Turkish Journal of Zoology

Volume 42 | Number 4 Article 10

1-1-2018

Diel and seasonal activity of ground dwelling spiders (Araneae) in a sandy grassland habitat

ANNA KRÓL

IZABELA HAJDAMOWICZ

CEZARY TKACZUK

TÜBİTAK

Turkish Journal of Zoology

http://journals.tubitak.gov.tr/zoology/

Research Article

Turk J Zool
(2018) 42: 439-448
© TÜBİTAK
doi:10.3906/zoo-1802-46

Diel and seasonal activity of ground dwelling spiders (Araneae) in a sandy grassland habitat

Anna KRÓL[1,*], Izabela HAJDAMOWICZ[2], Cezary TKACZUK[1]

[1]Department of Plant Protection and Breeding, Faculty of Natural Sciences, Siedlce University of Natural Sciences and Humanities, Siedlce, Poland

[2]Department of Zoology, Institute of Biology, Faculty of Natural Sciences, University of Natural Sciences and Humanities, Siedlce, Poland

Received: 02.03.2018 • **Accepted/Published Online:** 14.05.2018 • **Final Version:** 26.07.2018

Abstract: The paper concerns the diel and seasonal activity of ground dwelling spiders on a sandy grassland in the Bug River Valley in East-Central Poland. The spiders were captured using pitfall traps in 2009 and 2010 from May to July. The material was collected one day a week, day and night. Traps were checked every 3 h, eight times a day. It was found that for spiders with larger bodies, from the families Lycosidae and Philodromidae, the peak of their activity was in the afternoon, and smaller spiders belonging to the families Linyphiidae and Tetragnathidae showed the greatest activity in the morning. Species *Pardosa palustris* and *Xerolycosa miniata* were dominant spiders of the studied grassland. The time of their highest diel activity was different by several hours. It was observed that *P. palustris* individuals were more numerous in that habitat in early June and *X. miniata* spiders from mid-June. Spiders of the dominant family Lycosidae were in the highest numbers in the second half of May and in early June, while most of the spiders of other families were captured before or after the period of prevailing presence of dominant spiders.

Key words: Species competition, cooccurrence, *Xerolycosa miniata*, *Pardosa palustris*

1. Introduction

In the course of evolution, organisms have evolved in terms of a variety of diel and seasonal rhythms, synchronizing their vital functions with the cyclic changes in their habitat, in its temperature, and in the amount of light it receives (Bell-Pedersen et al., 2005). Diel activity of predatory arthropods, including spiders, is determined by many factors such as tolerance to high temperatures and humidity, activity of potential preys, and the activity time of higher-order predators threatening them (Romero and Harwood, 2010; Watts et al., 2015). Different distributions of the activity of species with similar requirements in a given habitat during a 24-h cycle and throughout the season can be an important factor in reducing competition and enabling them to cohabit (Bayram, 1966; Krumpalova and Tuf, 2013).

Most spider species living around the world are active at night. This is mainly due to lower overnight pressure from predators such as birds or reptiles, and the availability of a large number of preys, mainly insects (Van Berkum, 1982; Mestre et al., 2013). Many species of spiders have perfectly adapted to nightlife; web spiders can build their webs with little light and catch a prey even in total darkness. In Central Europe, however, most spiders are active during the day (Krumpalova and Tuf, 2013). Spiders that are active during the day are usually those species that use their sense of sight to hunt successfully. These are mainly spiders of the families Salticidae and Thomisidae, and a majority of the species of the family Lycosidae. Representatives of those families actively hunt their prey without using webs. There are also spiders that are active both at night and during the day, such as species of the family Oxyopidae (Foelix, 1996; Uetz et al., 1999).

The literature provides information categorizing most of the known species and families of spiders as nocturnal or diurnal (Foelix, 1996; Uetz et al., 1999). However, the diel activity of only a few European species was described in detail (Alderweireldt, 1994; Lundgren et al., 2009; Krumpalova and Tuf, 2013). Such information may be relevant for plant protection against pests. It is widely known that spiders belong to the most abundant invertebrate predators capable of reducing populations of insects, some of which are harmful to crops (Symodson et al., 2002; Harwood et al., 2004, 2005; Chatterjee et al.,

* Correspondence: anna.krol@uph.edu.pl

2009). Furthermore, crop fields are mainly colonized by species living in open habitats like grasslands (Nyffeler and Sunderland, 2003).

Abundance peaks of various spider families can occur in different months. Relatively big spiders of the family Lycosidae mostly have one abundance peak in the growing season, which is from May to July, but it fluctuates throughout the year for species belonging to the family Linyphiidae (Bel'skaya and Esyunin, 2003; Jõgar et al., 2004). Phenological differences in the species of spiders depending on the environment type were also noted in the literature (Szymkowiak and Woźny, 1998; Samu and Szinetar, 2002).

The knowledge of the exact time of the activity of individual spider species during the day and throughout the season could be used to increase the efficiency of spiders as biological control agents against insects feeding on crop plants and to determine the optimum time of plant protection product application so that beneficial organisms are not harmed (Lundgren et al., 2009; Romero and Harwood, 2010).

The aim of the present study was to learn about the composition of species and to describe patterns of daily and seasonal activity of ground dwelling spiders on a sandy grassland area, as a model habitat with small spatial diversity of vegetation. The present study tried to answer the questions of whether the species with small and large body sizes had different diel and seasonal activity peaks and whether dominant species were different from each other in their highest activity time during the day and the season.

2. Materials and methods

The present study was carried out in the Bug River Valley in East-Central Poland in the Bug Valley Landscape Park. A sandy grassland habitat of 210 m^2 was selected in the Commune of Korczew, Masovian Voivodeship (52°24′N, 22°34′E). Those grasslands are characterized by relatively rare and low vegetation (Matuszkiewicz, 2006). The area where the study was conducted was floodplain with desiccated alluvial soil. The study plot was surrounded mostly by mesic and wet meadow habitats. The surface vegetation was classified as the *Sileno-Festucetum trachyphyllae* community with *Koelerion glaucae* belonging to the class *Koelerio-Corynephoretea* (Matuszkiewicz, 2006). The average vegetation cover was assessed as 70%–80%, and the dominant species in that habitat were *Sedum sexangulare*, *Thymus serphyllum*, *Arenaria serphyllifolia*, *Poa angustifolia*, and *Silene otites*.

The study was conducted in 2009 and 2010 from May to July in the period of the greatest seasonal activity of spiders. The material was collected during a 24-h cycle one day a week, and the spiders were captured with pitfall traps. The data obtained with this method consist of the number and activity of arthropods, informing about the so-called activity density (Thomas et al., 2006). In the present study, 30 traps were set every 2 m in two rows that were 7 m apart from each other. Cups with a diameter of 68 mm and a depth of 70 mm were filled with 50% glycol, and detergent was added to reduce the surface tension of the liquid. There were eight collections every 3 h during 24 h, and the cups were checked at 0300, 0600, 0900, 1200, 1500, 1800, 2100, and 2400 hours. The collected material was placed in test tubes filled with 75% ethanol. The spiders were assigned to species after studying their morphological features on the basis of copulating organs observed under an SMZ 2B Nikon stereoscopic microscope. To determine the species, identification keys of Roberts (1996) and Nentwig et al. (www.araneae.unibe.ch) were used.

The significance of the differences among the number of dominant species during the season was determined with the Mann–Whitney U test. Statistical analysis was performed with Statistica 12.5. Daily activity patterns of families of spiders were evaluated with correspondence analysis (CA) using Past 2.17c. Spider taxa and body size categories were listed according to the directory of Platnick (http://research.amnh.org/iz/spiders/catalog.html).

3. Results

During the course of the present study, a total of 1732 specimens of spiders were captured, of which 1699 adult spiders were used for the analysis. Forty-three species belonging to 12 families were identified (Table 1). The most numerous families were Lycosidae and Philodromidae. Species belonging to the family Lycosidae, *Pardosa palustris* and *Xerolycosa miniata*, were the two main dominant species. They accounted for more than 80% of all the gathered individuals. The third but far less numerous species was *Thanatus arenarius*, belonging to the family Philodromidae, constituting 5% of the spider assemblage. The spiders of the families Thomisidae, Linyphiidae, and Tetragnathidae had an above 1% share (Table 1).

3.1. Diel activity

Spiders from the most abundant families (Lycosidae, Linyphiidae, Tetragnathidae, Philodromidae, and Thomisidae) were captured during the day and at night. However, by far the greatest number of individuals were active during the day. The only one captured only at night was the largest species, *Trochosa ruricola*, belonging to the family Lycosidae (Table 1). Other spiders could be divided into two groups. The first group, with larger body sizes, consisted of spiders from the families Lycosidae, Philodromidae, and Thomisidae. Representatives of the family Lycosidae were active all day (from 0600 to 2100 hours), and the peak of their activity was between 1200 and 1500 hours. Spiders of *T. arenarius*, the only representatives

Table 1. The number of adult individuals of ground dwelling spiders collected in the sandy grassland habitat at particular times of the day.

Species and families	Pitfalls checking time (hours)							
	0300	0600	0900	1200	1500	1800	2100	2400
Theridiidae								
Enoplognatha latimana					1			
Asagena phalerata						1		
Linyphiidae								
Erigone atra				1				1
Erigone dentipalpis	5	3	10	10	4		3	2
Erigonoplus foveatus						1		
Agyneta affinis		1		2		1		
Agyneta rurestris			1			1		
Metopobactrus prominulus				3				
Microlinyphia pusilla					1	2		
Pelecopsis parallela		6	1	1	1			1
Trichopterna cito			1	2				
Walckenaeria atrotibialis			1	1	2			
Tetragnathidae								
Pachygnatha clercki	1							
Pachygnatha degeeri	1	1	6	3		1	1	1
Araneidae								
Mangora acalypha				1				
Lycosidae								
Alopecosa cuneata	2		1		13	7	2	
Alopecosa pulverulenta					1			
Pardosa agricola						2		
Pardosa amentata				1				
Pardosa lugubris							1	
Pardosa monticola						1	1	
Pardosa paludicola		1						
Pardosa palustris	3	7	64	144	222	116	12	6
Pardosa prativaga			1		5	5	2	
Pardosa pullata							1	
Pirata hygrophilus		1						
Trochosa ruricola	2	1	1	1			4	7
Xerolycosa miniata	15	33	84	148	179	195	132	51
Hahniidae								
Hahnia nava				1				
Eutichuridae								
Cheiracanthium campestre	2							
Clubionidae								
Clubiona neglecta		1	1					

Table 1. (Continued).

Gnaphosidae								
Drassyllus praeficus			1	1		2		
Drassyllus pusillus			1			1		
Haplodrassus signifer		1				1		1
Zelotes electus							1	
Zelotes longipes						1		
Philodromidae								
Thanatus arenarius		1	1	22	37	27		
Thomisidae								
Ozyptila scabricula			1	1	1			1
Xysticus cristatus				7	6	1	2	
Xysticus kochi				3	1	5		
Salticidae								
Phlegra fasciata					2			
Talavera aequipes				1				
Heliophanus flavipes						1		
Total	31	57	176	354	476	372	162	71

of the family Philodromidae, were active from 0900 to 1800 hours with the peak of their activity between 1200 and 1500 hours. Thomisid spiders were captured between 0900 and 2100 hours. The other group of spiders, those of small and medium size, showed greater activity at earlier times of the day. The peak of the Linyphiidae activity was from 0900 to 1200 hours, although some individuals were captured 24 h a day. Representatives of the family Tetragnathidae showed the greatest activity from 0600 to 2100 hours, but they were captured 24 h a day with the exception of the period between 1200 and 1500 hours (Figure 1). CA showed that the diel activity patterns of spiders with smaller body sizes, i.e. Linyphiidae and Tetragnathidae, active in the morning, were the least similar to the rest of the larger spiders belonging to the families Lycosidae, Philodromidae, and Thomisidae (Figure 2). On the left side of the graph, families with afternoon activity were grouped, and on the right side families with morning activity. Axis number 1, which can be considered as a time axis, explained 70% of the variability in the diel activity among the spider families. The next axis, number 2, was responsible for 21% of the activity variability that can be explained by different but hard to recognize factors.

3.2. Seasonal activity

In the studied habitat, the period of the highest abundance and activity of Lycosidae spiders with body sizes of 5–20 mm was in the second half of May and in early June. Large numbers were also observed in the third week of June (Figure 3a). A small number of spiders from other families made data interpretation difficult; however, even with relatively few individuals, some trends were observed. In the case of the spiders from the family Philodromidae (4–12 mm), the majority of specimens were captured in the second half of May, and smaller-sized Linyphiidae individuals (1.2–5 mm) showed their greatest activity in July, outside the time of the activity of the rest of the spider assemblage (Figure 3b).

3.3. Seasonal changes in diel activity of dominant species

The two dominant species, *P. palustris* and *X. miniata*, were characterized by a similar body size (5 to 7.6 mm). They had the same time of the highest diel activity in May only, which was the month with the largest number of *P. palustris* and a relatively small number of *X. miniata.* While *P. palustris* spiders had the activity peak always at the same time during the day, for *X. miniata* it changed in consecutive months (Figures 4a–4f).

During all three months of the research, the activity peak of *P. palustris* spiders was between 1200 and 1500 hours. In May, the activity of individuals of this species was observed from 0900 to 1500 hours (Figure 4a), in June only between 1200 and 1500 hours (Figure 4c), and in July between 0900 and 1800 hours (Figure 4e).

In May, the spiders belonging to *X. miniata* were most active from 0900 to 1500 hours with a slight increase in their activity between 1200 and 1500 hours (Figure 4b). In June, they were most active after the time of the greatest activity of *P. palustris*, from 1500 to 1800 hours with quite a lot of activity occurring from 1200 to 1500 hours and between 1800 and 2100 hours (Figure 4d). However, in July, the activity of the spiders of this species decreased,

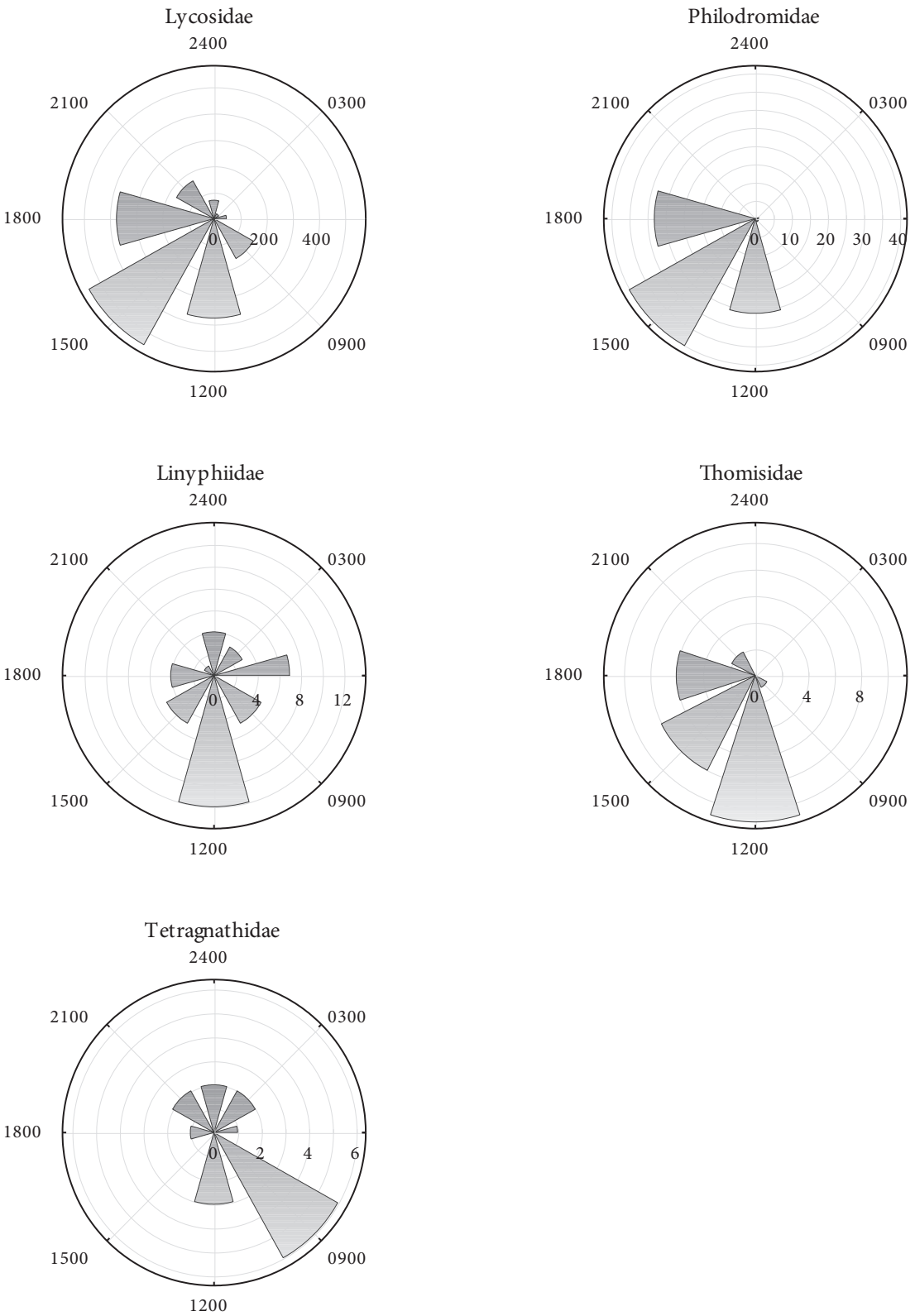

Figure 1. Diel activity of the dominant ground dwelling spider families of sandy grassland. The number of individuals collected at consecutive pitfall checking (for example: spiders collected at 1200 hours were active between 0900 and 1200 hours).

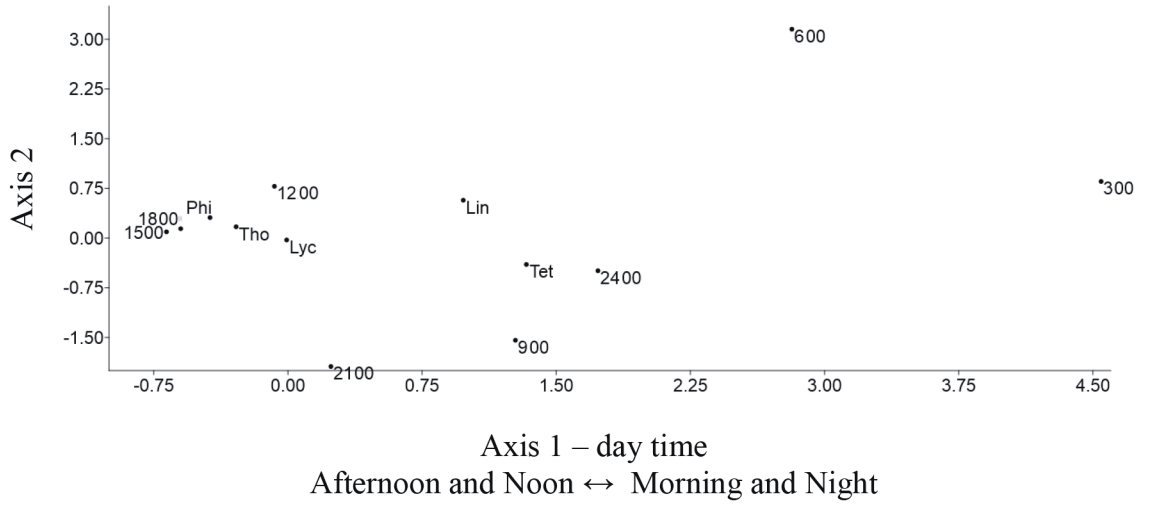

Figure 2. Correspondence analysis of diel activity of the dominant spider families in the sandy grassland habitat.

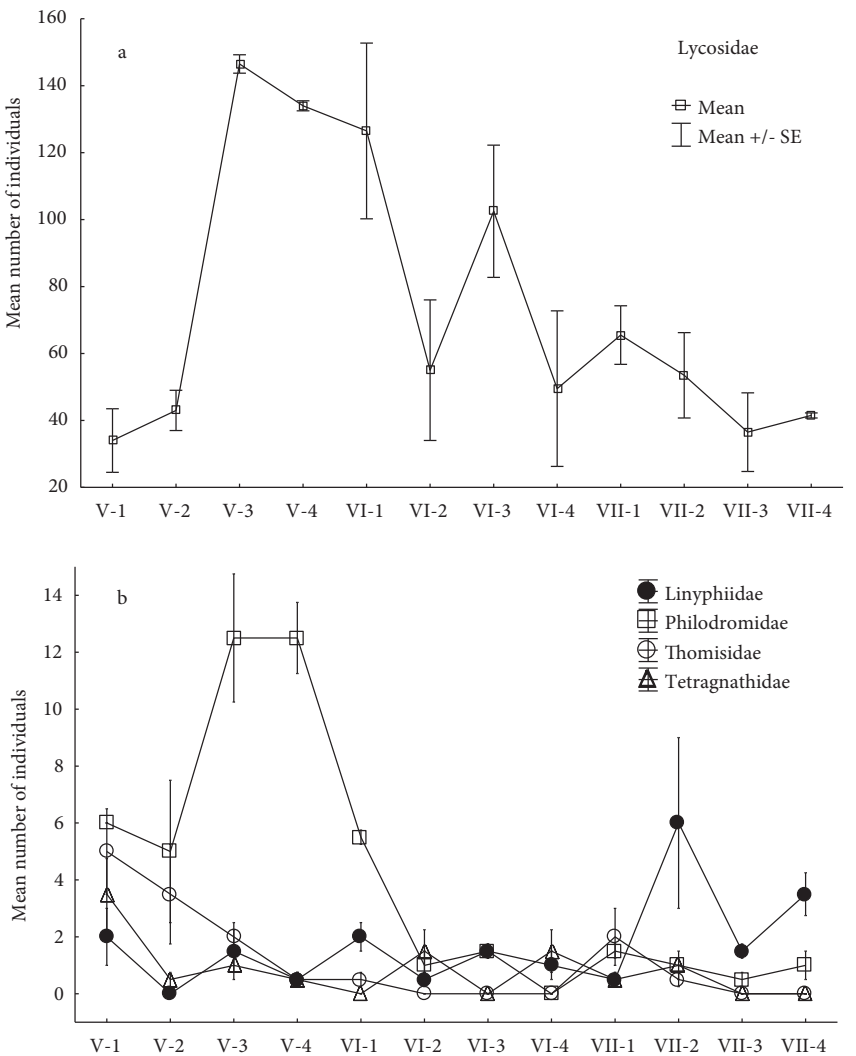

Figure 3. Seasonal dynamics of the number of spiders from particular families (Roman numerals represent months, while Arabic numerals are the subsequent weeks of the month).

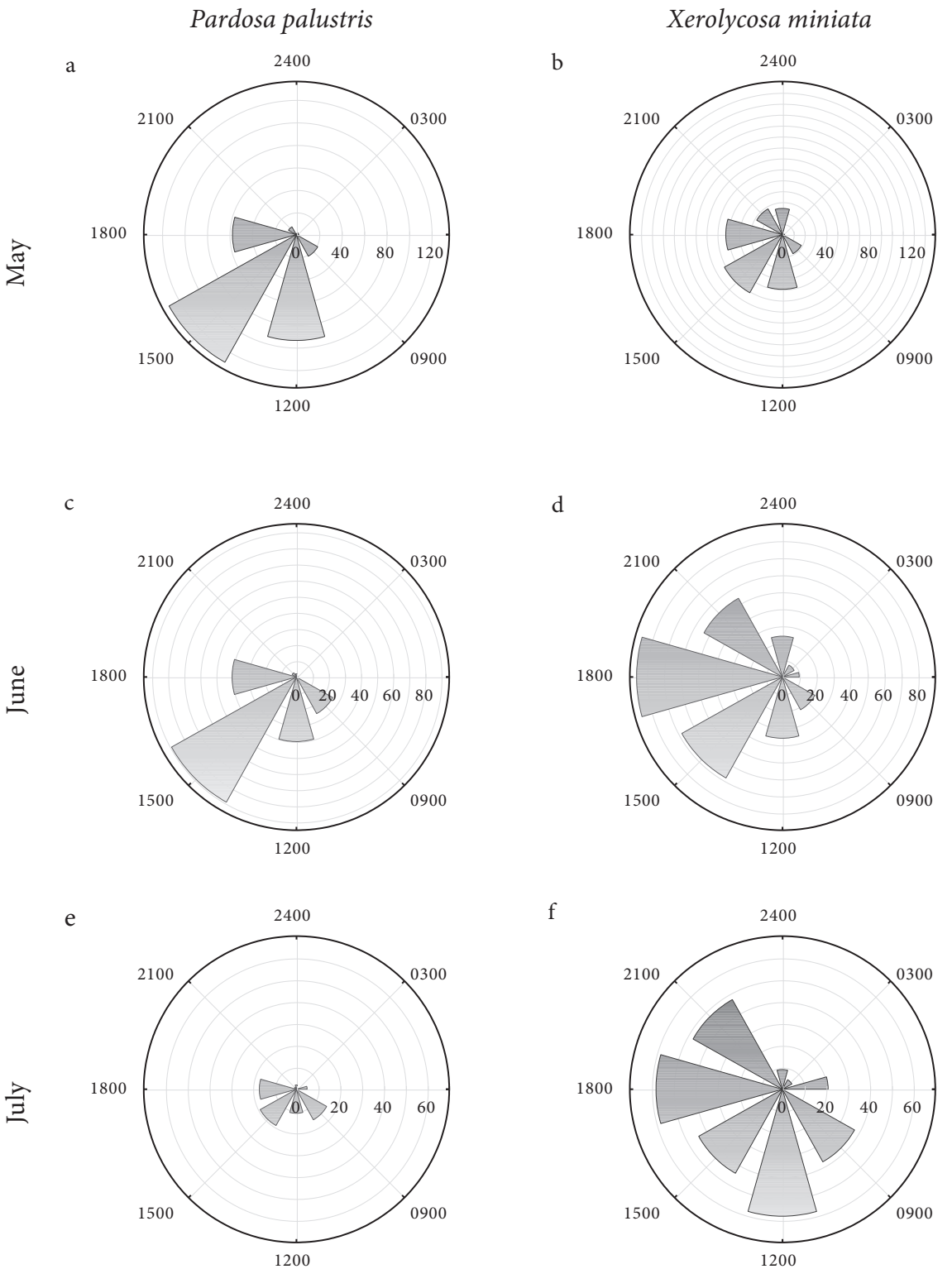

Figure 4. Seasonal changes in the diel activity of dominant spider species in the sandy grassland habitat.

and they were by far more numerous than the individuals of *P. palustris*. Relatively high activity of *X. miniata* was observed in July from 0600 to 2100 hours with peak activity between 0900 and 1200 hours and a decrease between 1200 and 1500 hours (Figure 4f).

3.4. Seasonal activity of the dominant species

The peak of seasonal activity of *P. palustris* was in May and in early June, and then it fell sharply. The activity of *X. miniata* was relatively steady from the third week of May to the end of July (Figure 5). The number of spiders belonging to those two species differed significantly in May and July 2009 and in June and July 2010, and after summarizing the results from both years, there were differences in each month throughout the season (Table 2).

4. Discussion

In the study area, the family Lycosidae dominated among ground dwelling spiders. They are active hunters that use the sense of sight to acquire food. Low and quite rare vegetation of sandy grasslands is a good habitat for spiders hunting this way (Honek, 1988). A significant dominance of just two species of spiders, *P. palustris* and *X. miniata*, belonging to the family Lycosidae, could partially be caused by the small variety of vegetation structure in this habitat. Diverse vegetation provides spatial niches and positively affects the abundance and diversity of insect and spider species living there (Pfiffner and Luca, 2003). Because of the uniform and low vegetation of the area, the spider species used the same food resources, which made them compete with each other. Additionally, spiders belong to the generalist predators feeding primarily on insects, but also on other spiders (Harwood and Obrycki, 2005; Samiayyan, 2014). When the allocation of niches in the area is limited, the activity distribution of dominant species throughout the day and the season may be more important.

We observed that spiders with larger bodies from the families Lycosidae and Philodromidae were most active in the afternoon and smaller spiders belonging to the families Linyphiidae and Tetragnathidae showed the greatest activity before noon. Similar dependencies were found by Krumpalova and Tuf (2013), who studied the diel activity of ground spiders in lowland forests and a surrounding open environment. Both in their study and in the present study, the largest species were active at night. Big spiders, which are more visible to birds as prey, are nocturnal, avoiding the pressure of these predators (Van Berkum, 1982).

The distribution of diel and seasonal activity of spiders was influenced also by the circadian rhythm and phenology of their potential preys. For spiders living on the ground, most of their diet is arthropods running around on the surface of the soil, largely represented by springtails (Collembola) with small body size (Nyffeler and Benz, 1988). In an open environment, such as grassland, they demonstrate mainly daily activity (Frampton et al., 2001; Krumpalova and Tuf, 2013). Other potential preys of ground spiders are aphids, which, according to the research of Ximenez-Embun et al. (2014), carried out in fields of alfalfa, are available for the spiders throughout the growing season with a peak of their activity during the afternoon. Different aphid species falling on the surface of the soil, or feeding on the lower parts of the plants, are common food for spiders living on the ground (Nyffeler and Sunderland, 2003; Schmidt et al., 2012; Chapman et al., 2013). In turn, many-legged Myriapoda, active at night,

Table 2. The results of the Mann–Whitney U test comparing the abundance of *Pardosa palustris* and *Xerolycosa miniata* species in particular months and years of research.

	Test value	P
2009		
May	4.33*	0.000015
June	−0.31	0.755736
July	−4.27*	0.000019
2010		
May	1.66	0.097092
June	−3.63*	0.00028
July	−4.56*	0.000005
2009 and 2010		
May	3.79*	0.000148
June	−2.65*	0.007941
July	−4.52*	0.00006

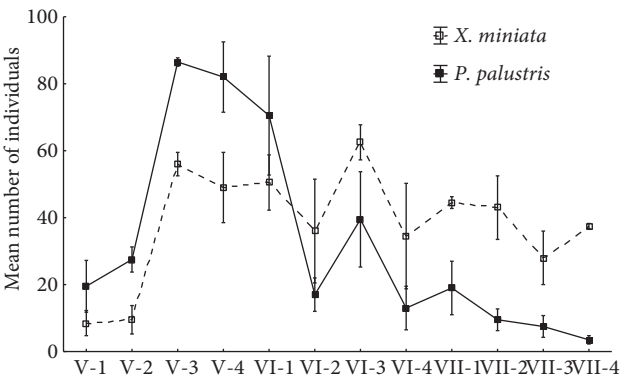

Figure 5. Seasonal changes in the number of spider species dominating in the sandy grassland habitat (average of two years of research ± SE).

are among bigger preys eaten by spiders with larger bodies (Tuf et al., 2006). Active hunters, including terrestrial spiders, prey on moving preys, thus synchronizing their daily activity cycle with that of their preys (Welch and Harwood, 2014).

Jõgar et al. (2004) indicated that the reason for seasonal dynamics of abundance of spiders in the family Lycosidae is, in addition to the availability of their preys, the impact of the habitat where they live. In May and in early June, in the fields of wheat and rape treated with chemical plant protection products, they found that those spiders were most active as late as July, while in the present study, in a sandy area, the largest activity of this family was in the second half of May and in early June.

The difference in the distribution of daily activity of large spiders of the families Lycosidae and Philodromidae and the small Linyphiidae spiders makes it possible that smaller spiders avoid the time of higher activity of the former ones (Lundgren et al., 2009). Although little spiders in the habitat were active also during the whole day, they were more active before the larger spiders exhibited the most increased activity. Those different activity times are also indicated by seasonal distribution of the abundance of spiders from different families. Most spiders belonging to the family Linyphiidae were captured in July when all of the larger species had diminished their activity. Spiders of the families Philodromidae and Tetragnathidae began their activity in the season before the population of the species from family Lycosidae became numerous. Szymkowiak and Woźny (1998) observed a similar phenomenon by examining the activity of ground spiders on pastures. They noticed that spiders of the families with smaller body sizes, including Linyphiidae, were mostly captured in late summer, when larger spiders of the family Lycosidae were caught in far smaller numbers.

In a similar way, it is possible to explain the distribution of seasonal changes in the diel activity of *P. palustris* and *X. miniata* species of similar sizes dominant on the ground (Roberts, 1996). During the research period, adult individuals of *P. palustris* were invariably most active between 1200 and 1500 hours. Perhaps because of the competition with *P. palustris*, *X. miniata* was the most active in June before or after that time. Thanks to the phenomenon of two species not being active at the same time, species with similar niches can coexist in the same habitat (Lundgren et al., 2009). Only in May, the time of higher activity of both species was similar, when the population of *X. miniata* was not too large yet. The latter species showed far greater activity in June and July when individuals of *P. palustris* ceased to be active. Another explanation, but not excluding the previous one, could be that *X. miniata* is more resistant to higher temperatures that occur in June and July. The effect of soil surface temperature on ground dwelling spiders' activity was observed by Krumpalova and Tuf (2013).

The finding that species with small bodies avoid large spiders was also confirmed by Birkhofer et al. (2008), who found a numerous population of Linyphiidae spiders, while in the same habitats, the density of spiders of the genus *Pardosa* was very low. A similar relationship was observed by Hajdamowicz et al. (2015) in a group of spiders on a seasonal island on the river Pripyat (Belarus). They found that the number of spiders with smaller body sizes was negatively correlated with the number of large spiders.

The diversity of diurnal and seasonal activity patterns of spider species inhabiting the same habitat is one of the factors enabling their cooccurrence, which may be especially important for spiders with similar body sizes.

Acknowledgment

The results of the research carried out under the research theme No. 360/13/S were financed by the science grant granted by the Ministry of Science and Higher Education.

References

Alderweireldt M (1994). Day/night activity rhythms of spiders occurring in crop-rotated fields. Eur J Soil Biol 30: 55-61.

Bayram A (1996). A study on the diel activity of *Pardosa* spiders (Araneae, Lycosidae) sampled by the time sorting pitfall trap in different habitats. Turk J Zool 20: 381-387.

Bell-Pedersen D, Cassone VM, Earnest DJ, Golden S, Hardin PE, Thomas TL, Zoran MJ (2005). Circadian rhythms from multiple oscillators: lessons from diverse organisms. Nat Rev Genet 6: 554-556.

Bel'skaya EA, Esyunin SL (2003). Arachnids (Arachnidae) in a spring wheat agrocenosis in southern Sverdlovsk oblast and the effect of treatment with Decis, a pyretroid insecticide, on their populations. Russ J Ecol+ 5: 395-398.

Birkhofer K, Fließbach A, Wise DH, Scheu S (2008). Generalist predators in organically and conventionally managed grass-clover fields: implications for conservation biological control. Ann Appl Biol 153: 271-280.

Chapman EG, Schmidt JM, Welch KD, Harwood JD (2013). Molecular evidence for dietary selectivity and pest suppression potential in an epigeal spider community in winter wheat. Biol Control 65: 72-86.

Chatterjee S, Isaia M, Venturino E (2009). Spiders as biological controllers in the agroecosystem. J Theor Biol 258: 352-362.

Foelix RF (1996). Biology of Spiders. 2nd ed. New York, NY, USA: Oxford University Press.

Frampton GK, Van Den Brink PJ, Wratten SD (2001). Diel activity patterns in arable collembolan community. Appl Soil Ecol 17: 63-80.

Hajdamowicz I, Pilacka L, Meissner W (2015). Spider assemblages and dynamics on seasonal island in the Pripyat River, Belarus. Turk J Zool 39:1-11.

Harwood JD, Obrycki JJ (2005). Web-construction behavior of linyphiid spiders (Araneae, Linyphiidae): competition and co-existence within a generalist predator guild. J Insect Behav18: 593-607.

Harwood JD, Sunderland KD, Symodson WO (2004). Prey selection by linyphiid spiders: molecular tracking of the effects of alternative prey on rates of aphid consumption in the field. Mol Ecol 13: 3549-3560.

Harwood JD, Sunderland KD, Symodson WO (2005). Monoclonal antibodies reveal the potential of the tetragnathid spider *Pachygnatha degeeri* (Araneae: Tetragnathidae) as an aphid predator. B Entomol Res 95: 161-167.

Honek A (1988). The effect of crop density and microclimate on pitfall trap catches of Carabidae, Staphylinidae (Coleoptera) and Lycosidae (Araneae) in cereal fields. Pedobiologia 32: 233-242.

Jõgar K, Metspalu L, Hiiesaar K (2004). Abundance and dynamics of spiders (Lycosidae) in different plant communities. Agronomy Research 2: 145-152

Krumpalova Z, Tuf IH (2013). Circadian rhythms of ground living spiders: mechanisms of coexistence strategy based on the body size. Pol J Ecol 61: 575-586.

Lundgren JG, Nichols S, Prischmann DA, Elsbury M (2009). Seasonal and diel activity patterns of generalist predators associated with *Diabrotica virgifera* (Coleoptera: Chrysomelide). Biocontrol Sci Techn 19: 327-333.

Matuszkiewicz W (2006). Przewodnik Do Oznaczania Zbiorowisk Roślinnych Polski. Warsaw, Poland: Wydawnictwo Naukowe PWN (in Polish).

Mestre L, Garcia N, Barrientos JA, Espadaler X, Pinol J (2013). Bird predation affects diurnal and nocturnal web-building spiders in a Mediterranean citrus grove. Acta Oecol 47: 74-80.

Nyffeler M, Benz G (1988). Feeding ecology and predatory importance of wolf spiders (*Pardosa* spp.) (Araneae, Lycosidae) in winter wheat fields. J Appl Ecol 106: 123-134.

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

Pfiffner L, Luca H (2003). Effects of low-input farming systems on carabids and epigeal spiders - a paired farm approach. Basic Appl Ecol 4: 117-127.

Roberts MJ (1996). Collins Field Guide. Spiders of Britain and Northern Europe. London, UK: Harper Collins Publishers.

Romero SA, Harwood JD (2010). Diel and seasonal patterns of prey available to epigeal predators: evidence for food limitation in a linyphiid spider community. Biol Control 52: 84-90.

Samiayyan K (2014). Spiders - The Generalist Super Predators in Agro-ecosystems. In: Abrol DP, editor. Integrated Pest Management. Current Concepts and Ecological Perspective. San Diego, CA, USA: Academic Press, pp. 283-310.

Samu F, Szinetar C (2002). On the nature of agrobiont spiders. J Arachnol 30: 389-402.

Schmidt JM, Harwood JD, Rypstra AL (2012). Foraging activity of a dominant epigeal predator: molecular evidence for the effect of prey density on consumption. Oikos 121: 1715-1724.

Symodson WOC, Sunderland KD, Greenstone MH (2002). Can generalist predators be effective biocontrol agents? Annu Rev Entomol 47: 561-594.

Szymkowiak P, Woźny M (1998). Dominance structure and seasonal changes in the abundance of dominant epigeic spiders in pastures of Northern Greater Poland. In: Selden PA, editor. Proceedings of the 17th Colloquium of Arachnology; 14–18 July 1997. Edinburgh, UK: British Arachnological Society, pp. 245-252.

Thomas CFG, Brown NJ, Kendall DA (2006). Carabid movement and vegetation density: Implications for interpreting pitfall trap data from split-field trials. Agr Ecosyst Environ 113: 51-61.

Tuf IH, Tufova J, Jerabkova E, Dedek P (2006). Diurnal epigeic activity of myriapods (Chilopoda, Diplopoda). Norwegian Journal of Entomology 53: 335-344.

Uetz GW, Halaj J, Cady AB (1999). Guild structure of spiders in major crops. J Arachnol 27: 270-280.

Van Berkum FH (1982). Natural history of a tropical, shrimp-eating spider (Pisauridae). J Arachnol 10: 117-121.

Watts JC, Ross CR, Jones TC (2015). Diel life-history characteristics of personality: consistency versus flexibility in relation to ecological change. Anim Behav 101: 43-49.

Welch KD, Harwood JD (2014). Temporal dynamics of natural enemy-pest interactions in a changing environment. Biol Control 75: 18-27.

Ximenez-Embun MG, Zaviezo T, Grez A (2014). Seasonal, spatial and diel partitioning of *Acyrthosiphon pisum* (Hemiptera: Aphididae) predators and predation in alfalfa fields. Biol Control 69: 1-7.