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Spider (Arachnida: Aranei) Communities in Mountain-Hollow Steppes of Southeastern Altai and Tuva

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Abstract—Spider communities in the intermontane hollows of southeastern Altai and Tuva have been studied for the first time using the catena approach. It is revealed that their abundance is very low and their taxonomical composition is very poor. The catenas of the Chuya hollow are dominated by subarid species, while polyzonal species prevail in the Kurai hollow in the valley of the large Chuya River. As in the Chuya hollow, the driest conditions of the catena in the Tannu-Ola mountain range (Ubsu-Nur hollow, western sector) have determined the predominance of subarid faunal elements in Tuva. For the same reason, these two catenas are characterized by the largest proportion of representatives of Central Palaearctic fauna. The catenas near lakes Khadyn (Ulug-Khem hollow) and Tore-Khol (Ubsu-Nur hollow, eastern sector), where the accumulative positions have a high humidity, are dominated by subboreal humid species. West Palaearctic species prevail on the catenas of the Kurai steppe and near Lake Khadyn, while there are no dominant species with some certain longitudinal type of range on the catena near Lake Tore-Khol. The dynamic density of spiders is usually highest at the lower catena positions. Under extremely arid conditions, the maximum dynamic density in the Chuya and Ubsu-Nur (Tannu-Ola) hollows is recorded at the uppermost catena positions. In the mountain hollows of southeastern Altai and Tuva, wolf spiders (Lycosidae) and gnaphosids (Gnaphosidae) are most abundant and diverse in spider communities. Specific spider faunas are formed in isolated conditions of separate hollows. The similarity by the community structure is observed only between the transitive and accumulative positions on the catena in the Kurai hollow.

Keywords: catenas, communities, dominant species, diversity, mountain hollows, Kurai hollow, Chuya hollow, Ubsu-Nur hollow, Ulug-Khem hollow

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INTRODUCTION

The fauna of the Russian part of the mountainous Altai and Tuva has been well studied to date based on active arachnological studies in southern Siberia in recent decades (Marusik et al., 2000; Azarkina and Trilikauskas, 2012, 2013a, 2013b). In addition to their unusual variety of landscapes, these regions are also characterized by the richest araneofauna, which makes them extremely promising and interesting for studying different aspects of spider ecology. Therefore, one should particularly note unique landscape objects, such as vast intermontane hollows surrounded by highlands, on the territory of these regions. The climate of these hollows is extreme continental, which is expressed in negative average annual temperatures, long winters with little snow, short growing seasons, and dry springs and autumns. Most of the scanty precipitation (120–250 mm per year) falls in the second half of summer. The steppe and desert phytocenoses located on the bottoms of these hollows are characterized by a sparse vegetation cover (the projective cover is not more than 30–40%) and its low height (from 3 to 15 cm, depending on humidity conditions).

The communities of ground invertebrates (herpetobionts) in Altai and Tuva mountain hollows are dominated by ants (Formicidae), coleopterans of two families (darkling beetles (Tenebrionidae) and ground beetles (Carabidae)), and spiders (Aranei). The composition, spatial distribution, and structure of the communities were studied for ants (Zhigul'skaya, 1968, 2009, 2011), ground beetles, and darkling beetles (Mordkovich, 1968). The fauna is depleted and the number of representatives of these groups decreases with an increase in aridity from north to south and from west to east due to a lack of humidity and heat. The diversity and total abundance of herpetobium sharply increases in sites where one of these limiting factors is at least partially less effective. Abiotic conditions prove to be somewhat softer at the foot of mountain ranges (i.e., at the very edges of hollows) and on their bottoms near moisture sources. Under these conditions, the community of the studied invertebrates is distributed extremely heterogeneously and determined by macro- and mesorelief elements at the macroscale and by the location of separate phytocenotic contours and even large plant specimens at the microscale (Stebaev et al., 1968).

Although being very detailed, this information is not only somewhat outdated due to climatic changes in recent decades (most studies on herpetobiont communities in these hollows were carried out more than 50 years ago), but it also does not provide any data on the synecology of one important and taxonomically and ecologically diverse group of arthropods, namely, spiders. The only paper on Altai spiders in which the title declares the study of spider communities in the mountain hollows of the region is actually not related to this topic and analyzes the biotopic distribution of spiders in the vicinity of the town of Biysk and village of Chemal (Volkovskii and Romanenko, 2010). Therefore, there are currently only some faunistic papers that provide no more than fragmentary data on the ecology of spiders in intermontane hollows (Logunov and Marusik, 1994; Marusik et al., 1996).

The purpose of our research was to study the spatial distribution and structure of spider (Arachnida; Aranei) communities in extreme continental mountain areas in the south of Siberia: the Kurai and Chuya hollows in southeastern Altai and Ubsu-Nur and Ulug-Khem hollows in Tuva. The study used the catena approach: material collection points (sites) are ordered along the geomorphological gradients from the edge of the hollow to its lowermost parts.

MATERIALS AND METHODS

Field studies were carried out in the Ubsu-Nur and Ulug-Khem hollows in the third decade of July 2018 and in the Kurai and Chuya hollows in the second decade of July 2018 and third decade of the same month in 2020. Inventories were performed on one catena in the Kurai hollow and on two catenas in the Chuya hollow (near the village of Kokorya in 2018 and near the village of Ortalyk in 2020). The geographical coordinates and a brief description of the positions of the studied catenas are given in Table 1.

In the Ubsu-Nur hollow, studies were carried out on two catenas: in the western, more arid sector (from the southern macroslope of the Tannu-Ola range towards Lake Ubsu-Nur) and in the eastern (more humid) sector (on the southeastern shore of Lake Tore-Khol). In the Ulug-Khem hollow, the spider community was studied on the catena near Lake Khadyn.

Study sites were selected using the catena method, which served as a basis for our recently published research on spiders in Central Kazakhstan (Trilikauskas and Lyubechanskii, 2020). Taking into account the diversity of habitats, we studied three positions on each catena in the Kurai and Chuya hollows (eluvial, transitive, and accumulative positions), four positions in Tuva hollows (two transitive positions on catenas near each of the two lakes, Tore-Khol and Khadyn), and two eluvial positions on the southern macroslope of the Tannu-Ola range.

Spiders were collected using pitfall traps (plastic cups 6.5 cm in diameter fixed in 3% vinegar solution, 10 cups per each position).

Species whose proportion was no less than 10% of the total community were considered dominants and species with an abundance of no less than 30% were considered superdominants.

In this study, we analyzed the ranges of spider species based on the typology of species ranges that was developed for ground beetles (Coleoptera, Carabidae) (Dudko and Lyubechanskii, 2002) and adapted for spiders (Trilikauskas and Lyubechanskii, 2020). According to the latitudinal component of species ranges, spider species were grouped into boreal, subboreal humid, subarid, and polyzonal species; according to the longitudinal component, they were classified into west, central, and east Palaearctic and Transpalaearctic species. The spectra of species ranges for each habitat make it possible to assess how northern or southern (western or eastern) the species composition in a certain habitat is.

The species nomenclature is given according to the World Spider Catalog (2021).

Cluster analysis was performed in PAST 4 (Hammer et al., 2001). The Raup–Crick index of faunistic similarity and Morisita similarity index were calculated; the cluster was built by the unweighted pair-group method using arithmetic averages (UPGMA).

RESULTS

Taxonomic Analysis of Araneofauna

Southeastern Altai. The spider community (Table 2) in the mountain hollows of the region is characterized by a low taxonomic diversity. Seventeen species were recorded on the Kurai steppe catena. These are mainly representatives of the two largest families of wandering spiders: Gnaphosidae and Lycosidae (six and seven species, respectively). At the species level, the taxonomic diversity was higher at the transitive position located on the river terrace with clumps of treelike sagebrush (*Artemisia santolinifolia* Turcz. ex Bess.), feather grass, and sparse larch trees. At the genus level, the taxonomic diversity of spiders did not differ at different positions of the catena. The largest number of families was recorded in the feather grass steppe at the upper position of the catena. Against the background of general low taxonomic diversity, the differences in the number of taxa are insignificant at different positions of the catena. Gnaphosid spiders were represented by three species at all catena positions. Wolf spiders were more diverse at the transitive and accumulative positions. In the collections, this group was represented exclusively by juvenile individuals of Lycosidae only in the feather-grass steppe at the upper position and it was impossible to determine the num-

Table 1. Brief description of the studied habitats in Altai and Tuva mountain hollows

Designation	Coordinates	Brief description, altitude above sea level
K18, Altai, Kurai hollow, July 10–15, 2018; K20, same positions, July 21–August 1, 2020		
K18EL, K20EL	50°15′21.2″ N 87°57′50.2″ E	True feather-grass steppe in the lower part of the mountain slope, with sagebrush, hawkweed, and thyme. Projective cover (PC) 60–70%. *H* = 1626 m
K18TR, K20TR	50°15′4.0″ N 87°57′22.2″ E	River terrace with clumps of treelike sagebrush, feather grass, and separate larch trees. *H* = 1607 m
K18AC, K20AC	50°14′57.8″ N 87°57′17.3″ E	Lower terrace of the Kuraika River floodplain, short-grass meadow with sagebrush clumps. *H* = 1606 m
C18, Altai, Chuya hollow, July 10–15, 2018		
C18EL	49°55′34.9″ N 89°3′6.2″ E	Desert at the bottom of the slope. *H* = 1929 m
C18TR	49°55′8,7″ N 89°03′8.1″ E	Desert on the piedmont plain. *H* = 1904 m
C18AC	49°54′51.5″ N 89°03′11.6″ E	Saline meadow in the valley of an intermittent stream. *H* = 1883 m
C20, Altai, Chuya hollow, July 21–August 1, 2020		
C20EL	50°04′24.9″ 88°32'39,1″	South-facing slope, bottom. Sagebrush rocky desert with ephedra and grasses. *H* = 2050 m
C20TR	50°04′05.6″ 88°32′13.0″	Edaphic desert on the piedmont plain, PC 30–40%. Sagebrush, astragalus, ephedra, small umbelliferae and small sod grasses, and crucials on loose rubble-loam soil. *H* = 1985 m
C20AC	50°03′56.9″ 88°31′56.3″	Solonetz with cheegrass, orach, low bunchgrasses, and sagebrush. PC 80%. *H* = 1975 m
U, Tuva, Ubsu-Nur hollow, western part, southwest of the Irbitei River. Macrocatena from the southern macroslope of the Tannu-Ola Range to Lake Ubsu-Nur. July 22–29, 2018		
U-EL1	50°45′44.4″ N 93°2′21.1″ E	Upper part of the piedmont plain, bottom of the runoff hollow. The vegetation cover contains large-sod grasses, polster plants, and pea shrub. Soil is gravel–sandy, light. PC 20–30%. *H* = 1143 m
U-EL2	50°45′37″ N 93°2′19.5″ E	Small terrace with gravelly soil in the same site. Sagebrush, polster plants, and grasses. PC 15–25%. *H* = 1135 m
U-TR	50°43′0.9′ N 93°3′42.1″ E	Nanophyton desert, PC 10–20%. Separate sods of low bunchgrasses (5–8 cm). Bare gravelly soil. *H* = 840 m
U-AC	50°40′15.3″ N 93°3′36.2″ E	Wild-rye meadow with herbs on solonetz. PC up to 20%. *H* = 785 m
T, Tuva, Ubsu-Nur hollow, eastern part. Southeastern shore of Lake Tore-Khol. Sandy steppe on dunes. July 24–29, 2018		
T-EL	50°2′45.9″ 95°7′20.4″	Steppe on a dissected piedmont plain. *H* = 1248 m
T-TR1	50°2′45.9″ N 95°7′20.4″ E	Sandy steppe with *Caragana bungei* on dune tops in the center of the hollow. PC 20–30%. *H* = 1235 m
T-TR2	50°2′52.5″ N 95°7′23.7″ E	Psammophytic vegetation at the foot of the sandy dune. PC 10%. *H* = 1195 m
T-AC	50°3′11.6″ 95°7′23.6″	Swampy tussock meadow in front of the lake embankment. Heavy grazing. PC 70%. Sedges, dandelion, yarrow, and lady's-mantle. *H* = 1147 m
H, Tuva, Ulug-Khem hollow, Lake Khadyn. July 21–30, 2018		
H-EL	51°18′39.7″ N 94°29′23.6″ E	Feather-grass steppe with sagebrush and peashrub at the top of the steep slope. PC 50%. *H* = 755 m
H-TR1	51°18′46.4″ N 94°29′30.5″ E	Sagebrush site with fescue, feather grass, aster, and cinquefoil. PC 30%. *H* = 742 m
H-TR2	51°18′52.9″ N 94°29′47.2″ E	Short-grass June-grass–sagebrush steppe on the lower ancient lake terrace. PC 50%. *H* = 715 m
H-AC	51°18′54.8″ N 94°29′52.4″ E	The edge of the reed water meadow, 50 m from the water edge; transition to solonetz with licorice. PC 70–80%. *H* = 712 m

EL, eluvial position of the catena; TR, transitive position; and AC, accumulative position.

Table 2. Dynamic density (ind. per 100 trap-days) of spiders (Arachnida, Aranei) at positions of the studied catenas in the mountain hollows of southeastern Altai

Type of range	Locality	Kurai hollow			Chuya hollow (Kokorya), 2018			Chuya hollow (Ortolyk), 2020		
	Species	catena position								
		EL	TR	AC	EL	TR	AC	EL	TR	AC
	GNAPHOSIDAE	**14/9**	**10/7**	**0/5**	**0**	**2**	**9**	**3**	**3**	**2**
SA WP	*Berlandina cinerea* (Menge, 1872)	6/7						1		
P EP	*Drassodes neglectus* (Keyserling, 1887)		4/0							
	Drassodes sp.1			0/1						
	Drassodes sp.2							1		
B TP	*Haplodrassus kulczynskii* Lohmander, 1942	4/0								
SH TP	*Micaria guttulata* (C. L. Koch, 1839)						1			
P TP	*Micaria lenzi* Bösenberg, 1899						4			2
P WP	*Micaria silesiaca* L. Koch, 1875								2	
SH WP	*Zelotes electus* (C.L. Koch, 1839)		0/2	0/1						
	Zelotes cf. *eugenei* KOvblyuk, 2009						1			
P TP	*Zelotes longipes* (L. Koch, 1866)	0/1	0/4	0/3						
SA EP	*Zelotes potanini* Schenkel, 1963								1	
	Not ident.	4/1	6/1			2	3	1		
	LINYPHIIDAE	**0/0**	**0/0**	**0/0**	**0**	**0**	**0**	**0**	**10**	**0**
BM CP	*Incestophantes bonus* Tanasevitch, 1996								1	
	LYCOSIDAE	**4/14**	**70/29**	**42/38**	**1**	**2**	**25**	**9**	**5**	**9**
SH EP	*Alopecosa* cf. *albostriata* (Grube, 1861)		0/1							
	Alopecosa sp.(*borea* gr.)		0/1							
	Alopecosa sp.*1*				1	2	2			
	Alopecosa sp.*2*							5		4
P WP	*Alopecosa cursor* (Hahn, 1831)			0/1						
SH TP	*Alopecosa mariae* (Dahl, 1908)		0/1							
	Pardosa sp. (*bifasciata* gr.)		70/19	40/30						
SA CP	*Pardosa mongolica* Kulczyński, 1901						17			
SA CP	*Pardosa haibeiensis* Yin, Wang, Peng & Xie, 1995									4
%%	*Pardosa* cf. *palustris* (Linnaeus, 1758)			0/2						
%%	*Pardosa* cf. *wagleri* (Hahn, 1822)							1		
SA CP	*Pardosa zyuzini* Kronestedt & Marusik, 2011						4			
SH WP	*Xerolycosa miniata* (C.L. Koch, 1834)		0/1	0/1						
	Not ident.	4/14	0/6	2/4			2	3	5	1
	PHILODROMIDAE	**2/0**	**0/0**	**0/0**	**2**	**2**	**0**	**3**	**1**	**0**
	Thanatus sp.(*formicinus* gr.)					2				
	Thanatus cf. *mikhailovi* Logunov, 1996				2					
SA CP	*Thanatus tuvinensis* Logunov, 1996							3	1	
	Thanatus sp. (juvenile)	2/0								
	SALTICIDAE	**10/2**	**0/2**	**10/4**	**1**	**5**	**3**	**0**	**4**	**0**
P TP	*Aelurillus v-insignitus* (Clerck, 1757)	0/1	0/2	0/4						
SA CP	*Asianellus ontchallan* Logunov & Hęnciak, 1996					4				
	Yllenus sp. (juvenile)				1		3			
	Not ident.	10/1		10/0		1				
	THERIDIIDAE	**0/1**	**0/0**	**0/0**	**0**	**0**	**0**	**0**	**4**	**0**
P TH	*Steatoda albomaculata* (De Geer, 1778)	0/1							4	
	THOMISIDAE	**0/0**	**2/1**	**0/4**	**1**	**0**	**0**	**0**	**0**	**0**
	Ozyptila sp.				1					
SH WP	*Psammitis ninnii* (Thorell, 1872)	0/0	2/1	0/4						
	Total density	**30/26**	**82/39**	**52/61**	**5**	**11**	**37**	**15**	**14**	**11**
	Number of species	**7**	**10**	**9**	**7**	**3**	**7**	**5**	**5**	**3**

Type of range, latitudinal component: B, boreal type; SH, subboreal humid type; SA, subarid type; and P, polyzonal type. Longitudinal component: WP, West Palaearctic type; CP, Central Palaearctic type; EP, East Palaearctic type; TP, Transpalaearctic type; and TH, Transholarctic type. Not ident. indicates juvenile spider individuals identified only to the family level. Data from the Kurai hollow for 2018/2020 divided by slash (/).

ber of species living there. With respect to the spider fauna of the Kurai hollow, one should note the almost complete absence of crab spiders of the genus *Thanatus* in the collections, although it is steppe areas where many representatives of this group were recorded (Logunov and Marusik, 1994).

According to the results of collections, there are 21 spider species on two catenas (11 species per each catena) in the Chuya steppe, which is significantly lower than their number in the Kurai steppe. Here, the families Gnaphosidae and Lycosidae are represented by the largest and approximately equal numbers of species. However, whereas the collections from the catena near the village of Kokorya in 2018 included only three species of each of these families, there were five gnaphosid species on the catena near Ortolyk in 2020. The only linyphiid species, *Incestophantes bonus,* described in the materials from the studied Altai and Tuva catenas (Tuvan highlands) was also recorded here (Tanasevich, 1996, 2013). It should also be noted that leaping spiders (the family Salticidae) (including representatives of the genus *Yllenus* characteristic of arid areas) were found only in the collections of 2018 from the Chuya steppe.

The species diversity of spiders on the catena near the village of Kokorya was significantly lower at the transitive position than at the marginal positions. At the genus level, the number of taxa at this position was inferior only to that at the accumulative position; however, the number of families was higher at the transitive position. The accumulative position on the Ortalyk catena (2020) was lower than the transitive and upper positions at all taxonomic levels. On the catena where studies were carried out in 2018, the accumulative position was a meadow near a small watercourse and differed from that in 2020 in more humid conditions and type of vegetation. The taxonomic diversity of spiders was significantly higher at all levels at the accumulative position of the first catena than at the accumulative position of the second catena. In addition, the differences in the taxonomic diversity were more significant at different positions on the second catena. The spider community was more diverse here in the transitive position at all taxonomic levels.

Tuva. Twenty-three spider species were recorded on the catena in the Ulug-Khem hollow near Lake Khadyn (Table 3). The taxonomic diversity of spiders increased from the upper to the lower position at all levels, in particular, at the species level. Almost half of the species identified at the accumulative position were wolf spiders. Crab spiders of the family Thomisidae and small cribellate dictynid spiders were found only at this position (at the edge of a reed water meadow developing into solonetz). At the same time, representatives of the family Liocranidae that were found at all other positions of this catena were absent here.

A similar pattern, albeit not so clearly defined, was observed on the catena in the eastern sector of the Ubsu-Nur hollow, near Lake Tore-Khol. The lower position of this catena (a swampy tussock meadow) was a habitat with the largest number of spider species, genera, and families on the catena. At the same time, the first of the transitive positions was characterized by the lowest taxonomic diversity at all levels. The number of species, genera, and families was somewhat higher at the eluvial position. The accumulative position of the catena near Lake Tore-Khol included two linyphiid species of the genus *Erigone* and orb-weaving spiders of the genus *Pachygnatha*, which do not build their webs at adult age and often become a component of herpetobium communities in humid habitats. The total taxonomic diversity of spiders was the lowest on this catena among the studied Tuvan catenas.

Eighteen spider species were recorded in the spider community of the catena located on the southern macroslope of the Tannu-Ola range (the western sector of the Ubsu-Nur hollow). At the species and genus levels, the taxonomic diversity was higher on this catena than on the Tore-Khol catena, with the number of families being the same. The number of taxa of all levels decreases here from the second eluvial to the accumulative position, which sharply differs from the lower positions of other Tuvan catena in dryness and low projective vegetation cover. Five species of wandering crab spiders of the genus *Thanatus* were recorded on the catena of the Tannu-Ola range, while they were absent on the other catenas of the region.

Figure 1a shows a dendrogram built by the unweighted pair-group method using arithmetic averages (UPGMA) with calculation of the Raup–Crick index of faunistic similarity. Two clusters are clearly distinguished: one small cluster with faunas of accumulative positions of catenas near lakes Khadyn and Tore-Khol and one large cluster with faunas of positions of all other catenas. The lower positions included in the small cluster were not determined by the similarity of their species compositions, since they were the wettest among all the studied habitats; they were determined by sharp differences of their fauna from that at positions of other catenas.

The cluster analysis also showed a very high degree of faunistic similarity between the eluvial positions of the Ubsu-Nur catena and upper and first transitive positions on the catena near Lake Khadyn, as well as between the faunas of the accumulative and transitive positions on the catena in the Kurai hollow (data for 2020).

Areographic Analysis

An analysis of spider ranges by their latitudinal component showed that subarid species prevailed on catenas in the Chuya hollow of southeastern Altai and on the Tannu-Ola range in Tuva (Fig. 2a). Despite a significant difference in the altitudinal location of

Table 3. Dynamic density (ind. per 100 trap-days) of spiders (Arachnida, Aranei) at positions of the studied catenas in Tuva mountain hollows

Type of range	Locality	Lake Khadyn (Ulug-Khem hollow)				Tannu-Ola range (Ubsu-Nur hollow, western sector)				Lake Tore-Khol (Ubsu-Nur hollow, eastern sector)			
	Species	catena position											
		EL	TR1	TR2	AC	EL1	EL2	TR	AC	EL	TR1	TR2	AC
	DICTYNIDAE	**0**	**0**	**0**	**2**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
SH WP	*Argenna patula* (Simon, 1874)				2								
	GNAPHOSIDAE	**7**	**14**	**16**	**9**	**16**	**31**	**1**	**12**	**6**	**0**	**6**	**4**
SA WP	*Berlandina cinerea* (Menge, 1872)	2	10	8		10	19	1	4				
SH TP	*Drassyllus pusillus* (C.L. Koch, 1833)				6								
	Gnaphosa sp.*1*			4									
	Gnaphosa sp.*2*					3	4		4				
	Not ident.					1							
P TP	*Micaria lenzi* Bösenberg, 1899						1						
	Micaria cf. *lenzi* Bösenberg, 1899											2	
B WP	*Micaria nivosa* L. Koch, 1866				1								
SH WP	*Zelotes electus* (C.L. Koch, 1839)					1						4	
SH WP	*Zelotes latreillei* (Simon, 1878)				1								
P TP	*Zelotes longipes* (L. Koch, 1866)	3	3										
SA WP	*Zelotes mundus* (Kulczyński, 1897)				1								4
SA EP	*Zelotes potanini* Schenkel, 1963	2							4				
P TH	*Zelotes puritanus* Chamberlin, 1922						4			4			
	Not ident.		1	4		1	3			2			
	LIOCRANIDAE	**1**	**4**	**6**	**0**	**9**	**1**	**1**	**3**	**0**	**0**	**0**	**0**
SA EP	*Agroeca mongolica* Schenkel, 1936	1	4	6		9	1	1	3				
	LINYPHIIDAE	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**32**
P TP	*Erigone dentipalpis* (Wider, 1834)												10
SH EP	*Erigone sinensis* Schenkel, 1936												22
	LYCOSIDAE	**3**	**6**	**10**	**147**	**1**	**10**	**0**	**0**	**6**	**4**	**8**	**156**
SH EP	*Alopecosa* cf. *albostriata* (Grube, 1861)	3	4	2								2	
	Alopecosa cf. *cuneata* (Clerck, 1757)				1								
	Alopecosa sp.									2	2		
SA CP	*Alopecosa zyuzini* Logunov & Marusik, 1995										2	2	
SA CP	*Evippa sibirica* Marusik, 1995						7						
B TP	*Pardosa atrata* (Thorell, 1873)				1								
SH EP	*Pardosa hanrasanensis* Jo & Paik, 1984		2										
SA WP	*Pardosa luctinosa* Simon, 1876				27								
SH TP	*Pardosa plumipes* (Thorell, 1875)			8	111								10
	Pardosa sp.				1								
SA CP	*Pardosa zyuzini* Kronestedt & Marusik, 2011												142
SH WP	*Xerolycosa miniata* (C.L. Koch, 1834)				6								
	Not ident.					1	3			4		4	4
	PHILODROMIDAE	**0**	**0**	**1**	**0**	**6**	**8**	**5**	**0**	**0**	**0**	**0**	**0**
B TH	*Thanatus arcticus* Thorell, 1872			1									

Table 3. (Contd.)

Type of range	Locality	Lake Khadyn (Ulug-Khem hollow)				Tannu-Ola range (Ubsu-Nur hollow, western sector)				Lake Tore-Khol (Ubsu-Nur hollow, eastern sector)			
	Species	catena position											
		EL	TR1	TR2	AC	EL1	EL2	TR	AC	EL	TR1	TR2	AC
	Thanatus cf. *altimontis* Gertsch, 1993							1					
	Thanatus sp.						1						
SA CP	*Thanatus stepposus* Logunov, 1996					3	3						
SA EP	*Thanatus tuvinensis* Logunov, 1996					3	4						
SA CP	*Thanatus ubsunurensis* Logunov, 1996							4					
	SALTICIDAE	**0**	**1**	**5**	**1**	**0**	**2**	**0**	**0**	**2**	**0**	**2**	**0**
P TP	*Aelurillus v-insignitus* (Clerck, 1757)						1						
SH TP	*Asianellus festivus* (C.L. Koch, 1834)		1	1									
B TP	*Calositticus caricis* (Westring, 1861)				1								
SA CP	*Phlegra profuga* Logunov, 1996						1						
	Not ident.			4						2		2	
	TETRAGNATHIDAE	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**8**
SA TH	*Pachygnatha clercki* Sundevall, 1823												8
	THERIDIIDAE	**0**	**0**	**0**	**0**	**0**	**0**	**6**	**0**	**0**	**0**	**0**	**0**
P TH	*Steatoda albomaculata* (De Geer, 1778)							6					
	THOMISIDAE	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**2**
SH TH	*Ozyptila trux* (Blackwall, 1846)				1								
SH EP	*Xysticus hedini* Schenkel, 1936												2
	Total density	**11**	**25**	**38**	**160**	**32**	**52**	**13**	**15**	**14**	**4**	**8**	**202**
	Number of species	**5**	**6**	**7**	**13**	**8**	**11**	**5**	**4**	**2**	**2**	**4**	**7**

See the notes in Table 2.

these catenas, they are similar in the extreme dryness of the studied habitats and low projective vegetation cover. The catena near Lake Khadyn at a relatively low altitude above sea level, characterized by different variants of steppe vegetation with a high projective cover, was dominated by subboreal humid species; the proportion of boreal species was also significant here. The intermediate variant against this background is the species structure grouped by the latitudinal component of the range on the catena near Lake Tore-Khol. Here, despite the humidity of the accumulative position, the vegetation cover is sparse at the upper positions of catenas and loose sandy soils cannot retain moisture. The ratio of subboreal humid and subarid species was approximately equal under these conditions.

The catena in the Kuraika River valley, located in the narrow Kurai hollow sandwiched between high ranges, occupied an isolated position against the general background during assessment of the latitudinal component of the ranges of species living there. It was dominated by polyzonal elements with a significant proportion of subboreal humid elements. Apparently, polyzonal species penetrate here via the valley of the Chuya River, one of the largest rivers in Altai. The dominance of polyzonal and subboreal humid species characterizes the spider fauna on the Kurai catena as nonspecific for the steppe hollow.

An analysis of the spider fauna on the catena of mountain hollows in southeastern Altai and Tuva by the longitudinal component of ranges (Fig. 2b) also revealed a similarity between the Chuya and Ubsu-Nur catenas. The species inhabiting these hollows were dominated by representatives of Central Palaearctic fauna. West Palaearctic species prevailed on catenas near Lake Khadyn and in the Kurai hollow. The main difference of the catena near Lake Tore-Khol was the most uniform distribution of the proportions of different longitudinal elements at a slight predominance and equal proportions of western and eastern Palaearctic species.

Analysis of Spider Dynamic Density

Among the five studied hollows, the highest values of the dynamic density of spiders were recorded on

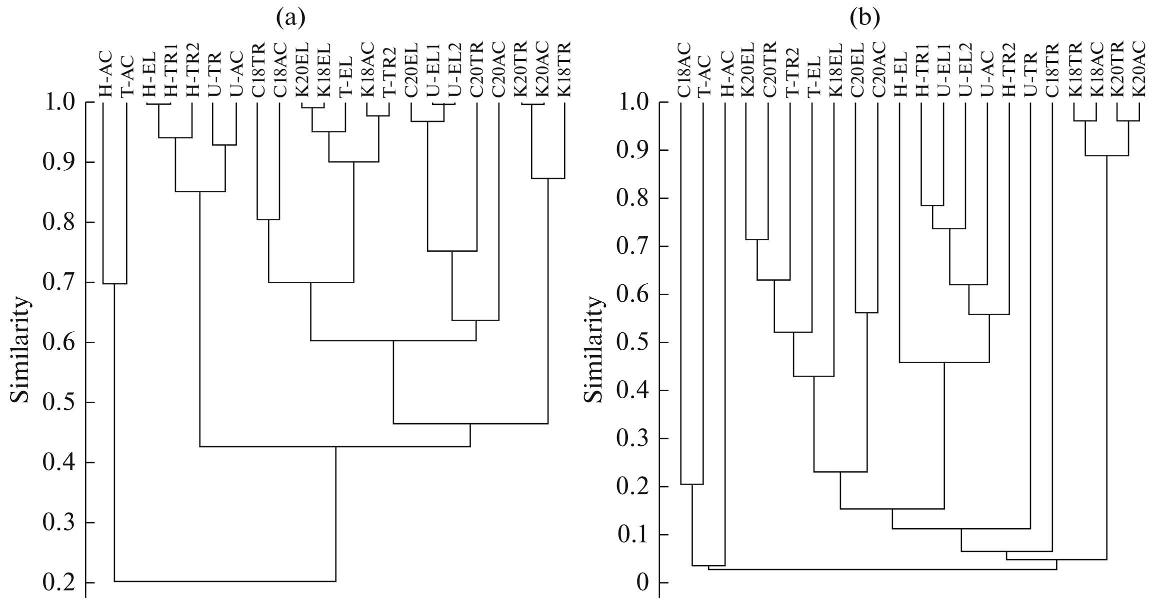

Fig. 1. Dendrograms of the faunistic similarity of species compositions ((a) Raup–Crick index, UPGMA) and similarity of spider communities ((b) Morisita index, UPGMA) of catena positions in southeastern Altai and Tuva. Dendrograms are built by the unweighted pair-group method using arithmetic averages (UPGMA). See notes in Table 1.

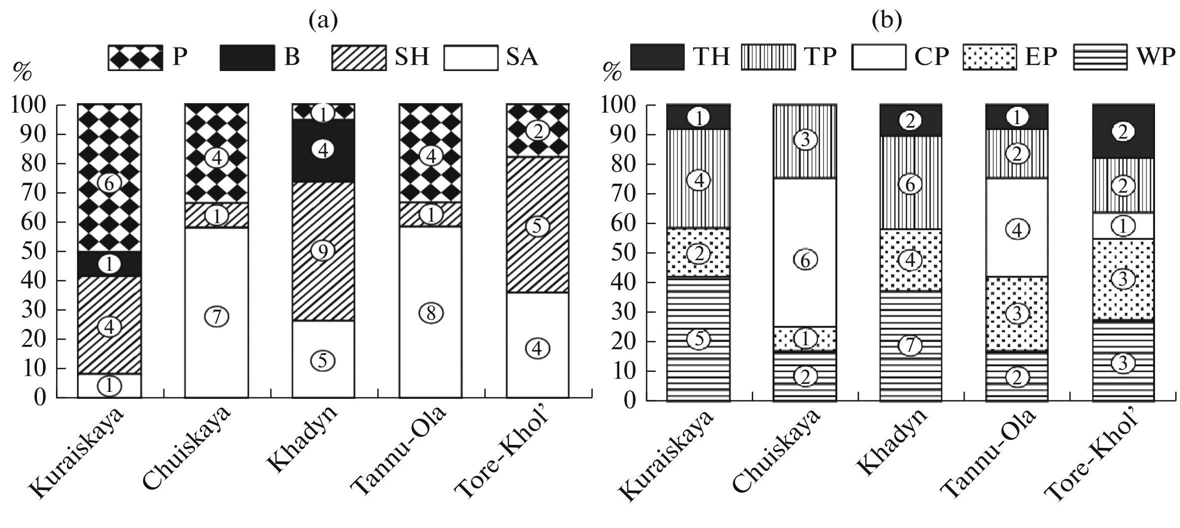

Fig. 2. Spectra of areographic spider groups on the studied catenas of southeastern Altai and Tuva. (a) latitudinal component of the range: B, boreal species; SH, subboreal humid species; SA, subarid species; and P, polyzonal species. (b) Longitudinal component: WP, West Palaearctic type; CP, Central Palaearctic type; EP, East Palaearctic type; TP, Transpalaearctic type; and TH, Transholarctic type.

catenas near lakes Khadyn and Tore-Khol (Table 4). Here, the accumulative positions were characterized by a high humidity; the dynamic density was maximal and sharply differed in its value from the other positions. Its value near Lake Tore-Khol exceeded 200 specimens per 100 trap-days. The lowest values of the dynamic density were observed on catenas in the Chuya hollow and on the Tannu-Ola range (Ubsu-Nur hollow).

Dominant Complexes (Tables 2, 3)

Southeastern Altai. In the second decade of July (2018), two representatives of the family Gnaphosidae, *Berlandina cinerea* and *Haplodrassus kulczynskii,* were among the dominants at the upper position of the catena in the Kurai steppe. At the same time, a significant part of the material was represented by unidentified (juvenile) individuals from the families Gnaphosidae (over 10%), Lycosidae (over 10%), and Salticidae (over 30%), which makes it impossible to determine the full complex of dominants at this position. During the research in the third decade of July in 2020, *Berlandina cinerea* retained its dominant position. At the same time, over 53% of the material was represented by immature wolf spider individuals, while adult specimens were completely absent, which made the identification of the dominant species at this position even more problematic. At the transitive position of this catena, the superdominant was a small wolf spider species, *Pardosa* sp. (*bifasciata* gr.), both in the second and third decades of July. In 2020, the dominant complex also included a representative of the family Gnaphosidae, *Zelotes longipes,* as a dominant species at this position. The proportion of unidentified lycosid individuals was over 15%. *Pardosa* sp. (*bifasciata* gr.) also remained superdominant at the accumulative position of this catena both in the second and third decades of July (2018 and 2020). In 2018, almost 20% of individuals recorded here were juvenile leaping spider individuals, which probably also included some of the unidentified species of the dominant complex.

The abundance of the spider community was extremely low at the upper positions of catenas in the Chuya steppe. In 2018, all the individuals occasionally recorded here were almost exclusively immature and unidentified. On the catena where studies were carried out in 2020, *Thanatus tuvinensis* and large individuals of the genus *Alopecosa* (which were not determined to the species level, since the collections contained only older immature individuals of this genus) were attributed to the dominants at the eluvial position. At the transitive position of the catena near the village of Kokorya, *Asianellus ontchallan* was the superdominant and *Thanatus* sp. (*formicinus* gr.) was the dominant species. *Steatoda albomaculata* was dominant on the catena near the village of Ortolyk, where studies were carried out in 2020. At the same time, more than one-third of the population was represented by unidentified lycosid individuals. Wolf spiders of the genus *Pardosa* were superdominant at the accumulative positions of both catenas of the Chuya hollow. In 2018, *Pardosa mongolica* was over 45% of the community abundance at the lower position. The dominant complex also included *Pardosa zyuzini* and *Micaria lenzi* as dominants. In 2020, the superdominants at the accumulative position included *Pardosa haibeiensis,* which was recorded in Russia for the first time, and the large unidentified species of the genus *Alopecosa* that was mentioned above for the upper position. *Micaria lenzi* was also dominant here.

Tuva. At the upper position of the catena near Lake Khadyn, the distribution of species was fairly even in the small spider community. All of them except *Agroeca mongolica* can formally be attributed to dominants. It should be noted that these are mainly representatives of the family Gnaphosidae. A typical inhabitant of steppe landscapes, *Berlandina cinerea,* became the superdominant at the first transitive position of this catena. The dominant complex proved to be taxonomically quite diverse here and included representatives

Table 4. Average dynamic density and most abundant position on the studied catenas

Catena	Average dynamic density on the catena (individuals per 100 trap-days)	Catena position with maximum dynamic density
Chuya hollow (Ortolyk), 2020	13.3 ± 1.2	EL
Chuya hollow (Kokorya), 2018	17.7 ± 9.8	AC
Tannu-Ola range	28.0 ± 9.1	EL2
Kurai hollow, 2020	42.0 ± 10.2	AC
Kurai hollow, 2018	54.7 ± 15.1	TR
Lake Tore-Khol	57.0 ± 48.4	AC
Lake Khadyn	58.5 ± 34.3	AC

of three families. *Zelotes longipes* (Gnaphosidae), *Agroeca mongolica* (Liocranidae), and *Alopecosa* cf. *albostriata* (Lycosidae) were dominant here. At the second transitive position of the catena near Lake Khadyn, *Berlandina cinerea* and *Agroeca mongolica* were still among dominants in the dominant complex; in addition, *Pardosa plumipes* and *Gnaphosa* sp. also supplemented this complex. There were no superdominants here. *Pardosa plumipes*, characteristic of meadow sites, became superdominant at the lower position. The dominant complex also included *Pardosa luctinosa* as a dominant, while it was not found at other positions of this catena.

At both upper positions of the Ubsu-Nur catena, the superdominant was *Berlandina cinerea*, while the proportion of *Agroeca mongolica* was slightly less than 30% of the community at the first eluvial position and the dominant species at the second position was *Evippa sibirica*, which was not recorded at any other catena or other positions of the Ubsu-Nur catena. The abundance of the community in the Ubsu-Nur hollow was low at the transitive position. Here, the proportion of each of the two species, *Thanatus ubsunurensis* and *Steatoda albomaculata*, was 30%. Only four species, *Berlandina cinerea*, *Gnaphosa* sp., *Zelotes potanini*, and *Agroeca mongolica*, were recorded at the lower position; they were distributed almost evenly, each being no less than 20% of the total community.

At the upper position of the catena near Lake Tore-Khol, the dominant complex included *Zelotes puritanus* and *Alopecosa* sp. Unidentified representatives of the families Lycosidae and Salticidae were more than one-third of the total community at this position. Only four spider specimens of two species of the genus *Alopecosa* were collected at the first transitive position. The second transitive position included two dominants: *Zelotes electus* and *Alopecosa* cf. *albostriata,* the former being twofold predominant. At the accumulative position of the catena, the spider community was abundant, but taxonomically poor. Here, over 70% of the community were specimens of *Pardosa zyuzini*—a widespread species in Tuva, which was previously also recorded near Lake Tore-Khol (Kronestedt and Marusik, 2011). The dominant species at this position was the *Erigone sinensis*, a small cobweb-producing spider. Two representatives of this genus and family Linyphiidae were recorded exclusively at the lower position of the catena near Lake Tore-Khol.

Figure 1b shows a dendrogram that was built by the unweighted pair-group method using arithmetic averages with calculation of the Morisita index, taking into account the species abundance. Two well-defined clusters, the small and large ones, can be seen. The small cluster is formed by the communities of accumulative positions of the Chuya (2018), Tore-Khol, and Khadyn catenas with superdominants distinguished markedly in their abundance. A small subcluster is clearly distinguished in the large cluster; this small cluster combines taxocenes of the transitive and accumulative positions of the Kurai hollow catena in different inventory years. They proved to be most similar with respect to the taxocene structure. It should be noted that the transitive and accumulative positions on the catena in the Kurai hollow were also very similar in the species composition according to the inventory data in 2020, while they had significant differences in 2018. Along with the occurrence of superdominants, their taxocenes are characterized by a relatively large trail of low-abundance species. Transitive positions of the Ubsu-Nur and Chuya (2018) catenas with small communities and a high abundance of two species are clearly distinguished in the remaining part of the cluster. In the remaining part of the large cluster, the lower and upper positions of the driest catenas—Ubsu-Nur and Chuya catenas (2020)—are most closely located to each other, while these positions are significantly distant from each other on other catenas.

DISCUSSION

The data of our research indicate an extremely low general taxonomic diversity of spiders in the mountain hollows of southeastern Altai. The main representatives of the spider community are wandering forms belonging to the families Gnaphosidae and Lycosidae. As can be assessed by the whole cenotic diversity of mountain-hollow steppes, these areas, located at high altitudes under harsh and dry climate conditions, represent an extreme living habitat for spiders. The low projective cover, absence of any significant layer of plant remains in harsh winters, and low amount of precipitation allow only a very small number of species to survive in such conditions.

An analysis of the structure of the fauna of the studied hollows by their latitudinal component showed that subarid species with a relatively southern distribution prevailed on catenas in arid conditions, where there are desert and semidesert sites at eluvial and transitive positions. In more humid conditions of lake hollows with humid habitats, the proportion of subboreal humid species is high at accumulative positions; they are generally distributed to the north of the range of subarid species. Well-drained sandy soils at upper positions under high moisture conditions at the lower position equalize the proportions of subboreal humid and subarid species. Wide river valleys can facilitate the penetration of polyzonal elements into mountain hollows.

With respect to the longitudinal component of the range, autochthonous Central Palaearctic species prevailed under extremely arid climate conditions of the Chuya and Ubsu-Nur hollows (even against the background of other hollows in the mountains of southern Siberia). The comparatively humid conditions of other mountain hollows, where there are water bodies near the accumulative positions, determined a significant proportion of West Palaearctic elements, which possibly penetrated into the hollows relatively recently.

A clearly defined trend towards an increase in the dynamic density of spiders from the upper to the lower position was observed on catenas near Lake Khadyn, in the Chuya hollow near the village of Kokorya in 2018, and in the Kurai hollow in 2020. In 2018, the maximum dynamic density on the latter catena was recorded at the transitive position, which directly borders on the accumulative one. The high dynamic density of spiders at the lower positions of the catenas was observed in areas where these positions differed markedly from the upper and transitive positions in high humidity. On dry catenas, where the soil cover was dry and vegetation was low and had a low projective cover at all positions, the maximum dynamic density of spiders was observed at upper positions.

The use of the catena method for studying the spatial species distribution showed that the habitats adjacent to water bodies (accumulative positions of catenas) under moisture conditions are distinguished among the hollow sites by a high dynamic density of spiders and the predominance of subboreal humid elements, which are longitudinally widespread in most of the Palaearctic. In other exclusively arid conditions of catenas, where desert and semidesert habitats are formed, spiders are not numerous at all positions and are represented mainly by species with the subarid latitudinal and Central Palaearctic longitudinal components of the range. The results of an analysis of the taxocene of spiders in the studied regions are generally similar to the related data on the communities of other herpetobiont invertebrates: ants and ground and darkling beetles (Mordkovich, 1968; Stebaev et al., 1968).

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflicts of interest.

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