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Spatial and temporal structure of the spider community in the clay semi-desert of western Kazakhstan

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Abstract: The spatial and temporal structure of spider communities was studied in the clay semi-desert of the north-western Caspian Lowland, western Kazakhstan (49°23' N, 46°47' E). The soils and vegetation are complex, being composed of a mosaic of desert and steppe plant communities. Besides the native associations, there are plantations of different tree species. The ground-dwelling spider assemblages in the native habitats are the most diverse. The number of species inhabiting forest plantations is three times as small. Gnaphosidae is the leading family in the ground layer. They show high abundance and diversity levels during the whole season. Thomisidae, Lycosidae, Philodromidae, and Salticidae are abundant as well. The species diversity of herbage-dwelling spiders in different open native habitats is very similar. The spectrum of dominant families (Thomisidae, Oxyopidae, Araneidae, and Salticidae) and the seasonal dynamics of their ratio in desert and steppe associations have much in common. Spider assemblages of native and artificial habitats are characterised by change from multispecies polydominant spring-summer communities to impoverished imbalanced autumn ones. Seasonal changes in the species structure of mature spider groupings in native habitats are well pronounced, while the impact of seasonal conditions is even stronger than between-habitat differences. Complexes of typical species with different levels of habitat preference are revealed.

Key words: Araneae, ecology, habitat preference, seasonal dynamics

Spiders of steppe and semi-desert regions of the Palaearctic, unlike those of the temperate zone, are still poorly studied. There is some faunistic information (e.g. PONOMAREV 1981, 1988, 2005, 2008, PONOMAREV & TSVETKOVA 2003, PONOMAREV & TSVETKOV 2004a, 2004b, POLCHANINOVA 1992, 1995, 2002, KOVBLYUK 2006, EFIMIK et. al. 1997, ESYUNIN & EFIMIK 1998, ESYUNIN et al. 2007, TUNEVA & ESYUNIN 2003), but very little attention has been paid to such ecological aspects as the structure of populations, their dynamics, and the mechanisms of community function in arid and semi-arid conditions (ESYUNIN 2009).

This paper is focused on studying the spatial and temporal structure of spider assemblages in the clay semi-desert in the Volga and Ural rivers' interfluve. The research was carried out in the environs of the Dzhanybek Research Station of the Russian Academy of Sciences (49°23'N, 46°47'E), located on the border between the Western Kazakhstan Province of the Republic of Kazakhstan and the Volgograd Province of the Russian Federation. The area studied is a flat, nearly undrained plain in the north-western Caspian Lowland, a semi-desert zone (MILKOV & GVOZDETSKY 1986).

Study area, material and methods

The Dzhanybek plain is the most arid area in the Ciscaspian semi-desert due to both internal drainage and soil salinity, despite its northernmost location. The climate of the territory is characterised by high atmospheric drought and aridity. Hot summers and severe winters are typical: the summer temperatures exceed 40°C, the winter temperatures sink lower than -35°C. The average annual air temperature (for 1951–2003) is 7.3°C; 18°C during the warm period and -3.5°C during the cold period. The average annual precipitation (for 1951-2003) is 295 mm, ranging from 44 (in 1984) to 354 mm (in 1993) (SAPANOV 2006). The sharp disparity of heat and moisture causes the very low humidity of the territory. The evaporative power reaches 1000 mm, which is 3 times the total rainfall. In addition, the meteorological conditions of the region are characterised by long-term fluctuations with regular cyclic reiterations of drought and moist periods (RODE 1959, LINDEMAN et al. 2005, SAPANOV 2006).

Another characteristic feature of the study area is a well pronounced complex pattern of soils and vegetation, with a combination of typical desert, semi-desert and steppe habitats. The co-existence of such

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contrasting biotopes is caused by pronounced microrelief and, consequently, differences in moisture, soil substrates and their properties (Rode & Polskikh 1961).

Microelevations are occupied by plant communities of the desert type, with *Kochia prostrata*, *Artemisia pauciflora*, and *Salsola laricina* on saline soils. The groundwater is saline. Forb-grass vegetation (*Stipa* spp., *Festuca valesiaca*, *Agropyron cristatum*, etc.) on dark chestnut and meadow chestnut soils with fresh groundwater occupies microdepressions (down to 0.4 m deep); they represent steppe habitats. This mosaic of elements constitutes most of the territory. Large depressions (down to 1-1.5 m deep, area of 1-100 hectares) with steppe plant communities take up about 10–15 % of the area. These large depressions are best supplied with water, due to runoff from the surrounding area. Besides these mentioned native associations, there are 50-year-old plantations composed of different tree species.

Material for this work was collected by the author (April-October 2004-2005) and Dr. K.G. Mikhailov (June-September 1984) in three native habitats (desert associations of microelevations, and steppe associations of large depressions, and microdepressions) and three artificial ones: oak (*Quercus robur*) forest belts, oak patch in a park, and elm (*Ulmus pumila*) forest belts. The collections in the latter habitat took place only in 1984. In recent years, the vitality of the forest-belt has become very poor; the trees are very sparse so the conditions in it have approached those of an open habitat.

Traditional collecting methods were used: pitfall trapping (one transect – 10 traps), hand-sorting of soil and litter samples (0.25 x 0.25 m, 10 samples) and sweeping (one sample – 4 x 25 sweeps, 3 times a day, at 00:00, 8:00 and 16:00). Sampling was carried out every 7-10 days. Pitfall traps were set in microelevations, microdepressions and woody plantations. Soil and litter samples were taken in all studied habitats. As the plantations had a rather poor and scattered herbaceous layer, sweeping was undertaken only in native habitats.

The material includes a total of 15000 pitfall days, 570 soil and litter samples, and 268 sweeping samples.

One of the most important features of the spider population in the clay semi-desert is its strongly pronounced seasonality and vertical stratification. Thus, I analysed the structure of spider complexes separately by layer, i.e. ground and herbaceous layers, and seasons, i.e. spring, summer and autumn. When calculating the ratio of families, I considered spiders of all instars. With respect to the seasonal changes in species compositions I used mature spiders only, although I suggest that the differences revealed might reflect certain phenological trends.

Taxa with a relative abundance of ≥5 % were considered predominat. The habitat preference of species was calculated using Pesenko's coefficient (F_{ij}) (Pesenko 1982), which represents a mathematical transformation of the share of a species in a single biotope to its share in all other biotopes:

$$F_{ij} = (n_{ij}/N_j - n_i/N)/(n_{ij}/N_j + n_i/N),$$

where n_{ij} – number of specimens of *i*-species in samples from *j*-biotope with total volume N_j; n_i – number of specimens of *i*-species in all other biotopes with total volume *N*. Single records of species were omitted from the calculation.

The choice of this coefficient was based on the variety of the collecting methods used, which caused the heterogeneity of the data obtained and the difficulties in their unification. Using relative indices (not absolute ones) simplifies the interpretation of data and makes miscellaneous information comparable. The value of the coefficient ranges from –1 (absolute avoidance) to +1 (absolute preference).

Statistical data analysis was performed using Statistica 6.0.

Results

About 20000 spider specimens were captured and studied, with about 7000 of these spiders being mature. Altogether, 172 species from 88 genera and 21 families were recovered. Taking into account the scant information published previously, the spider fauna of the Dzhanybek Station amounts to 184 species from 93 genera and 22 families. A checklist and the distribution of species between the study habitats has been made available elsewhere (Piterkina 2009, Piterkina & Mikhailov 2009). Since the time of these mentioned papers some taxonomical changes have taken place or some identifications were refined, thus some species names may not coincide. Namely, *Ero* sp. turned out to be *Ermetus inopinabilis* Ponomarev, 2008, *Theridion* cf. *uhligi* Martin, 1974 – *T. uhligi*, *Thanatus constellatus* Charitonov, 1946 – *T. oblongiusculus* (Lucas, 1846), and *Eresus cinnaberinus* (Olivier, 1789) – *E. kollari* Rossi, 1846.

Species structure of spider communities and its seasonal dynamics

The communities of ground-dwelling spiders in the native habitats – microelevations and microdepressions – are the most diverse (about 90 species). The number of species inhabiting forest plantations is three times as small (about 30 species) (Tab. 1).

The activity of spiders in the open habitats fluctuates from 20 to 70 ind. / 100 pitfall-days, with the highest numbers in spring and summer. The amplitude of its fluctuation is much higher in the forest plantations (from 3-4 to 100 ind./100 pitfall-days). The density of the spider population, based on soil and litter samples, reaches its highest values in autumn (up to 117 ind. /m^2).

Gnaphosidae is the dominant family in the native associations. They exhibit high abundance and diversity levels (about 50 %) during the whole vegetation season, this being quite typical of arid and semi-arid landscapes. The proportions of Lycosidae and Salticidae are less, but also stable. Linyphiidae predominate in spring and autumn, Oxyopidae in summer, Titanoecidae in spring and summer, Thomisidae in summer and autumn. The dominant complex of the tree plantations is less diverse. The proportion of Gnaphosidae is significantly lower than in native habitats (about 20–30 %), while the abundance of Thomisidae is high and stable during the entire vegetation season (about 30–50 %). Pisauridae show a peak in their abundance in spring and autumn, whereas Liocranidae peak in summer.

Seasonal change in species dominance is well pronounced and the species set is relatively stable across different years (Tab. 1). For example, in the desert habitats, *T. veteranica*, *Haplodrassus* cf. *soerenseni*, *E. eltonica*, *D. rostratus*, *Z. orenburgensis* predominate in spring populations in both years of study. The stable summer dominants are *P. braccatus*, *H. horridus*, *Oxyopes* cf. *xinjiangensis*, *D. rostratus* and *Z. orenburgensis*. The autumn populations are rather imbalanced. Characteristic is a high level of predominance of 1-2 species that can change in different years (*Z. orenburgensis*, *X. marmoratus* or *D. rostratus*). The dominant complexes of oak plantations have much in common and include several species abundant during the whole vegetation season (*Z. gallicus*, *O. praticola*, *X. luctator*) (Tab. 1). The species diversity of herbage-dwelling spiders in the open native habitats is very similar: about 50 species (Tab. 2). The abundance of hortobiotic spiders fluctuates with a high amplitude, reaching its maximum in summer (about 100 ind. / 100 sweeps). The spectrum of predominating families and the seasonal dynamics of their proportion in desert and steppe associations have much in common. Uloboridae and Linyphiidae are abundant in spring, Araneidae and Oxyopidae in spring and autumn, Salticidae in sum-

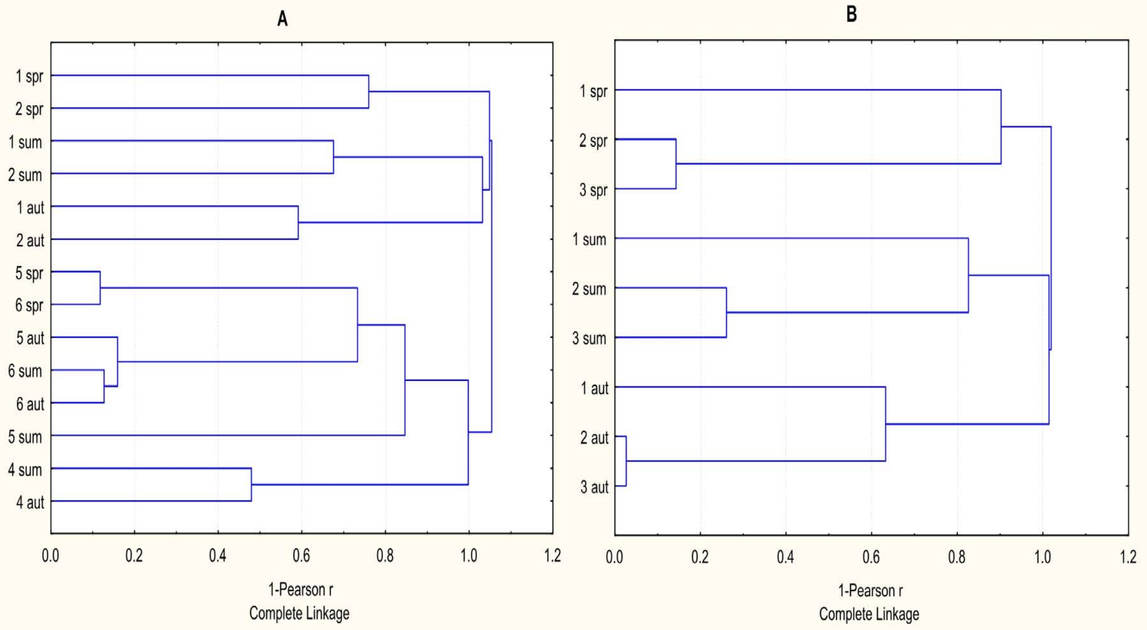

Figure 1: Clustering the mature spider complexes for separate seasons: A – ground-dwelling spiders, B – herbage-dwelling spiders. Habitats: 1: microelevations, 2: microdepressions, 3: large depressions, 4: elm shelter-belt, 5: oak shelter-belt, 6: oak patch in a park. Seasons: spr – spring, sum – summer, aut – autumn.

mer and autumn. Philodromidae, Clubionidae and Miturgidae are numerous during the whole vegetative period.

The seasonal change of the predominant complexes of species is also well-pronounced (Tab. 2). In spring and, especially, summer, the sets of abundant species are not stable in different years. On the contrary, the autumn populations of all habitats are very similar. They are mainly formed by two species, *Xysticus marmoratus* and *X. striatipes*. Co-dominance of *Cheiracanthium* cf. *virescens* adds originality to the autumn assemblages of microelevations, *E. michailovi* to those of microdepressions, and *H. lineiventris* to those of large depressions (Tab. 2).

Clustering the mature spider complexes for separate seasons (Fig. 1) yielded interesting results. Two large clusters were revealed among ground-dwelling spiders: assemblages of native biotopes and of forest plantations (Fig. 1A). Within them, the populations were not united by habitat, as one would expect, but by season. The cluster of open habitats includes populations of microelevations and microdepressions during spring, summer and autumn. Microclimatic conditions in woody plantations were presumably comparatively smoother, even though no direct abiotic measurements were taken. The cluster of artificial forests appears to be less differentiated. The same tendency is also obvious when clustering the herbage-dwelling spider complexes: three pronounced clusters united spring, summer and autumn assemblages of microelevations, microdepressions and large depressions respectively (Fig. 1B).

Habitat preferences of species

Spider assemblages of desert associations are the most specific. The share of species collected only in microelevations is highest (24 %), whereas it is half this in the other biotopes. Most of unique species, with few exceptions, exhibit low abundance levels and hardly play coenotic roles (Tab. 3).

Table 1: Species structure of populations of mature ground-dwelling spiders. Numbers in brackets show relative abundance in %.

Microelevations (desert habitats)

Characteristics	Spring		Summer		Autumn		
	2004	2005	1984	2004	1984	2004	2005
Number of species	99						
	45	39	49	32	24	22	13
Predominating species	*Titanoeca veteranica* (12) *Haplodrassus* cf. *soerenseni* (8) *Micaria pallipes* (7) *Evippa eltonica* (6) *Drassodes rostratus* (6) *Gnaphosa steppica* (5) *Zelotes orenburgensis* (5)	*Evippa eltonica* (34) *Titanoeca veteranica* (13) *Haplodrassus* cf. *soerenseni* (10) *Zelotes orenburgensis* (5)	*Heriaeus horridus* (14) *Oxyopes* cf. *xinjiangensis* (14) *Zelotes orenburgensis* (13) *Gnaphosa steppica* (9) *Evippa eltonica* (9) *Phaeocedus braccatus* (8) *Drassodes rostratus* (6)	*Gnaphosa lucifuga* (16) *Phaeocedus braccatus* (11) *Heriaeus horridus* (10) *Nurscia albomaculata* (10) *Zelotes orenburgensis* (9) *Drassodes rostratus* (9) *Oxyopes* cf. *xinjiangensis* (6)	*Zelotes orenburgensis* (48) *Drassodes rostratus* (21) *Ozyptila lugubris* (7)	*Xysticus marmoratus* (44) *Thanatus pictus* (18) *Xysticus striatipes* (7) *Drassodes rostratus* (7) *Zelotes orenburgensis* (5)	*Drassodes rostratus* (36) *Xysticus marmoratus* (21) *Zelotes orenburgensis* (17) *Talanites strandi* (5)

Microdepressions (steppe habitats)

Characteristics	Spring		Summer		Autumn		
	2004	2005	1984	2004	1984	2004	2005
Number of species	84						
	46	40	17	38	6	29	24
Predominating species	*Thanatus arenarius* (15) *Berlandina cinerea* (11) *Zelotes electus* (11) *Haplodrassus kulczynskii* (8) *Gnaphosa taurica* (6) *Alopecosa taeniopus* (5)	*Berlandina cinerea* (20) *Thanatus arenarius* (19) *Gnaphosa taurica* (11) *Haplodrassus* cf. *soerenseni* (7) *Haplodrassus kulczynskii* (6) *Zelotes electus* (6) *Haplodrassus signifier* (5)	*Xysticus ninnii* (26) *Thanatus atratus* (14) *Aelurillus v-insignitus* (14) *Zelotes electus* (6)	*Xysticus ninnii* (12) *Berlandina cinerea* (11) *Gnaphosa lucifuga* (10) *Thanatus atratus* (10) *Zelotes caucasius* (7) *Gnaphosa steppica* (6) *Gnaphosa taurica* (5) *Nurscia albomaculata* (5)	*Phlegra bicognata* (36) *Aelurillus v-insignitus* (27)	*Thanatus pictus* (20) *Xysticus marmoratus* (19) *Xysticus striatipes* (15) *Haplodrassus isaevi* (14) *Trichopterna cito* (7)	*Alopecosa schmidti* (13) *Xysticus striatipes* (13) *Xysticus marmoratus* (12) *Thanatus pictus* (7)

Elm shelter-belt

Characteristics	1984	
	Summer	Autumn
Number of species	30	
	26	11
Predominating species	*Xysticus ninnii* (22) *Zelotes gallicus* (16) *Titanoeca schineri* (9) *Pardosa xinjiangensis* (8) *Drassyllus pusillus* (8) *Pisaura mirabilis* (5)	*Zelotes gallicus* (44) *Gnaphosa taurica* (28)

Oak shelter-belt

Characteristics	Spring		Summer	Autumn	
	2004	2005	2004	2004	2005
Number of species	39				
	14	18	17	9	5
Predominating species	*Pisaura mirabilis* (31) *Drassyllus pusillus* (14) *Zelotes gallicus* (13) *Ozyptila praticola* (11) *Gnaphosa taurica* (6) *Xysticus luctator* (6) *Zora pardalis* (6)	*Xysticus luctator* (39) *Pisaura mirabilis* (18) *Ozyptila praticola* (10) *Zora pardalis* (9) *Drassyllus pusillus* (8) *Zelotes gallicus* (8)	*Titanoeca schineri* (42) *Pisaura mirabilis* (9) *Zora pardalis* (8) *Zelotes gallicus* (7) *Ozyptila praticola* (7) *Xysticus ninnii* (7) *Oxyopes lineatus* (5) *Xysticus luctator* (5)	*Ozyptila praticola* (43) *Alopecosa taeniopus* (24)	*Ozyptila praticola* (44) *Zelotes longipes* (22) *Xysticus luctator* (22) *Zelotes gallicus* (11)

Oak patch in a park

Characteristics	Spring		Summer	Autumn	
	2004	2005	2004	2004	2005
Number of species	31				
	17	17	13	5	4
Predominating species	*Xysticus luctator* (19) *Ozyptila praticola* (18) *Zelotes gallicus* (15) *Pisaura mirabilis* (12) *Drassyllus pusillus* (12) *Gnaphosa taurica* (6)	*Xysticus luctator* (45) *Drassyllus pusillus* (15) *Ozyptila praticola* (12) *Pisaura mirabilis* (5)	*Ozyptila praticola* (45) *Titanoeca schineri* (13) *Drassyllus pusillus* (12) *Sitticus zimmermanni* (6) *Xysticus luctator* (5) *Xysticus robustus* (5)	*Ozyptila praticola* (78) *Sitticus zimmermanni* (11) *Berlandina cinerea* (6) *Zelotes electus* (6)	*Zelotes gallicus* (27) *Aelurillus v-insignitus* (27) *Agroeca cuprea* (27) *Ozyptila praticola* (18)

Table 2: Species structure of populations of mature herbage-dwelling spiders. Numbers in brackets shows relative abundance in %.

Microelevations (desert habitats)

Characteristics	Spring		Summer		Autumn		
	2004	2005	1984	2004	1984	2004	2005
Number of species	48						
	24	14	14	20	3	8	4
Predominating species	*Lasaeola tristis* (15) *Gibbaranea bituberculata* (14) *Microlinyphia pusilla* (9) *Agyneta saaristoi* (8) *Archaeodictyna consecuta* (7) *Cheiracanthium* cf. *virescens* (6) *Uloborus walckenaerius* (5)	*Gibbaranea bituberculata* (21) *Clubiona genevensis* (13) *Lasaeola tristis* (13) *Alopecosa cronebergi* (8) *Robertus arundineti* (8)	*Oxyopes* cf. *xinjiangensis* (61) *Dictyna latens* (8) *Cheiracanthium* cf. *virescens* (6) *Aculepeira armida* (6)	*Oxyopes* cf. *xinjiangensis* (24) *Micaria pallipes* (12) *Thanatus constellatus* (12) *Dictyna latens* (10) *Pellenes albopilosus* (6) *Gibbaranea bituberculata* (6) *Lasaeola tristis* (6)	*Xysticus striatipes* (69) *Oxyopes* cf. *xinjiangensis* (23) *Dictyna latens* (7)	*Xysticus marmoratus* (60) *Cheiracanthium* cf. *virescens* (19) *Xysticus striatipes* (9)	*Xysticus marmoratus* (65) *Xysticus striatipes* (25) *Thanatus constellatus* (5) *Cheiracanthium* cf. *virescens* (5)

Microdepressions (steppe habitats)

Characteristics	Spring		Summer		Autumn		
	2004	2005	1984	2004	1984	2004	2005
Number of species	53						
	29	14	23	21	5	11	6
Predominating species	*Gibbaranea bituberculata* (21) *Evarcha michailovi* (16) *Trichopterna cito* (11) *Clubiona genevensis* (10) *Cheiracanthium* cf. *virescens* (6)	*Cheiracanthium* cf. *virescens* (32) *Clubiona genevensis* (15) *Thanatus arenarius* (10) *Trichopterna cito* (8) *Gibbaranea bituberculata* (5) *Mangora acalypha* (5) *Philodromus histrio* (5) *Microlinyphia pusilla* (5)	*Heliophanus lineiventris* (13) *Thanatus mikhailovi* (13) *Heliophanus koktas* (9) *Aculepeira armida* (8) *Cheiracanthium* cf. *virescens* (7) *Cheiracanthium pennyi* (6) *Xysticus ninnii* (5) *Dictyna latens* (5) *Uloborius walckenaerius* (5)	*Thanatus constellatus* (23) *Neoscona adianta* (8) *Xysticus marmoratus* (8) *Thanatus atratus* (8) *Evarcha michailovi* (6) *Thomisus onustus* (6) *Oxyopes lineatus* (6)	*Xysticus striatipes* (73) *Cercidia levii* (18) *Heliophanus koktas* (5)	*Xysticus striatipes* (57) *Evarcha michailovi* (16) *Xysticus marmoratus* (12) *Cercidia levii* (5)	*Xysticus striatipes* (78) *Evarcha michailovi* (9) *Xysticus marmoratus* (7)

Big depressions (steppe habitats)

Characteristics	Spring		Summer		Autumn		
	2004	2005	1984	2004	1984	2004	2005
Number of species	52						
	19	11	18	20	12	8	6
Predominating species	*Gibbaranea bituberculata* (33) *Uloborius walckenaerius* (11) *Cheiracanthium* cf. *virescens* (9) *Agyneta* spp. (♀) (6) *Trichopterna cito* (6) *Archaeodictyna consecuta* (6)	*Cheiracanthium* cf. *virescens* (35) *Evarcha michailovi* (19) *Cheiracanthium pennyi* (12) *Philodromus histrio* (8)	*Aculepeira armida* (27) *Dictyna latens* (16) *Oxyopes* cf. *xinjiangensis* (10) *Heliophanus lineiventris* (8) *Thanatus oblongiusculus* (8) *Cheiracanthium* cf. *virescens* (5)	*Thanatus oblongiusculus* (34) *Oxyopes lineatus* (16) *Neoscona adianta* (9) *Oxyopes heterophthalmus* (9) *Thomisus onustus* (6)	*Xysticus striatipes* (56) *Xysticus marmoratus* (15)	*Xysticus striatipes* (62) *Xysticus marmoratus* (18) *Heliophanus lineiventris* (7)	*Xysticus striatipes* (70) *Heliophanus lineiventris* (19)

Table 3: Unique species per type of habitat.

	number	%
Microelevations	28	23.7
Microdepressions	10	8.9
Large depressions	7	13.4
Elm shelter-belt	3	10.3
Oak shelter-belts	6	15.4
Oak patch in a park	4	12.9

As many as 25 species occur in all native habitats, another five in all forest plantations. Two species, *Lathys stigmatisata* and *Xysticus ninnii*, are ubiquitous and inhabit all studied habitats.

However, finding the species in a particular habitat does not necessarily indicate habitat preference. In order to estimate preference level, Pesenko's coefficient (F_{ij}) was used. A complex of species, including taxa both with high (F_{ij}≥0.7) and relatively low (0.3≥F_{ij}>0.7) levels of habitat preference, was revealed for each habitat (Tab. 4).

Discussion

It is well known that the denser the vegetation the greater is density of spiders, and the greater the diversity of vegetation the greater the spider species diversity (DUFFEY 1962). But the spider assemblages of both the ground and herbaceous layers of open native habitats (microelevations, microdepressions and large depressions) are very similar not only in species diversity but also in density. This was rather surprising as the low, sparse and rather poor desert plant communities look much more miserable compared to the dense forb-grass vegetation of steppe habitats. This reveals a complex of species well adapted to the extreme conditions of desert associations. On the contrary, the communities of forest plantations appear to be significantly impoverished. The poorness of soil fauna under Dzhanybek plantations was demonstrated for other arthropods as well (CHERNOVA 1971, KRIVOLUTSKII 1971, etc.).

Calculating the level of habitat preference (F_{ij}) revealed complexes of typical species for each habitat (Tab. 4). In spite of mosaic structure and a comparatively small size of desert and steppe elements (some tens of square meters) in complex Northern Caspian semi-desert, the spider groupings formed on them are rather specific and contain sets of species associated with the particularities of the substrate (soil) and vegetation of those elements. The complexes of typical species of native habitats – microelevations and microdepressions – are the richest (35-40 species). Most of the typical species in desert associations are dwellers of arid and semi-arid landscapes: these are steppe (*D. rostratus*, *Z. orenburgensis*, *G. steppica*, etc.), semi-desert (*S. crassipedis*, *T. mikhailovi*, *W. stepposa*) and steppe-desert species (*H. horridus*, *O. lugubris*); with some participation of nemoral-steppe and nemoral ones. The share of steppe species (*B. cinerea*, *G. leporina*, *H. isaevi*, etc.) decreases significantly in associations of microdepressions and large depressions, while nemoral-steppe (*E. michailovi*, *Z. electus*, *T. arenarius*, etc.) and nemoral-subtropical species (*P. chrysops*, *P. fasciata*, *A. lobata*, etc.) prevail. Most of the typical species are quite abundant and predominate in these biotopes.

In addition, there is a complex of species which can inhabit several types of native habitats with similar probability levels (except for woody plantations). These are *Trichoncoides* cf. *piscator*, *G. bituberculata*, *A. v-insignitus*, *A. cursor*, *P. histrio*, *Z. segrex*, etc.

Complexes of typical species of woody plantations are poor and include 12-15 species, although the level of habitat preference is very high (Tab. 4). Most of them are nemoral species. Populations in the plantations are very likely composed of highly eurytopic species (*D. pusillus*, *Z. gallicus*, *P. mirabilis*) and typical dwellers of intrazonal associations (*S. zimmermanni*, *T. schineri*) with a small participation of forest species (*O. praticola*) which could be introduced with plant material.

On the other hand, the structure of spider assemblages is heavily determined by macroclimatic conditions and their seasonal changes. The analysis of seasonal features of population structure shows that the spring and summer spider assemblages of both ground and herbaceous layers are characterised by high species diversity levels and a relatively high number of predominating species, as opposed to the impoverished, imbalanced autumn populations (Tab. 1-2). The same pattern was recovered by ESYUNIN (2009) for spiders of steppe and steppe-like habitats in the Ural Mountains.

Clustering the spider complexes for separate seasons confirmed the prevailing role of seasonal differences in species proportions for mature spider groupings of native habitats when comparing between-habitat differences (Fig. 1). The populations of native associations were not united by habitats, but by seasononality. A similar trend has been also shown by ESYUNIN (2009) for the spider populations of steppe-like habitats in the Ural Mountains.

It is interesting to note that such a tendency was

Table 4: Pesenko's coefficient of a habitat preference (*Fij*) of spiders. Species are grouped according to their preference to a certain habitat. Within the groups species are ranked in order of decreasing the values of *Fij*. Grey background: high level of habitat preference (0.7 ≤ F_{ij} ≤ 1.00); bold: relatively low level of habitat preference (0.3 ≤ F_{ij} < 0.7). Habitats as in Fig. 1.

Species	Number of specimens	Habitats					
		1	2	3	4	5	6
Chalcoscirtus nigritus	17	**1.00**	-1.00	-1.00	-1.00	-1.00	-1.00
Heriaeus horridus	54	**1.00**	-1.00	-1.00	-1.00	-1.00	-1.00
Lepthyphantes spasskyi	7	**1.00**	-1.00	-1.00	-1.00	-1.00	-1.00
Micaria guttulata	7	**1.00**	-1.00		-1.00	-1.00	-1.00
Nomisia aussereri	4	**1.00**	-1.00		-1.00	-1.00	-1.00
Robertus arundineti	5	**1.00**	-1.00	-1.00	-1.00	-1.00	-1.00
Urozelotes sp.	4	**1.00**	-1.00		-1.00	-1.00	-1.00
Evippa eltonica	189	**0.98**	-0.94		-1.00	-1.00	-1.00
Titanoeca veteranica	115	**0.96**	-0.90		-1.00	-1.00	-1.00
Zelotes orenburgensis	204	**0.93**	-0.82		-1.00	-0.94	-1.00
Drassodes rostratus	153	**0.91**	-0.78	-1.00	-1.00	-0.92	-1.00
Lasaeola tristis	23	**0.91**	-0.75	-0.85			
Phaeocedus braccatus	47	**0.91**	-0.77		-1.00	-1.00	-1.00
Micaria pallipes	56	**0.89**	-0.71	-1.00	-1.00	-1.00	-1.00
Oxyopes cf. *xinjiangensis*	114	**0.82**	-0.92	-0.36	-1.00	-1.00	-1.00
Thanatus mikhailovi	22	**0.80**	-0.51	-1.00	-1.00	-1.00	-1.00
Microlinyphia pusilla	16	**0.71**	-0.26	-0.76	-1.00	-1.00	-1.00
Silometopus crassipedis	23	**0.71**	-0.35	-0.59	-1.00	-1.00	-1.00
Talanites mikhailovi	10	**0.71**	-0.35		-1.00	-1.00	-1.00
Trachyzelotes adriaticus	5	**0.71**	-0.35		-1.00	-1.00	-1.00
Talanites strandi	14	**0.69**	-0.31		-1.00	-1.00	-1.00
Xysticus marmoratus	278	**0.66**	-0.44	-0.41	-1.00	-1.00	-1.00
Gnaphosa lucifuga	79	**0.65**	-0.23	-1.00	-1.00	-1.00	-1.00
Theridion uhligi	6	**0.64**	-0.21		-1.00	-1.00	-1.00
Ozyptila lugubris	19	**0.62**	-0.18		-1.00	-1.00	-1.00
Theridion innocuum	8	**0.62**	-0.26	-0.54	-1.00	-1.00	-1.00
Drassyllus sur	33	**0.60**	-0.16		-1.00	-1.00	-1.00
Nurscia albomaculata	36	**0.59**	-0.15		-1.00	-1.00	-1.00
Ozyptila pullata	22	**0.58**	-0.13	-1.00	-1.00	-1.00	-1.00
Pellenes albopilosus	26	**0.57**	-0.11	-0.63	-1.00	-1.00	-1.00
Archaeodictyna consecuta	18	**0.53**	-0.41	-0.18			
Ceratinella brevis	3	**0.50**	-0.02		-1.00	-1.00	-1.00
Euophrys frontalis	3	**0.50**	-0.02		-1.00	-1.00	-1.00
Gnaphosa steppica	72	**0.50**	-0.08		-1.00	-0.83	-0.77
Walckenaeria stepposa	3	**0.50**	-0.02		-1.00	-1.00	-1.00
Haplodrassus cf. *soerenseni*	102	**0.42**	0.05		-1.00	-0.88	-0.83
Aelurillus m-nigrum	5	**0.39**	0.13		-1.00	-1.00	-1.00
Cheiracanthium cf. *virescens*	99	**0.36**	-0.15	-0.20	-1.00	-1.00	-1.00
Phlegra bicognata	24	**0.36**	0.16		-1.00	-1.00	-1.00
Uloborus walckenaerius	26	**0.35**	-0.22	-0.12	-1.00	-1.00	-1.00
Zelotes caucasius	39	**0.32**	0.10		-0.08	-0.71	-1.00
Improphantes contus	7	-1.00	**1.00**		-1.00	-1.00	-1.00
Heliophanus flavipes	4	-1.00	**1.00**	-1.00			
Phlegra fasciata	10	-1.00	**1.00**	-0.05	-1.00	-1.00	-1.00
Walckenaeria alticeps	4	-1.00	**1.00**	-1.00	-1.00	-1.00	-1.00
Haplodrassus kulczynskii	48	-0.94	**0.98**		-1.00	-1.00	-1.00
Trichopterna cito	169	-0.98	**0.96**	-0.43	-0.19	-0.91	-1.00
Berlandina cinerea	139	-0.83	**0.92**		-1.00	-1.00	-0.76
Cercidia levii	37	-1.00	**0.92**	-0.80	-1.00	-1.00	-1.00
Trichoncus villius	28	-0.79	**0.92**	-1.00	-1.00	-1.00	-1.00
Thanatus arenarius	140	-0.76	**0.90**	-0.54	-1.00	-0.91	-1.00
Zelotes electus	73	-0.96	**0.90**		**0.31**	-0.83	-0.77
Haplodrassus isaevi	37	-0.69	**0.88**		-1.00	-1.00	-1.00

Species	Number of specimens	Habitats					
		1	2	3	4	5	6
Gnaphosa leporina	24	-1.00	**0.81**		-1.00	-1.00	0.30
Thanatus atratus	45	-0.52	**0.81**	**0.40**	-1.00	-1.00	-1.00
Zelotes longipes	60	-0.62	**0.79**		-0.29	-0.63	-1.00
Evarcha michailovi	77	-0.92	**0.77**	-0.52	-1.00	-1.00	-1.00
Heliophanus koktas	19	-1.00	**0.77**	-0.50			
Pardosa plumipes	5	-0.45	**0.77**		-1.00	-1.00	-1.00
Drassodes lapidosus	4	-0.33	**0.71**		-1.00	-1.00	-1.00
Clubiona genevensis	27	-0.26	**0.66**	-0.74	-1.00	-1.00	-1.00
Drassodes villosus	7	-0.25	**0.66**		-1.00	-1.00	-1.00
Alopecosa schmidti	31	-0.24	**0.65**		-1.00	-1.00	-1.00
Thanatus pictus	96	-0.11	**0.57**	-0.16	-1.00	-1.00	-1.00
Thanatus sp.	8	0.00	**0.49**	-0.05	-1.00	-1.00	-1.00
Alopecosa taeniopus	41	-0.65	**0.47**		0.25	0.30	-0.63
Agyneta saaristoi	30	-0.05	**0.43**	-0.54	-1.00	-0.39	-1.00
Haplodrassus signifer	45	0.05	**0.42**		-1.00	-1.00	-0.65
Eresus kollari	13	0.13	**0.39**		-1.00	-1.00	-1.00
Gnaphosa taurica	135	-0.31	**0.38**		**0.35**	-0.36	-0.10
Xysticus striatipes	426	-0.60	**0.35**	-0.03	-0.29	-0.80	-1.00
Agroeca maculata	61	0.15	**0.33**		-1.00	-1.00	-0.73
Philaeus chrysops	5	0.20	**0.32**	-1.00	-1.00	-1.00	-1.00
Simitidion simile	9	0.12	**0.32**	-0.54	-1.00	-1.00	-1.00
Scotargus pilosus	4	0.20	**0.32**		-1.00	-1.00	-1.00
Xysticus cristatus	43	0.20	**0.32**	0.22	-1.00	-1.00	-1.00
Trichoncoides cf. *piscator*	11	**0.41**	**0.32**	-1.00	-1.00	-1.00	-1.00
Zelotes segrex	15	0.26	0.26		-1.00	-1.00	-1.00
Aelurillus v-insignitus	30	0.20	0.13		-1.00	-1.00	0.01
Alopecosa cursor	34	0.26	0.27		-1.00	-1.00	-1.00
Gibbaranea bituberculata	82	0.09	0.02	-0.10	-1.00	-1.00	-0.90
Philodromus histrio	18	-0.01	-0.11	0.12	-1.00	-1.00	-0.90
Oxyopes lineatus	43	-1.00	-0.62	**0.84**	-1.00	-1.00	-1.00
Neoscona adianta	23	-1.00	-0.42	**0.73**			
Argiope lobata	4	0.03	-1.00	**0.69**			
Thanatus oblongiusculus	99	-0.51	-0.53	**0.67**			
Aculepeira armida	53	-0.49	-0.53	**0.66**	-1.00	-1.00	-1.00
Oxyopes heterophthalmus	29	-0.60	-0.43	**0.64**	-1.00	-1.00	-1.00
Thomisus onustus	20	-0.71	-0.23	**0.54**			
Dictyna latens	45	0.02	-0.63	**0.50**			
Agyneta spp. (♀)	29	-0.01	-0.38	**0.34**	-1.00	-0.25	-0.09
Heliophanus lineiventris	75	-0.38	0.01	0.22	-1.00	-1.00	-1.00
Heriaeus melloteei	10	-0.04	-0.15	0.18	-1.00	-1.00	-1.00
Pardosa xinjiangensis	6	-1.00	-1.00		**1.00**	-1.00	-1.00
Micaria rossica	7	-0.25	-0.13		**0.92**	-1.00	-1.00
Pseudeuophrys obsoleta	5	-1.00	-1.00		**0.91**	**0.63**	**0.40**
Ermetus inopinabilis	8	-0.33	-1.00		**0.90**	**0.59**	-1.00
Titanoeca quadriguttata	3	-1.00	-0.02		**0.88**	**0.53**	-1.00
Zelotes atrocaeruleus	6	-0.14	-0.02		**0.88**	-1.00	-1.00
Xysticus ninnii	85	-0.79	0.24	0.22	**0.86**	0.04	-0.42
Tibiaster djanybekensis	24	**0.56**	-1.00	-1.00	**0.83**	-0.49	-1.00
Zelotes gallicus	96	-1.00	-1.00		**0.83**	**0.75**	**0.47**
Mangora acalypha	5	0.23	**0.49**	-1.00	**0.69**	-1.00	-1.00
Cheiracanthium pennyi	24	-1.00	0.10	0.10	-1.00	**1.00**	-1.00
Pisaura mirabilis	105	-1.00	-1.00		0.13	**0.91**	**0.37**
Zora pardalis	56	-1.00	-0.68		0.10	**0.88**	0.28
Lathys stigmatisata	93	-0.80	-0.25	-0.25	0.21	**0.70**	**0.37**
Titanoeca schineri	73	-1.00	-1.00		**0.55**	**0.87**	**0.44**
Xysticus luctator	198	-1.00	-0.98		-1.00	**0.73**	**0.80**

Species	Number of specimens	Habitats					
		1	2	3	4	5	6
Drassyllus pusillus	90	-1.00	-1.00		**0.40**	**0.63**	**0.83**
Sitticus zimmermanni	29	-1.00	-0.87		**0.42**	**0.55**	**0.84**
Ozyptila praticola	155	-1.00	-1.00	-1.00	-1.00	**0.60**	**0.88**
Xysticus robustus	10	-1.00	-1.00	-1.00	-1.00	**0.68**	**0.84**
Zelotes subterraneus	3	-1.00	-1.00		-1.00	-1.00	**1.00**
Philodromus cespitum	5	-1.00	0.10	0.10	-1.00	-1.00	**1.00**
Agroeca cuprea	4	-1.00	-1.00		-1.00	-1.00	**1.00**

not revealed for snout-beetles (Coleoptera, Curculionoidae) investigated at the Dzhanybek Station during the same period. These phytophagous insects showed that the influence of between-habitat differentiation on the structure of their populations – which was determined by their close links with the plants on which they forage (Khruleva et al. in press) – was much stronger than seasonal changes. Spiders being a group of mobile generalist predators are more likely to be influenced by abiotic factors.

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