

Assemblages of herb-dwelling spiders (Araneae) of various steppe types in Ukraine and the Central Chernozem region of Russia

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doi: 10.5431/aramit4312

Abstract: A total of 107 spider species from 15 families were recorded in the herbaceous vegetation of the steppe ecosystems of Ukraine and the Central Chernozem region of Russia. Araneidae, Thomisidae, Salticidae and Theridiidae were the most species-rich. The species composition depended on the steppe type; adjacent forest habitats influenced steppe fauna in the forest-steppe and northern part of the steppe natural zone. The number of generalist, forest and wetland dwelling species in the steppe vegetation showed a tendency to decrease towards the south. Dominance of herb-dwelling spiders was specific to each steppe type; no single species was found to predominate in all the steppe habitats.

Key words: dominance structure, species distribution, spider communities, steppe ecosystems

Steppes are the most transformed ecosystem in Ukraine. The steppe natural zone comprises 40% of the country and about 80% of this territory was once covered with steppe vegetation. Presently, only 3% of relatively undisturbed virgin steppes have survived intact. They are preserved mainly in nature reserves or on gully slopes and saline lands not suitable for agriculture (KOTENKO 1996).

All steppe reserves are isolated to various degrees, such that they can be considered as ecological islands, surrounded by agricultural landscapes (MALYSHEV 1980). Different components of the steppe biota respond to isolation in different ways (KOTENKO 1996, HANSER & HUNTLY 2006, LAIOLO & TELLA 2006). Spiders move quite easily from natural habitats to agricultural fields, however many of them do not penetrate beyond the field margins. Crops are populated mainly by eurytopic species typical of meadows or disturbed habitats (SEYFULINA & TCHERNYSHEV 2001, SEYFULINA 2010).

Adjacent habitats have an undeniable impact on steppe communities (CHERNOV & PENEV 1993), especially in the forest-steppe zone where forest and steppe are both zonal plant formations, and an active species interchange can be supposed to take place. To the north and to the south the difference in microclimatic conditions between zonal and intrazonal habitats increases, which results in higher species specificity of their animal and plant

assemblages (CHERNOV 1975). Habitat preference of species depends on the natural zone (KÜHNELT 1943, WALTER 1960, BEI-BIENKO 1966). According to the so-called 'principle of zonal change of habitats' (BEI-BIENKO 1966), or the principle of 'relative stenotopy' (SCHAEFER 1992), widespread species moving northwards can change their habitats to dryer warmer open sites with sparse vegetation, while going southwards, the same species inhabit moister and shadier habitats with dense vegetation cover. These two phenomena were illustrated by the example of spider communities of the Urals transect (ESYUNIN 2009), oak forests of the East European Plain (ESYUNIN et al. 1994), and Ukrainian steppes (POLCHANINOVA 1990a, 1996). Investigation of the spider fauna and ecology in the area in question began in the 1980s in the Central Chernozem Reserve of Russia (PICHKA 1984, 1984b) and in the steppe reserves of Ukraine (POLCHANINOVA 1988, 1990b). Based on the data obtained, a first attempt was made to analyze the fauna and spider communities of the steppe ecosystems of Ukraine (POLCHANINOVA 1990b). Further research focused on all steppe reserves in Ukraine (GURIANOVA & KHOMENKO 1991, POLCHANINOVA 1998, POLCHANINOVA & PROKOPENKO 2007a, PROKOPENKO 2001, PROKOPENKO et al. 2008) and the adjacent territory of Russia (POLCHANINOVA 2003, 2009, PONOMAREV 2005, 2010). Thus, it became possible to analyse the species composition and dominance structure of spider assemblages to see whether they depend on the steppe type. The present paper is part of a comprehensive study of spider communities of steppe ecosystems of Ukraine and European Russia and concerns herb-dwelling spiders only.

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Materials and methods

The material was collected from three localities in the Central Chernozem region of Russia, and eight localities in the Left-bank Ukraine (Fig. 1). Central Chernozem is a segment of the Eurasian chernozem (black soil containing a high percentage of humus) belt that lies within the East European Plain (also known as the Russian Plain). It is a well-delimited geographical and administrative region. The Left-bank Ukraine in the present context is a territory that stretches from the left bank of the Dnieper River eastward to the border of the state.

We investigated five types of fragments of virgin steppes in the East European Plain (classification according to GRIBOVA et al. 1980). Meadow, forb-bunchgrass and bunchgrass steppes belong to the category of zonal steppes, while sandy and chalky steppes belong to the azonal steppes. In Russian geobotany, meadow steppes situated in the forest steppe natural zone are called ‘northern steppes’ in contrast to genuine steppes, which form two subzones of the steppe natural zone (Fig. 1, Tab. 1). We regard sandy steppes situated in different steppe subzones separately as northern and southern variants. The studied localities, investigation period and abbreviations used further in the tables and graphs are given in



Fig. 1: Map of localities (I – forest-steppe zone, II – steppe zone: IIa – subzone of forb-bunchgrass steppes, IIb – subzone of bunchgrass steppes. For number of locality, see Tab. 1).

Tab. 1. Here and additionally in the graphs and tables, the localities are arranged from north to south. Names of settlements and nature reserves are translated from Russian and Ukrainian respectively.

Tab. 1: List and characteristics of study sites including type of steppe habitat.

Nature zone/ subzone	Name of locality	Steppe type	Years of study	site area (ha)	abbrev.	Region
Forest-steppe zone	1. Streltsovskaya steppe	meadow steppe	1998 1999 2007	730	mead1	Kursk Area, Central Chernozem Res. 51°36'N 36°12'E 248 m a.s.l.
	2. Kazatskaya steppe	meadow steppe	1999 2000 2007	1010	mead2	Kursk Area, Central Chernozem Res. 51°32'N 36°20'E 230 m a.s.l.
	3. Yamskaya steppe	meadow steppe	2001 2002	500	mead3	Belgorod Area, Belogorye Res. 51°11'N 37°45'E 193 m a.s.l.
	4. Mikhailivska Tsilyna	meadow steppe	1985 1986 1988	160	mead4	Symska Area Ukrainian steppe Res. 50°34'N 44°12'E 172 m a.s.l.

Nature zone/ subzone	Name of locality	Steppe type	Years of study	site area (ha)	abbrev.	Region
Steppe zone: Northern subzone of forb- bunchgrass steppe	5. Striltsivskiyi step	forb-bunchgrass steppe	1986 1988 2009	1000	forb1	Luhansk Area, Luhanskyi Natural Res. 49°17'N 40°00'E 147 m a.s.l.
	6. Khomutivskiyi step	forb-bunchgrass steppe	1982 1983 2004	1000	forb2	Donetsk Area, Ukrainian steppe Res. 47°17'N 38°10'E 57 m a.s.l.
	7. Striltsivskiyi zakaznyk	chalky steppe	2009 2011	80	chalk	Luhansk Area 49°18'N 39°50'E 100 m a.s.l.
	8. Dnieprovsko- Orilskiyi Res.	Northern sandy steppe	1999 2000 2003	300	sandN	Dnipropetrovsk Area 48°30'N 34°45'E 53 m a.s.l.
Steppe zone: Southern subzone of bunchgrass steppe	9. Askania-Nova Res.	bunchgrass steppe	1984 1985 1988	11000	bunch	Kherson Area, 46°28'N 33°58'E 29 m a.s.l.
	10. Ivano- Rybalchanskyi	Southern sandy steppe	1989 1990 1991	2074	sandS1	Kherson Area, Chernomorskyi Res. 46°27'N 32°07'E 6 m a.s.l.
	11. Solenoozernyi	Southern sandy steppe	1995 1996 1998	1325	sandS2	Kherson Area, Chernomorskyi Res. 46°27'N 31°58'E 1 m a.s.l.

In each locality, investigations were carried out for two consecutive years. The material was collected by sweeping with an entomological net ($d=30$ cm), as well as by hand collecting. Quantitative samples were taken every month from May to September, five samples of 50 sweeps each. The material obtained from two vegetation seasons was considered as a general sample. For comparative analysis, we chose plots in nature reserves with strictly protected steppe, because traditional regime management such as hay mowing dramatically impacts upon species composition and structure of spider communities (POLCHANINOVA 2004). In order to obtain more information on the spider species composition of local faunas and various steppe types, we conducted additional research in different years, and also used the data from available publications (PICHKA 1984a, 1984b, GURYANOVA & KHOMENKO 1991, PROKOPENKO 2001). In total, more than 12,000 spider specimens were collected. A list of species is given in the Appendix. Species are arranged by families according to PLATNICK (2012).

With the method of net sweeping, a large number of juvenile spiders were collected. In many cases, they could be identified to species level as they belonged to a single species of the genus in a given locality, or differed in period of maturity. For the genera whose

immature specimens could not be distinguished, we considered the genus as a whole in general quantitative analysis, and then species relationships within the genus were estimated separately based on mature individuals.

In order to determine relative abundance, we used the Tischler rating scale, where eudominant $n \geq 10\%$, dominant $5 \leq n < 10\%$, subdominant $2.5 \leq n < 5\%$, recent $1 \leq n < 2.5\%$, and subrecent $n < 1\%$ (TISCHLER 1949). We considered eudominants and dominants together as a dominant complex. The ecological groups of species were determined based on the data on their habitat preference within the forest-steppe and steppe zones of the East European Plain (Tab. 2). We define grassland species as species occurring in all habitats with predominance of herbaceous vegetation, in our case meadows, steppes, and open slopes of gullies. We consider permanent residents of one or more steppe types to be typical species. Sometimes they may occur in other habitats as rare finds.

Similarity of spider assemblages of the studied habitats was determined by cluster analysis performed in Statistica 7 (STATSOFT INC. 2004). Two year quantitative samples (see above) were pooled together and a percentage of each species of the total sample at each site was calculated. We used the Ward's algorithm as a

cluster method and Euclidian distance as a similarity measure.

Results

Species composition and species richness

A total of 107 spider species from 15 families were recorded in herbaceous vegetation at 11 study sites. Four families were the most species-rich: Araneidae (20 species, 18.7% of total species in study sites), Salticidae (19 species, 17.8%), Thomisidae (18 species, 16.8%), and Theridiidae (13 species, 12.1%). Only Araneidae were distributed quite evenly, ranging from 22% of the species in forb steppes to 27% in the sandy ones. Linyphiidae and Clubionidae occurred mainly in meadow steppes (Appendix). Thomisidae reached their maximum of species richness in bunchgrass steppes (23%) and fell to a minimum in meadow steppes (13%). Salticidae are known to increase in terms of the number of species towards the south (NENILIN 1984, MIKHAILOV 1997). In our collection, we found unexpectedly few salticid species in the bunchgrass steppe (4 species, 10%); in the other steppe types this increase could be seen not in absolute but only in relative numbers because of impoverishment of the species composition in the southern steppes (9 species, 15% in meadow steppes, 11 species, 17% in forb steppes, 9 species, 20% in northern sandy steppes, 7 species, 21% in the southern ones).

A third of the species found in meadow steppe have not been recorded southwards in genuine

steppe. The spider fauna of meadow steppe situated in forest-steppe zone differs significantly from that of steppe habitats in steppe zone. Within the steppe zone, spiders are more evenly spread, and the fauna of each steppe type has only 7-12% of species not found in other steppe types.

Species richness of herb-dwelling spiders was maximal in both fragments of the forb steppe and minimal in both fragments of the southern sandy steppe (Appendix). In the largest steppe fragment (bunchgrass steppe in Askania-Nova) the species richness was slightly lower than that in the smallest one (chalky steppe in Milove District).

Ecological groups of species

Meadow steppes are characterized by a large number of forest and wetland species (Tab. 2). Some of them appear in the steppe in wet years, and nine species are permanent residents. The number of wetland and forest species gradually decrease towards the south. In different steppe types, generalist species comprised 15-20%. The number of steppe species at all sites was significantly lower than that of species widely distributed in grasslands. In meadow steppes, we found no steppe species.

There were no specialist species in the herb layer of steppe vegetation. Eight species which were considered to be typical were also found in other habitats; however, they reached their maximal abundance only in a certain steppe type. These species are *Run-*

Tab. 2: Ecological groups of spiders of various steppe types.

Ecological groups	Number of species in steppe type					
	meadow steppe	forb-bunch-grass	chalky	sandy N	bunch-grass	sandy S
generalist	10	11	9	8	6	5
wetland + forest	17	7	2	4	3	1
forest	7	3		1		
wetland	7	2		2		
grassland + forest edges	5	10	9	9	5	6
grassland	9	12	10	11	9	8
steppe		8	6	2	6	2
unspecified	6	9	2	4	7	5
typical		1				
		1				
			2			1
				1	1	
						3

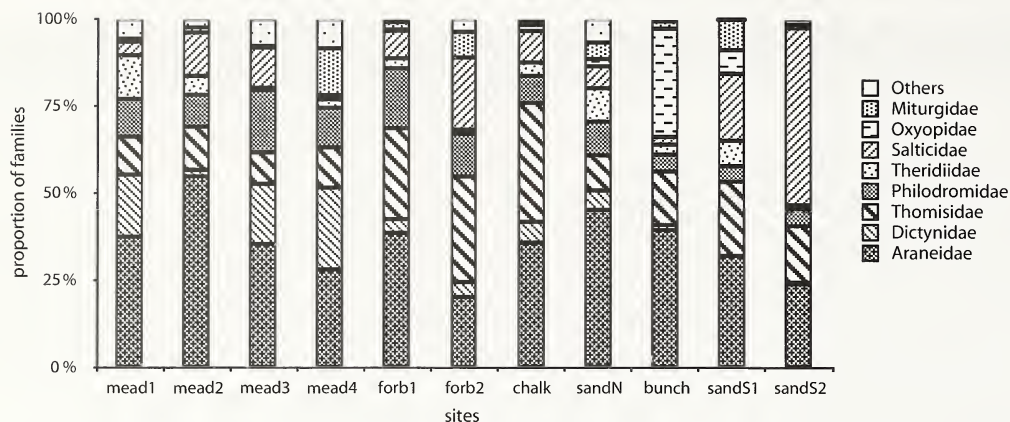


Fig. 2: Family abundance (proportion of total numbers of families at each site) in spider assemblages of herbaceous vegetation of steppe habitats. Sites are arranged from north to south.

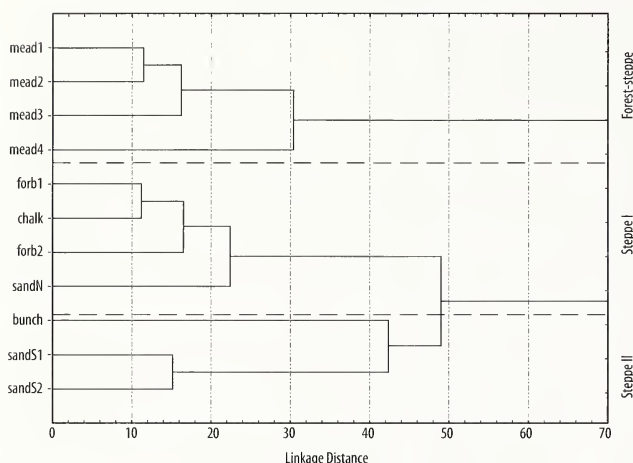


Fig. 3: Dendrogram of biocoenotic similarity of herb dwelling spider assemblages of various sites based on the % of each species in the two year samples in each site using Ward's method as cluster algorithm and Euclidian distance as similarity measure.

cinia grammica, *Pellenus seriatus* and *Yllenus vittatus* in southern sandy steppe, *Heliophanus lineiventris* in southern sandy and bunchgrass steppe, and *Uloborus walckenarius* in sandy and chalky steppes.

Thirteen generalist and grassland dwelling species occurred in almost all investigated steppe fragments (Appendix). Four species found in steppes of the forest-steppe and northern steppe subzone changed their habitat preference to forests or wetlands in the southern subzone. Ten wetland species spread to the south through steppe fragments no further than sites 'forb1' and 'sandyN'; southwards they also moved into intrazonal habitats. Five steppe species were widely spread in the steppe zone, but absent in meadow steppes; three species occurred in meadow steppes only in the site 'mead3'. It is the driest eastern site with a character of vegetation closer to genuine steppes.

Among five steppe species of the southern steppe subzone, three species occurred in sandy and chalky steppes of the northern subzone while two species did not extend beyond zonal boundaries. We did not find tendencies in distribution of the other species; 22 species were found as singletons, therefore we cannot judge their habitat preference.

Family abundance

The herbaceous vegetation of steppe habitats was dominated by Araneidae at all sites (Fig. 2). The second largest family Thomisidae preferred forb and chalky steppes. The relative number of Dictynidae went down from meadow steppes to bunchgrass and southern sandy ones. Philodromidae, likewise, were least abundant in the three southern sites while they reached a maximum in forb steppes and in the 'mead4'

site. The distribution of Salticidae did not show a latitudinal trend. An unusually large individual number of this family was found in one of the sandy steppe sites. A characteristic feature of the spider assemblage of the bunchgrass steppe was the high abundance of Oxyopidae.

Biocoenotic similarities

A dendrogram of biocoenotic similarity of spider assemblages of various sites brings them together based on a zonal-subzonal principle (Fig. 3). First, two clusters of the sites of the forest-steppe and steppe zone are separated, and then the sites of northern and southern subzones are divided into two groups. As expected, assemblages of two neighbouring fragments of southern steppes were similar, however, their similarity was less manifest than that of the two

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adjacent meadow steppe plots and even of the forb and chalky ones.

Dominance structure

In the study areas, 13 species occurred in all steppe habitats. In addition, two species were found sporadically in both northern and genuine steppes. However none of them dominated in all steppe types.

Neoscona adianta was distinguished by the widest habitat spectrum (Tab. 3). It is common in various

grasslands, but in the south it is particularly abundant. *Phylloneta impressa*, another dry grassland species, preferred sandy and chalky steppes. *Dictyna arundinacea*, by contrast, was eudominant in meadow steppes and occurred in high numbers in the forb ones. This species is characteristic of grasslands and forest edges in the forest-steppe and northern part of the steppe zone. The group of species with a narrower dominance spectrum was represented by *Neottiura bimaculata* and *Araneus quadratus* in meadow steppes, and by *Thomisus*

Tab. 3: Dominant spider species in different steppe habitats.

● – eudominant $n \geq 10\%$, ● – dominant, $5 \leq n < 10\%$, ● – subdominant $2,5 \leq n < 5\%$, ● – recedent $\leq n < 2,5\%$, ● – subrecedent $n < 1\%$ of spiders collected in each locality

Species	Localities										
	1	2	3	4	5	6	7	8	9	10	11
<i>Neottiura bimaculata</i>	●	●	●		●						
<i>Araneus quadratus</i>	●	●	●		●	●					
<i>Cheiracanthium punctatorium</i>		●	●	●	●	●					
<i>Evarcha</i> spp.	●	●	●	●	●	●		●			
<i>Dictyna arundinacea</i>	●	●	●	●	●	●	●	●	●		●
<i>Tibellus</i> spp.	●	●	●	●	●	●	●	●	●		●
<i>Xysticus</i> spp.	●	●	●	●	●	●	●	●	●	●	●
<i>Agalenatea redi</i>	●	●	●		●	●	●	●	●	●	●
<i>Mangora acalypha</i>	●	●	●	●	●	●	●	●	●	●	●
<i>Neoscona adianta</i>	●	●	●	●	●	●	●	●	●	●	●
<i>Heliophanus</i> spp.	●	●	●	●	●	●	●	●	●	●	●
<i>Phylloneta impressa</i>	●	●	●	●	●	●	●	●	●	●	●
<i>Cheiracanthium pennyi</i>		●			●	●	●	●	●	●	●
<i>Philaeus chrysops</i>					●	●	●		●		●
<i>Thomisus onustus</i>					●	●	●	●	●	●	●
<i>Uloborus walckenaerius</i>							●	●		●	●
<i>Oxyopes heterophthalmus</i>							●	●	●	●	●

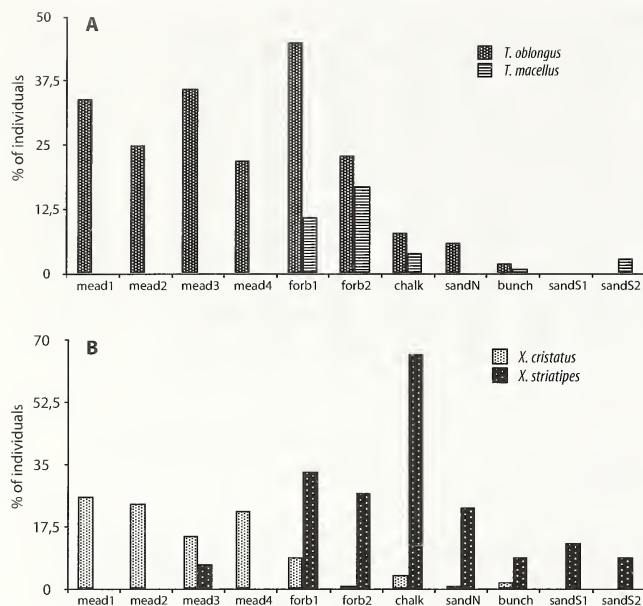


Fig. 4: Relative abundance (% of individuals out of the total number of spiders collected at each site) of (A) *Tibellus oblongus* and *T. macellus* and (B) *Xysticus cristatus* and *X. striatipes* in herbaceous vegetation of different steppe habitats. Sites are arranged from north to south.

onustus and *Philaeus chrysops* in genuine steppes. Six species were dominants at only one site (*Uloborus walckenaerius*, *Cheiracanthium pennyi*, *C. punctorum*, *Philodromus histrio*, *Pellenes seriatus*, and *Yllenus vitatus*).

Of further interest are the latitudinal changes of abundance of common species of the same genus. In the pairs *Tibellus oblongus*–*macellus* and *Xysticus cristatus*–*striatipes*, the first species of each pair was abundant in the forest-steppe and in the north of the steppe zone (Fig. 3). The second species of each pair appeared in genuine steppes, and in case of *Xysticus*, replaced the first one. Further to the south they all decreased in number or disappeared in steppe plots, although they remained quite common in adjacent forest stands (POLCHANINOVA 1990a). *Heliophanus flavipes* occurred in all steppe types. In the three southern sites, *H. lineiventris* co-occurred with *H. flavipes* and together they made up a significant proportion of the individuals found in these sites (Tab. 3). *Evarcha arcuata* was common in meadow steppes and in the northern sandy steppe. *E. michailovi* occurred in forb steppes and penetrated into one site of meadow steppes. Southward in the subzone of bunchgrass steppes, neither of these species was found.

Despite the local differences in species composition and dominance structure of spider assemblages, a number of characteristic features can be distinguished for every steppe type. All the spider complexes of steppe herbage had a polydominant structure.

In the four sites of meadow steppes, the group of dominants consisted of *Dictyna arundinacea* (16.0–24.3%), *Tibellus oblongus* (8.7–14.2%) and *Xysticus cristatus* (6.0–9.3%). *Araneus quadratus* was a member of this complex in three sites, *Neottiura bimaculata*, *Larinioides patagiatus*, *Cheiracanthium punctorum*, *Evarcha arcuata*, and *Neoscona adianta* were local dominants in not more than one site each. *Marpissa pomatia*, *Hypsosinga sanguinea*, and *Singa hamata* were subdominants in the meadow steppes. Southwards in genuine steppes they did not occur, or were found only as a few specimens. However we can not consider them to be typical species of meadow steppes because they were also numerous in wetlands (personal observation). The specificity of the spider assemblage of the driest eastern site 'mead4' is worth mentioning. The abundance of *Neoscona adianta* and the appearance of *Evarcha michailovi* and *Xysticus striatipes* make it similar to the assemblages of forb steppes.

Xysticus striatipes (9.3–15.7%), *Tibellus* spp. (10.7–12.6%), and *Neoscona adianta* (8.0–9.7%) were common dominants of forb steppes, with *Agalenatea redii* and *Mangora acalypha* co-occurring with them in the northern site, and *Philaeus chrysops*, *Evarcha michailovi*, *Heliophanus flavipes* and *Thomisus onustus* in the southern one. A range of species typical of dry grasslands appear in these steppes (*Heterotheridion nigrovariegatum*, *Theridion innocuum*, *Heriaeus oblongus*, *Tibellus macellus*, *Xysticus marmoratus*, *Synageles hilarulus*, and *Philaeus chrysops*). However, we found no species specific for the forb steppes only.

The dominance complex of chalky steppe included *Xysticus striatipes* (25.5%), *Agalenatea redii* (11.6%), *Neoscona adianta* (10.0%), *Tibellus* spp. (6.4%), *Philaeus chrysops* (6.7%), and *Dictyna arundinacea* (5.8%). In the northern sandy steppe it consisted of *Neoscona adianta* (14.9%), *Xysticus striatipes* (11.0%), *Mangora acalypha* (8.9%), *Dictyna arundinacea* (5.8%), *Philodromus histrio* (7.7%), and *Uloborus walckenaerius* (5.3%). In the area investigated, the latter two species are associated with vegetation of sandy soil. They were also common in calcareous lands (POLCHANINOVA

2010). *Simitidion simile* and *Cyclosa oculata* preferred the same habitats but they had larger ecological flexibility, inhabiting meadows, shrubby steppes and even open deciduous forests (POLCHANINOVA & PROKOPENKO 2007b). *Gibbaranea bituberculata* and *G. ullrichi* came to the steppe plots from neighbouring pine forests.

The spider assemblage of the bunchgrass steppe was characterized by large numbers of three eudominants *Neoscona adianta* (29.8%), *Oxyopes heterophthalmus* (26.2%), and *Thomisus onustus* (14.0%), the occurrence of one subdominant *Xysticus striatipes*, and single finds of other species. Southern sandy steppes were dominated at both sites by *Heliophanus flavipes*, *H. lineiventris* (15.6–20.0%), *Neoscona adianta* (11.0–12.2%), and *Phylloneta impressa* (5.6–6.3%). In one of them (Ivano-Rybalchansky site) the dominance complex was supplemented with *Oxyopes heterophthalmus*, *Cheiracanthium pennyi*, *Thomisus onustus*, and *Runcinia grammica*, and in the other one (Solenoozerny) with *Pellenes seriatus* and *Yllenus vittatus*. The presence of the latter three species and the abundance of *H. lineiventris* is characteristic of the southern sandy steppes.

Discussion

Spider species richness of the investigated steppe fragments depended on the steppe type. The low number of species on the largest site of bunchgrass steppes can be explained by the monotonous plain relief and absence of neighbouring intrazonal habitats. Presumably, invertebrate communities within small sites increase in species richness due to species exchange with adjacent habitats (MAGURA & KODOBOCZ 2007). This statement is true for the forest-steppe and northern part of the steppe zone where an active interchange takes place (CHERNOV 1975). In our investigations, we recorded the presence of forest and wetland species in meadow steppes. However in the south of the steppe zone, despite a rich local fauna in general and the existence of neighbouring forest stands and lakes, the species composition of spiders of steppe fragments remained the poorest. Only one wetland species was found there.

About 12% of the species of the investigated area occurred in all steppe types. Another 12% changed their habitat preference spreading from north to south and moved from steppe sites to shaded and moist ones. These data illustrate well the 'principle of zonal change of habitats' by BEI-BIENKO (1966). Some of them, such as *Neottiura bimaculata*, changed

both habitat and vegetation layer moving from herbs to the ground (POLCHANINOVA 1990a). A group of southern species which spread to the north through the dry open sites made up only 4% of the species found in the steppe habitats. Our data confirm a decrease of generalist, forest and wetland dwelling species to the south and predominance of grassland species in genuine steppes. The same tendencies in distribution of ecological groups of spiders were shown by ESYUNIN (2009) in a transect through the Urals.

The relative abundance of spider families in steppe vegetation changes depending on the steppe type. This is confirmed by data on steppe localities in other regions. Thus, in mountain steppes of Bashkiriya (Southern Urals), Tetragnathidae, Thomisidae, and Araneidae were dominants in numbers, while Thomisidae comprised the main part of the biomass (EFIMIK 1989). According to our data, Araneidae was the most abundant family while Tetragnathidae occasionally occurred in steppe as rare finds. In the east of the Russian Plain, in stony and forb steppes of Samarskaya Luka, Thomisidae reached the highest abundance followed by Araneidae and Salticidae (KRASNOBAEV 2003). In eastern Hungary (Great Hungarian Plain), dry sandy grassland communities that are close to sandy steppes were also dominated by Araneidae and Thomisidae while Salticidae and Dictynidae comprised a second-ranked group (HORVATH et al. 2009).

No single species dominated in all the steppe types and even within one type, a dominance complex was composed of different species. Meadow steppes were dominated by wetland species and genuine steppes by wide-spread grassland species. In azonal steppes, the complex included species inhabiting sparse vegetation of sandy and chalky soils. Dominant spider species of steppe and steppe-like habitats of the Urals also vary depending on zonal and local conditions (ESYUNIN 2009).

In conclusion the spider assemblages of the northernmost meadow steppes and the southernmost sandy steppes differed dramatically, as expected, because of zonal-climatic differences. From a zonal standpoint, the first have much in common with meadows (PONOMAREV & POLCHANINOVA 2006), and the latter with brackish meadows and salt-marshes with dense vegetation (POLCHANINOVA 1998). In our study, the most specific were herb dwelling spider assemblages of the bunchgrass steppe represented in Ukraine by a single site in the middle of plowed Dnieper lowland.

The second specific groups were assemblages of sandy steppes in the northern steppe subzone because these fragments are isolated and differ in microclimatic conditions and vegetation structure from other grasslands. Steppes of a certain type are formed under both climate and soil conditions of the zone and local topography (GRIBOVA et al. 1980). Accordingly, the structure of the animal communities of the steppes is a reflection of these conditions (MORDKOVITCH 1982). Assemblages of herb-dwelling spiders are characteristic of each steppe type and differ in species composition and dominance structure.

Acknowledgements

The author is grateful to J. Gergerich for revising the first draft of the English manuscript and to A. Atemasov for the map design.

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Appendix: Occurrence of herbaceous vegetation spiders in investigated steppe habitats of Ukraine and Central Chernozem Russia. For a description of the localities, see Tab. 1.

Ecological groups: gn – generalist species, wf – wetland and forest, for – forest, wt – wetland, grf – grassland and forest edges, gr – grassland, st – steppe, un – unspecified, typ – typical.

Species	ecological group	Type of steppe habitats										
		meadow steppe				forb – bunchgrass		chalky	sandy Northern	bunchgrass	sandy Southern	
		1	2	3	4	5	6	7	8	9	10	11
Mimetidae												
<i>Ero furcata</i> (Villers, 1789)	for	+		+								
Uloboridae												
<i>Uloborus walckenaerius</i> Latreille, 1806	typ							+	+		+	+
Theridiidae												
<i>Dipoena coracina</i> (C.L. Koch, 1837)	un									+		
<i>Enoplognatha latimana</i> Hippa & Oksala, 1982	un				+					+		
<i>E. ovata</i> (Clerck, 1757)	wf	+			+	+	+					
<i>Euryopis saukea</i> Levi, 1951	st					+		+				
<i>Heterotheridion nigrovariegatum</i> (Simon, 1873)	st					+		+				
<i>Neottiura bimaculata</i> (Linnaeus, 1767)	wf	+	+	+	+	+						
<i>Parasteatoda simulans</i> (Thorell, 1875)	for			+								
<i>Phylloneta impressa</i> (L. Koch, 1881)	grf	+	+	+	+	+	+	+	+	+	+	+
<i>Simitidion simile</i> (C.L. Koch, 1836)	grf					+		+	+		+	+
<i>Theridion innocuum</i> Thorell, 1875	typ					+	+	+	+	+		
<i>T. melanurum</i> Hahn, 1831	un								+			
<i>T. mystaceum</i> L. Koch, 1870	yn			+								
<i>T. pinastri</i> L. Koch, 1872	for			+								
Linyphiidae												
<i>Dactylopisthes mirificus</i> (Georgescu, 1976)	un					+	+					
<i>Erigone dentipalpis</i> (Wider, 1834)	wtf	+	+		+					+		
<i>Floronia bucculenta</i> (Clerck, 1757)	wtf	+	+									
<i>Gonatium paradoxum</i> (L. Koch, 1869)	wtf			+								
<i>Hylyphantes nigrinus</i> (Simon, 1881)	wtf		+									
<i>Linyphia hortensis</i> Sundevall, 1830	wtf	+										
<i>L. tenuipalpis</i> Simon, 1884	gn			+			+	+				
<i>L. triangularis</i> (Clerck, 1757)	gn	+	+	+		+	+	+				
<i>Russocampus polchaninovae</i> Tanasevitch, 2004	un			+								
Tetragnathidae												
<i>Metellina segmentata</i> (Clerck, 1757)	wtf			+								
Araneidae												
<i>Aculepeira ceropegia</i> (Walckenaer, 1802)	un					+				+		
<i>Agelenatea redii</i> (Scopoli, 1763)	gr	+	+	+		+	+	+	+	+	+	+
<i>Araneus diadematus</i> Clerck, 1757	for		+	+			+					
<i>Araneus quadratus</i> Clerck, 1757	wt	+	+	+	+		+					
<i>Araniella cucurbitina</i> (Clerck, 1757)	wtf				+		+	+				
<i>Argiope bruennichi</i> (Scopoli, 1772)	gr	+	+	+	+	+	+	+	+	+	+	+
<i>A. lobata</i> (Pallas, 1772)	st							+	+	+	+	
<i>Cercidia prominens</i> (Westring, 1851)	gn	+	+	+	+	+	+	+		+	+	+
<i>Cyclosa conica</i> (Pallas, 1772)	for	+		+								
<i>C. oculata</i> (Walckenaer, 1802)	grf			+		+		+	+			
<i>Gibbaranea bituberculata</i> (Walckenaer, 1802)	grf								+	+		

Species	ecological group	Type of steppe habitats										
		meadow steppe				forb – bunchgrass		chalky	sandy Northern	bunchgrass	sandy Southern	
		1	2	3	4	5	6	7	8	9	10	11
<i>G. ullrichi</i> (Hahn, 1835)	typ								+			
<i>Hypsosinga albovittata</i> (Westring, 1851)	un					+		+			+	+
<i>H. pygmaea</i> (Sundevall, 1831)	gr	+	+	+			+		+	+	+	
<i>H. sanguinea</i> (C.L. Koch, 1844)	grf	+		+		+	+	+	+			
<i>Lariniioides patagiatus</i> (Clerck, 1757)	wt		+	+	+				+			
<i>L. suspicax</i> (O. Pickard-Cambridge, 1876)	wt				+							
<i>Mangora acalypha</i> (Walckenaer, 1802)	gn	+	+	+	+	+	+	+	+	+	+	+
<i>Neoscona adianta</i> (Walckenaer, 1802)	gr	+	+	+	+	+	+	+	+	+	+	+
<i>Singa hamata</i> (Clerck, 1757)	wt	+	+			+			+			
Pisauridae												
<i>Pisaura mirabilis</i> (Clerck, 1757)	wtf	+	+	+			+		+			
Oxyopidae												
<i>Oxyopes heterophthalmus</i> (Latreille, 1804)	typ					+		+	+	+	+	+
<i>O. lineatus</i> Latreille, 1806	un											+
Dictynidae												
<i>Archaeodictyna consecuta</i> (O. Pickard-Cambridge, 1872)	un								+			
<i>A. minutissima</i> (Miller, 1958)	un									+		
<i>Dictyna arundinacea</i> (Linnaeus, 1758)	grf	+	+	+	+	+	+	+	+	+	+	+
<i>D. latens</i> (Fabricius, 1775)	grf					+	+	+		+	+	
<i>D. uncinata</i> Thorell, 1856	wtf			+	+							
Miturgidae												
<i>Cheiracanthium elegans</i> Thorell, 1875	un						+					
<i>C. erraticum</i> (Walckenaer, 1802)	grf	+	+	+			+					
<i>C. pennyi</i> O. Pickard-Cambridge, 1873	gr					+	+	+	+	+	+	+
<i>C. punctorium</i> (Villers, 1789)	wt	+	+	+	+	+	+					
Clubionidae												
<i>Clubiona caerulescens</i> L. Koch, 1867	for	+										
<i>Clubiona diversa</i> O. Pickard-Cambridge, 1862	wt		+	+								
<i>C. lutescens</i> Westring, 1851	wtf				+							
<i>C. neglecta</i> O. Pickard-Cambridge, 1862	wtf	+	+	+	+							
<i>C. pseudoneglecta</i> Wunderlich, 1994	gn					+	+					
Sparassidae												
<i>Micrommata virescens</i> (Clerck, 1757)	wtf	+	+	+	+	+			+	+	+	
Philodromidae												
<i>Philodromus cespitum</i> (Walckenaer, 1802)	gn	+	+	+	+	+	+	+	+	+		
<i>P. histrio</i> (Latreille, 1819)	gn					+	+	+	+	+	+	
<i>Thanatus atratus</i> Simon, 1885	un									+	+	
<i>T. pictus</i> L. Koch, 1881	un						+			+		
<i>T. vulgaris</i> Simon, 1870	un						+					
<i>Tibellus macellus</i> Simon, 1875	st					+	+	+		+		
<i>T. oblongus</i> (Walckenaer, 1802)	gn	+	+	+	+	+	+	+	+	+		+
Thomisidae												
<i>Embrechtella tricuspidata</i> (Fabricius, 1775)	gn	+	+	+	+	+	+	+	+			
<i>Heriaeus oblongus</i> Simon, 1918	grf					+	+	+	+	+	+	
<i>Misumena vatia</i> (Clerck, 1757)	gn	+	+	+	+		+		+			
<i>Runcinia grammica</i> (C.L. Koch, 1837)	typ										+	+
<i>Synema globosum</i> (Fabricius, 1775)	un									+		

Species	ecological group	Type of steppe habitats										
		meadow steppe				forb – bunchgrass		chalky	sandy Northern	bunchgrass	sandy Southern	
		1	2	3	4	5	6	7	8	9	10	11
<i>Thomisus onustus</i> Walckenaer, 1805	gr				+	+	+	+	+	+	+	+
<i>Tmarus piger</i> (Walckenaer, 1802)	for						+		+			
<i>Xysticus acerbus</i> Thorell, 1872	gr					+	+		+			
<i>X. cristatus</i> (Clerck, 1757)	gn	+	+	+	+	+	+	+	+	+	+	+
<i>X. kochi</i> Thorell, 1872	gn			+	+	+	+	+	+	+		+
<i>X. laetus</i> Thorell, 1875	gr					+		+		+		
<i>X. lanio</i> C.L. Koch, 1835	for					+						
<i>X. luctuosus</i> (Blackwall, 1836)	for	+										
<i>X. marmoratus</i> Thorell, 1875	st						+			+		
<i>X. mongolicus</i> Schenkel, 1863	un								+			
<i>X. ninnii</i> Thorell, 1872	st					+		+		+		
<i>X. striatipes</i> L. Koch, 1870	gr			+		+	+	+	+	+	+	+
<i>X. ulmi</i> (Hahn, 1831)	wtf	+	+	+	+							
Salticidae												
<i>Carrhotus xanthogramma</i> (Latreille, 1819)	grf					+	+	+			+	
<i>Evarcha arcuata</i> (Clerck, 1757)	gn	+	+	+	+	+	+	+	+			
<i>E. falcata</i> (Clerck, 1757)	wtf		+			+			+			
<i>E. laetabunda</i> (C.L. Koch, 1846)	un			+		+						
<i>E. michailovi</i> Logunov, 1992	un			+		+	+					
<i>Heliophanus auratus</i> C.L. Koch, 1835	gn		+	+	+	+	+	+	+			
<i>H. cupreus</i> (Walckenaer, 1802)	wtf		+			+	+	+	+	+		
<i>H. flavipes</i> (Hahn, 1832)	gr	+	+	+		+	+	+	+	+	+	+
<i>H. lineiventris</i> Simon, 1868	typ									+	+	+
<i>Marpissa pomatia</i> (Walckenaer, 1802)	wtl	+	+	+								
<i>Myrmarachne formicaria</i> (De Geer, 1778)	un						+					
<i>Pellenes seriatus</i> (Thorell, 1875)	typ										+	+
<i>Philaeus chrysops</i> (Poda, 1761)	st					+	+	+	+	+	+	
<i>Salticus scenicus</i> (Clerck, 1757)	un							+	+			
<i>Sibianor aurocinctus</i> (Ohlert, 1865)	un	+		+								
<i>Synageles hilarulus</i> (C.L. Koch, 1846)	un					+						
<i>S. subcingulatus</i> (Simon, 1878)	grf						+		+			
<i>Yllenus borvathi</i> Chyzer, 1891	un											+
<i>Y. vittatus</i> Thorell, 1875	typ								+		+	+
Total number of species in locality		36	35	46	33	50	50	41	45	39	29	24
Total number of species in steppe type		61				64		41	45	39	33	

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Jahr/Year: 2012

Band/Volume: [43](#)

Autor(en)/Author(s): Polchaninova Nina Y.

Artikel/Article: [Assemblages of herb-dwelling spiders \(Araneae\) of various steppe types in Ukraine and the Central Chernozem region of Russia 66-78](#)