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Distribution of Spiders (Arachnida: Araneae) in the Zonal–Catena Matrix of the Central Kazakhstan Steppes

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Abstract—Spider communities (Arachnida: Aranei) have been studied in central Kazakhstan along 70° E longitude in the subzones of typical, dry, and desert steppes on catenas, including eluvial, transitive, and accumulative positions. In total, 79 spider species belonging to 33 genera and 11 families have been identified. The bulk of the spider population consists of gnaphosid ground spiders, which are typical for arid zones and arid habitats. Wolf spiders (Lycosidae) are also abundant in the study area; they are most numerous in the lower, more humid catena positions. An increase in the proportion of jumping spiders (Salticidae), as well as their taxonomic diversity in the spider population, has been observed in the direction from north to south, from typical to desert steppes. In contrast to the species richness of ground beetles (Coleoptera, Carabidae), which decreases in the series of these habitats from north to south, the number of spider species increases, and this is similar to the species richness of darkling beetles. Within the latitudinal gradient from north to south, at the upper positions of the catena, the dynamic density of spiders decreases, while the ecological diversity of spider taxocenes increases. Catena positions that are similar in faunal composition are, as a rule, also similar in the structure of the spider population. The transition from typical to desert steppes is accompanied by a decrease in the number of widespread species of subboreal distribution, and the number of species typical for steppe and semidesert habitats and for solonchaks increases.

Keywords: spiders, spatial distribution, range, fauna, population, salinity, aridization, catena

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INTRODUCTION

Spiders are increasingly being used as a model ecological object for studying the state and dynamics of the natural environments (Trilikauskas, 2010; Piterkina, 2011; etc.). This is an extremely diverse group of arthropods both in taxonomic and ecological terms. Spider-population characteristics can be reliable indicators of temporal and spatial changes in different habitats.

Studies of spiders on the territory of Kazakhstan have not yet covered its central part and, in most cases, described faunal patterns (Savelieva, 1970, 1979; etc.). Active research began only at the beginning of this century. There is a number of faunistic works for East Kazakhstan (Tuneva, 2004; Marusik and Logunov, 2011); however, synecological and zoogeographical studies of spiders have not yet been carried out on this territory. Spiders of West Kazakhstan are being studied more actively (Ponomarev, 2007a, 2007b, 2008). The structure of spider communities in semideserts of this region is summarized in the work of Piterkina (2011). Thus, the fauna and ecology of spiders in the steppes of central Kazakhstan remain unexplored.

The plains of central Kazakhstan are characterized by continental climate and poorly expressed relief and can serve as a matrix of environmental factors. A wide range of environmental conditions of the steppes of central Kazakhstan is expressed on a geographical scale in the form of a system of latitudinal zones and subzones that form a regular gradient and, on a local scale, in the form of catenas (drainage series of biocenoses), along which moisture and salinity change regularly.

In general, the amount of heat increases from the northern boundaries of the steppe zone to the southern ones; the amount of atmospheric precipitation decreases; and evaporation, moisture deficit, and general aridization of habitats increase. The seasonal patterns of precipitation changes in the same direction: precipitation maximums shift from July to the spring–early summer period (*Prirodnye usloviya*..., 1969; Beresneva, 2006).

The purpose of this work is to investigate the distribution of representatives of such a large and diverse taxocene as spiders in the environmental zonal–catena matrix and determine the zoogeographic and ecological patterns of their spatial distribution in the steppes of central Kazakhstan.

MATERIALS AND METHODS

The material was collected in three geographical points located approximately along 70° E: in the typical steppe on the southern chernozem in the vicinity of the village of Shortandy (51°34′ N, 71°17′ E) from May 31 to June 8, 2018; in the dry steppe on dark chestnut soil in the vicinity of the village of Arykty (50°32′ N, 70°27′ E, Akmola region, Republic of Kazakhstan) from June 1–7, 2018; and in the desert steppe in the vicinity of the village of Barshyn (49°37′ N, 69°28′ E; Karaganda region) from the June 2–7, 2018.

The studies were carried out according to the catena approach, which consists of the synchronous acquisition of data not only from zonal landscapes, but also from intrazonal positions, preselected and marked (Mordkovich et al., 1985): eluvial (EL; corresponds to the zonal landscape), transitive (TR), and accumulative (AC). The nomenclature proposed by Glazovskaya and Gennadiev (1995) was used to indicate the study sites. Two transitive positions were distinguished on the catenas at Shortandy and Arykty (transeluvial TR1 and transaccumulative TR2) and, in Barshyn, due to the high diversity of habitats, three positions were distinguished (additional TR3). Thus, the counts were simultaneously carried out in 13 habitats (catena positions). Their descriptions are presented in Table 1.

The spiders were collected by pitfall traps. In each position, ten traps were placed in one line 3–4 m from each other. The distance between the positions ranged from 100 to 300 m. For unification, the data reduced to 100 trap days.

An analysis of the spider fauna was carried out according to areageographical (range) approach. It is based on the typology of range types developed for ground beetles (Coleoptera, Carabidae) (Dudko and Lyubechanskii, 2002) and adapted for spiders (Lyubechanskii and Azarkina, 2017; Azarkina et al., 2018). The latitudinal component of the range of each species is considered. The boreal, subboreal humid, subarid, and polysonal groups have been distinguished. It is important to note that the names of areageographical groups reflect only the geographical distribution of the species and do not characterize their habitat preferendum. The northern boundary of the species of the boreal group runs in the tundra or forest–tundra zone. In the south, boreal species can penetrate into the steppe zone in the central sector of Palaearctic, or into the zone of deciduous forests in its western and eastern sectors. We consider species that are not found to the north from the middle taiga subzone in the central sector of the Palaearctic as subboreal humid. The southern boundary of this group distribution runs along the steppe zone. The subarid group includes species whose distribution to the north is limited by the forest-steppe zone. The distribution of polysonal species in the north is similar to that of boreal ones; in the south they penetrate into the semidesert zone or even further. The range spectra of spider species in each habitat make it possible to gauge about the "northern" or "southern" nature of the species composition in a particular habitat.

Data analysis was performed using the PAST v. 3.26b software (Hammer et al., 2001). Simpson, Shannon, and Berger–Parker indices of the species diversity, as well as Raup-Crik coefficients of the faunistic similarity and Morisita index for the population similarity, were calculated.

Characteristics of the dynamic density of spiders at the family level were calculated both with and without juveniles (Table 2). To assess the proportion of representatives of individual families, juveniles were taken into account, since they are easily identified for the family level. Juvenile individuals were not considered in analyses of the species structure according the species abundance.

The dominant complex in this work includes subdominant (2.1–5% in the total taxocene structure), dominant (5.1–10%), and superdominant (>10%) species.

RESULTS AND DISCUSSION

Taxonomic Analysis

On Shortandy catena (typical steppe subzone), the greatest taxonomic diversity of spiders was registered in the meadow community (AC) (Table 3). In total, 30 species of spiders belonging to 18 genera and 9 families were recorded on this catena. Representatives of three families (Linyphiidae, Phrurolithidae, and Tetragnathidae) were not determined on other catenas. It should be noted that the families Lycosidae, Liocranidae, and Thomisidae in the typical steppe subzone were represented by a greater number of species than on other catenae, while the family Gnaphosidae, on the contrary, had half the amount. Jumping spiders were represented here by the only species of very small dark-colored spiders from the genus *Chalcoscirtus* (Salticidae).

On Arykty catena (subzone of dry steppe), the investigated positions were located from a dry *Stipa lessingiana* steppe (EL) to a solonchak along a salt lake shore (AC). On the solonchak (AC) and the first transitive site with a thin vegetation cover (TR1), the taxonomic diversities of spiders were similar and the most diverse in comparison with the rest of the positions of the catena. Also, 30 species of spiders from 18 genera were recorded here, but the number of families represented was less than in the typical steppe subzone (7). The first (TR1) and second transitive (TR2) positions of this catena were characterized by the only species of cobweb spiders, *Steatoda albomaculata*. On the catena in the dry steppe subzone, the species diversity of gnaphosid ground spiders doubles and two species of jumping spiders which have not been noted in the typical steppe subzone appear.

Table 1. Brief description of the catena positions in the steppes of central Kazakhstan

Position, coordinates, altitude a.s.l.	Characteristics
Shortandy (S). Subzone of typical steppes. A site of virgin typical steppe with an area of about 200 ha, approximately 20 km southeast of Shortandy (Akmola Region, Kazakhstan)	
EL 51°33′57.7″ N, 71°16′50.3″ E 422 m	Feather steppe, projective cover (PC) 70%. Among the grasses there are a lot of herbs: sage, cinquefoil, hawkweed, lousewort, lampwick plant, wormwoods. Due to the cold spring, the vegetation is poorly developed
TR1 51°33′55.1″ N, 71°17′05.2″ E 421 m	Feather grass, mesophilic grasses, wormwoods. Steppe with elements of transformation to meadows and solonetz-forming process. PC 40–50%
TR2 51°34′00.5″ N, 71°17′25.9″ E 419 m	Meadow solonetz. Feather grass, spots of wormwood. Small grazing impact of sheep and horses. No flowering plants on May 31. PC 30–40%
AC 51°33′58.2″ N, 71°17′28.9″ E 420 m	Coastal meadow with willow bushes along the water's edge (a pond formed by an anti-erosion dam, dam broken several years ago). Line of pitfall traps located 3–5 m from the water. Meadow with mesophilic grasses with wormwood, flooded with water in spring. Further from the coast, there are long-term persistent puddles with treelike wormwood. There are traces of solonetz-forming process in the soil. PC 60–70%
Arykty (A). Subzone of dry steppes. An area of at least several thousand hectares, 11.5 km southwest of the village of Arykty (Akmola Region, Kazakhstan). Ridgeline plains are either plowed up or fallowed.	
EL 50°32′38.9″ N, 70°27′47.9″ E 359 m	*Stipa lessingiana* steppe with forbs. Eluvial transitive position, PC 40–50%. Moderate grazing
TR1 50°32′34.4″ N, 70°27′38.0″ E 354 m	*Stipa lessingiana* steppe. Significantly less vegetation cover than at the eluvial position. PC 30–40%
TR2 50°32′33.0″ N, 70°27′35.4″ E 353 m	Solonet with a mosaic of feather grass and ferula spots. PC on solonetz 30–40%, on feather grass sites 60–70%
AC 50°32′29.7″ N, 70°27′34.9″ E 353 m	Solonchak. Dominants: *Atriplex* and *Goniolimon*. The distance from the line of pitfall traps to the edge of the solid salt cover is about 5 m. Features of heavy grazing
Barshyn (B). Subzone of desert steppes. Plot 6 km south-southwest from the village of Barshino, the shore and the vicinity of Lake Saryzhol	
EL 49°37′31.7″ N, 69°28′21.8″ E 371 m	Soddy–grass steppe on the top of a gentle hill. PC 40–50%
TR1 49°37′23.7″ N, 69°28′17.4″ E 370 m	Feather steppe with spirea in the upper part of the slope. PC 70%
TR2 49° 37′20.5″ N, 69° 28′18.5″ E 369 м	Wormwood desert steppe at a convex site at the bottom of the slope. PC 30–40%. There are a lot of small stones on the soil surface
TR3 49°37′12.9″ N, 69°28′28.3″ E 361 m	Feather steppe on the solonetz. PC 40–50%
AC 49°37′11.3″ N, 69°28′35.1″ E 359 m	Halocnemum solonchak near the coast. PC about 30%. Grazing features

Table 2. Composition and dynamic density of spiders (ind./100 trap days) in the steppes of central Kazakhstan

Range	Study area	**Shortandy**				**Arykty**				**Barshyn**				
	Catena location	EL	TR1	TR2	AC	EL	TR1	TR2	AC	EL	TR1	TR2	TR3	AC
	GNAPHOSIDAE	**21.5**	**20.9**	**32.7**	**5.2**	**38.4**	**25.1**	**22.7**	**35.1**	**18.0**	**20.0**	**22.0**	**34.0**	**56.0**
	With juveniles	**24.0**	**29.2**	**35.2**	**5.2**	**38.4**	**33.5**	**26.9**	**36.8**	**18.0**	**20.0**	**24.0**	**40.0**	**62.0**
SA	*Berlandina cinerea* (Menge, 1868)	1.3	9.7		1.3	1.7				2.0	16.0			
SA	*Civizelotes pygmaeus* (Miller, 1943)						1.7							
SA	*Drassodes chybyndensis* Esyunin et Tuneva, 2002								1.7					
P	*Drassodes cupreus* (Blackwall, 1834)						1.7							
B	*Drassodes katunensis* Marusik, Hippa et Koponen, 1996	1.3	4.2	1.3									2.0	
SH	*Drassodes longispinus* Marusik & Logunov, 1995							2.1						
SA	*Drassodes rostratus* Esyunin et Tuneva, 2002							2.1	3.3				2.0	2.0
SH	*Drassyllus pusillus* (C.L. Koch, 1833)	1.3		1.3										
SA	*Drassyllus sur* Tuneva et Esyunin, 2003					15.0								10.0
SA	*Gnaphosa cumensis* Ponomarev, 1971													4.0
SA	*Gnaphosa betpaki* Ovtsharenko, Platnick et Song, 1992													2.0
SA	*Gnaphosa jucunda* Thorell, 1875				1.3									
?	*Gnaphosa* cf. *kompirensis* Bösenberg & Strand, 1906?												2.0	
B	*Gnaphosa lapponum* (L. Koch, 1866)							2.1	21.7				6.0	8.0
P	*Gnaphosa leporina* (L. Koch, 1866)		4.2	25.0	1.3									
P	*Gnaphosa lucifuga* (Walckenaer, 1802)					1.7		2.1					14.0	2.0
P	*Gnaphosa lugubris* (C.L. Koch, 1839)	5.0		2.5										
SA	*Gnaphosa mandschurica* Schenkel, 1963							1.7						
SA	*Gnaphosa mongolica* Simon, 1895					1.7				8.0		4.0		
SA	*Gnaphosa saurica* Ovtsharenko, Platnick & Song, 1992								1.7					8.0
SA	*Gnaphosa steppica* Ovtsharenko, Platnick et Song, 1992	8.8				8.3		4.2	3.3				4.0	8.0
SA	*Haplodrassus alexeevi* Ponomarev & Shmatko, 2017					1.7			1.7					
SA	*Haplodrassus kulczynskii* Lohmander, 1942		2.8	1.3			1.7	2.1		4.0	4.0			2.0
P	*Haplodrassus signifer* (C.L. Koch, 1839)	3.8			1.3		1.7	2.1						4.0
P	*Micaria rossica* Thorell, 1875									2.0		2.0		2.0
SA	*Shaitan elchini* Kovblyuk, Katrygina et Marusik, 2013						5.0							
SA	*Trachyzelotes chybyndensis* Tuneva & Esyunin, 2002												2.0	
SH	*Zelotes electus* (C. L. Koch, 1839)							4.2						

Table 2. (Contd.)

Range	Study area	Shortandy				Arykty				Barshyn				
	Catena location	EL	TR1	TR2	AC	EL	TR1	TR2	AC	EL	TR1	TR2	TR3	AC
P	*Zelotes longipes* (L. Koch, 1866)			1.3										
SA	*Zelotes mikhailovi* Marusik in Eskov et Marusik, 1995													4.0
SA	*Zelotes orenburgensis* Tuneva & Esyunin, 2003												2.0	
SA	*Zelotes potanini* Schenkel, 1963									2.0		16.0		
SA	*Zelotes segrex* (Simon, 1878)					8.3	13.3							
SA	*Urozelotes trifidus* Tuneva, 2003								1.7					
	LIOCRANIDAE		**1.4**		**2.5**				**1.7**					
SH	*Agroeca cuprea* Menge, 1873								1.7					
SH	*Agroeca dentigera* Kulczyński, 1913				2.5									
SH	*Agroeca maculata* L. Koch, 1879		1.4											
	LINYPHIIDAE				**5.1**									
P	*Hypomma bituberculatum* (Wider, 1834)				1.3									
SH	*Tallusia experta* (O. PickardCambridge, 1871)				3.8									
	LYCOSIDAE	**22.7**	**48.7**	**21.4**	**116.3**		**5.0**		**6.7**	**2.0**	**2.0**	**4.0**	**6.0**	**17.0**
	With juveniles	**22.7**	**48.7**	**22.7**	**125.1**		**5.0**		**6.7**	**2.0**	**2.0**	**4.0**	**6.0**	**19.0**
SA	*Alopecosa cronebergi* (Thorell, 1875)												6.0	
SH	*Alopecosa cuneata* (Clerck, 1758)	1.3	2.8	3.8										
P	*Alopecosa cursor* (Hahn, 1831)	11.3	30.6	15.0			3.3							
SH	*Alopecosa pulverulenta* (Clerck, 1758)				7.5									
SH	*Alopecosa schmidti* (Hahn, 1835)	1.3		1.3										
	Alopecosa sp.								1.7					
SA	*Evippa eltonica* Dunin, 1994													12.0
	Lycosa sp.									2.0	2.0			
SA	*Mustelicosa dimidiata* (Thorell, 1875)											4.0		
P	*Pardosa italica* Tongiorgi, 1966													5.0
SH	*Pardosa paludicola* (Clerck, 1758)				55.0									
?	*Pardosa sp.*(*luctinosa gr*)	8.8	15.3	1.3	6.3									
SA	*Pardosa zonsteini* Ballarin, Marusik, Omelko, Koponen, 2012						1.7							
P	*Trochosa robusta* (Simon, 1876)								5.0					
SH	*Trochosa ruricola* (De Geer, 1778)				47.5									
	PHILODROMIDAE		**1.4**	**3.8**				**4.2**			**4.0**	**2.0**		
SA	*Thanatus arenarius* Thorell, 1872		1.4	3.8				4.2			4.0			
	Thanatus kitabensis Charitonov, 1946											2.0		
	PHRUROLITHIDAE		**1.4**											
SA	*Phrurolithus pullatus* Kulczyński in Chyser et Kulczyński, 1897		1.4											
	SALTICIDAE				**1.3**		**3.3**	**2.1**	**6.7**	**8.0**	**4.0**	**6.0**	**8.0**	**6.0**
	With juveniles				**1.3**		**3.3**	**2.1**	**6.7**	**8.0**	**4.0**	**8.0**	**8.0**	**8.0**

Table 2. (Contd.)

Range	Study area	Shortandy				Arykty				Barshyn				
	Catena location	EL	TR1	TR2	AC	EL	TR1	TR2	AC	EL	TR1	TR2	TR3	AC
SA	*Aelurillus mnigrum* Kulczyński, 1891												4.0	
P	*Aelurillus vinsignitus* (Clerck, 1757)						3.3	2.1	5.0	4.0	4.0			
SA	*Attulus avocator* (O. PickardCambridge, 1885)								1.7					
SH	*Chalcoscirtus nigritus* (Thorell, 1875)									2.0		2.0	2.0	
	Chalcoscirtus sp.(juv)				1.3									
SA	*Pellenes nigrociliatus* (Simon in L. Koch, 1875												2.0	
SA	*Pellenes pseudbrevis* Logunov, Marusik et Rakov, 1999													6.0
SA	*Phlegra bicognata* Azarkina, 2004											2.0		
	Phlegra sp.									2.0				
SA	*Pseudomogrus vittatus* (Thorell, 1875)											2.0		
	TETRAGNATHIDAE				**42.6**									
SH	*Pachygnatha degeeri* Sundevall, 1830				3.8									
B	*Pachygnatha listeri* Sundevall, 1830				38.8									
	THERIDIIDAE						**3.3**	**2.1**						**2.0**
P	*Steatoda albomaculata* (De Geer, 1778)						3.3	2.1						2.0
	THOMISIDAE	**6.3**	**1.4**		**20.1**	**1.7**			**6.7**					**4.0**
SA	*Ozyptila inaequalis* (Kulczyński, 1901)													2.0
SA	*Ozyptila pullata* (Thorell, 1875)													2.0
SH	*Ozyptila scabricula* (Westring, 1851)	1.3												
SH	*Ozyptila trux* (Blackwall, 1846)				1.3									
SH	*Xysticus cristatus* (Clerck, 1758)	5.0	1.4											
SH	*Xysticus viduus* Kulczyński, 1898 sensu Utotschkin, 1968				18.8									
?	*Xysticus* cf. *urgumchak* Marusik & Logunov, 1990					1.7			6.7					
	TITANOECIDAE										**4.0**		**2.0**	**10.0**
SA	*Titanoeca liaoningensis* Zhu, Gao & Guan, 1993										4.0			
SA	*Titanoeca turkmenia* Wunderlich, 1995												2.0	10.0
	Total	**50.5**	**75.2**	**57.9**	**193.8**	**40.1**	**36.7**	**31.1**	**56.9**	**28.0**	**34.0**	**34.0**	**50.0**	**95.0**
	Total with juveniles	**53.0**	**83.5**	**61.7**	**202.6**	**40.1**	**45.1**	**35.3**	**58.6**	**28.0**	**34.0**	**38.0**	**56.0**	**105.0**

Designations: type of area: B, boreal species; P, polysonal; SH, subboreal humid; and SA, subarid. Catena positions: EL, eluvial; TR, transitive; and AC, accumulative.

In the subzone of the desert steppe on the Barshyn catena, five positions were studied: from the zonal landscape at the top of a gentle hill (EL) to a solonchak (AC) near the lake shore. The spider population of solonchak is distinguished by the highest taxonomic diversity not only on this catena, but also in the entire study area. However, the catena in the desert steppe subzone is characterized by a significant variation in the number of spider species, genera, and families at different positions. For example, on TR1, the taxonomic diversity of spiders at the species and genera levels was the lowest for the entire study area. In total,

Table 3. Characteristics of species compositions and population of spiders at catena positions in the steppe subzones of central Kazakhstan

Geographical site	Typical steppe, Shortandy						Dry steppe, Arykty						Desert steppe, Barshyn						
Catena location	D	EL	TR1	TR2	AC	N	D	EL	TR1	TR2	AC	N	D	EL	TR1	TR2	TR3	AC	N
Gnaphosidae	23.39	45.2	35.7	57.2	2	10	75.71	95.9	75	75	63	20	62.84	64.3	55.5	63	72.4	56.2	19
Linyphiidae	1.27				2.5	2						0							0
Liocranidae	0.97		1.7		1.3	2	0.95				2.9	1							0
Lycosidae	54.79	42.9	57.5	36.7	62.5	7	6.53		10.8		11.4	4	12.64	7.1	5.6	10.5	10.4	21.9	6
Philodromidae	1.3		1.7	6.1		1	2.35			12.4		1	2.3		11.1	5.3			2
Phrurolithidae	0.35		1.7			1						0							0
Salticidae	0.32				0.5	1	6.76		7.1	6.3	11.4	2	13.79	28.6	11.1	21.2	13.8	7.4	8
Tetragnathidae	10.65				21.3	2						0							0
Theridiidae						0	3.02	4.2	7.1	6.3		1	0.77					1.8	1
Thomisidae	6.95	11.9	1.7		9.9	4	4.69				11.4	1	1.53		5.6				3
Titanoecidae						0						0	6.13		11.1		3.4	9.1	2
Species		12	11	11	15	30		8	15	11	14	30	62.84	9	6	9	13	21	40
Genera		9	10	8	14	18		6	12	7	11	18		8	6	8	9	13	23
Families		3	6	3	7	9		2	4	4	5	7		3	6	4	4	6	8
S		0.85	0.77	0.73	0.8			0.76	0.88	0.9	0.82			0.83	0.7	0.79	0.87	0.93	
H		2.14	1.82	1.7	1.9			1.68	2.36	2.34	2.18			1.91	1.47	1.86	2.29	2.84	
H/S		0.71	0.56	0.5	0.45			0.67	0.71	0.95	0.63			0.84	0.73	0.71	0.76	0.81	
B–P		0.24	0.41	0.43	0.29			0.38	0.2	0.14	0.37			0.29	0.5	0.38	0.26	0.11	

Legend: D, share of spider families for the catena; N, number of spider taxa for the catena. EL, TR, and AC, catena positions; **S**, Simpson index; **H**, Shannon index; **H/S**, evenness; **B–P**, Berger–Parker index.

at least 40 species of spiders from 23 genera and 7 families were recorded on this catena. Spiders of the family Liocranidae, common on the Shortandy and Arykty catenas, did not occur at this geographical point, while only two species of spiders from the family Titanoecidae, ecologically associated with the presence of the stones under which they settle, were reordered. One important feature of the taxonomic composition of spiders on the Barshyn catena, the southernmost of the three studied ones, is the high species diversity of jumping spiders. This family was represented here by seven species.

In general, 79 spider species from 33 genera and 11 families were registered in the steppes of central Kazakhstan. The arid climate of this region is responsible for the high diversity of members of the family Gnaphosidae.

A comparison of the species composition of spiders of 13 studied positions of three catenas was carried out on the basis of multidimensional scaling of the Raup-Crick index (Fig. 1).

On the diagram, the most isolated position was occupied by all four positions of the catena in the subzone of the typical steppe (Shortandy). The taxocenes of the three upper (EL, TR1, and TR2) and two lowest positions (AC and TR3) of the Barshyn catena (subzone of the desert steppe) are noticeably different from each other according to the set of species. The taxocene of spiders in the upper position (EL) of the Arykty catena (dry steppe subzone) was found to be very similar in species composition to the upper positions of the southernmost of the studied catenas (Barshyn), and the set of species of the lowest position (AC) of the Arykty catena was similar with that from the lower positions of the desert steppe catena (AC and TR3). Two transitive positions of the catena in the dry steppe subzone were characterized by a relatively distinct position.

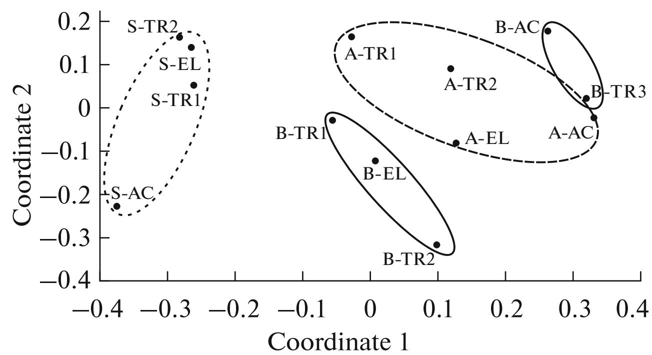

Fig. 1. Multidimensional scaling of species compositions of spiders in the steppes of central Kazakhstan (Raup-Crick similarity index). S, Shortandy; A, Arykty; B, Barshyn; EL, eluvial position of the catena; TR, transitive position of the catena; and AC, accumulative position of the catena.

Areageographical Analysis

The number and proportion of subarid species in the spider fauna increases along with the latitudinal gradient from north to south. This increase occurs both due to the enrichment of the fauna and due to a strong reduction in the number of subboreal humid species with a more "northern" range (Fig. 2a). The number of even more "northern" boreal species, as well as polysonal ones, changes little and irregularly. However, a consideration of the distribution of species with different types of ranges over the catena positions shows that, in the typical steppe, boreal species are found throughout the catena, although in the dry and desert steppes they were recorded only in the lower, more humid positions. The number of polysonal species was the highest in the typical and dry steppes at the transitive positions of the catena, while, in the desert steppe, it was at the accumulative position (Fig. 2b).

Analysis of Dynamic Density of Spiders

The dynamic density of spiders was the highest on the catena of the typical steppe subzone, 200 individuals per 100 trap days in the coastal meadow (AC) (Table 3). Among the two catenas located to the south, the Barshyn one (desert steppe subzone) was characterized by the highest amount of spiders: the highest dynamic density was observed on the solonchak near the lake shore (AC). In the dry steppe subzone (Arykty), this parameter was also the highest at the accumulative position (AC), but the number of spiders did not exceed 60 specimens per 100 trap days even taking into account juveniles.

On the catenas of the typical (Shortandy) and dry (Arykty) steppes, there is no trend towards an increase in the dynamic density of spiders in the direction from the upper position to the lower one. This parameter varies significantly in these areas. In the desert steppe (Barshyn), the dynamic density of spiders increases quietly from the top of the catena (EL) to the bottom (TR3) with a sharp increase in the accumulative position (AC).

The dynamic density of spiders decreases at the upper positions of the catena in the latitudinal gradient from north to south. This trend is not typical for other positions.

Table 3 presents the family-level population structure of spiders on the catena. In the typical steppe (Shortandy), ground wolf spiders and gnaphosids are most common at all positions of the catena. They dominate in the feather-grass steppe (EL) and meadow solonetz (TR2). Only at the accumulative position (AC) does the proportion of these spiders sharply decrease due to the high humidity of this habitat, while the proportion of wolf spiders is highest on the catena. More than 20% of the population here are represented by ground spiders of the genus *Pachygnatha* (Tetragnathidae) (registered nowhere else), which are typical for wet and floodplain habitats.

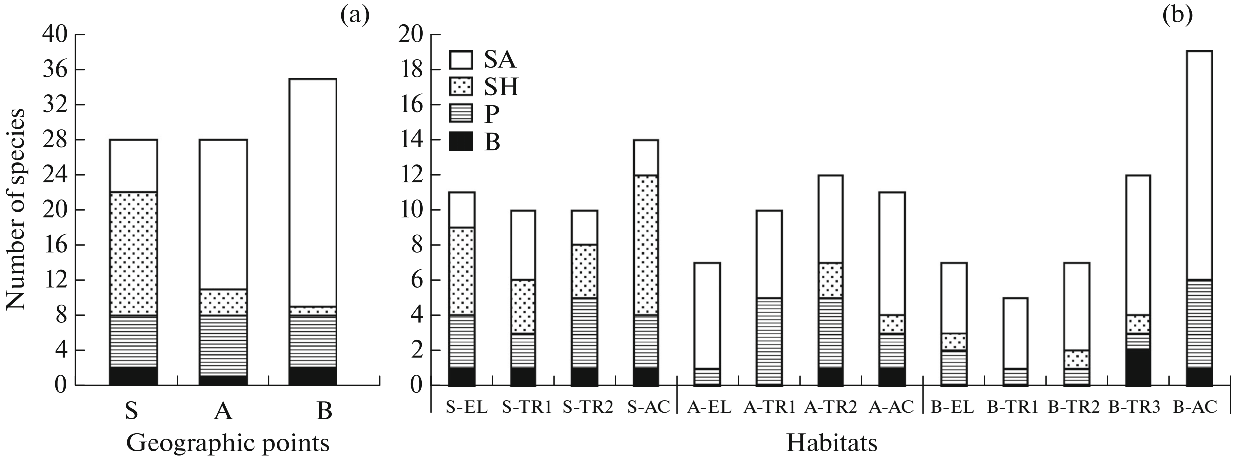

Fig. 2. Areageographical spectra of spider faunas in central Kazakhstan according to geographic regions (a) and catena positions (b). S, Shortandy; A, Arykty; B, Barshyn. B, boreal species; P, polysonal species; SH, subboreal humid species; and SA, subarid species.

On the dry steppe catena (Arykty), the proportion of wolf spiders is relatively small. They were not recorded in the zonal landscape (EL) or on solonetz (TR2). Their highest proportion was determined at the lowest position of the catena (AC). At the same time, the proportion of Gnaphosidae was very high in all positions. The proportion of jumping spiders noticeably increases at the transitive positions. Ground cobweb spiders (*Steatoda albomaculata*), typical for dry, warmed habitats, also appear here. On the coastal solonchak (AC), more than 10% of the population was represented by the crab spiders of the genus *Xysticus*.

In the spider population of the desert steppe catena (Barshyn), gnaphosid spiders retain the leading positions, while the proportion of the widespread wolf spiders at the lowest position near the waterbody (AC) exceeds 20%. The proportion of jumping spiders noticeably increases; in the eluvial position (EL), they accounted for almost one-third of the total spider population.

The calculation of diversity indices shows that, in the direction from north to south, from the typical steppe to the desert one, the ecological diversity of taxocenes of spiders increases (Table 3). In the typical steppe, the diversity and evenness indices decrease from the eluvial position (EL) to the transaccumulative (TR2), and then subsequently increase at the accumulative position (AC). In the dry steppe, a reverse dynamics with a subsequent decrease in the values of diversity and evenness indices at the accumulative position (AC) was observed. In the desert steppe, these indices do not show any directional dynamics, and, at the lowest position (AC), they are the highest on the catena and in the entire study area.

Dominant Complexes

The complex of dominants in the typical steppe (Shortandy) consists of 15 species. Most of them belong to the family Gnaphosidae. *Gnaphosa leporina* was a superdominant species on the lower catena position (AC) and *Alopecosa cursor* was one on TR1. The second species was the most numerous and widespread on this catena.

The dominant complex of dry steppe spiders (Arykty) according to the species composition differs from that of the typical steppe. Only *Gnaphosa steppica* and *Thanatus arenarius* are common dominant species of these two catenas. *Gnaphosa steppica*, the dominant species at the eluvial position (EL) of the typical steppe, was included in the complexes of dominants at all catena positions in the dry steppe (at the rank of dominant or subdominant). Looking ahead, we note that this species dominates or subdominates at three positions of the catena also in the desert steppe, thus being the most abundant and widespread in the steppes of central Kazakhstan. Two representatives of the family Gnaphosidae, *Drassyllus sur* and *Gnaphosa lapponum*, were found in the rank of superdominants at some positions of the dry steppe catena.

The dominant complex of the desert steppe catena (Barshyn) includes 23 species. Two species of gnaphosid spiders, *Berlandina cinerea* and *Zelotes potanini*, also superominated here. The first species was recorded on all catenas; however, it entered the dominant complex only on the southernmost one, in Barshyn. The second species was found neither in the typical steppe nor in the dry steppe. In the desert steppe, *Zelotes potanini* was recorded at the uppermost position of the catena (EL), as well as at TR2 in a convex site of the slope bottom. The highest richness of the dominant species of the wolf spider was determined on the southernmost catena; representatives of the genera *Evippa*, *Lycosa*, and *Mustelicosa* were recorded only at this geographical point. The family of jumping spiders was also represented by five species in the dominant complex of spiders of the desert steppe, while in the typical steppe this group was not included

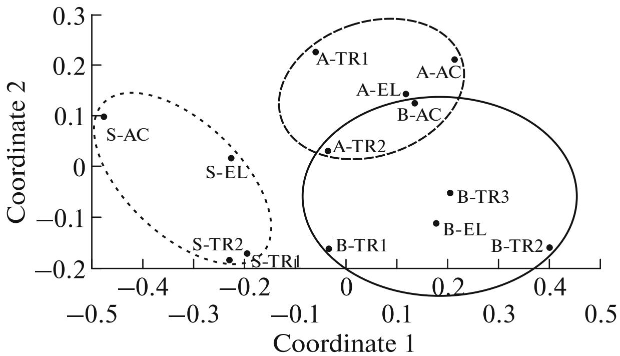

Fig. 3. Multidimensional scaling of the population of spiders in the steppes of central Kazakhstan (Morisita similarity index). See Fig. 1 for designations.

in the complex of dominants and in the dry steppe only one species was represented as a subdominant (Table 3).

Figure 3 shows a diagram obtained by the method of nonmetric multidimensional scaling and built on the basis of data on the abundance (in percent) of spider species at different positions of the three studied catenas (Morisita index). Similar to the comparison of the species composition similarity, all positions of the Shortandy catena are located on the left side of the diagram; however, according to the distribution of species (by abundance in the taxocene structure), only two transit positions (TR1 and TR2) turned to be close. The taxocene structure was quite close to them according to the species abundance at the first transitive position of the catena in Barshyn desert steppe. The distribution of species by abundance at the lowest position of the Shortandy catena turned out to be the most isolated and very distant even in comparison with the lower positions of the other two catenas. However it was nevertheless closer to the lower position of the Barshyn desert steppe catena than to the lower position of the Arykty catena, which is geographically closer. At first glance, the closeness of the upper position of the dry steppe catena and the lower position of the desert steppe catena (*Stipa lessingiana* steppe and *Halocnemum* solonchak, respectively) turned out to be paradoxical. However, this could be explained by the fact that, in the *Stipa lessingiana* steppe, 3 out of the 7 recorded species were not only common with the species list from the EL position in Barshyn, but in both cases were included in the complex of dominants.

In general, the positions of catena, similar to each other by the list of species, turned out to be similar in the structure of communities according to abundance, although with some exceptions (compare Fig. 1 and Fig. 3).

CONCLUSIONS

In total, 79 species of spiders from 33 genera and 11 families were recorded in the steppes of central Kazakhstan. Taxonomically, the most diverse spider populations were determined in the desert steppes. On the latitudinal gradient from north to south, there is a decrease in the dynamic density of spiders at the upper positions of the catena, while the ecological diversity of spider taxocenes increases. It was found that spiders were most numerous in the lowest positions of the studied catenas. A gradual increase in dynamic density from the upper to the lower position took place only on the desert steppe catena (Barshyn).

Both qualitatively and quantitatively, ground spiders of the family Gnaphosidae are the most important group in the study area, which is due to the arid features of the climate in this area. In dry and desert steppes, the proportion of representatives of this group at all positions of catena exceeded 50%. The most abundant and widespread species of central Kazakhstan steppes is *Gnaphosa steppica*.

The second most important group is represented by wolf spiders (Lycosidae), which are most numerous in the lower, more humid positions of the catena. Among them, some taxa are also associated with arid regions and dry stations. Thus, representatives of the genera *Evippa*, *Lycosa*, and *Mustelicosa* were recorded only on the desert-steppe catena.

Jumping spiders (Salticidae) in the study area were represented mainly by species typical for dry habitats. From north to south, from the typical to the desert steppe, the number of species of these spiders increases significantly, as does their proportion in the population structure.

An analysis of the species compositions and population of spiders at various positions of the catenas of central Kazakhstan showed that habitats similar in faunistic composition are, as a rule, similar in population structure.

The transition from typical steppes to desert ones is associated with a decrease in the number of species with a subboreal humid type of habitat and to an increase of the number of subarid species, most of which are recorded in steppe, semidesert, and solonchak habitats.

In contrast to the species richness of carabid beetles, which decreases in the series of these habitats from north to south, the number of spider species increases, and this is similar to the species richness of darkling beetles. The patterns of changes in areageographical spectra at the positions of the studied catenas in spiders and ground beetles are similar (Mordkovich et al., 2020). Therefore, we can support the effect of the principle of zonal change of habitats discovered on Acridoidea (Bei-Bienko, 1966) and confirmed on ground beetles (Lyubechanskii and Mordkovich, 1997).

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