) and between prey taxa ($F_{10,553} = 30.946$, $P < 0.001$). *Xysticus* spp. had prey with the widest, while *Clubiona* spp. had prey with the narrowest thorax (Table 2.2). The thorax-prosoma ratio differed among the spider groups ($F_{5,553} = 5.014$, $P < 0.001$), among the seasons ($F_{2,553} = 13.176$, $P < 0.001$) and among the different prey groups ($F_{10,553} = 24.222$, $P < 0.001$). Compared to their own size, *Ph. cespitum* and *C. xanthogramma* caught the smallest whereas *Xysticus* and *Clubiona* spp. caught the relatively largest prey items and the difference between the first two species and *Clubiona* spp. was significant (Fig. 2.9, Table 2.2). Furthermore, *C. xanthogramma* differed significantly from *Xysticus* spp. in niche width with respect to prey size (S^2 of thorax-prosoma ratios, Fig. 2.9).

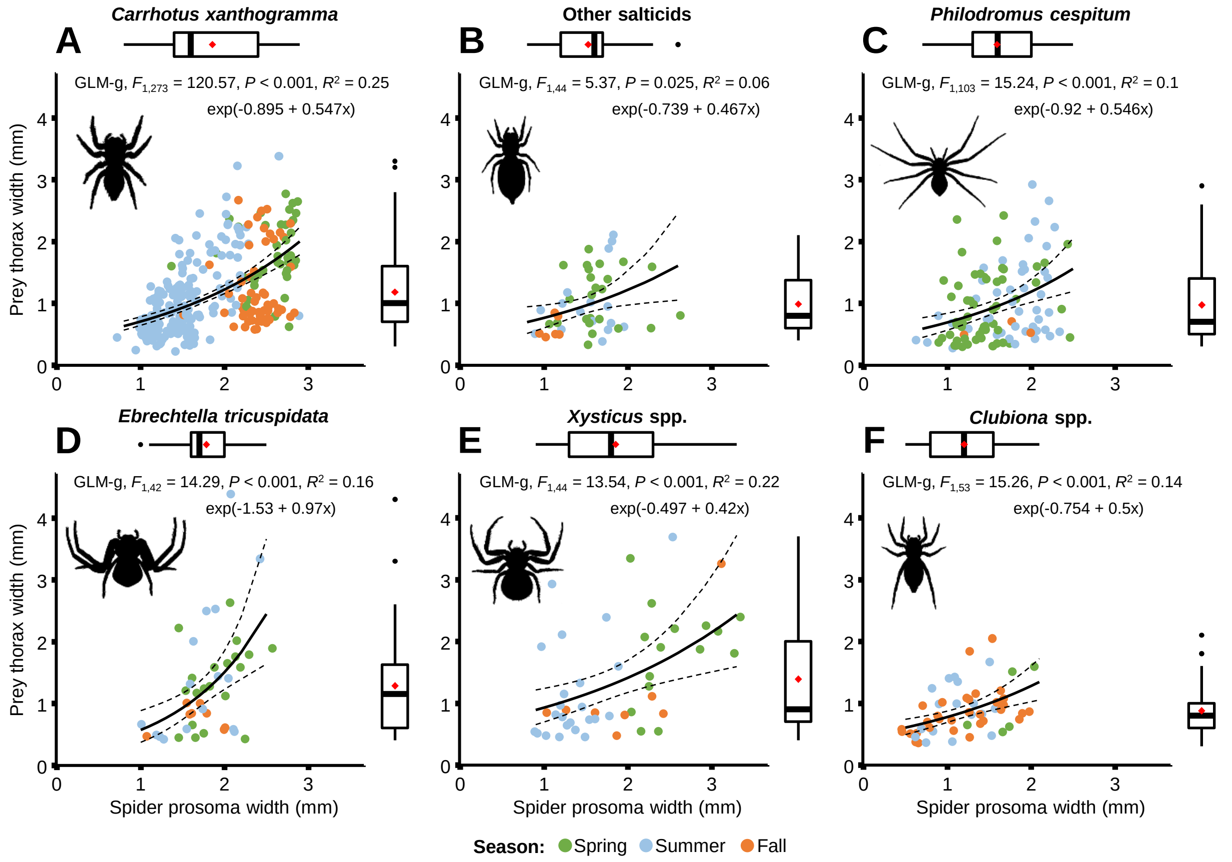

Figure 2.8: Relationship between spider and prey size (spider prosoma and prey thorax widths, jittered) for the most abundant arboreal hunting spider groups (**A**-**F**) in apple orchards. On the marginal boxplots red squares indicate means, see Table 2.2.

Table 2.2. Spider prosoma and prey thorax widths, and thorax-prosoma ratios (mean ± SD) for hunting spider groups and seasons.

Spider taxa						**Pooled**	**Season**		
Carrhotus xanthogramma	Other salticids	*Philodromus cespitum*	*Ebrechtella tricuspidata*	*Xysticus* spp.	*Clubiona* spp.		Spring	Summer	Fall
N*									
275	46	105	44	46	55	**571**	161	293	117
Spider prosoma width (mm)									
1.86 (0.56) C	1.53 (0.36) B	1.59 (0.42) B	1.78 (0.35) C	1.86 (0.68) BC	1.20 (0.43) A	**1.71 (0.55)**	1.92 (0.59) b	1.53 (0.39) a	1.89 (0.66) b
Prey thorax width (mm)									
1.18 (0.64) B	0.99 (0.49) AB	0.97 (0.61) A	1.28 (0.85) AB	1.39 (0.88) B	0.88 (0.39) A	**1.12 (0.66)**	1.30 (0.69) b	1.06 (0.66) a	1.03 (0.56) a
Thorax-prosoma ratio									
0.64 (0.28) A	0.66 (0.29) AB	0.62 (0.36) A	0.70 (0.41) AB	0.77 (0.50) AB	0.77 (0.30) B	**0.66 (0.33)**	0.68 (0.33) ab	0.69 (0.35) b	0.59 (0.27) a

Different capital letters indicate significant differences between spider groups, while different lowercase letters indicate significant differences between seasons at $P < 0.05$ level.

*Spiders with no prosoma or prey thorax width data were excluded.

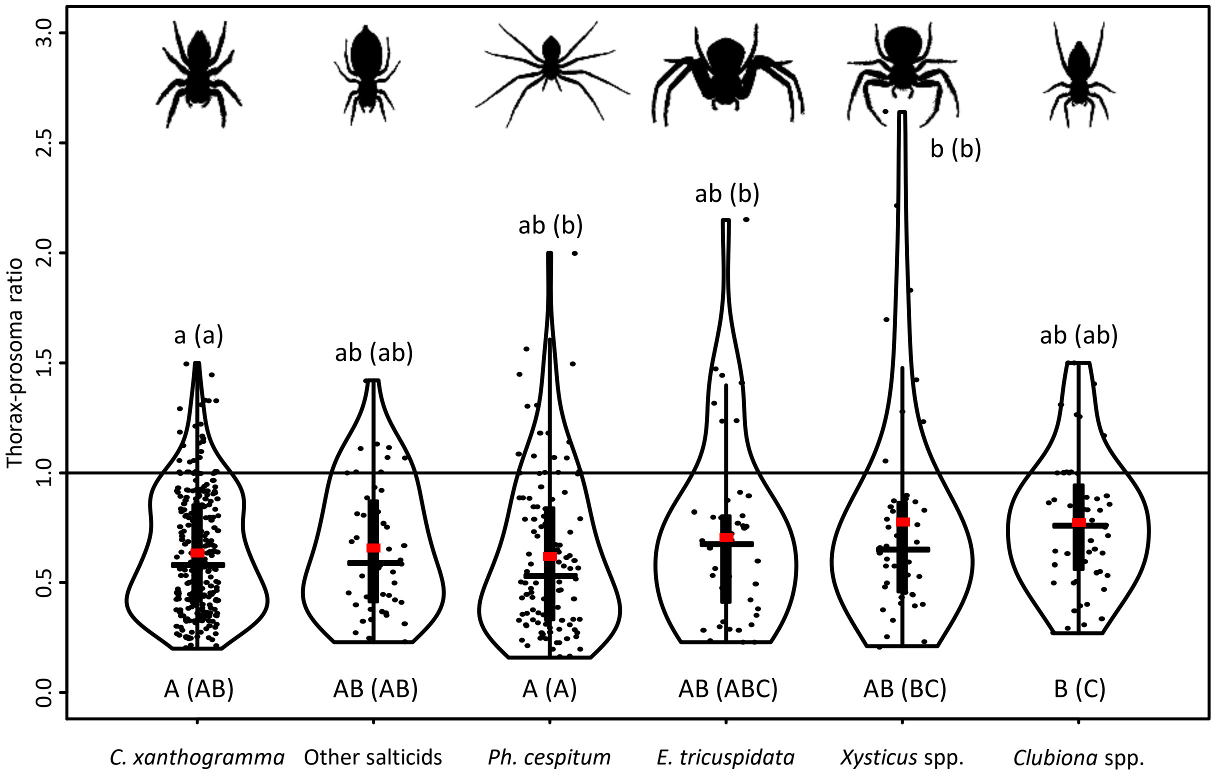

Figure 2.9: Prey-spider (prey thorax versus spider prosoma) size ratios (jittered) for the arboreal hunting spider groups. Red square – mean; black horizontal solid line – median; black vertical rectangle – interquartile range. Different capital letters indicate significant differences among means, while different lowercase letters indicate significant differences among variances at $P < 0.05$ level. Letters in parentheses refer to pairwise comparisons with unadjusted *P* values.

The size of spiders and prey items decreased from spring to summer. Spider size increased afterwards whereas prey size remained low (Table 2.2, Fig. S2.5). As a consequence, the thorax-prosoma ratio was identical in spring and summer ($P = 0.834$) and decreased in fall (compared to spring, $P = 0.054$; or summer, $P = 0.020$) (Table 2.2, Fig. S2.5). Analysed separately, the prey size was significantly related to spider size for all three main prey groups (Brachycera, Nematocera, Sternorrhyncha) (Fig. 2.10). However, the prey-predator (thorax-prosoma) size ratio was significantly different ($P < 0.001$ in all comparisons), with Brachycera being the largest prey caught by a same-sized spider, indicating that the taxonomic identity of the prey influenced the prey-predator ratio (Fig. 2.10).

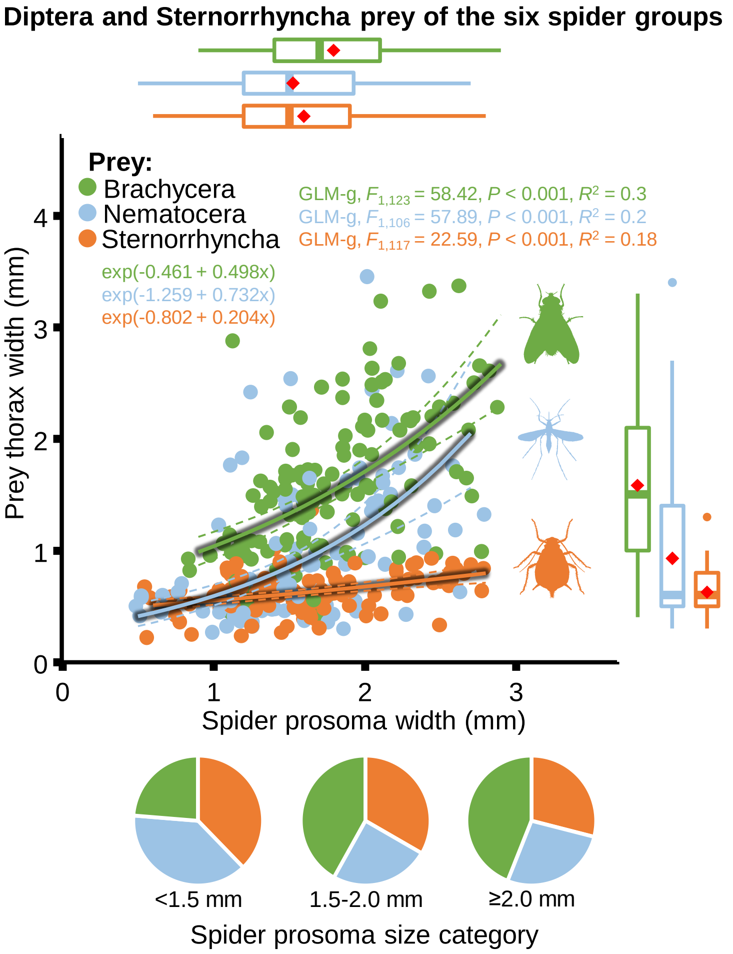

Figure 2.10: Relationship between spider and prey size (prosoma and thorax widths, jittered, N=352) for the arboreal hunting spider groups and their main prey taxa, Brachycera, Nematocera and Sternorrhyncha. On the marginal boxplots red squares indicate the mean. Pie charts show the relative frequency of the three main prey groups for three different spider size categories (N = 135, 117 and 100, respectively).

Life stages of C. xanthogramma and Ph. cespitum

Only *C. xanthogramma* and *Ph. cespitum* were collected in numbers high enough to analyse their prey in more detail. Comparing the prey of the spider life stages, the following results were obtained: *C. xanthogramma* adults had the widest trophic niche breadth (B = 6.76), followed by *C. xanthogramma* juveniles (B = 5.85), *Ph. cespitum* adults (B = 4.32) and *Ph. cespitum* juveniles (B = 2.51) (Table S2.14). Considering the taxonomic composition of their prey (Table S2.15), these four groups showed a high level of niche overlap (0.70 < NO) except for the lower overlap (NO < 0.54) between *Ph. cespitum* juveniles and both adults and juveniles of *C. xanthogramma* (Fig. 2.6B, Table S2.12). When *C. xanthogramma* and *Ph. cespitum* were split to juveniles and adults, spider groups displayed significant clustering across niche space regarding taxonomic composition (null model: 10 000 permutations, P < 0.001, Fig. 2.6B) and size of the prey (null model: 10 000 permutations, P = 0.008) and across niche space incorporating these two functional traits (null model: 10 000 permutations, $P < 0.001$, Fig. 2.6D). *Ph. cespitum* adults occupied a trophic niche different from that of juvenile conspecifics (null model: 10 000 permutations, $P = 0.001$), indicating an ontogenetic niche shift (Fig. 2.6B). Taking into account both niche dimensions (taxonomic identity and prey size), adults and juveniles of both species differed from each other in niche occupancy (*C. xanthogramma*: null model: 10 000 permutations, $P < 0.001$; *Ph. cespitum*: null model: 10 000 permutations, $P = 0.001$; Fig. 2.6D, Table S2.12).

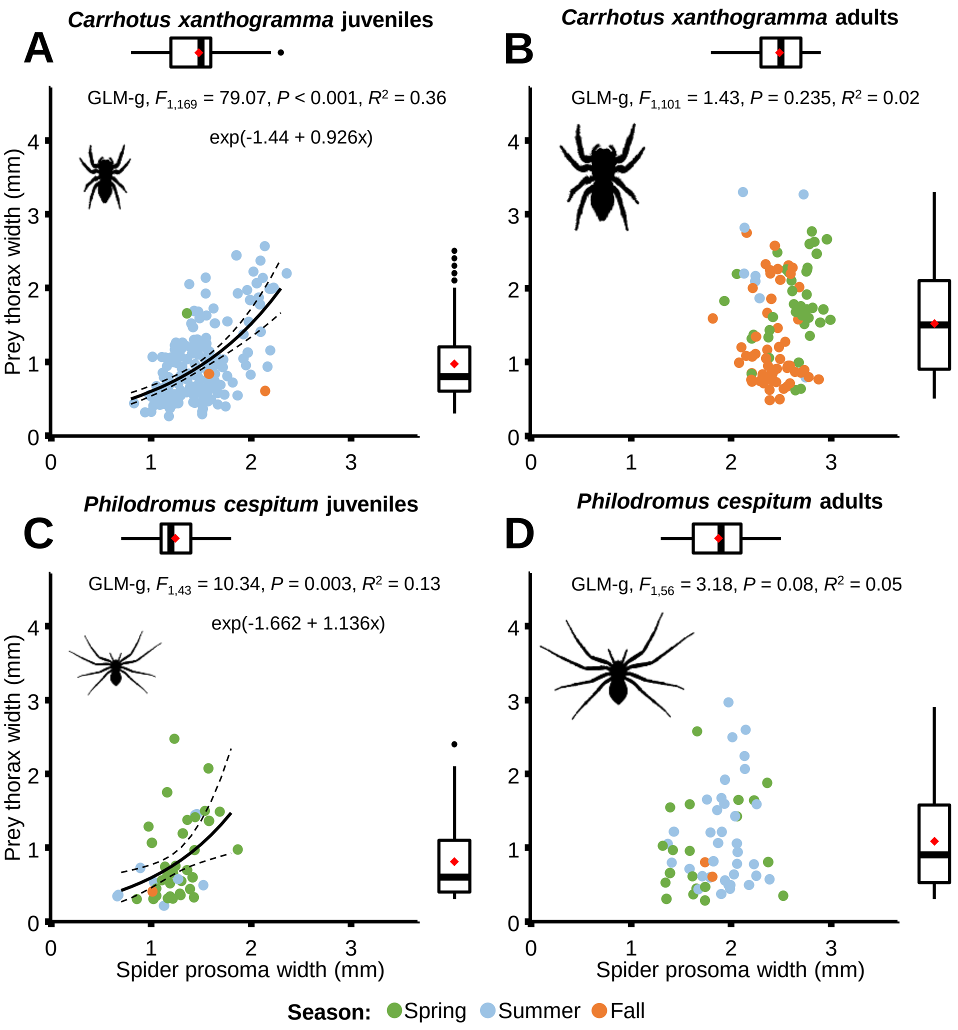

Figure 2.11: Relationship between spider prosoma and prey thorax widths (jittered) for juveniles and adults of *Carrhotus xanthogramma* (**A**, **B**) and *Philodromus cespitum* (**C**, **D**). Adults (**B**, **D**) comprise both subadult and adult individuals. On the marginal boxplots red squares indicate the mean values.

Although prey size was significantly related to spider size in both species (Fig. 2.8), different results were obtained when life stages were taken into consideration (Fig. 2.11). A significant relationship was found between predator and prey size for juveniles, but not for adults (Fig. 2.11). However, the thorax-prosoma size ratio was similar for the two life stage groups (*C. xanthogramma*: $F_{1,260} = 2.814$, $P = 0.095$; *Ph. cespitum*: $F_{1,91} = 1.288$, $P = 0.259$; Fig. S2.6), while it was different among the various prey groups (*C. xanthogramma*: $F_{10,260} = 24.133$, $P < 0.001$; *Ph. cespitum*: $F_{8,91} = 6.338$, $P < 0.001$). The three most abundant prey groups (Brachycera, Nematocera, Sternorrhyncha) differed from each other: (1) *C. xanthogramma*: Brachycera vs. Nematocera ($P < 0.001$), Brachycera vs. Sternorrhyncha ($P < 0.001$), Nematocera vs. Sternorrhyncha ($P = 0.001$) and (2) *Ph. cespitum*: Brachycera vs. Nematocera ($P < 0.001$), Brachycera vs. Sternorrhyncha ($P < 0.001$), Nematocera vs. Sternorrhyncha ($P = 0.019$) in relation to thorax-prosoma ratio, i.e. a spider of a given size mostly caught larger Brachycera prey items than those of Nematocera or Sternorrhyncha (Fig. S2.7). Among seasons, the size ratio was different for *C. xanthogramma* ($F_{2,260} = 9.776$, $P < 0.001$) but not for *Ph. cespitum* ($F_{2,91} = 0.358$, $P = 0.7$).

We found that *C. xanthogramma* adults had numerically lower size variance, while *Ph. cespitum* adults had significantly greater variance (S^2) in their size (prosoma width) compared to that in juveniles (Levene's tests: *C. xanthogramma*: $F_{1,272} = 3.319$, $P = 0.07$; *Ph. cespitum*: $F_{1,101} = 5.2$, $P = 0.025$). Adults of both species had significantly greater variance in the size of their prey (thorax width) than juveniles (Levene's tests: *C. xanthogramma*: $F_{1,277} = 19.282$, $P < 0.001$; *Ph. cespitum*: $F_{1,181} = 6.745$, $P = 0.01$). However, the variance of thorax-prosoma ratio (niche width with respect to prey size) was not different between the life stages (Levene's tests: *C. xanthogramma*: $F_{1,272} = 0.166$, $P = 0.685$; *Ph. cespitum*: $F_{1,101} = 0.252$, $P = 0.617$). For detailed data see Table S2.14.

Discussion

Based on 878 predator-prey records, we analysed the prey composition, biological control potential, and trophic interactions of arboreal hunting spiders in apple orchards. Although they were found to be polyphagous predators in general, hunting spiders selectively preyed upon canopy arthropods and the different spider species/groups differed from each other either in their diet composition or their prey size selection.

Prey composition, selectivity and efficiency in biological control

Two-thirds of the hunting spiders' prey were Sternorrhyncha, Brachycera or Nematocera (Fig. 2.1). Interestingly, these are also the main prey groups of the web-building spiders in agricultural ecosystems (*Birkhofer et al., 2018*) and are the groups most often consumed by spiders in general (*Birkhofer & Wolters, 2012; Michalko & Pekár, 2016*). Most Sternorrhyncha prey were aphids [mainly *Dysaphis plantaginea* (Passerini) and *Aphis pomi* De Geer]. Although aphids are regarded as a low-quality food (*Toft, 1995; Bilde & Toft, 2001; Toft, 2005*), they appear relatively frequently among the prey of spiders (e.g., *Alderweireldt, 1994; Harwood et al., 2005; Kerzicnik et al., 2012*). What is more, hunting spiders can contribute to aphid suppression in various agricultural habitats

(*Birkhofer et al., 2008; Boreau de Roincé et al., 2013; Lefebvre et al., 2017*). Ants [mainly *Lasius niger* (L.)] made up almost 8% of the prey of hunting spiders and comprised of both ant workers and winged males/queens. The fifth most frequent prey taxon was Araneae (e.g., theridiid or linyphiid males or other hunting spiders such as *C. xanthogramma, Ph. cespitum*), which comprised 6.5% of the total prey (Fig. 2.1). Intraguild predation is very common among hunting spiders (*Hodge, 1999; Birkhofer & Wolters, 2012; Mestre et al., 2013*) and spiders can make up to a quarter or a third of the hunting spiders' diet (*Michalko & Pekár, 2016*). Furthermore, in this study, we observed two unusual predation events: a *C. xanthogramma* and a *Heliophanus* sp. that both fed on stalked chrysopid eggs. Oophagy, although uncommon, has been found in salticids (*Nyffeler et al., 1990; Ahmed et al., 2018*), and predation on lepidopteran eggs by *C. xanthogramma* was observed by *Hirose et al. (1980).*

Some prey types were consumed significantly more or less often by the arboreal hunting spiders than expected from their respective abundances in the environment (Fig. 2.2-2.3, Table S2.7 and S2.10), indicating that these spiders are not strict opportunists and do not feed in a frequency-dependent manner. In general, the groups Brachycera and Nematocera (and possibly Other Hymenoptera, Lepidoptera and Sternorrhyncha) were overrepresented, while Coleoptera (and possibly Auchenorrhyncha) were underrepresented in the actual prey of the hunting spider community. Selective foraging was found both in epigeal (e.g., lycosids) and arboreal (e.g., philodromids) hunting spiders (*Michalko & Pekár, 2015; Whitney et al., 2018; Eitzinger et al., 2019*).

Hunting spiders preyed mostly (54% of the diet) on arthropods irrelevant to pest management in apple orchards in Central Europe such as Brachycera (excluding hoverflies), Nematocera, and Formicidae (Fig. 2.1). They also consumed a significant number (31%) of pests, e.g., aphids, *Phyllobius* spp. (Coleoptera: Curculionidae), *Metcalfa pruinosa* (Say) (Auchenorrhyncha: Flatidae), and psyllids, (Table S2.8) although some of these apple-feeding arthropods are considered only minor pests of apple in Hungary (e.g., *M. pruinosa*). The rest of the prey (15% of the diet) was made up of natural enemies such as spiders, zoophagous bugs, parasitic wasps, hoverflies and lacewings (Table S2.9).

The hunting spider assemblage showed the highest selectivity (positive preference) for neutral prey species, and spiders preyed on pests less than would be expected based on their availability in the canopy of apple trees (Fig. 2.2-2.4). Natural enemies were caught more often (but not significantly so) than their abundance would suggest. This implies that hunting spiders exerted a relatively lower predation pressure on pests than on neutral prey or even on natural enemies. The presence of alternative prey has been shown to disrupt biological control provided by generalist predators (e.g., *Koss & Snyder, 2005*), and in agreement with these findings, our results suggest that hunting spiders can easily switch from pests to neutral (or beneficial) prey hampering the effectiveness of conservation biological control in apple orchards. Although generalist predators (single species or assemblages) can reduce pest numbers (*Symondson et al., 2002*), intraguild predation often disrupts their action as biological control agents of herbivores (*Rosenheim et al., 1995; Rosenheim, 1998*) for example, in the case of unidirectional intraguild predation, where the intermediate predators (e.g., zoophagous bugs, parasitic wasps, hoverflies and lacewings) are more effective at suppressing the target prey (aphids) than the top predators (spiders) (*Vance-Chalcraft et al., 2007*). As spiders made up almost 45% of the spider-consumed natural enemies (Table S2.9), it would be difficult to calculate their negative effect on the biological control of pests. Nevertheless, our results suggest that, similar to several multi-enemy systems, hunting spider assemblages in general may often be unable to augment the pest suppression ability of local natural enemies, but instead reduce the overall predation pressure on pests via intraguild predation (*Rosenheim et al., 1993; Yasuda & Kimura, 2001; Finke & Denno, 2003, 2004, 2005*). However, there are some examples where presence of alternative prey has reduced the intensity of intraguild predation (e.g., *Rickers et al., 2006*).

Specific differences in the diet and in the pest control ability

We found that different spider species exerted different levels of predation on a given prey taxon (Fig. 2.5, Table S2.6). Although these trophic interactions strongly depended on both the abundances of predator and prey species and on the season (Fig. S2.2-S2.4), the fourth-corner analysis indicated an inherent species-specific prey selection pattern among hunting spiders (Fig. 2.7, Table S2.13). This suggests some selectivity in foraging behaviour (*Nentwig, 1980; Whitney et al., 2018; Eitzinger et al., 2019*), but the influence of other species-specific factors such as microhabitat preference (*Schmitz & Suttle, 2001*), hunting strategy (*Schmitz, 2008; Liu et al., 2015; Sanders et al., 2015*) or temporal niche (*Morse, 1981; Herberstein & Elgar, 1994; Mezőfi et al., 2019*) on the prey composition also cannot be excluded.

We observed relatively high levels of niche overlap, which indicates a functional redundancy (*Roubinet et al., 2018*) within hunting spiders in the canopy of apple trees (Fig. 2.6, Table S2.11-S2.12). Food web specialization was the highest in spring and the lowest in summer (Table 2.1) and was mainly driven by the prey groups Brachycera, Nematocera and Sternorrhyncha (Fig. S2.2-S2.4). Similarly, food web specialization was higher in the early than in the late period of the growing season in barley fields and this variation was suggested to be explained by prey availability dynamics (*Roubinet et al., 2018*). Species-level specialization was also the highest in spring in four out of six spider groups (Table 2.1). Overall, *Ph. cespitum* and *Xysticus* spp. showed the highest level of stenophagy and in accordance with that the narrowest niche breadth (Table 2.1) because *Ph. cespitum* mainly preyed on Nematocera and Sternorrhyncha while the diet of *Xysticus* spp. was comprised mostly of Formicidae and Coleoptera (Fig. 2.5, Table S2.6).

The prey composition of *Xysticus* spp. was very different from that of the other spider groups (Fig. 2.6, Table S2.11). Brachycera, Nematocera, and Sternorrhyncha were all consumed by *Xysticus* spp. in much lower proportions (16%) than by the other spiders (60–88%) (Fig. 2.5, Table S2.6). In contrast to our findings, *Xysticus* spp. was reported to prey intensively on Diptera in hay meadows, *X. cristatus* on aphids in winter wheat and *X. kochi* on thrips pests in greenhouse pepper (*Nyffeler & Breene, 1990; Birkhofer et al., 2008; Zrubecz et al., 2008*). Based on these findings it seems that although we found *Xysticus* spp. to be the most stenophagous hunting spider group, it had a high level of plasticity in its use of available resources.

Fourth-corner analysis showed that spider groups discriminated among prey taxa and each spider group had a certain degree of prey preference and avoidance. On a community level, different species of spiders partly complement each other via resource partitioning: if a particular prey group was avoided by one spider group, it was usually preferred by another (Fig. 2.7, Table S2.13). For example, compared to the other spiders, Coleoptera and Formicidae prey was rejected by *Ph. cespitum* but preferred by *C. xanthogramma* and *Xysticus* spp. Similar to our results, *Michalko & Pekár (2015)* found that the *Philodromus* species they studied rejected these two types of prey. The formicid prey of *C. xanthogramma* consisted almost exclusively of winged males as salticids usually refuse dangerous ant workers as prey (*Richman & Jackson, 1992; Huseynov, 2005*) but *Xysticus* species, as in our case, consume workers frequently (*Nyffeler & Breene, 1990; Huseynov, 2014*).

It would be expected that spider species within the same guild would exhibit more or less uniform resource utilization patterns (e.g., *Luiselli et al., 1998; Michalko et Pekár, 2016*), but our results do not support this view. In the canopy level of the studied apple orchards, we found marked intraguild differences and interguild similarities in the taxonomic composition of hunting spiders' prey or in their prey preferences (Fig. 2.6-2.7). These results agree with *Mestre et al. (2013)*, who reported trophic differences between spider species belonging to the same family. Overall, we found no evidence that hunting guild consistently determines prey composition. Possibly, the guild approach fails to identify finer trophic dynamics, and thus for a more accurate understanding of spider-prey community patterns, the use of (species-specific) functional traits is needed (*Fountain-Jones et al., 2015; Sanders et al., 2015*).

Hunting spiders, among prey designated as pest, most frequently consumed aphids (Table S2.8). Among hunting spiders, *Ph. cespitum* caught the most aphids in spring (Fig. S2.2) and possibly contributed to aphid control, especially in the early season by preying upon fundatrices and their larvae (*Boreau de Roincé et al., 2013; Michalko & Pekár, 2015; Lefebvre et al., 2017*). In addition, *Ph. cespitum* also feeds on other pests (*Klein, 1988; Wisniewska & Prokopy, 1997; Ghavami, 2008; Michalko et al., 2017*). This spider remains active during winter when other predators are dormant, and consequently, it can also reduce, for example, overwintering psyllid populations (*Pekár et al., 2015; Petráková et al., 2016*). *Philodromus cespitum* is among the most abundant hunting spiders in the canopy of apple orchards both in Europe (*Bogya et al., 1999a; Pekár, 1999; Pekár & Kocourek, 2004; Markó et al., 2009*) and North America (*Miliczky et al., 2008; Sackett et al., 2008*), and in our study it consumed the second-highest number of pests (following *Clubiona* spp.), compared to the number of natural enemies it consumed (Fig. 2.5, Table S2.6). Based on the above facts, this species could possibly be one of the most effective araneid biological control agents in the canopy of fruit trees in temperate regions, especially in the orchards with reduced use of insecticides (*Řezáč et al., 2010, 2019; Michalko & Košulič, 2016*). Beside *Ph. cespitum*, *Clubiona* spp. (mostly *C. frutetorum*) exerted considerable predation pressure on aphids, especially in autumn (Fig. 2.5, Fig. S2.4). There are some examples where spiders reduced aphid infestation by catching aphids immigrating back to the orchard in autumn (*Wyss et al., 1995; Cahenzli et al., 2017*) and possibly clubionids also have a high predation potential in this context. Furthermore, according to *Madsen et al. (2004)*, the level of predation on aphids by *Clubiona lutescens* Westring is not affected by the presence of alternative prey. Clubionids may also contribute to early season aphid control (Fig. S2.2; *Boreau de Roincé et al., 2013*) and they may reduce populations of lepidopteran pests by consuming both larvae and adults (Fig. 2.7; *Bogya, 1999*). The diet of *Clubiona* spp. had the lowest proportion of natural enemies (Fig. 2.4-2.5, Table S2.6), which suggests that clubionids are more compatible with biological control than several other hunting spiders. Meanwhile, *C. xanthogramma* is one of the most common species of spiders in the canopy of pome fruit orchards in Hungary where it can dominate the arboreal spider assemblage (*Bogya et al., 1999a, 2000; Markó & Keresztes, 2014*). Due to its high abundance, it exerts strong predation pressure on several prey taxa (Fig. 2.5, Table S2.6), but as *Markó & Keresztes (2014)* previously supposed, in this study, *C. xanthogramma* was found to be a significant intraguild predator of natural enemies, especially spiders (Fig. 2.5). Beside pests, its diet was comprised of a great number of beneficial prey as well (32% vs. 19%, respectively) and according to the fourth-corner analyses it proved to be the most araneophagic species compared to the other spider taxa examined (Fig. 2.7, Table S2.13). Due to its high level of intraguild predation and low abundance in spring, *C. xanthogramma* is possibly not an effective biological control agent. As intraguild predation on spiders is widespread among generalist salticids (*Markó & Keresztes, 2014*), the arboreal spider assemblage presumably has higher pest suppression potential in apple orchards in northern Europe, where the proportion of salticid spiders in the spider assemblages is lower, than in central or southern Europe where the proportion of salticid spiders is higher (*Bogya et al., 1999b*).

Although spiders are characterized as polyphagous predators with a high level of functional redundancy (Fig. 2.5-2.6; *Foelix, 2011; Roubinet et al., 2018*), they exert different predation pressure on different arthropod groups (Fig. 2.5, Fig. S2.2-S2.4) and have their own preferences towards certain prey taxa (Fig. 2.7; *Nentwig, 1986*), which means that the degree of pest suppression depends on the taxonomic composition of the hunting spider assemblage and on the taxonomic identity of the key pests. In other way, as *Birkhofer et al. (2008)* suggested, promoting particular species (in our context, *Ph. cespitum* and *Clubiona* spp.) or particular pest-consuming functional groups might be more effective in biological control rather than enhancing predator biodiversity, as the effect of increased diversity is highly context-dependent (*Markó & Keresztes, 2014; Michalko et al., 2019a*).

Predator– prey size relationships

The size of the prey was strongly related to the size of the hunting spiders, and on average, prey size was 67% that of the spider (see Fig. S2.1). Analysed separately, there was a significant exponential relationship between the six most abundant spider taxa and their prey, with prey size being 62–77% of predator size (Fig. 2.8, Table 2.2). Prey size relates to predator size in both hunting spiders (*Nentwig, 1982; Bartos, 2011*), web-builders (*Brown, 1981; Murakami, 1983*), but many other animals (*Luiselli et al., 1998; Amundsen et al., 2003*). This relationship suggests that the size of the prey has an important role in prey selection, especially in active hunters. Hunting spiders have to optimize their energy and nutritional intake while minimizing risk and therefore prefer prey items in the 60–80% range of their own size. However, they regularly captured prey that are larger or smaller than the preferred size (Fig. 2.8). Furthermore, without taking into account the shape of the spider prosoma, different species of spiders can prefer different prey size (thorax width) relative to their own size (prosoma width): *Ph. cespitum* caught the smallest prey items compared to their body size, followed by *C. xanthogramma*, while clubionids caught the largest prey (Fig. 2.9, Table 2.2). We also found a significant difference in niche width with respect to prey size: relative to their own size, *C. xanthogramma* caught prey from the narrowest prey size range, while *Xysticus* spp. caught prey from the broadest size range, suggesting that the size of the prey is not equally important for different hunting spider species (or for different hunting strategies) when choosing prey (Fig. 2.9). Prey-predator size ratios differed not only between spider groups but also between prey taxa (Fig. 2.10, Fig. S2.7). This shows that size and taxonomic identity of the prey are not independent factors. In this study, spiders of the same size caught larger

Brachycera than they did Nematocera prey. Finally, the prey-predator size ratio differed between summer and fall. This seasonal difference could be partly explained by prey availability dynamics or by the fact that both the spiders and their prey differed in size between seasons (Table 2.2, Fig. S2.5). Nevertheless, the prey-predator size ratios observed were possibly determined not only by the preferences of spiders but to some extent by the available range of prey size in the environment (*Tsai et al., 2016*). Overall, beside taxonomic identity, the size of the prey also matters in prey selection, though its importance may vary depending on the hunting strategy or spider species.

Ontogenetic niche shifts in Carrhotus xanthogramma and Philodromus cespitum

Ontogenetic niche shifts are common in the animal kingdom (Nakazawa, 2015). Such shifts are well documented e.g., in aquatic systems (*Amundsen et al., 2003*), but are largely understudied in spiders. In general, we observed that the diet of *C. xanthogramma* adults included more Coleoptera and Auchenorrhyncha, and fewer Formicidae and Nematocera, while the diet of *Ph. cespitum* adults comprised more Brachycera and Auchenorrhyncha and fewer Nematocera than did the diet of the juveniles (Table S2.15). However, an ontogenetic niche shift in prey type and size was observed only for *Ph. cespitum*; even though the sesonal occurrence of juveniles overlapped with that of the adults (Fig. 2.11, Fig. 2.6B). In contrast, *C. xanthogramma* exhibited ontogenetic shift only in prey size, despite little seasonal overlap between the two life stages (Fig. 2.11, Fig. 2.6D). There was no difference between the life stages in prey-predator size ratio (Fig. S2.6, Table S2.14). However, we found an ontogenetic shift in the niche breadth: the adults of *C. xanthogramma* and *Ph. cespitum* preyed upon a wider taxonomic and size range of prey than did their juveniles (Table S2.14). *Bartos (2011)* studied the natural prey of another salticid, *Yllenus arenarius* Simon and obtained similar results: the prey size, when standardized relative to spider size, did not differ between life stages, but the trophic niche width increased during the course of the predator's development. A similar increase in trophic niche width with ontogeny was reported for the philodromid, *Ph. dispar* Walckenaer (*Sanders et al., 2015*). In connection to the larger variance in prey size for adults, we found significant relationship between predator and prey size only in juveniles but not in adults (Fig. 2.11; but see the marginally significant relationship in *Ph. cespitum* adults). In a web-builder spider, *Argiope amoena* L. Koch, *Murakami (1983)* found a similar relationship: both prey size and prey size range increased with the increase of the prosoma width. A simple explanation for these findings would be that the prey size of spiders is (size-specifically) upper-bounded, but not lower-bounded, and therefore the larger spiders can choose from a wider size and taxonomic range of prey.

Conclusions

By analysing a total of 878 hunting spider prey items collected from the canopy of apple trees in apple orchards in Hungary we concluded that (1) although highly polyphagous, arboreal hunting spiders forage selectively and therefore cannot be considered as entirely opportunistic predators. We found that more Brachycera, Nematocera [and possibly Other (non-formicid) Hymenoptera, Lepidoptera and Sternorrhyncha] and less Coleoptera (and possibly Auchenorrhyncha) were consumed by the hunting spider assemblage than would be expected from their abundance in the canopy of apple trees. (2) Hunting spider assemblages consume a large number of pests. However, this beneficial effect is strongly constrained by the high predation levels on natural enemies (intraguild predation) and on neutral insects (propensity to switch from pests to alternative prey). In this study, the hunting spider assemblage showed positive selection for neutral prey, neutral selection for natural enemies and negative selection for pests. (3) In trophic webs, different hunting spider taxa/groups mediate different strengths of trophic effects on different prey taxa, and the web structure changes considerably with the season. (4) The natural prey of hunting spider species is highly overlapped, showing functional redundancy in their predation. (5) Nevertheless, hunting spider species show different trophic niche occupancy, also exhibit a certain level of stenophagy (species-specific prey preference) and select prey by its taxonomic identity and size. (6) The guilds do not determine the preferred or rejected prey types consistently, thus the diet of hunting spiders classified into the same guild can be considerably different. (7) From an economic point of view, *Ph. cespitum* and *Clubiona* spp. were found to be the most effective natural enemies because of their high level of aphid (*Ph. cespitum* and *Clubiona* spp.) and Lepidoptera (*Clubiona* spp.) consumption and low level of intraguild predation. (8) The trophic niche width of *C. xanthogramma* and *Ph. cespitum* increased during ontogeny where adults prey upon a wider taxonomic and size range of arthropods than juveniles. *Ph. cespitum* exhibited an ontogenetic shift in prey type, whereas no such pattern was observed for *C. xanthogramma*.

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STUDY3: CIRCADIAN RHYTHMS IN THE LOCOMOTOR ACTIVITY OF THE SPIDERS *CARRHOTUS XANTHOGRAMMA* (SALTICIDAE) AND *PHILODROMUS CESPITUM* (PHILODROMIDAE): TEMPORAL PATTERNS AND SEXUAL DIFFERENCES

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Abstract

Circadian rhythms play an essential role in the adaptation of organisms to the environment and may show species-specific or sex-specific differences even within a closely related taxonomic group. Although spiders (Araneae) are sexually dimorphic in several morphological and behavioural features, there are very few studies on the sex-specific differences in their biological rhythms. This study evaluated the circadian rhythm in the locomotor activity of two agrobiont hunting species of spider, *Carrhotus xanthogramma* (Latreille, 1819) (Salticidae) and *Philodromus cespitum* (Walckenaer, 1802) (Philodromidae), under natural photoperiod conditions. Particular attention was paid to possible differences between the sexes in both species. We found that *C. xanthogramma* is a strictly diurnal species with a mean activity peak in the morning in both sexes and the females are more active than males. The locomotor activity rhythm of males was richer in ultradian (shorter than a day but longer than an hour) components, although the relative power of these components was negligible compared to the main, 24-h period component. In accordance with these results, the diel pattern of locomotor activity of *C. xanthogramma* can be described by a unimodal cosine curve. In contrast to *C. xanthogramma,* both sexes of *Ph. cespitum* showed cathemeral activity (i.e., activity occurs within both the light and dark portions of the daily cycle) and females and males follow quite different activity schedules: females were most active at night, shortly before nautical dawn, whereas males were most active early in the morning. Unlike *C. xanthogramma*, *Ph. cespitum* has more ultradian components, with higher relative power especially in females, where besides the 24-h circadian component there is a particularly strong 12-h ultradian period. Based on these factors, females of *Ph. cespitum* show a bimodal and males a unimodal pattern.

Introduction

There are temporal periodicities in several physiological processes and behaviours of animals that are called circadian rhythms if the period is approximately 24 h. These rhythms are often regulated by both endogenous and exogenous cues. One of the most important exogenous cues is the natural light-dark cycle. A well synchronized circadian rhythm is an essential feature of the adaptation of organisms to their environment, as the entrained rhythm may allow the organism to act proactively to a periodic environmental stimulus (*Refinetti, 2016*). Furthermore, adaptation to different temporal niches (e.g., diurnal or nocturnal) affect resource availability, the risk of predation and rate of encounter with competitors (*Kronfeld-Schor & Dayan, 2003*). For example, the Batesian myrmecomorphic spider *Micaria sociabilis* Kulczyński, 1897 (Gnaphosidae), like the species it mimics, is diurnal, whereas its close relatives are nocturnal. Although this spider does not feed on ants, co-occurrence with its models seems to provide it with a defensive advantage (e.g., protection from model-averse predators) (*Pekár & Jarab, 2011*). In addition, the nature of a spider's diel activity pattern may influence the composition of its prey and, through this, the pest suppression ability of agrobiont spiders (*Herberstein & Elgar, 1994; Marc et al., 1999; Tietjen & Cady, 2007*).

Many studies report diel activity and biological rhythms in spiders (e.g., *Cloudsley-Thompson, 1981; Ortega et al., 1992; Kovoor et al., 1995, 1999; Yamashita & Nakamura, 1999; Ortega-Escobar, 2002a; Nørgaard et al., 2006; Jones et al., 2011, 2018; Moore et al., 2016*). The diel rhythm in locomotor activity in spiders can be circadian (*Cloudsley-Thompson, 1987, 2000*), higher-frequency (ultradian) endogenous rhythms can control their motor activity (*Suter, 1993*), they may not be purely nocturnal or diurnal (*Suter & Benson, 2014*) and even the locomotor activity of cave-dwelling species may be controlled by free-running circadian rhythms (*Soriano-Morales et al., 2013*). However, less attention has been given to sexual differences among spiders in either their rhythmic processes or diel activity (e.g., *Schmitt et al., 1990; Krumpalová & Tuf, 2013*).

Sex-specific selection pressures can result in sexual dimorphism in the physiology, morphology, or behaviour of animals (*Slatkin, 1984*). In the case of spiders, males are usually more active/mobile than females, partly because besides foraging they also must find females for mating (*Sullivan & Morse, 2004; Framenau, 2005; Foelix, 2011*). Pitfall traps tend to catch more males than females of spiders (e.g., lycosids, thomisids and salticids) (*Topping & Sunderland, 1992; Prószynski & Lubin, 1993; Fujii, 1997; Bogya & Markó, 1999*), while on trees, males of the nocturnal spiders *Cupiennius* spp. (Ctenidae) are more active than females (*Schmitt et al., 1990*). Furthermore, there might be differences between the sexes in when they are active (*Krumpalová & Tuf, 2013*), or other features such as body size (*Head, 1995*), certain morphological traits (*Albín* *et al., 2018*), metabolic rate (*Kotiaho, 1998*), or even immune response (*Rádai et al., 2018*), due to sex-specific selection pressures that may result in sex-specific differences in such features (*Turk et al., 2018*).

For this study, we chose two canopy dwelling hunting spider species, *Carrhotus xanthogramma* (Salticidae) and *Philodromus cespitum* (Philodromidae), which are very abundant and thus may play a role as natural enemies of certain invertebrate pests in Hungarian pome fruit orchards (*Mezőfi et al., 2018*).

Like other salticids (*Jackson & Pollard, 1996*), the jumping spider *C. xanthogramma* is a diurnal hunter with excellent eyesight that belongs to the guild of stalkers (*Uetz et al., 1999*). *C. xanthogramma* is distributed from Europe to Japan (*WSC, 2018*), and is one of the most common species of spider in the canopy of pome fruit orchards in Hungary (*Bogya et al., 1999a, b, 2000; Markó & Keresztes, 2014*). Mature individuals occur mostly in April and May. *C. xanthogramma* can dominate the arboreal spider assemblage in apple orchards, and presumably, it is a significant intraguild predator of other spiders (*Markó & Keresztes, 2014*). While a handful of earlier studies have dealt specifically with this species (e.g., *Yoshida & Suzuki, 1981; Maekawa & Ikeda, 1992; Fang et al., 2016*), none have examined its diel rhythm.

Philodromus cespitum is considered a diurnal hunter (*Pekár, 1999a; Korenko et al., 2010*), and, as with other philodromids, it belongs to the guild of ambush hunters (*Uetz et al., 1999*). *Ph. cespitum* is widely distributed in the Holarctic region (*WSC, 2018*) and while it can be the dominant species in canopy-dwelling spider assemblages in apple orchards in Europe (*Bogya et al., 1999b; Pekár, 1999b; Pekár & Kocourek, 2004*), it can also be abundant in North American orchards (*Miliczky et al., 2008; Sackett et al., 2008*). Adult *Ph. cespitum* are most common in June and July (*Miliczky et al., 2008*), and this species is a potential biological control agent (*Wisniewska & Prokopy, 1997; Ghavami, 2008; Michalko & Pekár, 2015; Pekár et al., 2015; Lefebvre et al., 2017; Michalko et al., 2017*), although pesticide applications could reduce its ability to suppress pests (*Řezáč et al., 2010; Michalko & Košulič, 2016*).

The aim of this study was to describe the diel pattern of locomotor activity and certain features of the rhythms, with special attention to sexual differences, in *C. xanthogramma* and *Ph. cespitum*, two hunting species of spider very abundant in fruit orchards in Hungary. We hypothesized that (1) both species are diurnal, i.e., activity is not uniformly distributed throughout the day, (2) their rhythms are circadian, and (3) the patterns contain ultradian components. Furthermore, we hypothesized that there is sexual dimorphism in certain features of the species' rhythms, i.e., (4) that males have higher locomotor activity compared to conspecific females, and, in connection with this, (5) locomotor activity rhythms of males contain more high-frequency components than those of females.

Material and methods

Test animals

Spiders used in the experiments were collected by beating the canopies of apple trees in various orchards in Hungary. The collected individuals were transported to the Department of Entomology at Szent István University, where the study was carried out. We collected 10 adult males and 11 adult females of *C. xanthogramma* (later one female had to be excluded from the analysis) in Újfehértó, on 16 April 2016. We also collected 312 *Philodromus* spp. individuals (mostly juveniles) for another study from various orchards between 9 and 26 May 2016. *Ph. cespitum* belongs to the *Ph. aureolus* species group, in which the species can be distinguished from one another only by the details of the copulatory organs (*Kubcová, 2004*), and thus juvenile specimens cannot be determined to species. The spiders were, therefore, raised to the adult stage (on *Drosophila hydei* Sturtevant, 1921) in the laboratory, and, when the vast majority of spiders had matured, we randomly selected 11 females and 11 males of *Ph. cespitum* (later two males had to be excluded from the analysis). Data on collected specimens and information on collecting sites are listed in Table S3.1.

The collected spiders (both *C. xanthogramma* and *Ph. cespitum*) were housed individually in plastic Petri dishes (height: 16 mm, outer diameter: 61 mm) and placed in random order on plastic trays. The sides of the Petri dishes were covered with white tape to reduce disturbance from neighbouring spiders. At the end of the study the body mass of *C. xanthogramma* and *Ph. cespitum* (see Table S3.1) were measured using an analytic scale (OHAUSE Adventurer Pro AV 114 C) and the previous identification of the specimens confirmed using the keys of *Kubcová (2004)* and *Nentwig et al. (2018)*.

Animal housing

All spiders were kept and our tests carried out in a behavioural laboratory at the Department of Entomology (Budapest, Hungary, 47°28′50″N, 19°02′25″E, 125 m a.s.l.). The plastic trays holding the Petri dishes with spiders were surrounded with a cardboard panel, and to minimize human disturbance, we only went into the room to check the experiment. Because the examination of circadian behaviour under more natural conditions allows a more accurate interpretation of certain rhythmic processes (*Vanin et al., 2012; Menegazzi et al., 2013*), the spiders' circadian activity was examined under natural light and photoperiod. The spiders were not exposed to direct sunlight, and the temperature and relative humidity in the room were approximately similar to outside conditions.

Recording locomotor activity

To monitor the spiders' locomotor activity, the activity of all individuals were simultaneously recorded with a video camera (Panasonic HC-X920 HD) for 72 h (as per *Schmitt et al., 1990*). During the scotophase, a red LED corn bulb (unbranded, 2.5 W, 200 Lm, emission peak at 632 nm wavelength) illuminated the recording area between 19:00 p.m. (before twilight) and 8:00 a.m. Because red light is on the verge of perception by spiders (*Yamashita, 2002*), exposure to red light did not influence their activity (*Ortega-Escobar, 2002b*). Activity was recorded from 26 to 29 April in the case of *C. xanthogramma* and 6–9 July in the case of *Ph. cespitum*. During these periods, the room temperature and the relative humidity were also recorded. Environmental conditions for the experiments are shown in Table 3.1. The exact time of sunrise, sunset, nautical and civil twilights (sun between 12°–6° and 6°–0° below the horizon) were calculated using the database available at the United States Naval Observatory (*USNO, 2018*), and the times were expressed as Central European Summer Time (CEST) (Table 3.1). To calculate the approximate photoperiods, civil twilight was used as a reference for the beginning and end of the day, because the start of civil twilight at dawn and the end of civil twilight at dusk are often considered the times of "lights on" and "lights off" for biological systems (*Hut et al., 2013*). Spiders were placed in the final layout three days before the tests and from this time to the end of the study food and water were not provided.

Table 3.1. Environmental conditions recorded during the experiment.

Species	Activity monitoring	Approx. Civil LD (h)[a]	Nautical Dawn[b]	Civil Dawn[b]	Sunrise[b]	Sunset[b]	Civil Dusk[b]	Nautical Dusk[b]	Avg. T (°C ± SE)[c]	Avg. Rel. Hum. (% ± SE)[c]
C. xanthogramma	2016.04.26. 8:00 - 2016.04.29. 8:00	15.5/8.5	4:16 - 4:58	4:58 - 5:32	5:32	19:50	19:50 - 20:24	20:24 - 21:07	18.5 (0.06)	39.6 (0.16)
Ph. cespitum	2016.07.06. 8:00 - 2016.07.09. 8:00	17/7	3:23 - 4:16	4:16 - 4:56	4:56	20:42	20:42 - 21:22	21:22 - 22:15	28.1 (0.03)	25.7 (0.20)

[a] approximate Light/Dark (LD) cycle where photophase was defined as time between the start of civil dawn and the end of civil dusk

[b] obtained from the online database of the United States Naval Observatory (*USNO, 2018*), three days average expressed as CEST

[c] measured during the experiment

Video recordings were analysed with a 10-min resolution. For this, the recordings were manually stopped at 10-min intervals using Solomon Coder software (*Péter, 2011*) and the same observer examined whether there was a movement within the given 10-min period. The level of activity was scored on a scale of 0–2 in each interval (0 – zero locomotion; 1 – minimal change in body position or the locomotion was shorter than the body length of the individual; and 2 – the locomotion was longer than the length of the individual). Applying this scoring procedure, we obtained a time series of 432 activity records (72-h long time series) for each individual.

Data analysis

(1) Quantifying the relative amount of activity: To quantify the relative amount of activity during the photophase and during twilight periods, we calculated diurnality and crepuscularity indices according to *Ensing et al. (2014)*. For the diurnality index, the light phase of the day was defined as the time between the start of civil dawn and the end of civil dusk, and the remainder of the day was considered "night". For the crepuscularity index, "twilight" was defined as the time from the start of nautical dawn until sunrise and from sunset until the end of nautical dusk (*Ensing et al., 2014*). The following equations were used to calculate the indices:

$$I_{diurnality} = \frac{act_{day} - act_{night}}{act_{day} + act_{night}}$$

and

$$I_{crepuscularity} = \frac{act_{twilight} - act_{non-twilight}}{act_{twilight} + act_{non-twilight}}$$

where act_{day} is the average activity level in the light phase of the day, act_{night} is the average activity level at night, $act_{twilight}$ is the average activity level during twilight, and $act_{non\text{-}twilight}$ is the average activity level during the remainder of the day (*Ensing et al., 2014*). Student's t-test was used to compare the means of the index values between sexes, and R software version 3.5.1 (*R Core Team, 2018*) was used for further analyses (but see Fourier analyses below).

(2) Circular statistical analysis of the activity pattern: Circular statistics were used to examine the temporal distribution of locomotor activity in different spider groups (females or males within a species) and to compare the diel activities of the sexes. For circular statistics, the activity dataset was transformed as follows: first, for each group, the average activity levels were computed at 10-min intervals; second, the computed activity values were rounded to one decimal place and multiplied by ten to get an integer. These integers were then treated as the activity level in a given 10-min interval for a particular group. Thereafter, as in *Fontúrbel et al. (2014)*, Rao's spacing test of uniformity was conducted to determine if the records were non-randomly distributed over the day. After this, the circular mean (the direction of the resultant vector or mean activity peak), the mean resultant length (*R*, a measure of data concentration or angular dispersion) and the bootstrap confidence intervals (95% CI) of mean direction were estimated. *R* values range from 0 to 1, where values close to 1 indicate an activity peak at a given moment and values close to 0 indicate a cathemeral activity pattern (i.e., activity at any time during the daily cycle) (*Tattersall, 1987; Ranganathan et al., 2010*). To compare activity patterns of the sexes, a nonparametric Watson's two-sample test of homogeneity (or Watson's U^2 test) was used. The square-roots of the activity levels throughout the day were plotted (at 30-min intervals) on a

circular histogram (rose diagram). For the circular statistics, the “circular” package in R environment was used.

(3) Comparing activity in different temporal windows: The observation days were divided into six temporal periods: nautical dawn ($dawn_n$), civil dawn ($dawn_c$), the period between sunrise and sunset (daytime), civil dusk ($dusk_c$), nautical dusk ($dusk_n$) and the period between the end of nautical dusk and the beginning of nautical dawn (night-time) (see details in Table 3.1). As the length of these temporal windows differed, the mean activity level (mean activity score per hour) was calculated for each individual and period in order to make the data comparable.

The relationships between activity levels and the temporal windows was analysed using a Linear Mixed-Effect Model (LMM) with the following statistical model structure applied to the “lme4” package in the R environment. We entered the standardized activity level as a response variable with temporal window as focal predictor. The variable containing the identification numbers of the focals were entered as a random factor. We ran the same statistical model structure for females and males of both species, but separately. For testing the post-hoc differences in the mean activity level between the different temporal windows within sexes, we applied Student’s t-test with the adjustment of the *P*-values using “Holm” correction due to the planned multiple comparisons.

(4) Analysis of the periodicities in activity patterns using discrete Fourier transformation: To examine the periodicities in the activity patterns (see Figs S3.1–S3.2), a discrete Fourier transform (DFT) analysis was applied, using self-made Matlab (*The MathWorks Inc., 2015*) routines. For this, the noisiness of the original 72-h-long time series was suppressed by compiling the moving averages with six-element (1 h) sliding-windows. This results in the spectral elements of the signal belonging to frequencies bigger than 1/h (24 cycles/day) were filtered out. On the other hand, the smallest limit of the investigated range of the spectra was set to 1/day, since the daily activity rhythm is already clearly exemplified by the three day long records of the spider’s movements. For both species, the biggest part of the power of the activity signals is contained by spectral components belonging to cycles below 20/day. It doesn’t necessarily demonstrate the absence of more frequent (frequencies bigger than 24/day) spider activities, but we suspect that the measurement procedure is simply not able to resolve finer details in the ultradian rhythms of the individuals. The statistical significance of the spectral peaks has been evaluated according to the method introduced by *Forrest & Suter (1994)*. Briefly, this method identifies a spectral peak as significant if the appearance of its power in the spectrum of a random process is less probable than a certain α threshold. In our analysis, we apply $\alpha = 0.01$ probability threshold that corresponds to a power limit L of $9.210/N$ (N being the number of signal elements), that is, any spectral peak

exceeding L were considered significant. In the following steps, we used the relative powers of the spectral components, computed as the ratio between the computed powers and the power limit, P/L. This choice enables the quantitative comparison of the statistical significance of spectral elements deriving from the analyses of different length time-series.

To investigate species-level behaviours, we constructed two types of bar graphs attributing the relevance of daily and ultradian periodicities for each species based on the spectral parameters of the individuals (see Figs S3.3–S3.6). The first bar plot (Fig. 3.4 left side) concerns the probability that a given cycle appears in the ultradian periodicities of a species. The bar heights in the plot represent the ratios of the number of spiders exhibiting periodical behaviour in a given cycle and the total number of spiders of a given sex analysed. The second bar graph (Fig. 3.4 right side) shows the mean values of the relative powers of the statistically significant peaks observed for any individuals of a given species or sex in terms of the number of ultradian cycles. The means are normalized relative to the largest mean value, i.e. the highest bar corresponds to a value of unity.

(5) Cosinor-based analysing of the activity rhythm: Fourier analysis indicated that a 24-h activity rhythm is prominent for the locomotor behaviour of both species; therefore we used cosinor-based rhythmometry to quantify and compare the circadian rhythms of activity in males and females (*Cornelissen, 2014*). First, we described the individual-based differences in the activity level by fitting Nonlinear Mixed-Effects Models (R package: “nlme”) characterized by a cosine function. We applied the following formula with a fixed 24-h period:

$y = p1 + p2 \times \cos[2\pi/24\ (x - p4)]$,

where y was the estimated activity level, x was the time in hours, p1 was the midline estimating statistic of rhythm (mesor), p2 was the distance above the mesor (amplitude) and p4 was the phase delay of the first peak.

The response variable of the statistical model was the diel activity rhythm (24 h-long, average of the three-day-long time series). The statistical model also included a variable containing the identification numbers of the observed individuals as a random factor. We ran these statistical models separately for each species. After the successful fitting of the cosine function, we also tested the significance of the model parameters of the nonlinear statistical model.

Second, based on the final model, we extracted the model parameters of the fitted model for characterizing the circadian rhythm of each individual. We calculated the following features: the activity level at the acrophase (time of maximum in the fitted curve, “Max”), the activity level at the bathyphase (time of minimum in the fitted curve, “Min”) and the average activity level (midline estimating statistic of rhythm – mesor, "Mean"). After this, we tested the potential differences of the function parameters between sexes within each species. We used LMM in which the calculated activity level was the response variable, while the sex, the type of the function parameter ("Max", "Mean" and "Min") and their interactions were entered as predictor variables in the model. The variable containing the ID numbers was present in the model as a random factor. We applied the Student's t-test for testing the post-hoc differences in the function parameters within and between sexes adjusting the *P*-values by "Holm" correction due to the planned multiple comparisons.

Finally, as a strong second frequency component with a 12-h period was found in the activity pattern of *Ph. cespitum* females, a bimodal cosine function was applied. The formula of the bimodal cosine function was:

$$y = p1 + p2\{\cos[2\pi/24\ (x - p4)])\} + p5\ \{\cos[4\pi/24\ (x - p4)]\},$$

where all parameters are already defined above in the formula of the unimodal cosine function except p5, which indicates the same parameter as p2 in the secondary cosine function.

Results

Activity indices

According to the calculated indices, *C. xanthogramma* was strictly diurnal and not crepuscular. Females and males did not differ significantly from each other in their relative amounts of diurnal or twilight activity (Fig. 3.1). *Ph. cespitum* was active during the whole 24 h period, and thus cannot be considered either strictly diurnal or nocturnal and cannot be characterized as crepuscular, although it was relatively more active during twilight than *C. xanthogramma*. According to the Student's t-test *Ph. cespitum* males were more active during daytime than the females, which were significantly more crepuscular than the males (Fig. 3.1).

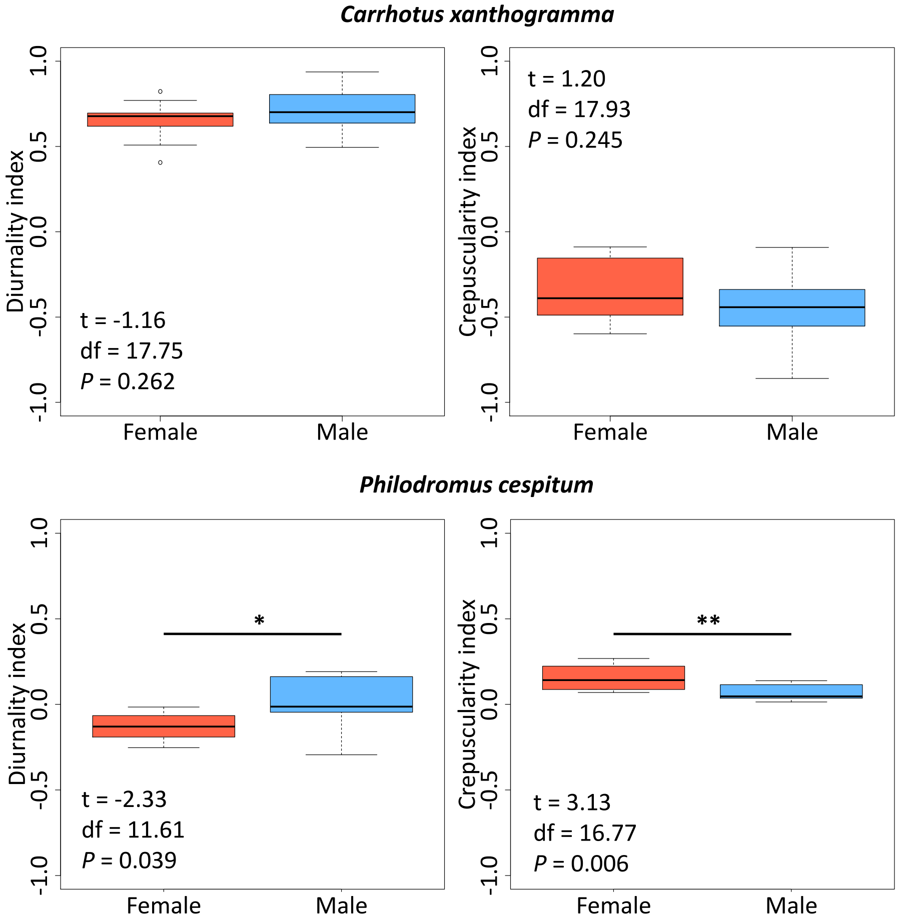


Figure 3.1: Diurnality and crepuscularity indices of *Carrhotus xanthogramma* (above) and *Philodromus cespitum* (below). The value 0.0 indicates similar activity in each of the periods of a day investigated. The significant differences are indicated by asterisks (* = *P* < 0.05, ** = *P* < 0.01).

Diel distribution of activity

Circular analysis revealed that the pattern in the locomotor activity of *C. xanthogramma* (Fig. 3.2) was not uniformly distributed throughout the day, either in females (Rao's spacing test; U = 325.532, $P < 0.001$) or males (Rao's spacing test; U = 313.879, $P < 0.001$). The mean peak of locomotor activity of females occurred at 10:51 (95% CI = 10:33 to 11:10; R = 0.437) and of males at 10:53 (95% CI = 10:32 to 11:14; R = 0.450). Activity patterns of the sexes did not differ (Watson's two-sample test; U^2 = 0.056, $P > 0.1$). As for *Ph. cespitum*, the activity of the females (Rao's spacing test; U = 324.396, $P < 0.001$) and males (Rao's spacing test; U = 329.506, $P < 0.001$) was also nonrandomly distributed throughout the day. The mean activity peak of the females occurred at 03:09 (95% CI = 01:19 to 04:58; R = 0.079) while that of males was at 07:07 (95% CI = 06:12 to 08:04; R = 0.138). The activity patterns (Fig. 3.2) of females and males of *Ph. cespitum* differed significantly (Watson's two-sample test; U^2 = 0.672, $P < 0.001$). For the activity patterns (activity matrices) based on untransformed time-series of the individual spiders of both species, see Figs S3.1–S3.2.

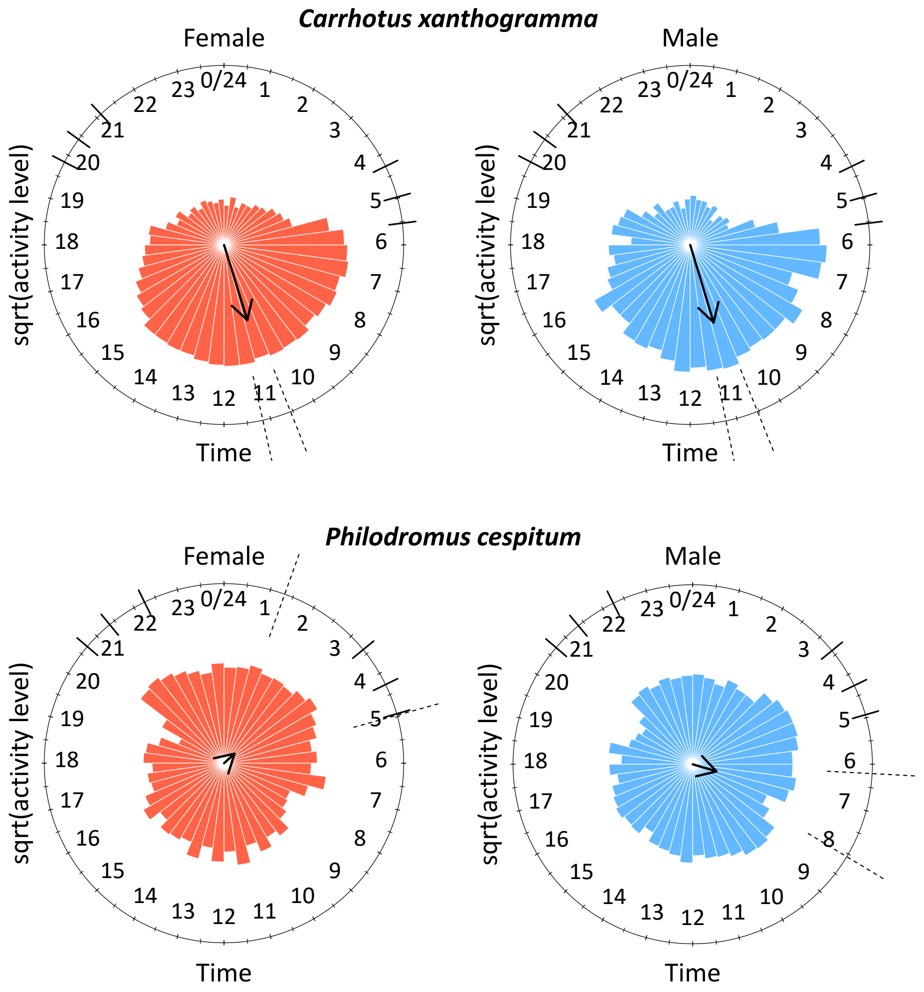


Figure 3.2: The activity pattern of *Carrhotus xanthogramma* (above) and *Philodromus cespitum* (below) females (left) and males (right). The mean activity peak (circular mean) is indicated by the arrow and its length is related to the mean resultant length (*R*). The square-root of the level of activity was plotted at 30 min intervals. Dashed lines indicate the 95% confidence intervals of the mean peak activity and the six shorter solid lines indicate the different twilight periods as follow: nautical dawn, civil dawn, sunrise, sunset, civil dusk and nautical dusk (see Table 3.1).

Analysing the average activity levels at different times in the day, we obtained the following results: the average activity levels of females and males of *C. xanthogramma* differed significantly throughout the day (females: $F_{5,45} = 21.697$, $P < 0.001$; males: $F_{5,45} = 22.703$, $P < 0.001$). Females were significantly more active during civil dawn and especially during daytime, while males were significantly more active in daytime than at other times of the day (Fig. 3.3). Comparing the mean activity level of females and males in the same temporal windows using Student's t-test, revealed that females were significantly more active than males during civil dawn and daytime (dawn_c: t = –2.45, df = 18.00, $P = 0.025$; daytime: t = –3.29, df = 17.98, $P = 0.004$; Fig. 3.3).

Ph. cespitum also differed in the activity levels recorded at different times of the day for both sexes (females: $F_{5,50} = 6.411$, $P < 0.001$; males: $F_{5,40} = 11.553$, $P < 0.001$). Females were least active during daytime and males most active during nautical- and civil dawn (Fig. 3.3). Comparison of the activity recorded at particular times of the day using Student's t-test revealed that the males were more active during civil dawn and daytime, and significantly less active during civil dusk than females (dawn$_c$: t = 3.33, df = 16.42, P = 0.004; daytime: t = 2.80, df = 14.32, P = 0.014; dusk$_c$: t = –2.60, df = 14.82, P = 0.021; Fig. 3.3).

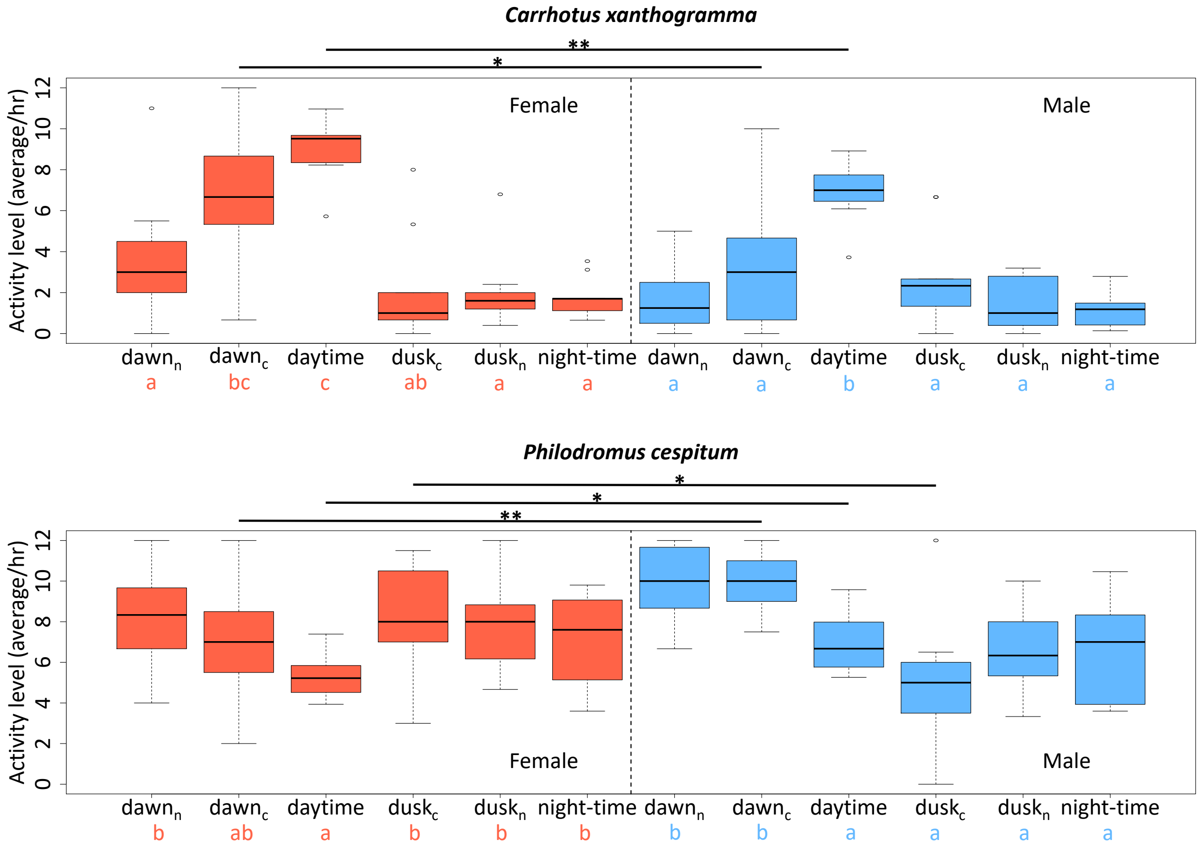
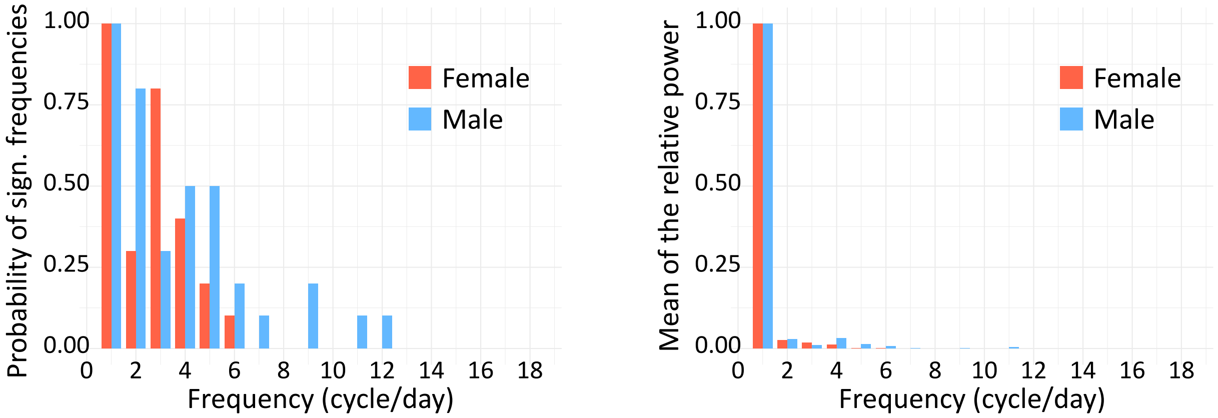


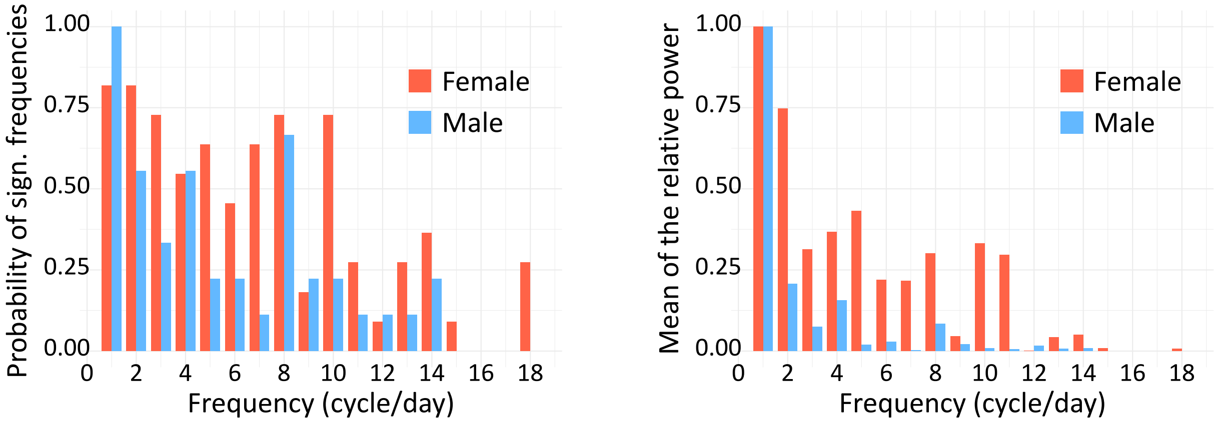
Figure 3.3: Mean activity levels (per hour) recorded in the following temporal windows: dawn$_n$ – nautical dawn, dawn$_c$ – civil dawn, daytime – the period between sunrise and sunset, dusk$_c$ – civil dusk, dusk$_n$ – nautical dusk, night-time – the period between the end of nautical dusk and the beginning of nautical dawn. Within females or males of the given species (above: *Carrhotus xanthogramma*, below: *Philodromus cespitum*) the different letters indicate significant differences at $P < 0.05$ level. The activity of females and males in the same temporal windows were compared separately and significant differences are indicated by asterisks (* = $P < 0.05$, ** = $P < 0.01$). (Note that the lengths of the temporal windows differed, see Table 3.1).

Circa- and ultradian rhythmicity

Fourier analysis revealed that the locomotor activity rhythms of *C. xanthogramma* and *Ph. cespitum* are circadian, as both species exhibited a single cycle per day as the main frequency component (Fig. 3.4). Furthermore, for both species, higher-frequency (ultradian), statistically significant components of activity were detected ($\alpha < 0.01$).



Carrhotus xanthogramma



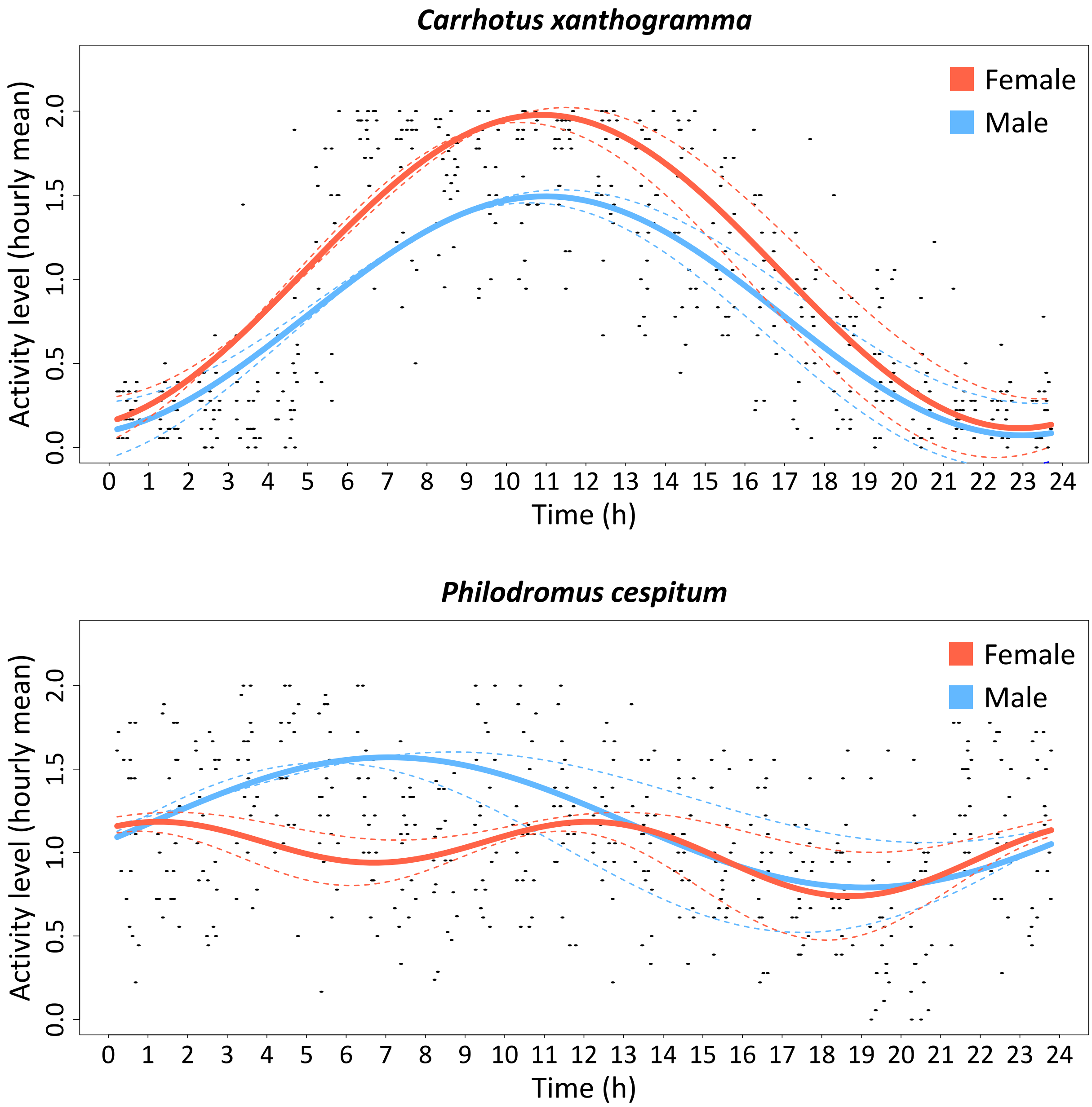
Philodromus cespitum

Figure 3.4: Results of the Fourier analysis of the time series (72 h long) recorded for *Carrhotus xanthogramma* (above) and *Philodromus cespitum* (below). On the left, we show the probabilities of the appearance of significant peaks in a given number of cycles per day. The probabilities are computed as the ratio between the number of individuals exhibiting a spectral peak (detected at $\alpha < 0.01$ level) in a given cycle and the total number of females and males studied. On the right, we show the individual means of the relative powers (i.e., the power of the peak divided by the limit of significance, see text) of the significant spectral peaks for the female and male spiders, in terms of the number of daily cycles. The plotted values are normalized relative to the largest mean value. Significant spectral components were not found beyond 18 cycles/day. (Note that the temporal resolution and high-pass filtering of the activity signals made it possible to clarify the spectral components in the frequency range of 0–24 cycles/day).

In *C. xanthogramma*, ultradian rhythmic components were generally more frequent in males than females, although their relative powers were negligible compared to the relative power of the main 24-h period (Fig. 3.4). Ultradian components present in the activity pattern of at least 50% of *C. xanthogramma* had a periodicity of 8 h (3 cycles/day) in females and 12 h (2 cycles/day), 6 h (4 cycles/day) and 4.8 h (5 cycles/day) in males (Fig. 3.4).

Philodromus cespitum showed more high-frequency oscillations than *C. xanthogramma*, and in contrast to *C. xanthogramma*, the high-frequency components were more common in *Ph. cespitum* females than males (Fig. 3.4). The most common (exhibited by at least 50% of the individuals) ultradian components in the locomotor activity of females and males had periods of 12 h (2 cycles/day), 6 h (4 cycles/day) and 4 h (8 cycles/day). The females displayed four additional high-frequency components, with periods of 8 h (3 cycles/day), 4.8 h (5 cycles/day), 3.4 h (7 cycles/day) and 2.4 h (10 cycles/day). Interestingly, all the cycles recorded for males were also recorded for females, but not vice versa. In addition, the means of the relative power of ultradian components recorded for females of *Ph. cespitum* was relatively higher than that recorded for conspecific males or *C. xanthogramma*. Nine of eleven *Ph. cespitum* females had particularly strong secondary components of activity, of two cycles per day (12 h), while in two of the 11 females, the 24-h period component was not detectable (at $\alpha < 0.01$ significance level) (Fig. 3.4). For the spectra and relative powers of the significant spectral peaks of the individual spiders in the case of both species, see Figs S3.3–S3.6.

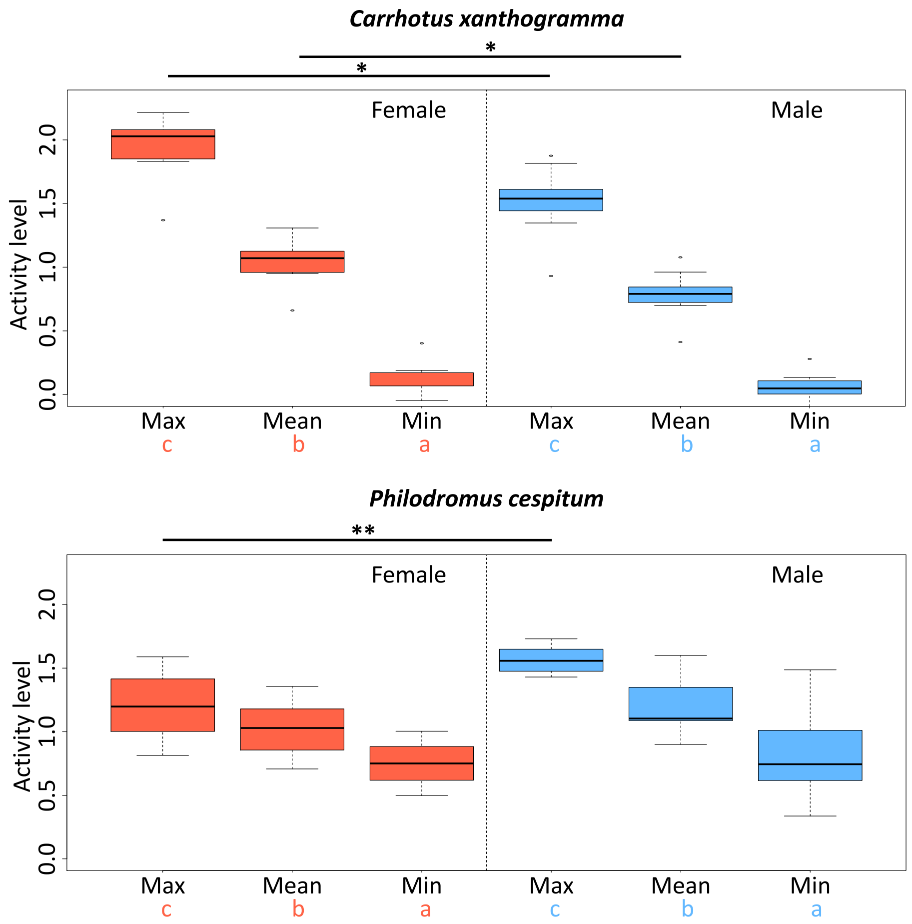
As the 24-h period had a major role in determining the pattern in motor activity, a simple cosine curve or double cosine curve (in *Ph. cespitum* females, due to the presence of a strong 12-h period component) with a 24-h fixed main period was fitted to the diel pattern of locomotor activity rhythm of both sexes for both species (Fig. 3.5). The simple cosine curve provided a good fit to the activity rhythms of *C. xanthogramma* females ($R^2 = 0.857$, $P < 0.001$), males ($R^2 = 0.807$, $P < 0.001$) and *Ph. cespitum* males ($R^2 = 0.622$, $P < 0.001$). The double cosine curve also provided a good fit to activity data of *Ph. cespitum* females ($R^2 = 0.226$, $P = 0.019$). Comparison of the different parameters obtained from the fitted curves revealed that the factor ‘phase of activity’ had a significant influence on the activity level of both species (*C. xanthogramma*: $F_{2,36} = 1696.41$, $P < 0.001$; *Ph. cespitum*: $F_{2,38} = 100.777$, $P < 0.001$). *C. xanthogramma* females were significantly more active at the maximum of the fitted curve and females also showed a significantly higher mean activity than males, while *Ph. cespitum* males were more active at the maximum of the curve than conspecific females (Fig. 3.6).



Carrhotus xanthogramma

Philodromus cespitum

Figure 3.5: Daily or 12 h (see text) locomotor activity rhythms recorded for *Carrhotus xanthogramma* (above) and *Philodromus cespitum* (below). Cosine-fitted curve based on the model parameters obtained using a fixed 24-h period. Each dot is the hourly average activity level (jittered) of one individual. Dashed lines indicate the 95% confidence intervals of the sex-specific fitted curves.


Carrhotus xanthogramma

Philodromus cespitum

Figure 3.6: Sex-related differences in the activity levels at different phases of cosine curve calculated for *Carrhotus xanthogramma* (above) and *Philodromus cespitum* (below). The activity levels at the maximum (Max – i.e. the activity levels at acrophase) and at the minimum (Min – i.e. the activity levels at bathyphase) of the fitted cosine curve and the mean levels of activity (Mean – i.e. the mesor of the fitted curves). Different letters indicate significant differences ($P < 0.05$) within males and females of a species while the asterisks indicate significant differences (* = $P < 0.05$, ** = $P < 0.01$) between the sexes.

Discussion

As we hypothesized, the activity of the species studied was not uniformly distributed throughout the day/night cycle, the rhythm was circadian and contained ultradian periodicities, although not both species proved to be diurnal. Nevertheless, as expected, a marked sexual dimorphism was also recorded in the features of the locomotor activity studied (e.g., in activity level, diel distribution, or spectral composition of the rhythm) of *C. xanthogramma* and *Ph. cespitum*; females and males of both species showed characteristic differences in the circadian rhythm of their locomotor activity.

Carrhotus xanthogramma

C. xanthogramma like other salticids has a strictly diurnal activity pattern (*Foelix, 2011*). Females and males have similar activity schedules (Figs 3.1 and 3.3) with their mean peak activities occurring in the morning, at similar times (Fig. 3.2). Their locomotor activity increases with increase in light intensity at dawn, although it seems that males react less strongly to the increase in light intensity than females (Figs 3.2–3.3). Nevertheless, contrary to what we predicted, the mean activity level was significantly higher in *C. xanthogramma* females than males (Figs 3.3 and 3.6). Although in most spiders the locomotor activity of males is greater than that of females (*Schmitt et al., 1990; Foelix, 2011*) and the same is true for many jumping spiders (*Prószynski & Lubin, 1993*), our results indicate the opposite pattern also occurs. A recent study (*Tork, 2018*) also reports higher activity in females of the jumping spider *Portia fimbriata* (Salticidae), suggesting that, in some species of jumping spiders, females are more active than males. One explanation for this might be that jumping spider females forage more intensively than males because they are larger and need more energy for egg production. In contrast, the most important objective for males is to find a mate (*Givens, 1978*). On the one hand, *C. xanthogramma* has a relatively narrow breeding window (April – May) (*Markó & Keresztes, 2014*), so that males need to find a mate as soon as possible in order to breed successfully, which would result in higher activity. On the other hand, although males are time minimisers in foraging (*Givens, 1978*) it does not necessarily mean that they spend most of their time searching for a mate. *C. xanthogramma* males might be exposed to greater risk of predation than females (*Markó & Keresztes, 2014*), and thus they may adopt a more careful and safer mate searching strategy requiring less movement in order to avoid predators and potentially dangerous conspecifics and so maximize their breeding success. Further studies are needed to clarify the mechanisms involved in this dynamic. Given that the sexes may differ in their metabolic rate (*Kotiaho, 1998; Schmitz, 2004*) and their activity levels may be correlated with metabolic rate (*Walker & Irwin, 2006*), it is important to have a better understanding of this aspect of their biology in order to interpret the sex-related differences recorded in activity levels of *C. xanthogramma*.

The locomotor activity of *C. xanthogramma* was circadian and the one cycle per day was the strongest pattern recorded for both sexes (Figs 3.4–3.5), while the other ultradian periodicities were less obvious, even though statistically they were significant. It should be noted that the ultradian periodicities were only recorded for some individuals. The presence of ultradian spectral components are reported in other spiders (*Suter, 1993; Suter & Benson, 2014*); however, their role is still not entirely clear. We hypothesized that the significant spectral components of the activities will be more numerous in males than in females and the males did indeed exhibit more ultradian periodicities than females, but not because they were more active. For rats, the appearance of various ultradian rhythmic components in the daily pattern of locomotor activity is also sex-specific and genetically fixed and might result from the different hormonal environments in the sexes (*Wollnik, 1985*). However, in spiders, further studies are needed to determine the exact ecological functions of these rhythms and the mentioned sexual differences.

Philodromus cespitum

As the activity index values (Fig. 3.1) and the mean resultant lengths (*R*, which is close to zero, Fig. 3.2) indicate that *Ph. cespitum* is not a diurnal hunter as previously thought (*Pekár, 1999a; Korenko et al., 2010*) but has a cathemeral activity pattern, which means this spider can be active both in the day and at night (*Tattersall, 1987*). Furthermore, *Ph. cespitum* females and males follow different activity schedules (Figs 3.1–3.3): females were significantly more active at night and twilight than males (Fig. 3.1) and they differed in mean time of their activity peaks. Females had a mean peak activity at night and that of males in the early morning, almost four hours later (Fig. 3.2). It is known that the females and males of small linyphiid spiders may have different activity patterns (*Krumpalová & Tuf, 2013*), which may be a kind of resource partitioning or it may be safer for the males to search for females when they are less active. Furthermore, *Ph. cespitum* females increase their activity immediately after the light intensity decreases, at civil dusk, whereas males increased their activity when light intensity increased at nautical dawn (Fig. 3.3). However, a moderate increase in activity also occurred at dawn in females and at dusk in males (Fig. 3.2). Somewhat similar bimodal activity rhythms (with two local peaks near dawn and dusk) are reported in other animal taxa (*Aschoff, 1966; Pittendrigh, 1981*), but in our case, females and males primarily react to two different stimuli (darkening, lightening), which is uncommon.

Our hypothesis that males of *Ph. cespitum* would be more active than the females was not confirmed (Figs 3.3, 3.5 and 3.6), as the mean activity levels of the sexes did not differ, although the mean activity of males was numerically greater and they were more active at the maximum of the fitted curve than the females. Furthermore, in contrast to our last hypothesis, the presence of ultradian components in the spectral activity pattern of females of *Ph. cespitum* were more frequent than in males (Fig. 3.4). Although daily locomotor activity of *Ph. cespitum* was found to be dominantly circadian, two females did not exhibit a daily activity cycle. *Suter & Benson (2014)* also report that some individuals of *Dolomedes triton* (Walckenaer, 1837) (Pisauridae) do not have a one cycle per day oscillation in their activity, whereas others do. Furthermore, unlike *C. xanthogramma*, the relative power of ultradian rhythmic components in *Ph. cespitum* was stronger, especially in females (Fig. 3.4). In females, the two cycle per day oscillation seems to be typical because it was recorded for the majority of the individuals and is of relatively high power (Fig. 3.4). The results of the Fourier analysis indicated a further important difference between the sexes:

males had unimodal while females had bimodal activity patterns (Figs 3.4–3.5). As *Ph. cespitum* has closely related sibling species [e.g., *Ph. aureolus* (Clerck, 1757), *Ph. buchari* Kubcová, 2004 or *Ph. longipalpis* Simon, 1870] in Europe (*Kubcová, 2004*), it would be worth studying the activity of these sibling species in order to learn more about the unusual activity pattern of philodromids and, potentially, about mechanisms for their reproductive isolation (*Schmitt et al., 1990*). The temporal shift in the diel activity of certain species or populations could be driven by predators that are active in the same time window or by the absence of prey (*Kronfeld-Schor & Dayan, 2003*). The observed sexual dimorphism in the activity of *Ph. cespitum* might, therefore, be explained by the different nutritional needs of the sexes, leading to activity (and foraging) peaks at different times of the day.

Conclusions

Summarizing the results we found the followings: (1) females of *C. xanthogramma* are more active than males, (2) whereas in *Ph. cespitum* the sexes have different patterns of activity, (3) based on the data for the two species studied the presence of ultradian components possibly does not depend on the total amount of activity, (4) sexes differ in their set of ultradian rhythmic components, (5) strictly diurnal species (*C. xanthogramma*) have fewer high-frequency oscillations in their locomotor activity rhythm with weaker relative power than in the cathemeral species (*Ph. cespitum*) and (6) for *Ph. cespitum*, in addition to one cycle per day (24-h) oscillation two cycles per day (12-h) oscillation can also play an important role in the temporal pattern in its locomotor activity.

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SUMMARY

Spiders (Araneae) form abundant and diverse assemblages in agroecosystems such as fruit orchards, and thus have an important role as natural enemies of orchard pests. Although spiders are often considered to be polyphagous and opportunistic predators in general, limited information is available on their natural prey at both species and community levels. Furthermore, many other aspects of the biology of the species with potential economic importance are poorly known. Thus, the aims of this thesis were (1) to provide new data on the taxonomic composition of spider assemblages inhabiting apple orchards; (2) to assess the natural prey (realized trophic niche) of arboreal hunting spiders, their role in trophic webs and their biological control potential with direct observation of predation events in apple orchards; and finally, (3) to get more information on the circadian biology regarding the locomotor activity of the two most abundant arboreal hunting spider species in apple orchards.

For the faunistic study, spiders were collected sporadically with a variety of collecting methods (hand collecting, beating, cardboard bands and litter sampling) in apple orchards located in various parts of Hungary, mainly in Bács-Kiskun, Pest, Szabolcs-Szatmár-Bereg and Tolna counties, from 2013 to 2016. For the assessment of the natural prey of hunting spiders, spiders with prey in their chelicerae were collected in the canopy of apple trees in organic apple orchards during the growing seasons between 2013 and 2019. Among others, the composition of the actual (captured by spiders) and the potential (available in the canopy) prey was compared, trophic niche and food web metrics were calculated, and some morphological, dimensional data of the spider-prey pairs were analysed. Finally, the circadian biology of two agrobiont hunting spider species, *Carrhotus xanthogramma* (Latreille, 1819) (Salticidae) and *Philodromus cespitum* (Walckenaer, 1802) (Philodromidae), was evaluated under natural photoperiod conditions. Particular attention was paid to possible differences between the sexes in both species.

This thesis reports the first records of two spider species for Hungary: *Cyclosa sierrae* Simon, 1870 (Araneidae) and *Porrhomma oblitum* (O. P.-Cambridge, 1871) (Linyphiidae). Among others, we provide new data for four further species collected in apple orchards: *Iberina microphthalma* (Snazell & Duffey, 1980) (Hahniidae), *Mermessus trilobatus* (Emerton, 1882) (Linyphiidae), *Pulchellodromus ruficapillus* (Simon, 1885) (Philodromidae) and *Lasaeola prona* (Menge, 1868) (Theridiidae).

By analysing a total of 878 prey items captured by spiders we concluded that arboreal hunting spiders forage selectively and consume a large number of apple pests; however, spiders' beneficial effects are greatly reduced by their high levels of intraguild predation and by a propensity to switch from pests to alternative prey. In the trophic web, the dominant hunting spider

taxa/groups (*Carrhotus xanthogramma*, *Philodromus cespitum*, *Clubiona* spp., *Ebrechtella tricuspidata, Xysticus* spp. and 'Other salticids') exhibit different levels of predation on different prey groups and the trophic web's structure changes depending on the time of year. Hunting spiders show a high functional redundancy in their predation. However, but contrary to their polyphagous nature, the examined spider taxa showed differences in their natural diet, exhibited a certain degree of prey specialisation and selected prey by size and taxonomic identity. Guilds (such as stalkers, ambushers and foliage runners) did not consistently predict either prey composition or predation selectivity of arboreal hunting spider species. From an economic point of view, *Ph. cespitum* and *Clubiona* spp. were found to be the most effective natural enemies of apple pests, especially of aphids. The trophic niche width of *C. xanthogramma* and *Ph. cespitum* increased during ontogeny, resulting in a shift in their predation.

And finally, we found that *C. xanthogramma* is a strictly diurnal species with a mean activity peak in the morning in both sexes and the females are more active than males. The locomotor activity rhythm of males was richer in ultradian (shorter than a day but longer than an hour) components, although the relative power of these components was negligible compared to the main, 24-h period component. In accordance with these results, the diel pattern of locomotor activity of *C. xanthogramma* can be described by a unimodal cosine curve. In contrast to *C. xanthogramma*, both sexes of *Ph. cespitum* showed cathemeral activity (i.e., activity occurs within both the light and dark portions of the daily cycle) and females and males follow quite different activity schedules: females were most active at night, shortly before nautical dawn, whereas males were most active early in the morning. Unlike *C. xanthogramma*, *Ph. cespitum* has more ultradian components, with higher relative power, especially in females, where besides the 24-h circadian component there is a particularly strong 12-h ultradian period. Based on these factors, females of *Ph. cespitum* show a bimodal and males a unimodal pattern.

ÖSSZEFOGLALÁS

Almaültetvények lombozatlakó vadászpókjai: taxonómiai összetétel, természetes zsákmány és cirkadián biológia

A pókok (Araneae) fajgazdag és nagy egyedsűrűségű ízeltlábú együtteseket alkotnak gyümölcsültetvényekben is, így fontos szerepük lehet egyes kártevők korlátozásában. A pókokat általában polifág és opportunista ragadozóknak tartja a szakirodalom, bár idáig viszonylag kevés feltáró kutatás készült az egyes fajok vagy pókegyüttesek természetes zsákmányspektrumáról. Mindemellett, sokszor még a kártevőgyérítés szempontjából fontosnak tartott fajok biológiája és ökológiai szerepe sem teljesen tisztázott. Ezért doktori disszertációmban a következő célkitűzéseket fogalmaztam meg: hogy (1) bővítsem ismereteinket az almaültetvények pókegyütteseinek taxonómiai összetételével kapcsolatban; hogy (2) terepi megfigyelésekkel felmérjem az almaültetvények lombkoronájában táplálkozó vadászpókfajok természetes zsákmányspektrumát, kártevőgyérítő képességét és elemezzem a vadászpókok és a lombozatlakó ízeltlábú együttes között kialakuló táplálékhálózatot; végezetül, hogy (3) jellemezzem a két leggyakoribb lombozatlakó vadászpókfaj, a *Carrhotus xanthogramma* (Latreille, 1819) (Salticidae) és *Philodromus cespitum* (Walckenaer, 1802) (Philodromidae) cirkadián aktivitási ritmusát.

Almaültetvények pókegyütteseinek faunisztikai vizsgálatához 2013-tól 2016-ig Magyarországon (főleg Bács-Kiskun, Pest, Szabolcs-Szatmár-Bereg és Tolna megyékben), több ültetvényben végeztem gyűjtéseket különböző gyűjtési módszerek (kopogtatás, egyelés, hullámpapír övek, avarminta-futtatás) segítségével. Lombozatlakó vadászpókok természetes zsákmányspektrumának meghatározásához 2013 és 2019 között, a vegetációs időszakban rendszeresen gyűjtöttem táplálkozó vadászpók egyedeket ökológiai művelésű almaültetvényekből. Többek között összehasonlítottam a pókok által fogyasztott aktuális és a lombkoronában elérhető potenciális préda összetételét, kiszámítottam a trofikus niche szélességeket, átfedéseket, illetve a táplálékhálózatra jellemző mérőszámokat és elemeztem a pók-préda párok morfológiai és méretbeli adatait. Végezetül természetes fotoperiódus mellett részletesen jellemeztem a *C. xanthogramma* és *Ph. cespitum* cirkadián aktivitási mintázatát, különös figyelmet szentelve az ivari különbségeknek.

Az almaültetvényekből gyűjtött pókanyagból Magyarország faunájára nézve újnak bizonyultak a *Cyclosa sierrae* Simon, 1870 (Araneidae) és *Porrhomma oblitum* (O. P.-Cambridge, 1871) (Linyphiidae) fajok és további értékes faunisztikai adatokat szolgáltattam kevéssé ismert fajokról, így többek között az *Iberina microphthalma* (Snazell & Duffey, 1980) (Hahniidae), *Mermessus trilobatus* (Emerton, 1882) (Linyphiidae), *Pulchellodromus ruficapillus* (Simon, 1885) (Philodromidae) és *Lasaeola prona* (Menge, 1868) (Theridiidae) pókfajok hazai elterjedéséről.

Összesen 878 táplálkozó vadászpók egyed zsákmányának elemzésével megállapítottam, hogy a lombozatlakó vadászpókok szelektíven táplálkoznak, és bár nagy mennyiségű almakártevőt fogyasztanak, hasznos tevékenységüket jelentősen korlátozza a gyakori intraguild predációjuk és hajlamuk arra, hogy kártevők zsákmányolása helyett alternatív prédára váltsanak. A táplálékhálózatban a domináns pókcsoportok (*C. xanthogramma*, *Ph. cespitum*, *Clubiona* spp., *Ebrechtella tricuspidata*, *Xysticus* spp. és „Egyéb ugrópókok") eltérő predációs nyomást fejtenek ki a különböző prédacsoportokra, ami szezonális különbségeket is mutat. A predációban megfigyelhető nagy funkcionális redundancia ellenére különbségek mutatkoznak a vizsgált pókcsoportok zsákmányösszetételében. Megállapítottam, hogy a vadászó pókfajok zsákmányösszetételét jelentősen befolyásolja a zsákmány mérete és taxonómiai hovatartozása, így zsákmányuk tekintetében a különböző fajok eltérő mértékű specializációval jellemezhetőek. A lombozatlakó vadászpókok guild szerinti csoportosítása (mint a cserkészők, lesből támadók és lombozaton futók) nem határozza meg következetesen azok zsákmányspektrumát vagy preferenciáit. Az almakártevők, és főleg a levéltetvek gyérítése szempontjából a *Ph. cespitum* és a *Clubiona* spp. fajok bizonyulnak a leghatékonyabb természetes ellenségeknek. Megállapítottam továbbá, hogy a *C. xanthogramma* és *Ph. cespitum* trofikus nicheszélessége az egyedfejlődésük során kiszélesedik. Eredményeim alapján a lombozatlakó vadászpókok nem tekinthetők opportunista ragadozóknak.

Végezetül megállapítottam, hogy a *C. xanthogramma* szigorúan nappali aktivitású faj, napi mozgási aktivitási mintázata egycsúcsú koszinusz görbével jól jellemezhető. Mindkét ivar esetében az átlagos aktivitási csúcs a délelőtti órákra esik, és a nőstények aktívabbak a hímeknél. A hímek lokomotoros aktivitási ritmusa több ultradián (24 óránál rövidebb periódusidejű) komponenst tartalmaz, mint a nőstényeké, habár ezek relatív amplitúdói jelentéktelenek a fő, 24 órás periódusidejű komponenshez képest. A *C. xanthogramma* fajjal ellentétben a *Ph. cespitum* egyedek katemerális (azaz napszaksemleges) aktivitást mutatnak, és az ivarok különböző napirendet követnek: a nőstények aktivitása kétcsúcsú, míg a hímeké egycsúcsú koszinuszgörbével jellemezhető. A nőstények éjszaka a legaktívabbak, röviddel a navigációs szürkület kezdete előtt, míg a hímek aktivitása a reggeli órákban tetőzik. A *C. xanthogramma* fajhoz viszonyítva a *Ph. cespitum* egyedek aktivitási ritmusa több ultradián komponenst tartalmaz, melyek relatív amplitúdói is magasabbak. Ez különösen a nőstények esetében szembetűnő, ahol a 24 órás periódusú cirkadián komponens mellett egy 12 órás periódusú komponens is jelentősen befolyásolja az aktivitást.

NEW SCIENTIFIC RESULTS

–As a result of my faunal studies in apple orchards, I reported *Cyclosa sierrae* and *Porrhomma oblitum* as new spider species for the fauna of Hungary (and *C. sierrae* also for Central Europe). *C. sierrae*, *P. oblitum*, *Iberina microphthalma*, *Mermessus trilobatus*, *Pulchellodromus ruficapillus* and *Lasaeola prona* were reported from apple orchards for the first time and *I. microphthalma* was proved to be not strictly associated with the ground level.

–By analysing a total of 878 hunting spider prey items collected from the canopy of apple trees I proved that although highly polyphagous, arboreal hunting spiders forage selectively and therefore cannot be considered as entirely opportunistic predators.

–I found that arboreal hunting spider assemblages show positive selection for neutral prey, neutral selection for natural enemies and negative selection for pests. Therefore, although hunting spiders consume a large number of apple pests, this beneficial effect is strongly constrained by intraguild predation and by propensity to switch from pests to alternative prey.

–Trophic web dynamics and trophic interactions between the most abundant hunting spider groups and the arthropod community were characterised at the canopy level in fruit orchards for the first time.

–Based on the natural prey, I described the trophic ecology of the most abundant arboreal hunting spider groups inhabiting apple orchards. Ontogenetic shifts in the trophic niche of *Carrhotus xanthogramma* and *Philodromus cespitum* were reported.

–Locomotor activity rhythms of *C. xanthogramma* and *Ph. cespitum* were characterized. I found that the females of *C. xanthogramma* are more active than the conspecific males which phenomenon is rare in spiders. The activity rhythm of *Ph. cespitum* proved to be cathemeral and the different sexes have different activity patterns. First time was found that spider sexes might have different sets of ultradian components, and their relative powers or importance are differ between sexes. Activity rhythms of *Ph. cespitum* females was proved to be bimodal rather than unimodal.

ACKNOWLEDGEMENTS

I am very grateful for the guidance of my supervisors, Viktor Markó and Gábor Markó. I would like to thank to my wife, Szilvia Mezőfi, for her support and patience during my research and the preparation of this thesis.

SUPPLEMENTARY MATERIALS

Supplemental Figures

Supplemental figures for Study2

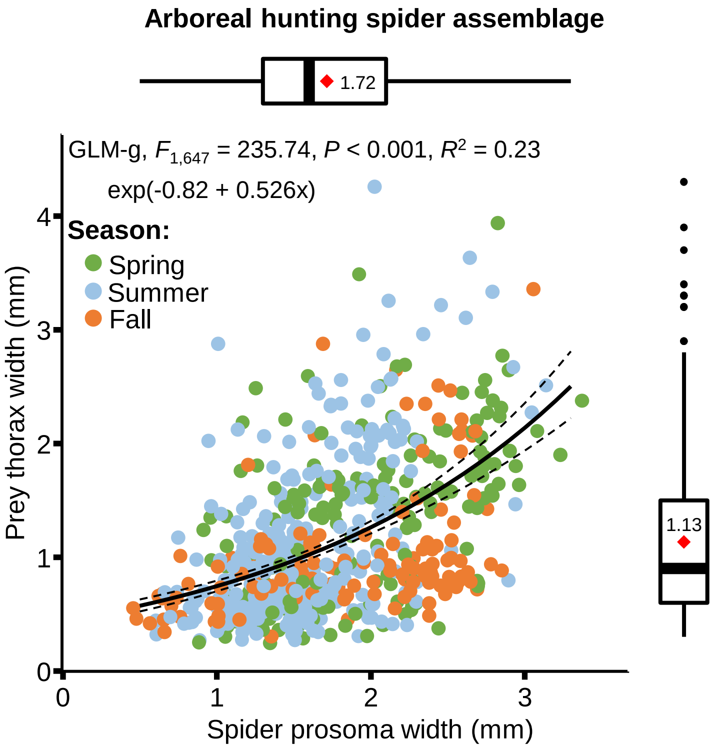

Figure S2.1: Relationship between spider prosoma and prey thorax widths (jittered, N=649) for the arboreal hunting spider assemblage. On the marginal boxplots red squares indicate the mean values.

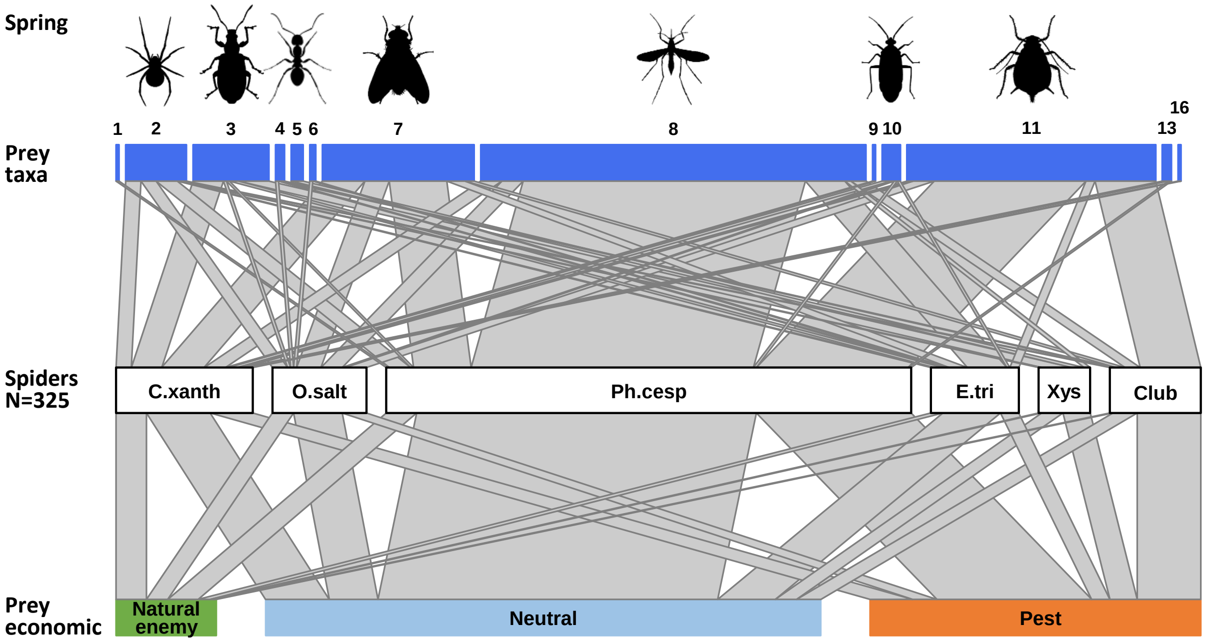

Figure S2.2: Spring aspect (N=325); throphic interactions between the most abundant hunting spider groups and the arthropod community in the canopy of apple trees in spring. The middle bars represent spider groups and upper and bottom bars represent the spiders' prey divided taxonomically and according their economic status. The width of the links between the trophic levels depict the frequency of interactions and bar widths indicate the relative abundance of each category. Numbers refer to following prey taxa: **1** Acari, **2** Araneae, **3** Coleoptera, **4** Lepidoptera, **5** Formicidae, **6** Other Hymenoptera, **7** Brachycera, **8** Nematocera, **9** Auchenorrhyncha, **10** Heteroptera, **11** Sternorrhyncha, **13** Neuroptera, **16** Trichoptera; Spiders: **C.xanth** = *Carrhotus xanthogramma*, **O.salt** = Other salticids, **Ph.cesp** = *Philodromus cespitum*, **E.tri** = *Ebrechtella tricuspidata*, **Xys** = *Xysticus* spp., **Club** = *Clubiona* spp.

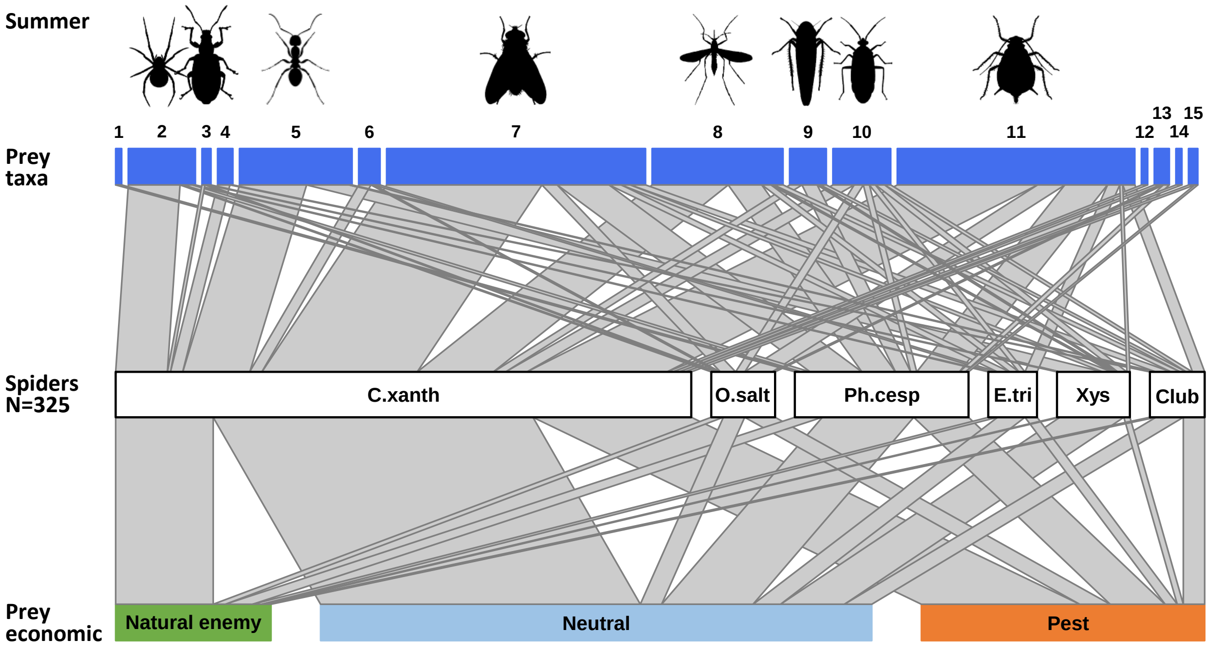

Figure S2.3: Summer aspect (N=325); throphic interactions between the most abundant hunting spider groups and the arthropod community in the canopy of apple trees in summer. The middle bars represent spider groups and upper and bottom bars represent the spiders' prey divided taxonomically and according their economic status. The width of the links between the trophic levels depict the frequency of interactions and bar widths indicate the relative abundance of each category. Numbers refer to following prey taxa: **1** Acari, **2** Araneae, **3** Coleoptera, **4** Lepidoptera, **5** Formicidae, **6** Other Hymenoptera, **7** Brachycera, **8** Nematocera, **9** Auchenorrhyncha, **10** Heteroptera, **11** Sternorrhyncha, **12** Ephemeroptera, **13** Neuroptera, **14** Psocoptera, **15** Thysanoptera; Spiders: **C.xanth** = *Carrhotus xanthogramma*, **O.salt** = Other salticids, **Ph.cesp** = *Philodromus cespitum*, **E.tri** = *Ebrechtella tricuspidata*, **Xys** = *Xysticus* spp., **Club** = *Clubiona* spp.

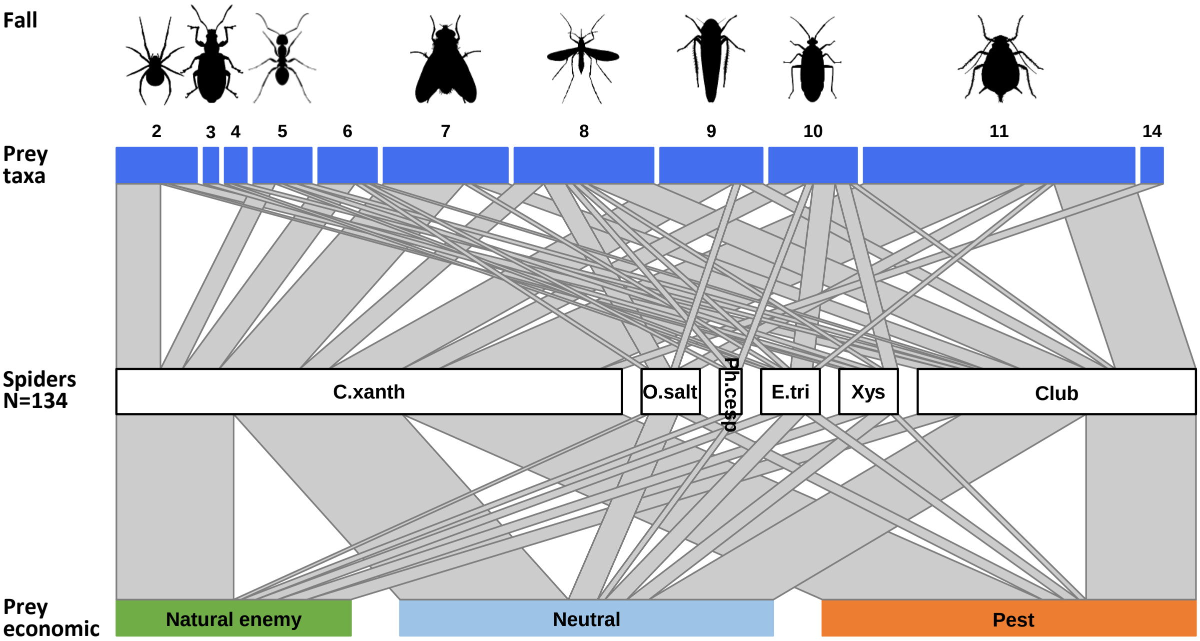

Figure S2.4: Fall aspect (N=134); throphic interactions between the most abundant hunting spider groups and the arthropod community in the canopy of apple trees in fall. The middle bars represent spider groups and upper and bottom bars represent the spiders' prey divided taxonomically and according their economic status. The width of the links between the trophic levels depict the frequency of interactions and bar widths indicate the relative abundance of each category. Numbers refer to following prey taxa: **2** Araneae, **3** Coleoptera, **4** Lepidoptera, **5** Formicidae, **6** Other Hymenoptera, **7** Brachycera, **8** Nematocera, **9** Auchenorrhyncha, **10** Heteroptera, **11** Sternorrhyncha, **14** Psocoptera; Spiders: **C.xanth** = *Carrhotus xanthogramma*, **O.salt** = Other salticids, **Ph.cesp** = *Philodromus cespitum*, **E.tri** = *Ebrechtella tricuspidata*, **Xys** = *Xysticus* spp., **Club** = *Clubiona* spp.

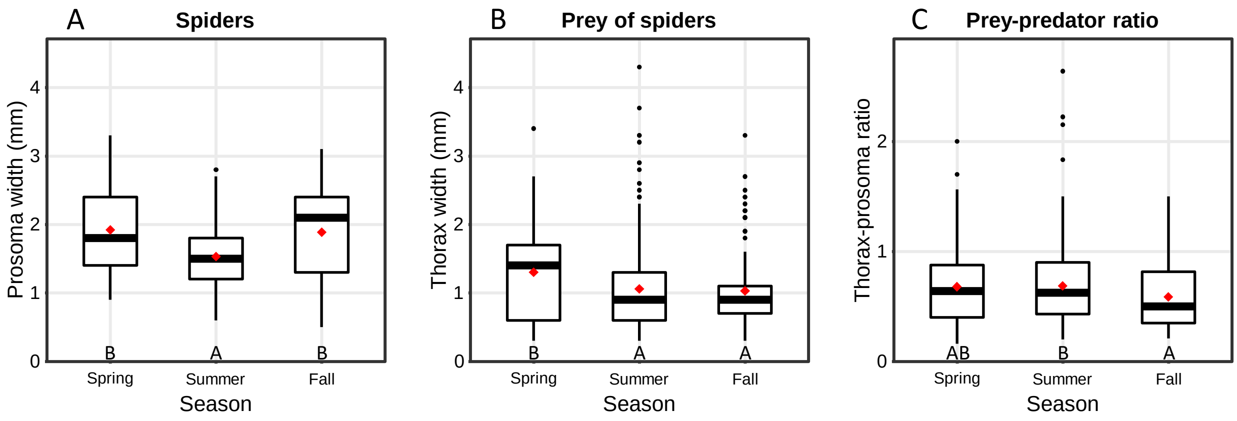

Figure S2.5: Seasonal variation in spider prosoma width (**A**), prey thorax width (**B**) and the prey thorax and spider prosoma ratio (**C**). On the boxplots red squares indicate the mean values. Different capital letters indicate significant differences between the seasons at *P* < 0.05 level.

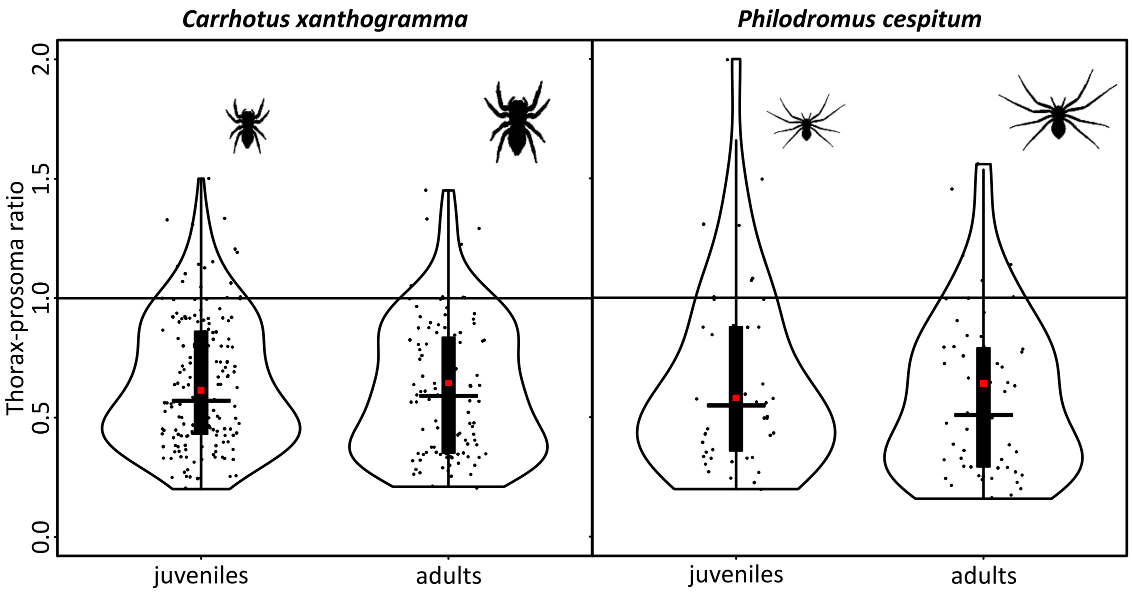

Figure S2.6: Prey thorax and spider prosoma ratios (jittered) for the juveniles and adults of *C. xanthogramma* and *Ph. cespitum*. Note that adults comprise both the subadult and adult individuals. Red square – mean; black horizontal solid line – median; black vertical rectangle – interquartile range.

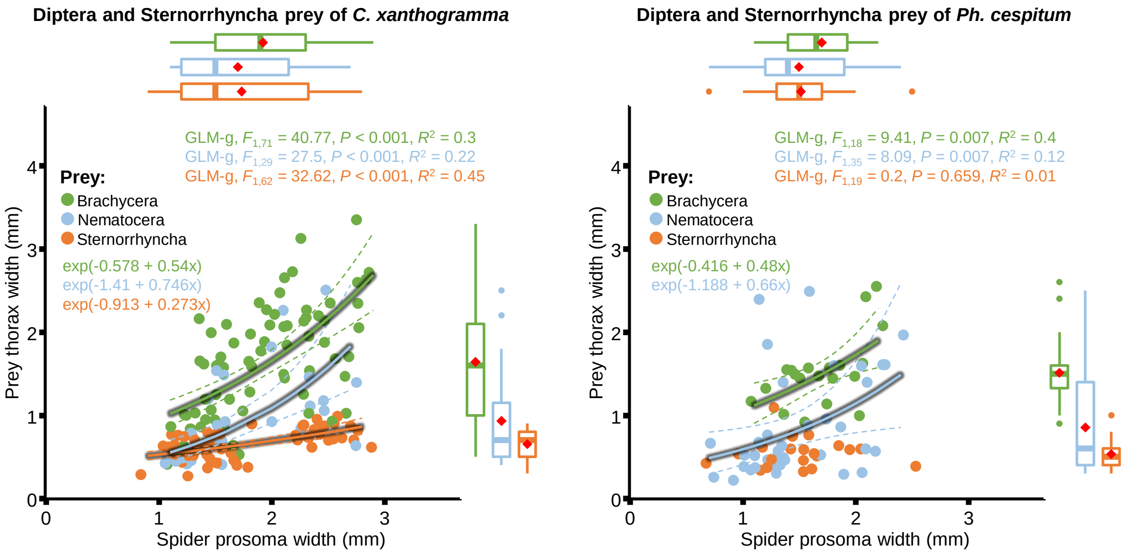

Figure S2.7: Relationship between spider prosoma and prey thorax widths (jittered) for the two most abundant arboreal hunting spider species, *Carrhotus xanthogramma* and *Philodromus cespitum*, and their main prey taxa (Brachycera, Nematocera and Sternorrhyncha) in apple orchards. On the marginal boxplots red squares indicate the mean values.

Supplemental figures for Study3

Notes on Figure S3.1–S3.2. Activity matrix for each species and sex based on individual activity scores:

We used the three-values (0, 1, 2) of the activity scores to quantify the activity of the spiders both at the individual- and species-levels. We provide a coloured activity matrix (based on the untransformed time-series) for each species and sex in which the numerical activity scores are in blue, green and yellow, which indicate whether the spiders were motionless, slightly active or active, respectively. The vertical dimension of the matrix exemplifies the temporal aspect of the spider's activity, while horizontally the coloured time-series for each individual belonging to the same species and sex are plotted, side by side. The colour textures of the matrices clearly represent the spider's activity rhythms, as well as the common behavioural patterns of the species.

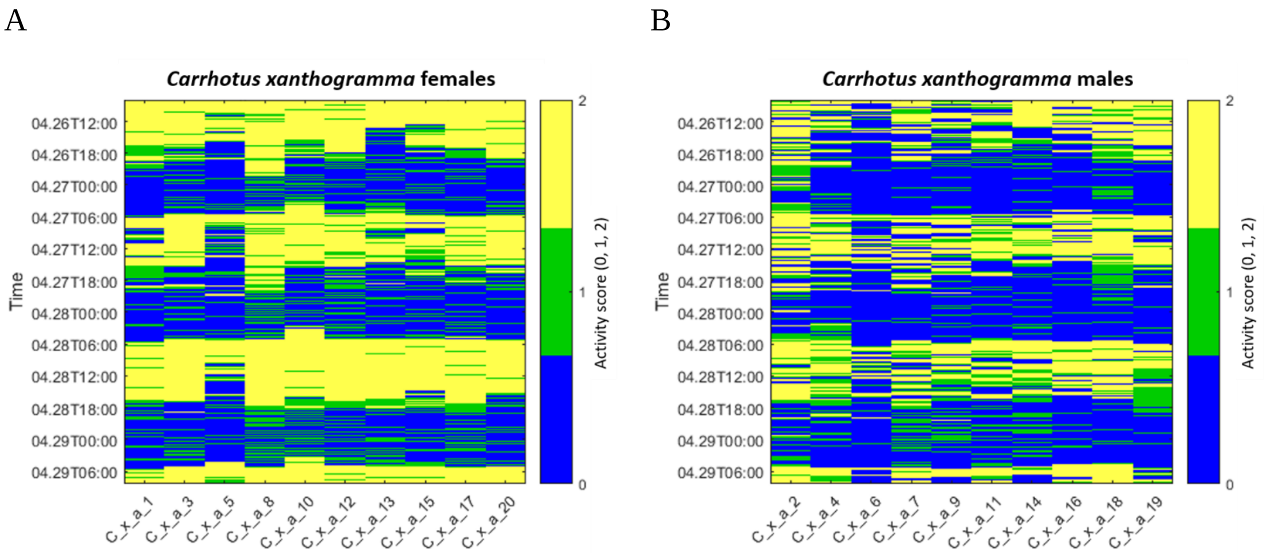

Figure S3.1: The coloured activity matrices of individual female (**A**) and male (**B**) *Carrhotus xanthogramma*. The blue, green and yellow colours correspond to motionless, slightly active and active states, respectively. The variation in the activity scores is indicated by the colours in terms of time (vertical dimension, at a 10-minute resolution) and individuals (horizontal dimension).

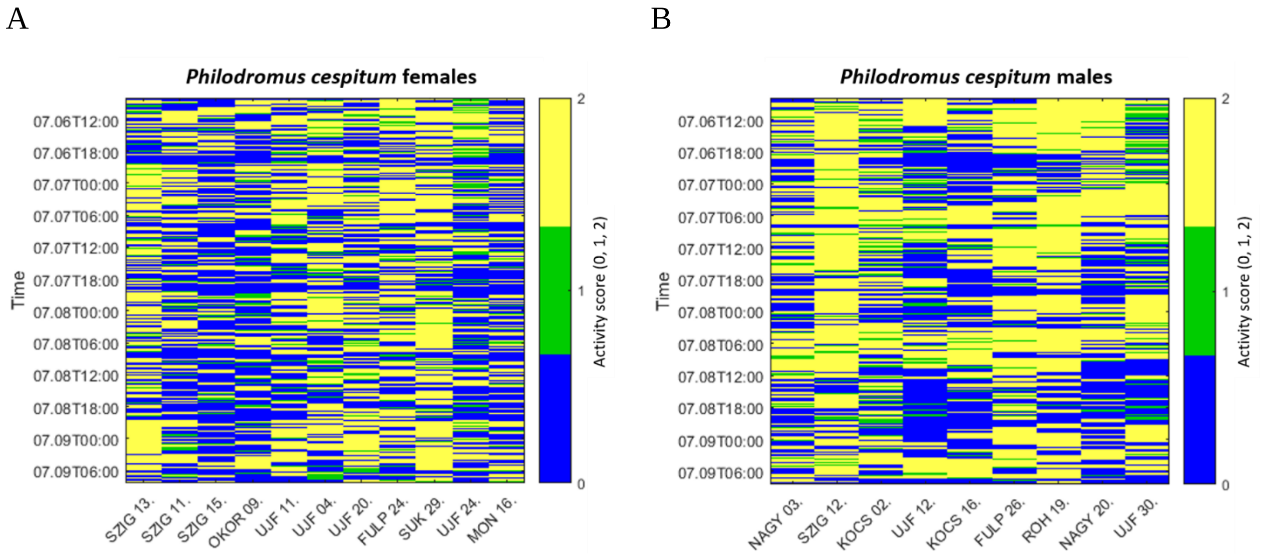

Figure S3.2: Same as Figure S3.1 for *Philodromus cespitum*

Notes on Figure S3.3–S3.6. Spectral parameters and relative powers of the significant spectral peaks of individual spiders:

The recorded power spectra are shown in Figs S3.3 and S3.4, where the frequency axes are scaled in terms of multiples of 1/day. The biggest frequency in the spectra is 24 in 1/day units, corresponding to the cut-off frequency of our low-pass filtering (1/hour).

In the spectra (Figs S3.3 and S3.4), the power limits are demarcated by the red horizontal lines while the statistically significant peaks in the spider's spectra are represented by red stars. In order to discriminate the significant periodicities in the spectra at an individual-level, as well as to check the relevance of the different spectral peaks, we present their relative powers (for the definition, see the main text) by different colours in filled discrete contour plots (Figs S3.5 and S3.6) where the horizontal and vertical dimensions belong, respectively, to different individuals and the n numbers of daily activity cycles. Since the frequency resolution of the spectra is better than the selected scale of the vertical dimension, the peak frequencies were binned with resolution of 1/day and the sum of the relative powers of bin elements were represented in the contour plots.

Note, that by comparing the positions of coloured boxes across the different columns, the plot displays the common activity features of species. For investigating the species-level behaviours, we constructed two additional types of bar graphs that display the relevance of daily and ultradian periodicities for a species, based on the spectral parameters of individual spiders (see the main text).

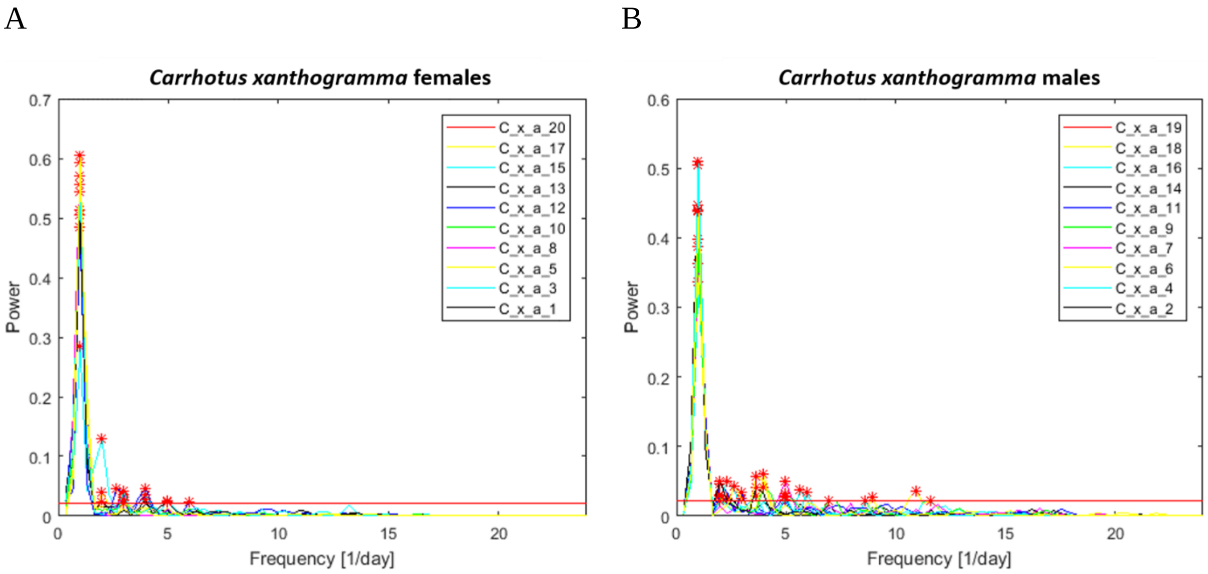

Figure S3.3: Power spectra of the low-pass filtered (see text) time series of individual female (**A**) and male (**B**) *Carrhotus xanthogramma*. The horizontal red line represents the power limit beyond which the spectral peaks are considered to be significant. The significant periodicities are indicated by red stars.

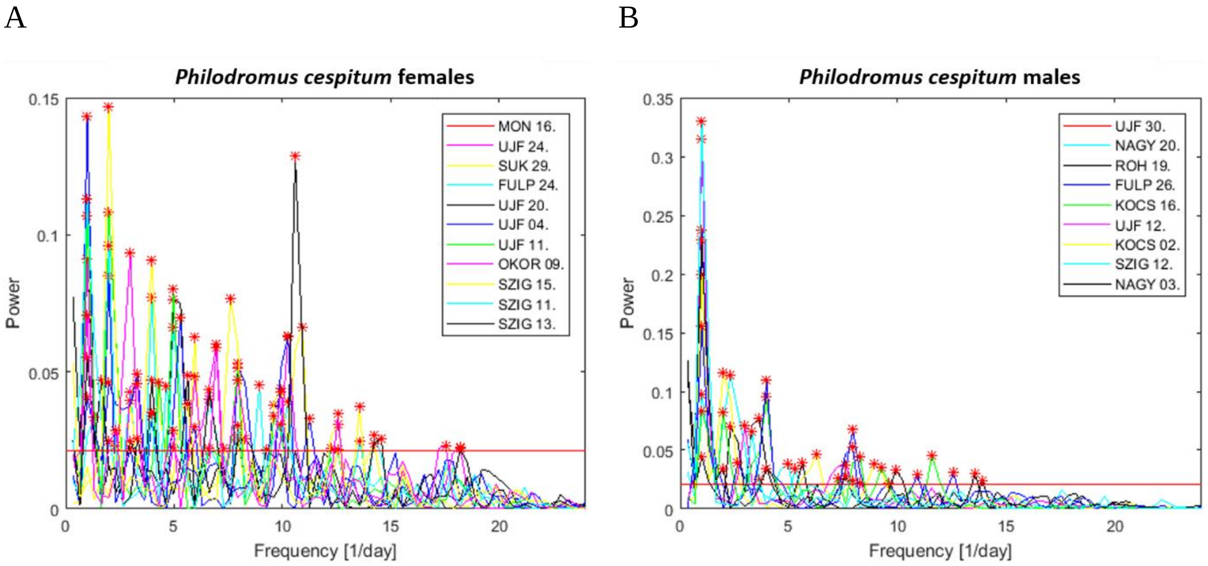

Figure S3.4: Same as Figure S3.3 for *Philodromus cespitum*

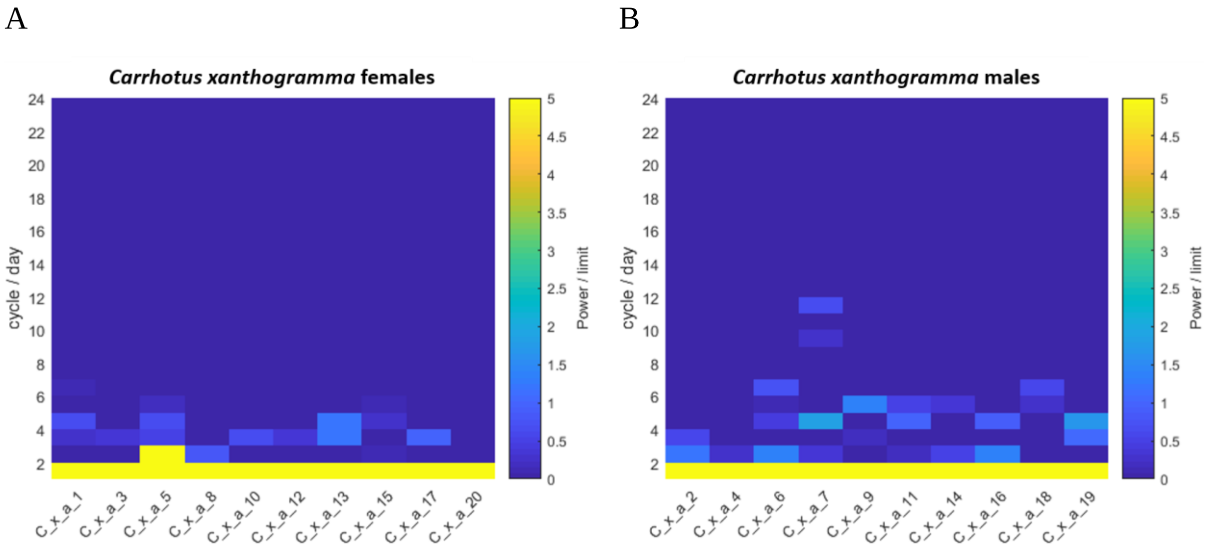

Figure S3.5: Colour-scale representation of the relative powers of the significant spectral peaks of individual female (**A**) and male (**B**) *Carrhotus xanthogramma* (individuals indicated along the X axis), in terms of frequency given in cycles/day.

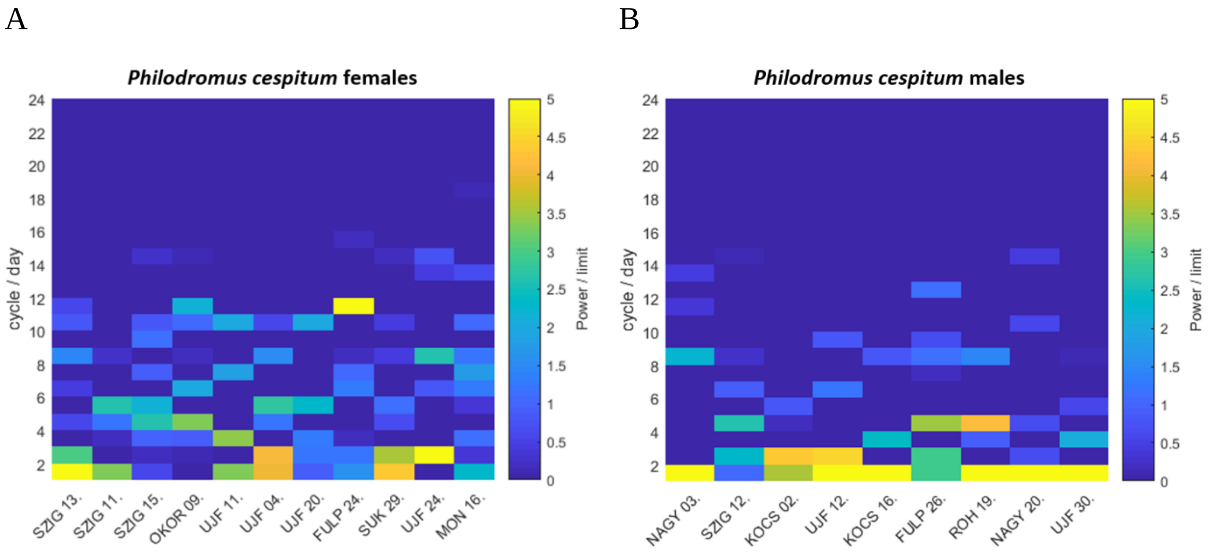

Figure S3.6: Same as Figure S3.5 for *Philodromus cespitum*

Supplemental Tables

Supplemental tables for Study2

Table S2.1. Species composition and abundance of hunting spiders collected in the canopy of apple trees in organic apple orchards

	All spiders collected with prey (from 2013 to 2019)		Újfehértó, 2016/17, spiders collected with prey		Újfehértó, 2016/17, suction sampled spiders	
Taxa	Abundance	%	Abundance	%	Abundance	%
Anyphaenidae	**0**	**0.0%**	**0**	**0.0%**	**1**	**0.3%**
Anyphaena accentuata	0	0.0%	0	0.0%	1	0.3%
Cheiracanthiidae	**20**	**2.3%**	**3**	**0.7%**	**8**	**2.6%**
Cheiracanthium cf. *virescens*	1	0.1%	0	0.0%	0	0.0%
Cheiracanthium sp.	19	2.2%	3	0.7%	8	2.6%
Clubionidae	**86**	**9.8%**	**57**	**12.6%**	**28**	**9.2%**
Clubiona frutetorum	10	1.1%	5	1.1%	4	1.3%
Clubiona sp.	76	8.7%	52	11.5%	23	7.5%
Porrhoclubiona leucaspis	0	0.0%	0	0.0%	1	0.3%
Oxyopidae	**17**	**1.9%**	**5**	**1.1%**	**1**	**0.3%**
Oxyopes ramosus	14	1.6%	4	0.9%	0	0.0%
Oxyopes sp.	3	0.3%	1	0.2%	1	0.3%
Philodromidae	**248**	**28.2%**	**76**	**16.8%**	**109**	**35.7%**
Philodromus cespitum	233	26.5%	73	16.2%	9	3.0%
Philodromus longipalpis	4	0.5%	0	0.0%	0	0.0%
Philodromus margaritatus	1	0.1%	0	0.0%	0	0.0%
Philodromus rufus	3	0.3%	2	0.4%	0	0.0%
Philodromus sp. (*aureolus* gr.)	5	0.6%	0	0.0%	100	32.8%
Tibellus oblongus	2	0.2%	1	0.2%	0	0.0%
Pisauridae	**2**	**0.2%**	**1**	**0.2%**	**1**	**0.3%**
Pisaura mirabilis	2	0.2%	1	0.2%	1	0.3%
Salticidae	**363**	**41.3%**	**240**	**53.1%**	**105**	**34.4%**
Ballus chalybeius	0	0.0%	0	0.0%	1	0.3%
Carrhotus xanthogramma	303	34.5%	214	47.3%	74	24.3%
Evarcha arcuata	2	0.2%	1	0.2%	0	0.0%
Evarcha falcata	2	0.2%	1	0.2%	0	0.0%
Heliophanus auratus	11	1.3%	3	0.7%	4	1.3%
Heliophanus cupreus	17	1.9%	5	1.1%	14	4.6%
Heliophanus sp.	1	0.1%	0	0.0%	0	0.0%
Macaroeris nidicolens	2	0.2%	0	0.0%	0	0.0%
Marpissa muscosa	2	0.2%	0	0.0%	0	0.0%
Pseudicius encarpatus	7	0.8%	4	0.9%	4	1.3%
Salticidae sp.	0	0.0%	0	0.0%	1	0.3%
Salticus scenicus	15	1.7%	12	2.7%	5	1.6%
Salticus sp.	1	0.1%	0	0.0%	2	0.7%
Thomisidae	**142**	**16.2%**	**70**	**15.5%**	**52**	**17.0%**
Ebrechtella tricuspidata	53	6.0%	24	5.3%	16	5.2%
Misumena vatia	24	2.7%	15	3.3%	11	3.6%
Runcinia grammica	1	0.1%	0	0.0%	0	0.0%
Synema globosum	4	0.5%	1	0.2%	0	0.0%
Tmarus piger	11	1.3%	8	1.8%	5	1.6%
Xysticus acerbus	3	0.3%	1	0.2%	0	0.0%
Xysticus cristatus	1	0.1%	1	0.2%	0	0.0%
Xysticus kochi	8	0.9%	4	0.9%	0	0.0%
Xysticus lanio	2	0.2%	2	0.4%	0	0.0%
Xysticus sp.	18	2.1%	7	1.5%	18	5.9%
Xysticus (*Spiracme*) *striatipes*	8	0.9%	3	0.7%	1	0.3%
Xysticus ulmi	9	1.0%	4	0.9%	1	0.3%
Sum	878	100.0%	452	100.0%	305	100.0%

Table S2.2. Taxonomic composition of the most abundant arboreal hunting spider groups collected in organic apple orchards

	All spiders collected with prey (from 2013 to 2019)		Újfehértó, 2016/17, spiders collected with prey		Újfehértó, 2016/17, suction sampled spiders	
Taxa	Abundance	%*	Abundance	%*	Abundance	%*
C. xanthogramma	303	34.5%	214	47.4%	74	24.3%
Other salticids	60	6.8%	26	5.8%	31	10.2%
Ph. cespitum	233	26.5%	73	16.2%	109	35.7%
E. tricuspidata	53	6.0%	24	5.3%	16	5.3%
Xysticus spp.	49	5.6%	22	4.9%	20	6.6%
Clubiona spp.	86	9.8%	57	12.6%	28	9.2%
Sum	784	89.3%	416	92.0%	278	91.2%

*Relative to the whole arboreal hunting spider assemblage

Table S2.3. Number of hunting spiders collected monthly by spider groups

Month/Taxa	*C. xanthogramma*	Other salticids	*Ph. cespitum*	*E. tricuspidata*	*Xysticus* spp.	*Clubiona* spp.*
All collected spiders with prey						
April	9	9	67	18	13	15
May	36	22	106	11	4	14
June	25	7	37	4	4	4
July	126	9	16	5	15	5
August	38	5	4	7	5	9
September	52	4	2	8	8	26
October	17	4	1	0	0	12
Újfehértó, 2016/17, collected spiders with prey						
April	4	4	28	8	7	9
May	18	6	17	6	1	4
June	23	3	11	2	1	2
July	110	6	14	4	8	5
August	27	2	1	3	5	7
September	15	1	1	1	0	17
October	17	4	1	0	0	12
Újfehértó, 2016/17, suction sampled spiders						
April	3	1	39	5	0	0
May	3	10	30	0	0	1
June	5	3	19	0	3	4
July	23	5	4	0	11	3
August	16	9	6	7	4	10
September	13	2	2	2	1	8
October	11	1	9	2	1	2

Two matrices were compared with Mantel test

*One record collected in March is not indicated in this Table.

Table S2.4. Number of the actual and potential prey items of arboreal hunting spiders by prey groups and months

Month/Taxa	Araneae	Coleoptera	Lepidoptera	Formicidae [a]	Other Hymenoptera	Brachycera	Nematocera	Auchenorrhyncha	Heteroptera	Sternorrhyncha [b]	Other [c]
All collected spiders - Actual prey											
April	6	8	4	6	1	15	58	0	4	42	3
May	14	23	1	7	2	40	80	1	2	46	2
June	1	1	0	6	0	34	12	2	2	35	2
July	15	3	4	33	8	36	26	8	4	37	12
August	6	1	2	1	1	26	8	4	14	7	0
September	14	3	4	11	8	15	14	13	14	20	4
October	1	0	0	4	0	3	7	2	2	20	0
Újfehértó, 2016/17, - Actual prey											
April	2	5	2	3	1	4	26	0	0	24	1
May	3	10	0	6	1	18	13	1	0	7	1
June	0	1	0	3	0	12	8	0	0	24	0
July	10	1	3	26	8	32	25	7	2	30	10
August	5	1	2	0	1	19	6	4	4	5	0
September	2	0	2	2	4	6	8	4	4	4	0
October	1	0	0	3	0	2	6	2	2	20	0
Újfehértó, 2016/17, suction sampled - Potential prey											
April	61	85	4	6	7	50	134	25	16	14	29
May	59	998	4	425	19	141	143	10	14	170	11
June	48	149	18	142	9	162	39	17	22	5996	25
July	62	52	8	42	15	39	75	136	37	16	15
August	56	30	13	24	6	18	14	195	62	5	13
September	45	53	8	5	12	47	62	248	137	5	17
October	65	49	3	3	21	27	260	246	25	70	28

Two matrices were compared with Mantel test

[a] One record collected in March is not indicated in this Table.

[b] Two records collected in March is not indicated in this Table.

[c] Acari, Ephemeroptera, Neuroptera, Psocoptera, Thysanoptera, Trichoptera, while in case of Potential prey, Orthoptera, Raphidioptera and Indet were also included.

Table S2.5. Prey items of the six most abundant arboreal hunting spider groups

Prey/Predator	*C. xanthogramma*	Other salticids	*Ph. cespitum*	*E. tricuspidata*	*Xysticus* spp.	*Clubiona* spp.
Újfehértó, 2016-2017						
Araneae	14	2	2	1	1	2
Coleoptera	6	1	1	2	5	0
Lepidoptera	4	0	0	1	0	3
Formicidae	22	0	0	0	8	3
Other Hymenoptera	6	1	1	3	0	1
Brachycera	60	7	8	5	3	5
Nematocera	26	7	30	8	1	13
Auchenorrhyncha	9	0	4	0	1	4
Heteroptera	6	0	1	0	3	2
Sternorrhyncha	53	8	22	4	0	24
Other prey*	8	0	4	0	0	0
All sites and sampling dates except 2016-2017, Újfehértó						
Araneae	14	4	8	1	1	3
Coleoptera	5	1	0	1	8	0
Lepidoptera	0	1	0	1	0	1
Formicidae	3	0	0	1	12	0
Other Hymenoptera	3	2	0	0	0	0
Brachycera	16	6	28	6	0	8
Nematocera	10	3	75	9	3	4
Auchenorrhyncha	6	1	1	0	0	1
Heteroptera	9	4	3	6	2	1
Sternorrhyncha	17	11	42	4	1	11
Other prey*	6	1	3	0	0	0

Two matrices were compared with Mantel test

*Acari, Ephemeroptera, Neuroptera, Psocoptera, Thysanoptera, Trichoptera

Table S2.6. Raw data of the trophic web (Fig. 2.5 based on abundance data).
Taxonomic and economic composition of natural prey of hunting spider groups for all sites and years

Prey/Predator	***C. xanthogramma***		**Other salticids**		***Ph. cespitum***		***E. tricuspidata***		***Xysticus* spp.**		***Clubiona* spp.**	
Acari	0	0.0%	0	0.0%	3	1.3%	0	0.0%	0	0.0%	0	0.0%
Araneae	28	9.2%	6	10.0%	10	4.3%	2	3.8%	2	4.1%	5	5.8%
Coleoptera	11	3.6%	2	3.3%	1	0.4%	3	5.7%	13	26.5%	0	0.0%
Lepidoptera	4	1.3%	1	1.7%	0	0.0%	2	3.8%	0	0.0%	4	4.7%
Formicidae	25	8.3%	0	0.0%	0	0.0%	1	1.9%	20	40.8%	3	3.5%
Other Hymenoptera	9	3.0%	3	5.0%	1	0.4%	3	5.7%	0	0.0%	1	1.2%
Brachycera	76	25.1%	13	21.7%	36	15.5%	11	20.8%	3	6.1%	13	15.1%
Nematocera	36	11.9%	10	16.7%	105	45.1%	17	32.1%	4	8.2%	17	19.8%
Auchenorrhyncha	15	5.0%	1	1.7%	5	2.1%	0	0.0%	1	2.0%	5	5.8%
Heteroptera	15	5.0%	4	6.7%	4	1.7%	6	11.3%	5	10.2%	3	3.5%
Sternorrhyncha	70	23.1%	19	31.7%	64	27.5%	8	15.1%	1	2.0%	35	40.7%
Ephemeroptera	2	0.7%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
Neuroptera	4	1.3%	1	1.7%	3	1.3%	0	0.0%	0	0.0%	0	0.0%
Psocoptera	5	1.7%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
Thysanoptera	2	0.7%	0	0.0%	1	0.4%	0	0.0%	0	0.0%	0	0.0%
Trichoptera	1	0.3%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
Natural enemy	58	19.1%	12	20.0%	21	9.0%	10	18.9%	6	12.2%	9	10.5%
Neutral	149	49.2%	27	45.0%	143	61.4%	31	58.5%	31	63.3%	34	39.5%
Pest	96	31.7%	21	35.0%	69	29.6%	12	22.6%	12	24.5%	43	50.0%
Sum:	303	100%	60	100%	233	100%	53	100%	49	100%	86	100%

Table S2.7. Taxonomic composition of actual and potential prey items of arboreal hunting spiders collected in apple orchards

	All collected spiders - Actual prey		Újfehértó, 2016/17, - Actual prey		Újfehértó, 2016/17, suction sampled - Potential prey	
Taxa	Abundance	%	Abundance	%	Abundance	%
Acari	3	0.3%	1	0.2%	14	0.1%
Araneae	57	6.5%	23	5.1%	396	3.5%
Coleoptera	39	4.4%	18	4.0%	1416	12.4%
Lepidoptera	15	1.7%	9	2.0%	58	0.5%
Formicidae	69	7.9%	44	9.7%	647	5.7%
Other Hymenoptera	20	2.3%	15	3.3%	89	0.8%
Brachycera	169	19.2%	93	20.6%	484	4.2%
Nematocera	205	23.3%	92	20.4%	727	6.4%
Auchenorrhyncha	30	3.4%	18	4.0%	877	7.7%
Heteroptera	42	4.8%	12	2.7%	313	2.7%
Sternorrhyncha	209	23.8%	116	25.7%	6276	55.0%
Ephemeroptera	3	0.3%	2	0.4%	1	0.0%
Neuroptera	8	0.9%	5	1.1%	92	0.8%
Psocoptera	5	0.6%	2	0.4%	15	0.1%
Thysanoptera	3	0.3%	2	0.4%	2	0.0%
Trichoptera	1	0.1%	0	0.0%	1	0.0%
Other*	0	0.0%	0	0.0%	13	0.1%
Sum	878	100.0%	452	100.0%	11421	100.0%

*Orthoptera, Raphidioptera, Indet

Table S2.8. Taxonomic composition of actual prey items of arboreal hunting spiders collected in apple orchards – pests. All sites and years are included.

Taxa	Abundance	%	Example
Auchenorrhyncha	**18**	**6.5%**	
Cicadellidae	2	0.7%	*Empoasca* sp.
Flatidae	16	5.8%	*Metcalfa pruinosa*
Coleoptera	**30**	**10.8%**	
Cerambycidae	1	0.4%	*Pogonocherus hispidus*
Curculionidae	29	10.5%	*Phyllobius betulinus*, *Ph. oblongus*, *Ph. virideaeris*, *Rhamphus* sp.
Heteroptera	**6**	**2.2%**	
Tingidae	6	2.2%	*Stephanitis pyri*
Lepidoptera	**14**	**5.1%**	
Arctiidae	1	0.4%	*Hyphantria cunea*
Gracillariidae	1	0.4%	*Phyllonorycter blancardella*
Indet leaf miners	2	0.7%	
Sesiidae	1	0.4%	*Synanthedon myopaeformis*
Tortricidae	9	3.2%	cf. *Recurvaria* sp.
Sternorrhyncha	**209**	**75.5%**	
Aphididae	198	71.5%	*Aphis pomi*, *Dysaphis devecta*, *D. plantaginea*
Psyllidae	11	4.0%	*Cacopsylla mali*, *C. melanoneura*
Sum	277	100.0%	

Table S2.9. Taxonomic composition of actual prey items of arboreal hunting spiders collected in apple orchards – natural enemies. All sites and years are included.

Taxa	Abundance	%	Example
Acari	**2**	**1.6%**	Trombidiidae sp.
Araneae	**57**	**44.5%**	
Araneidae	5	3.9%	*Cyclosa oculata*, *Mangora acalypha*
Cheiracanthiidae	1	0.8%	*Cheiracanthium* sp.
Clubionidae	5	3.9%	*Clubiona frutetorum*
Linyphiidae	3	2.3%	*Erigone dentipalpis*, *Gongylidiellum murcidum*, *Porrhomma microphthalmum*
Lycosidae	1	0.8%	
Philodromidae	9	7.0%	*Philodromus cespitum*
Salticidae	13	10.2%	*Carrhotus xanthogramma*, *Heliophanus auratus*, *H. cupreus*, *Salticus* sp.
Theridiidae	5	3.9%	*Dipoena melanogaster*, *Lasaeola prona*, *Theridion* sp.
Thomisidae	3	2.3%	*Ebrechtella tricuspidata*, *Ozyptila* sp., *Xysticus* sp.
Indet	12	9.4%	
Brachycera	**14**	**10.9%**	
Syrphidae	14	10.9%	*Episyrphus balteatus*, *Eupeodes corollae*
Coleoptera	**4**	**3.1%**	
Carabidae	1	0.8%	
Coccinellidae	2	1.6%	*Adalia decempunctata*, *Stethorus* sp.
Staphylinidae	1	0.8%	
Heteroptera	**26**	**20.3%**	
Anthocoridae	6	4.7%	*Orius* sp.
Miridae	20	15.6%	*Agnocoris* sp., *Campylomma verbasci*, *Deraeocoris ruber*, *Pilophorus perplexus*
Neuroptera	**8**	**6.3%**	Chrysopidae sp., Hemerobiidae sp.
Hymenoptera	**17**	**13.3%**	Hymenoptera Parasitica spp.
Sum	128	100.0%	

Table S2.10. Ivlev’s electivity indices based on the actual and potential prey of the arboreal hunting spider assemblage, Újfehértó, Hungary, 2016-2017. Comparison of the proportion of each prey group in the actual and potential prey based on model contrasts.

Taxa/Economic category	Ivlev's index	*P*[a]
Araneae	0.0568	0.7185
Coleoptera	-0.5472	0.0003
Lepidoptera	0.4897	0.0765
Formicidae	0.2080	0.1415
Other Hymenoptera	0.4986	0.0914
Brachycera	0.5789	0.0023
Nematocera	0.4018	0.0246
Auchenorrhyncha	-0.3143	0.0534
Heteroptera	-0.1067	0.2658
Sternorrhyncha	0.0191	0.0814
Other prey[b]	0.0295	0.8313
Natural enemy	0.0908	0.8941
Neutral	0.4084	0.0017
Pest	-0.3050	0.0023

[a] GLMM-b contrasts

[b] Acari, Ephemeroptera, Neuroptera, Psocoptera, Thysanoptera, Trichoptera

Table S2.11. Similarity (trophic niche overlap index) between the prey of the six hunting spider groups

	C. xanthogramma	Other salticids	*Ph. cespitum*	*E. tricuspidata*	*Xysticus* spp.
	Niche overlap based on prey taxonomic composition				
Other salticids	0.815	*	*	*	*
Ph. cespitum	**0.612**	**0.694**	*	*	*
E. tricuspidata	**0.663**	0.730	0.690	*	*
Xysticus spp.	**0.393**	**0.321**	**0.246**	**0.379**	*
Clubiona spp.	**0.703**	0.773	**0.709**	0.641	**0.294**
	Niche overlap based on prey size				
Other salticids	0.887	*	*	*	*
Ph. cespitum	0.833	0.840	*	*	*
E. tricuspidata	0.883	0.832	0.858	*	*
Xysticus spp.	0.898	0.806	0.764	0.893	*
Clubiona spp.	0.800	0.861	0.777	0.725	0.719
	Overall niche overlap				
Other salticids	0.851	*	*	*	*
Ph. cespitum	**0.722**	**0.767**	*	*	*
E. tricuspidata	**0.773**	0.781	0.774	*	*
Xysticus spp.	**0.645**	**0.563**	**0.505**	**0.636**	*
Clubiona spp.	**0.751**	0.817	**0.743**	**0.683**	**0.506**

0 index value means no overlap, whereas values close to 1 reflect similar resource utilization spectra.

Species pairs occupying statistically different niches, as identified by null model tests, are indicated in bold (adjusted $\alpha = 0.0033$).

Table S2.12. Similarity (trophic niche overlap index) between the prey of the six hunting spider groups.
C. xanthogramma and *Ph. cespitum* were split to juveniles and adults

	C. xanthogramma juveniles	*C. xanthogramma* adults	Other salticids	*Ph. cespitum* juveniles	*Ph. cespitum* adults	*E. tricuspidata*	*Xysticus* spp.
	Niche overlap based on prey taxonomic composition						
C. xanthogramma adults	0.784	*	*	*	*	*	*
Other salticids	0.801	0.783	*	*	*	*	*
Ph. cespitum juveniles	**0.542**	**0.465**	**0.588**	*	*	*	*
Ph. cespitum adults	0.737	0.702	0.804	**0.707**	*	*	*
E. tricuspidata	**0.637**	0.655	0.730	**0.622**	0.723	*	*
Xysticus spp.	**0.392**	**0.382**	**0.321**	**0.216**	**0.255**	**0.379**	*
Clubiona spp.	**0.707**	**0.647**	0.773	**0.604**	0.788	0.641	**0.294**
	Niche overlap based on prey size						
C. xanthogramma adults	**0.661**	*	*	*	*	*	*
Other salticids	0.912	**0.712**	*	*	*	*	*
Ph. cespitum juveniles	0.825	**0.629**	0.814	*	*	*	*
Ph. cespitum adults	0.837	**0.738**	0.852	0.855	*	*	*
E. tricuspidata	0.806	0.755	0.832	0.805	0.929	*	*
Xysticus spp.	0.795	0.785	0.806	**0.726**	0.831	0.893	*
Clubiona spp.	0.888	**0.598**	0.861	0.786	0.762	0.725	0.719
	Overall niche overlap						
C. xanthogramma adults	**0.723**	*	*	*	*	*	*
Other salticids	0.856	**0.748**	*	*	*	*	*
Ph. cespitum juveniles	**0.684**	**0.547**	**0.701**	*	*	*	*
Ph. cespitum adults	**0.787**	**0.720**	0.828	**0.781**	*	*	*
E. tricuspidata	**0.722**	**0.705**	0.781	**0.714**	0.826	*	*
Xysticus spp.	**0.594**	**0.584**	**0.563**	**0.471**	**0.543**	**0.636**	*
Clubiona spp.	0.798	**0.623**	0.817	**0.695**	0.775	**0.683**	**0.506**

0 index value means no overlap, whereas values close to 1 reflect similar resource utilization spectra.
Species pairs occupying statistically different niches, as identified by null model tests, are indicated in bold (adjusted $\alpha = 0.0018$).

Table S2.13. Coefficients of prey taxa vs. spider groups and the environmental predictors (fourth-corner model)

Prey taxa / Predictors	*C. xanthogramma*	Other salticids	*Ph. cespitum*	*E. tricuspidata*	*Xysticus* spp.	*Clubiona* spp.	Spring	Summer	Fall
Araneae	0.013	0.007	0	-0.046	0	0	0.069	0	0
Coleoptera	0.030	0	-0.157	0	0.265	-0.094	0.321	-0.030	0
Lepidoptera	-0.051	0	-0.095	0.046	0	0.087	0	0	0
Formicidae	0.039	-0.113	-0.188	0	0.303	0	-0.029	0.121	0
Other Hymenoptera	0	0.069	0	0.089	0	0	-0.035	0	0.095
Brachycera	0	0	0.029	0	-0.052	0	0	0	-0.117
Nematocera	-0.058	-0.039	0.115	0.021	-0.031	0	0.152	0	0
Auchenorrhyncha	0	0	0.072	-0.035	0	0.025	-0.164	0	0.111
Heteroptera	-0.030	0	-0.005	0.076	0.107	-0.012	-0.084	0	0.012
Sternorrhyncha	0	0.036	0.093	-0.029	-0.136	0.089	0.046	0	-0.015
Other prey*	0.044	0	0.102	0	0	-0.032	0	0.040	0

*Acari, Ephemeroptera, Neuroptera, Psocoptera, Thysanoptera, Trichoptera

Coefficients (in absolute value) ≥ 0.03 are highlighted in red (positive associations) or in blue (negative associations).

Table S2.14. Trophic niche widths (Levins' *B*), predator-prey size data and niche widths with respect to size (s^2) for different life stages of *C. xanthogramma* and *Ph. cespitum*

	C. xanthogramma juveniles	*C. xanthogramma* adults	*Ph. cespitum* juveniles	*Ph. cespitum* adults
B	5.851	6.762	2.509	4.322
Spider prosoma width (mm), mean (SD)	1.48 (0.30)	2.48 (0.23)	1.24 (0.24)	1.87 (0.30)
Prey thorax width (mm), mean (SD)	0.97 (0.51)	1.52 (0.69)	0.81 (0.52)	1.09 (0.65)
Thorax-prosoma ratio, mean (SD)	0.65 (0.27)	0.61 (0.28)	0.64 (0.38)	0.58 (0.33)
s^2 absolute predator size	0.09 A	0.05 A	0.06 a	0.09 b
s^2 absolute prey size	0.26 A	0.46 B	0.23 a	0.40 b
s^2 prey-predator size ratio	0.07 A	0.08 A	0.15 a	0.11 a

Different capital letters indicate significant differences in *C. xanthogramma* and different lowercase letters indicate significant differences in *Ph. cespitum* at $P < 0.05$ level.

Table S2.15. Natural prey of juveniles and adults (subadults + adults) of *Carrhotus xanthogramma* and *Philodromus cespitum*

	Carrhotus xanthogramma				*Philodromus cespitum*			
	Abundance		%		Abundance		%	
	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults
Acari	0	0	0.0%	0.0%	1	2	0.8%	2.0%
Araneae	17	11	9.2%	9.6%	5	5	3.8%	5.1%
Coleoptera	1	10	0.5%	8.8%	1	0	0.8%	0.0%
Lepidoptera	3	1	1.6%	0.9%	0	0	0.0%	0.0%
Formicidae	22	2	11.9%	1.8%	0	0	0.0%	0.0%
Other Hymenoptera	4	4	2.2%	3.5%	0	1	0.0%	1.0%
Brachycera	48	28	25.9%	24.6%	13	23	9.8%	23.5%
Nematocera	25	10	13.5%	8.8%	75	28	56.4%	28.6%
Auchenorrhyncha	4	11	2.2%	9.6%	0	5	0.0%	5.1%
Heteroptera	8	6	4.3%	5.3%	1	3	0.8%	3.1%
Sternorrhyncha	45	25	24.3%	21.9%	35	29	26.3%	29.6%
Ephemeroptera	2	0	1.1%	0.0%	0	0	0.0%	0.0%
Neuroptera	2	2	1.1%	1.8%	1	2	0.8%	2.0%
Psocoptera	2	3	1.1%	2.6%	0	0	0.0%	0.0%
Thysanoptera	2	0	1.1%	0.0%	1	0	0.8%	0.0%
Trichoptera	0	1	0.0%	0.9%	0	0	0.0%	0.0%
Sum:	185	114	100.0%	100.0%	133	98	100.0%	100.0%

Supplemental tables for Study3

Table S3.1. Spiders used in the experiment and information about the collecting sites

ID	Mass (mg)	Sex	Date collected	Collecting sites^a	Coordinates	Treatment
				Carrhotus xanthogramma		
C_x_a_1	13.10	female	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_2	26.30	male	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_3	24.20	female	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_4	22.00	male	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_5	21.10	female	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_6	23.10	male	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_7	29.20	male	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_8	27.90	female	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_9	27.10	male	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_10	25.10	female	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_11	30.80	male	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_12	21.30	female	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_13	28.20	female	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_14	30.70	male	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_15	21.60	female	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_16	18.80	male	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_17	26.80	female	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_18	22.60	male	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_19	22.40	male	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_20	23.60	female	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
C_x_a_21*	13.90	female	2016.04.16	Újfehértó	47°49'13"N 21°39'58"E	organic
				Philodromus cespitum		
NAGY_03	5.70	male	2016.05.09	Nagykálló	47°53'17"N 21°48'56"E	organic
SZIG_13	8.50	female	2016.05.26	Szigetszentmiklós	47°21'53"N 19°00'19"E	abandoned
SZIG_12	7.20	male	2016.05.26	Szigetszentmiklós	47°21'53"N 19°00'19"E	abandoned
SZIG_11	6.80	female	2016.05.26	Szigetszentmiklós	47°21'53"N 19°00'19"E	abandoned
KOCS_02	7.50	male	2016.05.10	Kocsord	47°56'26"N 22°24'13"E	IPM
SZIG_15	9.30	female	2016.05.26	Szigetszentmiklós	47°21'53"N 19°00'19"E	abandoned
UJF_12	6.40	male	2016.05.10	Újfehértó	47°49'13"N 21°39'58"E	organic
OKOR_09	11.50	female	2016.05.10	Ököritófülpös	47°55'21"N 22°27'51"E	organic
OKOR_16*	6.10	male	2016.05.10	Ököritófülpös	47°55'21"N 22°27'51"E	organic
UJF_11	9.50	female	2016.05.10	Újfehértó	47°49'13"N 21°39'58"E	organic
KOCS_16	10.20	male	2016.05.10	Kocsord	47°56'26"N 22°24'13"E	IPM
UJF_04	12.60	female	2016.05.10	Újfehértó	47°49'13"N 21°39'58"E	organic
UJF_19*	4.80	male	2016.05.10	Újfehértó	47°49'13"N 21°39'58"E	organic
UJF_20	8.90	female	2016.05.10	Újfehértó	47°49'13"N 21°39'58"E	organic
FULP_26	8.80	male	2016.05.10	Fülpösdaróc	47°56'18"N 22°29'17"E	organic
FULP_24	10.10	female	2016.05.10	Fülpösdaróc	47°56'18"N 22°29'17"E	organic
ROH_19	7.30	male	2016.05.09	Rohod	48°00'58"N 22°08'10"E	IPM
NAGY_20	7.40	male	2016.05.09	Nagykálló	47°53'17"N 21°48'56"E	organic
SUK_29	10.10	female	2016.05.17	Sükösd	46°17'60"N 19°00'21"E	organic
UJF_30	7.20	male	2016.05.10	Újfehértó	47°49'13"N 21°39'58"E	organic
UJF_24	9.80	female	2016.05.10	Újfehértó	47°49'13"N 21°39'58"E	organic
MON_16	8.40	female	2016.05.18	Monorierdő	47°19’11”N 19°31’13”E	organic

* specimens excluded from the analysis because of their early death

^{a} apple orchards