

Seasonal activity of wolf spiders (Araneae: Lycosidae) in coastal dune habitats at Akmensrags-Ziemupe Nature Reserve, Latvia

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Abstract

Observation of spider seasonal activity are needed to determine the complete spider fauna of investigated habitats. Spider seasonal dynamics have not been studied previously in Latvia. Here we present the first results on seasonal activity of Lycosidae spiders in dune habitats at the coast of Baltic Sea in Latvia. The spiders were collected with modified pitfall traps from April 2 until November 12, 2006. In total, 843 adult spiders of five genera and 15 species and 531 juvenile spiders were collected. High activity periods occurred in spring, summer and autumn, indicated by spider numbers. Specific species were characteristic for each season: *Alopecosa cuneata*, *Pardosa palustris*, *P. pullata*, *Trochosa ruficollis* and *T. terricola* – for spring; *Alopecosa pulverulenta*, *Pardosa palustris* and *Xerolycosa miniata* – for summer (the last two species were found only in summer) and *Alopecosa fabrilis* – for autumn and also spring. Males were more active than females. The activity of juveniles was positively correlated with mean air temperature during the observation period, while adults did not show this relationship.

Key words: coastal dunes, Lycosidae, phenology, spider species community.

Introduction

Coastal habitats are unique, dynamic systems due to significant disturbance of various origin and irregular frequency: wind erosion, sea water erosion and changes in soil salinity (Rove 2010). Additionally, dry soil conditions and increased insolation play important role. Invertebrate fauna of such habitats are characterised by irregular extinction and subsequent re-colonization (immigration) from neighbouring patches and habitats. Both habitat specialist and generalist species are found in dune habitats. Dune ecosystems are extremely fragile and can be easily destroyed by human activities: recreation or planting of trees for land management.

Spiders are an important part of dune fauna. Previously, spider fauna in dunes have been studied only in a few countries. Grey dunes (in comparison to other dune types) are inhabited by the largest number of dune-specific spider species (Bonte et al. 2000). Dune spiders have not been studied in Latvia until recently (Cera, Spuņģis 2010), and the spider fauna of Latvian dunes is virtually unknown. The dune-inhabiting species *Arctosa cinerea* is included in the Red Data Book of Latvia, category II – Vulnerable species (Šternbergs 1998) and in the list of Particularly Protected Species of Latvia (Anonymous 2000). Many more

species might be found in the dunes might be in need of conservation.

Wolf spiders (Lycosidae) are found in a variety of habitats and are active hunters. They have a two-year life cycle and usually hibernate as juveniles (Almquist 2005). Various aspects of Lycosidae biology have been studied: aerial dispersal (Richter 1971), fluctuation in population density of *Trochosa terricola* (Workman 1977), ballooning (Greenstone 1982), adaptations for prey capture (Rovner 1980), ecology in grasslands (Jocqué, Alderweireldt 2005), movement along pond edges (Ahrens, Kraus 2006) and community structure in woodland fragments of various sizes and shapes (Major et al. 2006). Maelfait et al. (1969) described fauna of Lycosidae along the coastline of Belgium.

There are only a few studies on seasonal activity of Lycosidae spiders in dune habitats. Almquist (1969) described activity of *Pardosa nigriceps*. The same author (Almquist 1973) conducted research on spider species (including *Pardosa nigriceps*) living in sand dunes, but more attention was paid on habitat preference change during the 17-months investigation. He used sieving of plant material for spider collecting. Bonte et al. (2000) described seasonal and diurnal migrations of spiders, including Lycosidae, in dune habitats. They used pitfall traps and sieving of litter samples as capture methods. Bonte and Maelfait (2001)

studied life cycle of *Pardosa monticola* collected with pitfall traps in the Flemish coastal dunes. Merrett (1967, 1968) studied the phenology of heathland spiders in Dorset, England by use of pitfall traps. Hollander (1971) analysed life cycle characters, such as *cephalothorax* growth of juveniles, seasonal adult spider occurrence and factors that may influence spider egg laying and abundance of species from *Pardosa pullata* subgroup: *P. pullata*, *P. fulvipes* and *P. prativaga* in their preferred habitat. Vlijm and Kessler-Geschier (1967) studied phenology of *Pardosa* species (*P. monticola*, *P. nigriceps* and *P. pullata*) in sand-dunes using pitfall traps and hand-sampling. Braun and Rabeler (1969) described the phenology of 17 species, and Schaefer (1976) determined the annual life cycles of spiders in different coastal habitats and described overwintering spiders.

The previous studies of Lycosidae cover the North-Western part of Europe – Sweden, Finland, England, Netherlands, Germany and Belgium. Seasonal studies of spiders have not been conducted in the Baltic countries and Eastern Europe where climatic conditions differ. Thus the aim of this study was to identify the occurrence of Lycosidae species in various dune habitats of Latvia during the non-frost season. This type of information is needed to determine factors affecting changes in activity, dominance and distribution of Lycosidae spiders in habitats over a season in dune habitats.

Materials and methods

Study site

Samples of ground-dwelling spiders were collected in the Ziemepe Nature Reserve (Natura 2000 site) near Akmensrags in the dunes along the Latvian coast of the Baltic Sea. The area is characterised by typical dune vegetation, including habitats of EU importance according to EU Habitats directive 92/43/EEK (Anonymous 1992; Rove 2010): 2120 – shifting dunes along the shoreline with *Ammophila arenaria* (white dunes) and 2130 – fixed coastal dunes with herbaceous vegetation (grey dunes).

Spider sampling and processing

Modified pitfall traps made from plastic cups (opening diameter 7.5 cm, height 9.0 cm, and volume 250 mL) were used. Traps were filled with 100 mL of 10% formaldehyde solution with additions of ethylene-glycol (10 mL) and a few drops of detergent. Forty traps were located on a 78-m transect extending from the white dune inlands, perpendicular to the coastline. The traps were renewed every two weeks in the period from April 2 until November 12, 2006. This period was chosen based on the season when air temperature was above 0 °C. Distance between traps was 2 m. The first 17 traps on the transect were located in the white dune and transition zone from white dune to grey dune (located 32 m from the beginning of transect). The next 13 traps (34 to 58 m) were in typical grey dune, and

the last 10 traps (60 to 78 m from the beginning of transect) represented the transition zone from grey dune to coastal meadow. Spiders from traps were sorted in vials with 70% ethanol. The adult spiders were identified to species by use of the identification key by Almquist (2005). Taxonomy follows Platnick (2010). Adults and juveniles was counted separately. All collected spiders are deposited in the collection of the Institute of Biology, University of Latvia.

Data analysis

The dominance of taxa was characterised in accordance with Engelmann (1978) classification.

Mean daily soil surface temperature for a two-week period was calculated by the data obtained from the Pāvilsta station of the Latvian Environment, Geology and Meteorology Centre (located at the Baltic Sea coast 12 km from the study site). Soil surface temperature was used for calculation of the Pearson rank correlation coefficient (Zar 1998) between temperature and spider activity. The difference in distribution of captured individuals per sampling period with the distribution for the entire sampling periods was tested by a χ^2 test (Zar 1998).

Results

In total 1374 spiders were collected (Table 1). The highest number of adult specimens was observed between April 30 and May 14, while for juveniles the highest numbers were observed between June 25 and July 23. No adult Lycosidae spiders were observed during the first two weeks of the study (April 2 to 15). During the last trapping period (October 29 – November 12) total number of adult spiders reached only 33 individuals and only one Lycosidae (juvenile) was captured.

In the wolfspider community, *Alopecosa cuneata* was eudominant (49.1% of the total number of adult spiders during the observation period), *Xerolycosa miniata* was dominant (18.51%), *Trochosa terricola* (9.96%), *Pardosa palustris* (7.24%) and *Alopecosa fabrilis* (5.46%) were subdominants, and the remaining species were recedent to subrecedent. The eudominant, dominant and subdominant species were encountered during most of 16 two-week observation periods (Table 1). *Arctosa perita* and *Trochosa ruricola* were exceptions, as they were only present in 10 and 6 periods respectively, but these species were recedent. The remaining species were observed in less than five two-week periods.

We identified specific activity periods for the most common species (Table 1). *Alopecosa cuneata* and *Trochosa terricola* had a spring-summer activity period as adults. *Pardosa palustris* had a late spring to early summer activity period, while *Xerolycosa miniata* and *Alopecosa pulverulenta* showed typical summer activity. *Alopecosa fabrilis* showed two peaks of activity, with the largest in autumn. *Arctosa perita* was observed during the most of the study period.

Table 1. Number of collected wolf spider individuals in different sampling periods of 2006 in Baltic Sea coastal dune habitats at Akmenrags in Ziemupe Nature Reserve in 2006

Species	Sampling period															
	02.04.- 16.04.	16.04.- 30.04.	30.04.- 14.05.	14.05.- 28.05.	28.05.- 11.06.	11.06.- 25.06.	25.06.- 09.07.	09.07.- 22.07.	22.07.- 06.08.	06.08.- 20.08.	20.08.- 03.09.	03.09.- 17.09.	17.09.- 01.10.	01.10.- 15.10.	15.10.- 29.10.	29.10.- 12.11.
<i>Alopecosa cuneata</i> (Clerck, 1757)	35	168	116	20	31	32	3	6	3	8	4	20	3	2		
<i>A. fabrilis</i> (Clerck, 1757)	1	1	1	2	4	1	1	1	1	8	4	20	3	2		
<i>A. pulverulenta</i> (Clerck, 1757)	1	1	1	1	8	12	2	1	3	2						
<i>Arctosa cinerea</i> (Fabricius, 1777)															2	
<i>A. perita</i> (Latreille, 1799)	1	1	1	1	1	1	1	1	1	1	1	2	7	1		
<i>Pardosa amentata</i> (Clerck, 1757)	1	1	1	1	1	1	1	1	1	1	1	2	7	1		
<i>P. paludicola</i> (Clerck, 1757)	1	1	1	1	1	1	1	1	1	1	1	2	7	1		
<i>P. palustris</i> (Linnaeus, 1758)				3	20	30	7	1								
<i>P. prativaga</i> (L. Koch, 1870)				1												
<i>P. pullata</i> (Clerck, 1757)				4	8	3	1									
<i>Pardosa</i> sp.																
<i>Trochosa ruricola</i> (De Geer, 1778)	1	4	4	1	2											
<i>T. spinipalpis</i> (F.O.P. Cambridge, 1895)				2												
<i>T. terricola</i> Thorell, 1856	31	27	10	5	4	3	1			1	2					
<i>Xerolycosa miniata</i> (C.L. Koch, 1834)				11	58	38	19	21	6	3						
Adults total	70	202	139	69	142	95	27	31	76	68	33	22	5	9	1	1
Juveniles total	5	45	2	15	0	93	86	50	76	68	33	22	5	9	2	1

For all dominant species, mostly males were collected (63 to 78%). Activity peaks for males and females differed, except for *Alopecosa cuneata*, for which both sexes were highly active between April 30 and May 14 (Fig. 2). The activity periods for the remaining species could not be evaluated because of small numbers of collected individuals.

Abundance of adults and juveniles, in relation to the mean soil surface temperature is shown in the Fig. 1. Adult spiders did not significantly depend on the temperature of soil surface ($r = 0.267$; n.s.; $n = 16$); in contrast the relationship with juvenile spiders was significant ($r = 0.546$; $p < 0.05$; $n = 16$).

Dominance of the most abundant species changed significantly among the two-week observation periods (Fig. 1). Two peak periods were observed for *Alopecosa cuneata*: between April 30 and May 14, and June 11 – July 9. A maximum between June 11 and June 25 was observed for *Xerolycosa miniata*, *Pardosa palustris* and *Alopecosa fabrilis*. The activity of *Alopecosa fabrilis* was much higher in autumn (eight individuals from August 20 to September 3 and 20 individuals from September 17 to October 1) than in the spring-summer period (four individuals). The highest activity of *Trochosa terricola* was observed from April 16 to May 30. The species was absent after July 23.

Discussion

Pitfall traps have been used in many studies of spider ecology (see review by Hänggi et al. 1995). In this review 76.6 % of all data in 223 publications were collected by the pitfall trap method. However, this method does have potential biases, such as trap spacing (Ward et al. 2001), trap diameter (Brennan et al. 2005) and others (e.g. layout and construction materials of traps, solution used in traps). Use of this method in an activity study assumes that trapability of a species is closely related with activity of the species.

All of the species we found at the Baltic Sea coast have also been found on various dune habitats in the other countries (Duffey 1968; Schultz, Finch 1996; Bell et al. 1998). Some of the species have been characterised as dune habitat indicator species (Bonte et al. 2002). A total of 17 Lycosidae species were collected in 16 Flemish dune habitat types in that study. Of those eight species were found in our study. In the study by Bonte et al. (2002) *Alopecosa cuneata* was characteristic of high dwarf shrubs, *A. fabrilis* for moss dominated dunes and Marram dunes near the inner dune front, *Trochosa terricola* for eutrophic vegetation, *T. ruricola* for short mesotrophic grasslands, *Pardosa palustris* and *P. pullata* for eutrophic wet dune valleys, *Arctosa perita* for meso-oligotrophic vegetation and *Xerolycosa miniata* for inundating mesotrophic grasslands.

Hänggi et al. (1995) provided a review of habitats of Central European spiders based on 223 publications. One of these species was found in our study – *Alopecosa fabrilis*, which is included in the list of species with insufficient

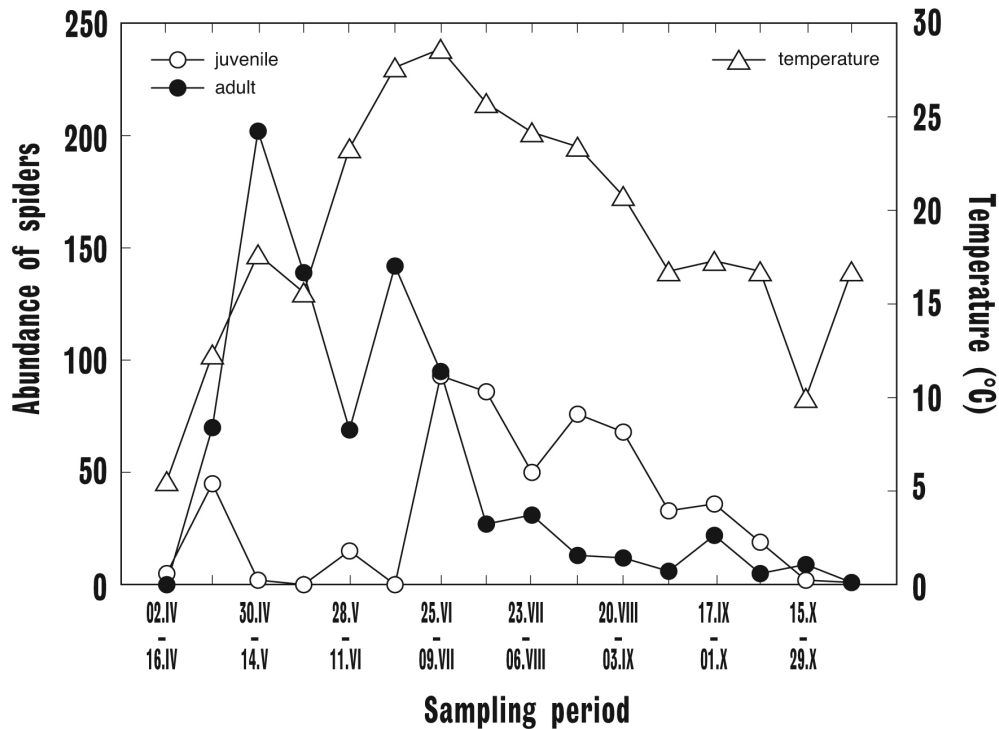


Fig. 1. Seasonal dynamics of adult and juvenile Lycosidae spiders in relation to the soil surface temperature in Baltic Sea coastal dune habitats at Akmenšrags in Ziemeņu Nature Reserve in 2006.

number of studies (less than 25). Thus, our study contributes to the knowledge on habitat use of *Alopecosa fabrilis* in Europe.

In total, there are 49 Lycosidae species known to the fauna of Latvia (Relys, Spunģis 2003; Cera, Spunģis 2008). In this study we found 14 species inhabiting coastal dunes. Five of them were abundant. The distribution of spider species in dune habitats of Latvia can be described as follows – *Pardosa palustris* and *Xerolycosa miniata* were observed at higher numbers in grey dunes, *Alopecosa fabrilis* occurred in all dune habitat types, and larger numbers of *Alopecosa cuneata* and *Trochosa terricola* occurred only in a transition zone from grey dune to dune meadows at the end of the transect, close to a pine forest.

Usually, spider seasonal activity has been studied for species groups (Merrett 1967; Vlijm, Kessler-Geschiere 1967; 1968; Almquist 1969; Braun, Rabeler 1969; Hollander 1971; Schaefer 1976 – coastal habitats; Bonte et al. 2000;) or only for one single species (Bonte, Maelfait 2001). Almquist (1969) described seasonal growth of 20 dune-living spiders species captured by hand from 1960 until 1962, from Lycosidae he described only *Pardosa nigriceps*. Meanwhile, Bonte et al. (2000) used data of a whole year of sampling by pitfall traps and frame method and observed only a few Lycosidae (*Arctosa perita*, *Trochosa terricola* and *Xerolycosa miniata*). *Pardosa nigriceps* juveniles leave cocoons in June, but some of them do not reach adult stage during the first summer and they hibernate and become adults during the next season in May or in June (Almquist

1969). Our study covered only spring, summer and autumn of one year. However, some species are also active in winter in Europe, including species of the Lycosidae family (Gunnarsson 1985; Aitchinson 1984). Compared to western Europe, winters in Latvia are normally snowy and have temperatures much below zero. Therefore, no activity of spiders can be expected in the cold period in Latvia. Thus, although our study covered only one season, it did show the seasonal activity of spiders. A repeated study might provide additional information about spider activity in coastal dunes, depending on annual climatic factor differences.

Almquist (2005) observed *Pardosa palustris* males to be active from beginning of May to mid June and females from mid May to mid October. Our results showed that male activity occurred somewhat later, from mid May to beginning of July, and females were active from end of May, but disappeared at the end of July, earlier in comparison to Almquist's study. These results could be explained by different spider collecting methods. Almquist (1969) used quadratic frame, which enables to catch also less active spiders (Vlijm, Kessler-Geschiere 1967), while pitfall traps used in our study failed to capture sedentary spiders that hide in the litter. The same explanation can be referred to other species.

Alopecosa fabrilis females were present in samples from mid April until August, and males from the end of August until end of October. In contrast, Almquist (2005) observed that males were active from beginning of October until June next year and females from end of the May until

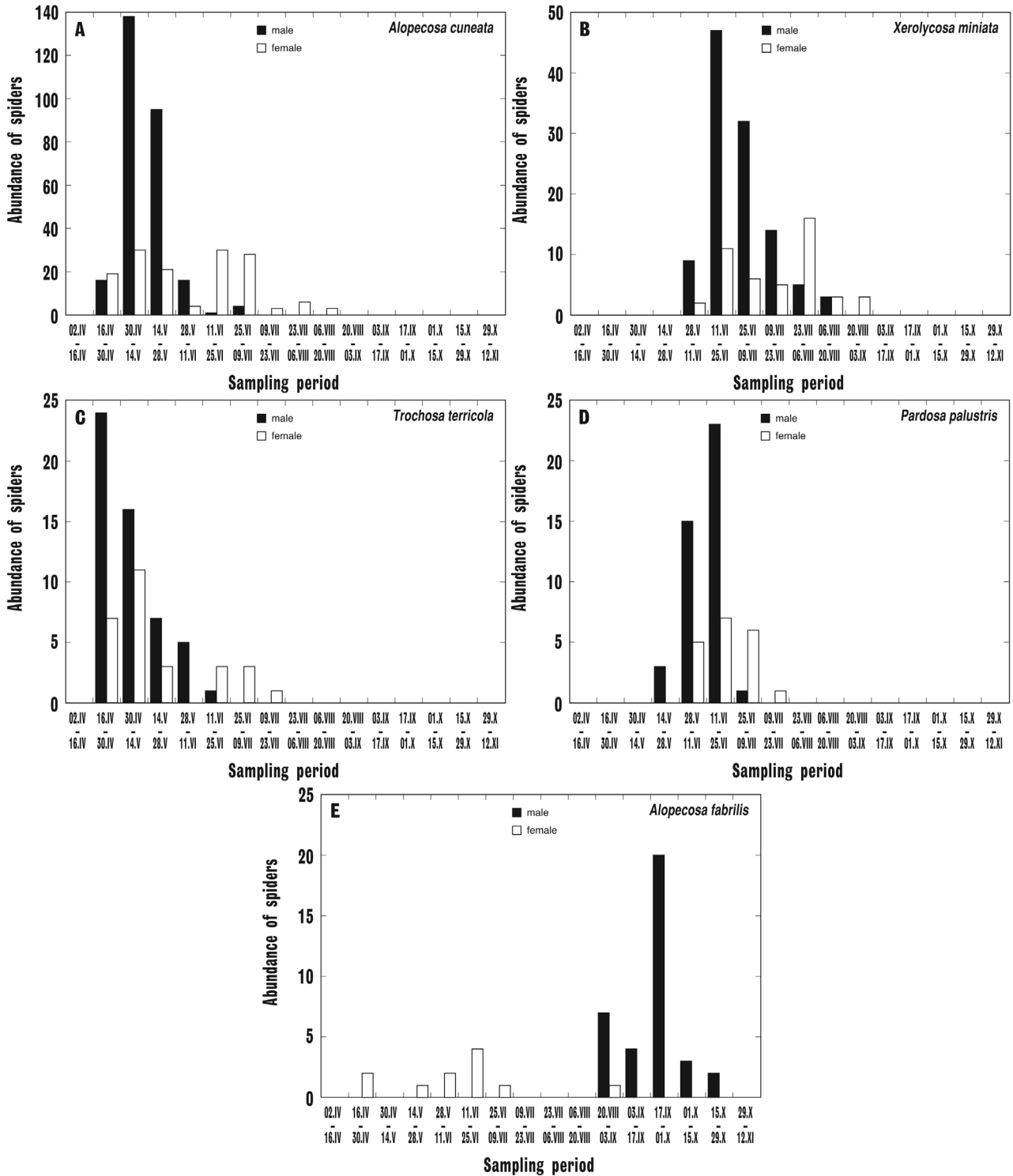


Fig. 2. Activity pattern of male and female spiders of the most abundant species, expressed as number of spiders captured in two week periods by pitfall traps in the coastal dune habitats of Baltic Sea at Akmenšrags in Ziemeņu Nature Reserve in 2006.

the beginning of September. Merret (1968) found that *Alopecosa fabrilis* was active from mid August until late October and the highest activity was observed in an early September. These differences in activity can be explained by differences in geographic region.

We found that *Alopecosa cuneata* were active from the end of April until mid August. Similarly, *Xerolycosa miniata* were active from beginning of May until beginning of September and *Trochosa terricola* – from April until November. Merrett (1968) found only one male of

Alopecosa cuneata during his study and he observed *Trochosa terricola* from the end of March until the end of October/beginning of November with a peak at the end of April. The higher activity of males can be explained by active search of females before copulation and decrease of later activity (Foelix 1996), as well as by availability of prey: a low prey density is associated with higher spider activity (Bonte et al. 2000). Due to increased seeking behaviour activity of males, they are more trapable by pitfall traps (Cady 1984). Female activity increases only after the young spiders hatch. This pattern might differ, if it was possible to separate juvenile males and females.

The climate in the northern and central Europe changes from maritime to continental in the direction west to east. Bonte et al. (2003) discussed regional differences of four large dune regions along the North Sea of Northern France, Belgium and the Netherlands as well as inland dunes from the German lowlands. He concluded that the main factor determining spider assemblages in their studied sites was sand dynamics. Our results share only four species with those recorded by Bonte et al. (2003), indicating that geographical differences occur, when assemblages are compared at a larger geographical scale. Almquist (1969) also discussed differences of spider development and life cycle in different climatic zones. Unfavourable conditions (i.e. high temperatures, low soil and air humidity) were mentioned as the main causes of absence of small stenotopic spider species in grey dunes in summer (Bonte et al. 2000). These conditions possibly may be caused by the absence of the main prey species springtails (*Collembola*). Larger species, including Lycosidae, were present in the Flemish dunes also in summer (Bonte et al. 2000).

The relationship between juvenile activity and soil temperature may be explained by development of spiderlings to adults during the season, and may be due to the characteristics of lycosid females to carry juveniles on their body during the first week after hatching (Almquist 2005). Spiderlings were taken into account in our study. Almquist (1970) studied lethal temperatures for some dune-living spiders, but he did not discuss influence of temperature on development of spiders. It is known that both soil and air temperature influence spider development and movement, soil temperature influences overwintering of offspring (Foelix 1996), and air temperature affects activity of hunting, reproduction, migration etc. Wind velocity (Richter 1970) and air humidity (Bonte et al. 2007) also affect aerial dispersal of some Lycosidae species.

The present paper describes seasonal activity of lycosid spiders during one season, and the effect of soil temperature influence on activity of juvenile spiders. The results are compared with data from other European studies. This is first study on seasonal activity of spiders in dune habitats of Latvia. In further studies more emphasis should be placed on seasonal activity of other spider families and species and on interrelations with environmental factors, as

discussed above. To explain impact of climate change on spider communities in dune habitats long-term studies are needed. Also knowledge of prey dynamics are needed to explain spider behaviour and activity.

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References

- Ahrens L., Kraus J. M. 2006. Wolf spider (Araneae, Lycosidae) movement along a pond edge. *J. Arachnol.* 34: 532–539.
- Aitchison C. W. 1984. Low temperature feeding by winter-active spiders. *J. Arachnol.* 12: 297–305.
- Almquist S. 1969. Seasonal growth of some dune-living spiders. *Oikos* 20: 392–408.
- Almquist S. 1970. Thermal tolerances and preferences of some dune-living spiders. *Oikos* 21: 230–236.
- Almquist S. 1973. Habitats selection by spiders on coastal sand dune in Scania, Sweden. *Insect Syst. Evol.* 4: 134–154.
- Almquist S. 2005. Swedish Araneae, part I – families Atypidae to Hahniidae. *Insect Syst. Evol.* 62: S1–S284.
- Anonymous 1992. European Council Directive 92/43/EEC of 21 May 1992 on the Conservation of natural habitats and of wild fauna and flora.
- Anonymous 2000. Regulations of the Cabinet of Ministers, Republic of Latvia No. 396 adopted on November 14, 2000: List of Specially Protected Species and Species with Exploitation Limits.
- Bell L.R., Haughton A.J., Cullen W.R., Wheeler C. . 1998. The zonation and ecology of a sand-dune spider community. In Selden A.P. (ed) *Proceedings of the 17th European Colloquium of Arachnology*, Edinburg, 1997, pp. 261–266.
- Bonte D., Baert L., Maelfait J.-P. 2002. Spider assemblage structure and stability in heterogenous coastal dune system (Belgium). *J. Arachnol.* 30: 331–343.
- Bonte D., Bossuyt B., Lens L. 2007. Aerial dispersal plasticity under different wind velocities in a salt marsh wolf spider. *Behav. Ecol.* 18: 438–443.
- Bonte D., Criel P., van Thournout I., Malfait J.-P. 2003. Regional and local variation of spider assemblages (Araneae) from coastal grey dunes along the North Sea. *J. Biogeography* 30: 901–911.
- Bonte D., Hoffmann M., Maelfait J.-P. 2000. Seasonal and diurnal migration patterns of the spider fauna of coastal grey dunes. *Ekológia* 19: S5–S16.
- Bonte D., Maelfait J.-P. 2001. Life history, habitat use and dispersal of a dune wolf spider (*Pardosa monticola* (Clerck, 1757) Lycosidae, Araneae) in the Flemish coastal dunes (Belgium).

- Belgian J. Zoology* 131: 145–157.
- Braun R., Rabeler W. 1969. Zur Autökologie und Phänologie der Spinnenfauna des nordwestdeutschen Altmoränengebietes. *Abh. Senckenberg. Nat. Ges.* 522: 1–89.
- Brennan K.E.C., Majer J.D., Moir M.L. 2005. Refining sampling protocols for inventorying invertebrate biodiversity: influence of drift-fence length and pitfall trap diameter on spiders. *J. Arachnol.* 33: 681–702.
- Cady A. B. 1984. Microhabitat selection and locomotor activity of *Schizocosa ocreata* (Walckenaer) (Araneae, Lycosidae). *J. Arachnol.* 11: 297–307.
- Cera I., Spunģis V. 2008. Spider (Araneae) species new to the fauna of Latvia. *Latvijas Entomologs* 45: 49.
- Cera I., Spunģis V. 2010. Distribution of spiders in dune habitats at the Baltic Sea coast at Akmenrags, Latvia. *Latvijas Entomologs* 49: 3–13.
- Duffey E. 1968. An ecological analysis of the spider fauna of sand dunes. *J. Animal Ecol.* 37: 641–674.
- Engelmann A.-D. 1978. Zur Dominanzklassifizierung von Bodenarthropoden. *Pedobiologia* 18: 378–380.
- Foelix R. F. 1996. *Biology of Spiders*. 2nd ed. Oxford University Press and Georg Verlag, New York, 311 p.
- Greenstone M. H. 1982. Ballooning frequency and habitat predictability in two wolf spider species (Lycosidae: Pardosa). *Florida Entomologist* 65: 83–90.
- Gunnarsson B. 1985. Interspecific predation as a mortality factor among overwintering spiders. *Oecologia* 65: 498–502.
- Hänggi A., Stöckli E., Nentwig W. 1995. Habitats of Central European spiders. Characterisation of the habitats of the most abundant spider species of Central Europe and associated species. *Miscellanea Faunistica Helvetica* 4: 1–460.
- den Hollander J. 1971. Life-history of species of the *Pardosa pullata* group, a study of ten population in the Netherlands (Araneae, Lycosidae). *Tijdschrift voor Entomologie* 114: 255–281.
- Jocqué R., Alderweireldt M. 2005. Lycosidae: the grassland spiders. *Acta Zoologica Bulgarica* 1: S125–S130.
- Maelfait J.-P., Alderweireldt M., Dessender K., Baer L. 1969. Lycosid spiders of the Belgian coast. *Bull. Annl. Soc. Roiale Belge Ent.* 125: 327–332.
- Major R. E., Gowing G., Christie F. J., Gray M., Colgan D. 2006. Variation in wolf spider (Araneae: Lycosidae) distribution and abundance in response to the size and shape of woodland fragments. *Biol. Conserv.* 132: 98–108.
- Merrett P. 1967. The phenology of spiders on heathland in Dorset: I. Families Atypidae, Dysderidae, Gnaphosidae, Clubionidae, Thomisidae and Salticidae. *J. Animal Ecol.* 36: 363–374.
- Merrett P. 1968. The phenology of spiders on heathland in Dorset: II. Families Lycosidae, Pisauridae, Agelenidae, Mimetidae, Theridiidae, Tetragnathidae, Argiopidae. *J. Zoology* 156: 239–256.
- Platnick N.I. 2010. The World Spider Catalog. Version 10.5 American Museum of Natural History. New York. Online at <http://research.amnh.org/entomology/spiders/catalog> (accessed: 14.07.2011).
- Relys V., Spunģis V. 2002. Check list of spiders (Arachnida, Araneae) of Latvia. Online at <http://leb.daba.lv/Aranea.htm> (accessed 12.02.2011).
- Richter C. J. J. 1970. Aerial dispersal in relation to habitat in eight wolf spider species (Pardosa, Araneae, Lycosidae). *Oecologia* 5: 200–214.
- Richter C. J. J. 1971. Some aspects of aerial dispersal in different populations of wolf spiders, with particular reference to *Pardosa amentata* (Araneae, Lycosidae). *Misc. Pap. Landbouw Hogeschool, Wageningen* 8: 77–88.
- Rove I. 2010. Coastal and inland dune habitats. In: Auniņš A. (ed) 2010. *Protected Habitats of European Union in Latvia. Identification Handbook*. Latvijas Dabas fonds, Riga: 21–87.
- Rovner J.S. 1980. Morphological and ethological adaptations for prey capture in wolf spiders (Araneae, Lycosidae). *J. Arachnol.* 8: 201–215.
- Schaefer M. 1976. Experimentelle Untersuchungen zum Jahreszyklus und zur Überwinterung von Spinnen (Araneida). *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 103: 127–289.
- Schultz W., Finch O.-D. 1996. *Biotoptypenbezogene Verteilung der Spinnenfauna der nordwestdeutschen Küstenregion*. Cuvillier Verlag, Göttingen. 141 S.
- Šternbergs M. 1998. *Arctosa cinerea* (Fabricius, 1777). In: Andrušaitis G. (ed) *Red Data Book of Latvia: Rare and Threatened Species of Plants and Animals*. Volume 4: Invertebrates. Institute of Biology, Riga, pp. 138–139.
- Vlijm L., Kessler-Geschiere M. 1967. The phenology and habitats of *Pardosa monticola*, *P. nigriceps* and *P. pullata* (Araneae, Lycosidae). *J. Animal Ecol.* 36: 31–56.
- Ward F.D., New T.R., Yen A.L. 2001. Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches. *J. Insect Conserv.* 5: 47–53.
- Workman C. 1977. Population density fluctuations of *Trochosa terricola* Thorell (Araneae: Lycosidae). *Ecol. Bull.* 25: 518–521.
- Zar J.H. 1998. *Biostatistical Analysis*. 4th ed. Prentice Hall, Upper Saddle River, New Jersey, USA. 929 pp.