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Effect of hay-mowing on spider communities of the meadow steppes of the central forest-steppe (Russia and Ukraine)

Влияние режима сенокошения луговых степей на население пауков в центральной лесостепи (Россия и Украина)

N.Yu. Polchaninova
Н.Ю. Полчанинова

Kharkov National University, 4 Svobody sqr, Kharkov, 61077, Ukraine. email: polchaninova@ukr.net
Харьковский национальный университет, пл. Свободы, 4, Харьков, 61077, Украина. email: polchaninova@ukr.net

ABSTRACT. The structure of spider communities of meadow steppes under the influence of different hay-mowing regimes is discussed. On the flat interfluve, the species composition is more diverse in the completely preserved steppe because of penetration by forest and forest-edge species. The density of both herb and low-mobile litter dwellers is also higher in the un-mowed steppe, whereas wandering species often show a preference for mowed plots. In relief depressions, in spite of annual hay-mowing, spider communities remain more stable and diverse, i.e., an orographic factor seems to play a pivotal role there, while hay-mowing is of secondary importance.

РЕЗЮМЕ. Приведен анализ формирования фауны и населения пауков в луговых степях Центральной лесостепи под воздействием различных режимов сенокошения. На плакоре видовой состав пауков наиболее разнообразен в абсолютно заповедной степи за счет добавления лесных и опушечных видов. На сенокосных участках видовое богатство уменьшается, но появляются стенобионтные виды. Плотность хортобионтов и малоподвижных герпетобионтов также выше в некосимой степи, бродячие формы часто предпочитают косимую степь. В понижениях рельефа, несмотря на ежегодный сенокос, аранеокомплексы остаются более стабильными и богатыми, т.е. орографический фактор играет главенствующую роль, а сенокошение отходит на второй план.

KEY WORDS: spiders, meadow steppes, mowing, management regime, nature reserves, central forest-steppe, Russia, Ukraine.
КЛЮЧЕВЫЕ СЛОВА: пауки, луговые степи, сенокошение, заповедный режим, заповедники, Центральная лесостепь, Россия, Украина.

Introduction

In Europe the virgin plain steppes have only remained in small territories of nature reserves, and implementation of a proper management regime for them is a very important and basic problem. According to many botanists, the lack of ungulates and natural fires leads to an accumulation of a thick litter layer; a process which causes a steppe's transformation into a more mesophytic community and further degeneration [Petrova, 1990; Sobakinskikh, 2002]. Hay-mowing is often used to prevent this process and affects different components of the steppe ecosystem in different ways, facilitating development of some species and suppressing others. For instance, a higher abundance of springtails [Arkhipova, 2002] and a higher species diversity and abundance of beetle-chortobionts [Tsirikov, 2002] in the 'Galitsya Gora' Reserve (Kursk region) were recorded on hay-mowed areas. On the contrary, the oribatids [Grechanichenko, 1997] and carabids [Grechanichenko & Chuvilina, 1997] of the 'Central-Chernozem' State Reserve were shown to predominate in both species diversity and abundance in the unmowed steppe. In the same reserve, the species composition of insects as a whole in the strictly preserved steppe ('Yamskaya Steppe') was higher than in its mowed areas [Yakushenko *et al*., 1984]. Currently, there is no agreement on the suitability of hay-mowing as a conservation management method in steppe nature reserves. The only way to tackle this problem is to undertake a thorough assessment on the effect of haymaking on the entire steppe biota. This paper aims to evaluate for the first time, the effects of different steppe mowing regimes on spider communities.

Material and methods

Investigations were carried out in the four nature reserves of the forest-steppe zone of the Central Russian Upland [Milkov, 1950]. The 'Streletskaya Steppe', 'Kazatskaya Steppe' and 'Yamskaya Steppe' reserves are situated in the Kursk and Belgorod regions of Russia, and 'Mikhailovskaya Tselina' reserve lies in the Sumy region of Ukraine. These sites differ in natural conditions, territory size and conservation management, which somewhat hinders their comparison.

According to the management regime, the territory of each nature reserve is subdivided into several areas: UMS = the strictly preserved (i.e., un-mowed) steppe, which has been excluded from a mowing rotation for 20–50 years; PMS = the periodically (mowed once every two or four years) mowed steppe; and AMS = the annually mowed steppe. Further subdivision included PMS-1, which was not mowed in the year prior to the start of this research, and PMS-2, which was mowed. The subsequent year following the onset of this research, they could either be mowed or not, according to the management regime of the reserve.

The 'Mikhailovskaya Tselina' was the smallest (200 ha) reserve studied, surrounded by forest shelterbelts, and with a small pond situated in a ravine mouth. The UMS and PMS were situated in a flat interfluve, and the AMS in a ravine. The mowing pattern was every other year, so the two PMS-plots were being mowed in turn. They were investigated throughout 1985–1986.

The territories of the other three reserves covered 500 to 2 000 ha and were structured according to the areas having different mowing regimes both on the plain, and on the ravine slopes. Everywhere, the steppe neighbours the plain and/or bairak (= growing in a ravine) oak-forests. The PMS plots had a five-year mowing rotation; they were not mowed every fifth year. In the 'Streletskaya Steppe', we found a plot just recovered from hay-mowing in 1997, but the next year it was mowed like the others. During the period of our research (2001–2002), the mowing regime in the 'Yamskaya Steppe' was changed, with some plots left unmowed for two–three years, hence the locations of the plots called PMS-2 and AMS were altered.

In each reserve, spiders were collected once a month, from May to September for two successive years. Each collection included five samples taken by sweeping (100 sweeps each), 16 samples using a 0.25 m^2 quadrat, ten pitfall traps (each set for five days), and some hand-collected material. The pitfall traps were plastic cups containing 4% formalin as a preservative. The 'Kazatskaya Steppe' was explored irregularly from time to time, and therefore insufficient data exists for this site. In total, *c*. 15 000 spiders belonging to 156 species in 19 families were collected from the sites. A list of species is given in the appendix and arranged according to Platnick [2003]. The material collected is kept in the author's collection (Kharkov National University, Ukraine) for future research purposes.

To determine the species dominance rate we used the Tishler scale (i.e., percent of total number of spiders in the sample) [after Engelmann, 1978], where: superdominant is $n \geq 10\%$; dominant is $5 \leq n < 10\%$; subdominant is $2.5 \leq n < 5\%$; recedent is $1 \leq n < 2.5\%$; subrecedent is $n < 1\%$. To determine the habitat preference, the percentage of specimens of a particular species collected in a particular habitat, was established based on the total number of specimens of that species collected in the whole reserve. As a rule, juveniles of species-dominants were possible to identify because these species were the sole representatives of their respective genera. For the genera which had more than one species recorded, the juveniles were counted together and this is specified in the text.

Table.
Spider species richness and abundance of the plots under different management regimes (first and second years of investigations separately; explanations in the text).

Таблица.
Видовое богатство и среднесезонная численность пауков на участках с различным заповедным режимом (первый и второй год исследований отдельно; объяснения в тексте).

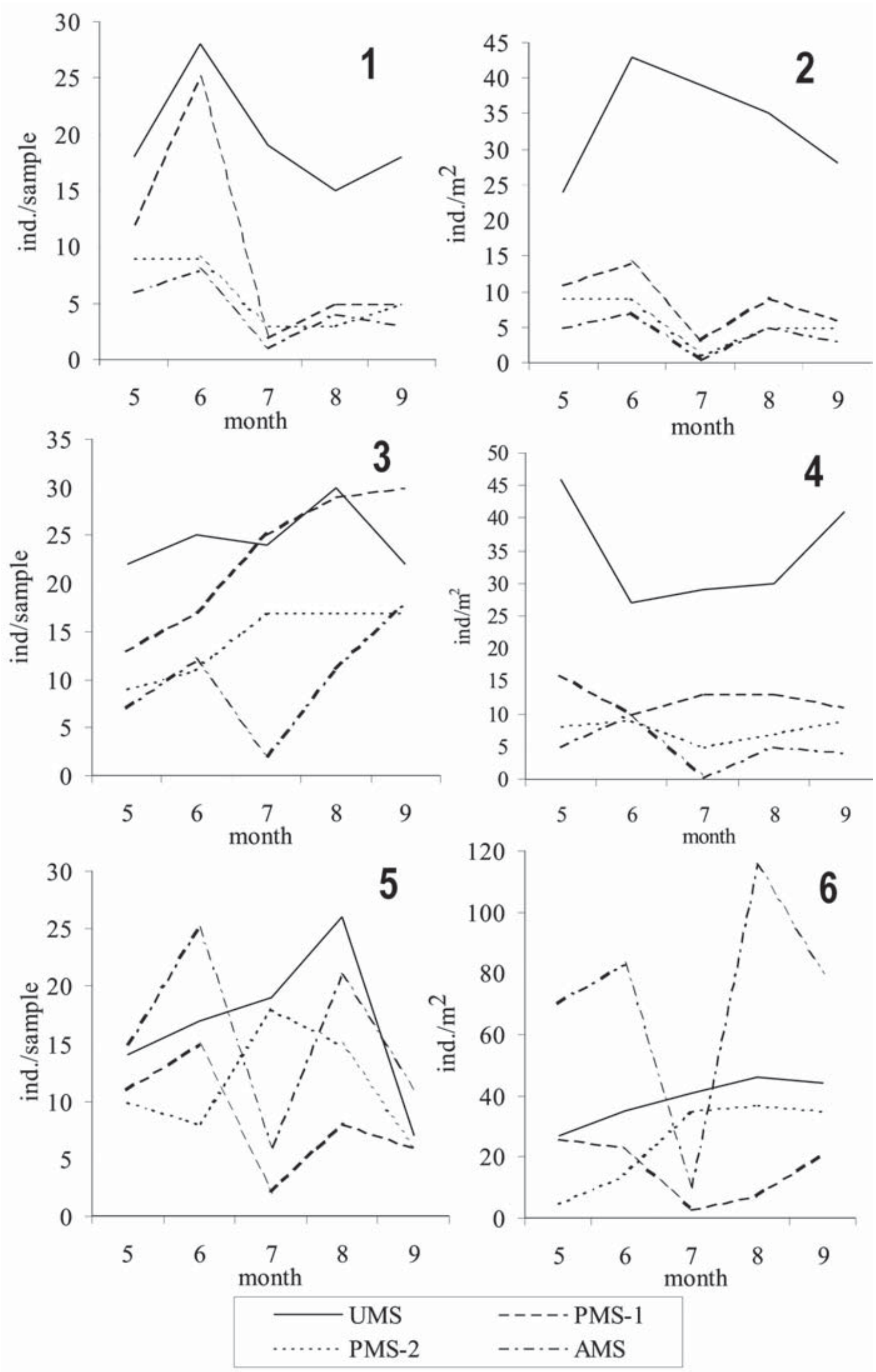
Nature reserves	Total number of species	Average number of individuals per season Herbage (ind./sample)		Litter (ind./m²)		(ind./10 trap-days)	
Streltsovskaya Steppe' 1998–1999							
UMS	77	20.2	25.4	33.0	35.0	17.2	15.7
PMS-1	58	12.0	7.8	24.0	11.5	12.2	10.8
PMS-2	53	5.8	5.0	7.8	10.8	12.0	11.2
AMS	41	4.7	5.2	6.6	5.8	10.5	8.0
'Yamskaya Steppe' 2001–2002							
UMS	89	29.3	25.8	32.2	32.6	15.6	17.8
PMS-1	68	21.4	23.2	9.8	10.8	6.3	6.7
PMS-2	50	7.0	13.3	5.4	5.0	5.2	4.8
AMS	60	9.5	14.4	4.8	5.0	4.0	4.6
'Mikhailovskaya Tselina' 1985–1986							
UMS	57	15.6	18.3	36.2	32.4	14.5	16.8
PMS-1	42	12.2	7.0	25.6	14.2	36.3	29.6
PMS-2	39	5.9	13.5	15.5	23.7	20.0	19.6
AMS	44	8.4	10.6	53.3	45.8	25.0	22.3

Results

The 'Streletskaya Steppe' Reserve

In total, 92 spider species were collected in the steppe part of the 'Streletskaya Steppe' nature reserve. Of these, 26 species were recorded either only in the UMS plot, or both in the UMS and in the forest plots. Nine species were represented by single specimens (here and subsequently, such species are excluded from analyses of their biotopic distributions); 13 species dominated in the oak-forest (*Ero furcata*, *Enoplognatha ovata*, *Entelecara flavipes*, *Neriene clathrata*, *Microneta viaria*, etc.); three dominated in the forest edges and glades (*Zelotes subterraneus*, *Misumena vatia*, *Misumenops tricuspidatus*), but can be encountered in the steppe occasionally. Only three species were simultaneously the dominants of the oak-forest and the subdominants of the steppe (viz., *Floronia bucculenta*, *Linyphia triangularis*, *Evarcha arcuata*). In this respect, it is interesting to notice that at least *F. bucculenta* and *L. triangularis* altered their vertical distribution, moving from trees, shrubs and the upper layer of herbage to the middle and lower layers of the herbage. On the other hand, the 13 species found in the mowed steppe were absent from the un-mowed plots. Seven of these (viz., *Steatoda phalerata*, *Agyneta saxatilis*, *Thanatus arenarius*, *T. formicinus*, *Ozyptila scabricula*, *Allochogna singoriensis* and *Pardosa agrestis*) occurred constantly in the mowed plots, whereas the others were rare, but were restricted to the mowed steppe (Table, see Appendix).

The typical seasonal dynamics of spider communities could be monitored only in the strictly protected steppe (UMS). In the herbage, the numbers of species and individuals were highest in June (Figs 1, 2, 7). In the litter, peaks of density were not stable: one year it was in June, and another it was in August. In early May the herbage was dominated by *Dictyna arundinacea* (accounting in different years for 35–46% of all collected spiders) and *Agalenatea redi* (12–14%). In late May–early June, the latter was replaced by *Mangora acalypha* (12%). In mid-June the most abundant were *Xysticus cristatus* (12%), *Tibellus oblongus* (13%), *Neottiura bimaculata* (18%); and in July–August *Araneus quadratus* (12%), *Argiope bruennichi* (9%) and *Theridion impressum* (8%) appeared. The total number of individuals, as a rule, was determined by juvenile spiders. From the end of May to July, half of the spiders collected consisted of juvenile Araneidae,



Figs 1–6. Seasonal dynamics of spider abundance in herbage (1, 3, 5) and litter (2, 4, 6) in steppe plots under different management regimes. Abbreviations as in the text. 1–2 — 'Streletskaya Steppe', 3–4 — 'Yamskaya Steppe', 5–6 — 'Mikhailovskaya Tselina'.

Рис. 1–6. Сезонная динамика численности пауков в травостое (1, 3, 5) и подстилке (2, 4, 6) на степных участках с разным режимом сенокошения. Сокращения в тексте. 1–2 — 'Стрелецкая Степь', 3–4 — 'Ямская Степь', 5–6 — 'Михайловская Целина'.

whereas *Xysticus*, *Agalenatea*, *Dictyna* and *Mangora*, each representing 12–18%, dominated from July to September.

In the gramineus associations a large number of spiders were concentrated in the space between withered leaves and the litter. There were lots of Linyphiidae (*Linyphia triangularis*, *L. hortensis*, *Floronia bucculenta*, *Stemonyphantes lineatus*) and other common species (*Neottiura bimaculata*, *Episinus angulatus*, *Zora spinimana*). In the shallow and moist litter, the spider density was low (no more than 10 ind./m^2; though on the whole, i.e., in the layer of withered leaves and the shallow litter, it reached 43 ind./m^2, Fig. 2) and except for *Agyneta rurestris* and *Zora spinimama* all species were rare. The forb-grass associations were dominated by the same spider species, but their spatial distribution was more even.

In PMS-1, the spring and early summer spider assemblages were close to those of UMS, with their species richness and abundance reducing insignificantly (Table). The only herb dweller, which preferred that plot, was *Xysticus cristatus* (22%). In the other plots (PMS-2 and AMS), the spring fauna was very poor, which seemed to be caused by hay-mowing the previous year, whereas the following July mowing broke the late summer assemblages. The nine common species (see above) were not found, and all the above-mentioned dominants occurred as singletons. Therefore, both the species richness and abundance decreased markedly (Table, Figs 1, 2, 7). In the litter, which usually takes many years to be formed, the number of spiders in PMS-1 was slightly higher than in PMS-2 (Table). Most of the species recorded were very rare, with only *Microlinyphia pusilla* and *Neottiura bimaculata* being subdominants.

In the second year of the investigation all the mowed plots were in the same condition, i.e., as they were after hay-mowing, with PMS-1 spider assemblages indistinguishable from those of PMS-2 and AMS (Table). Consequently, the advantage of not mowing had lasted only one season.

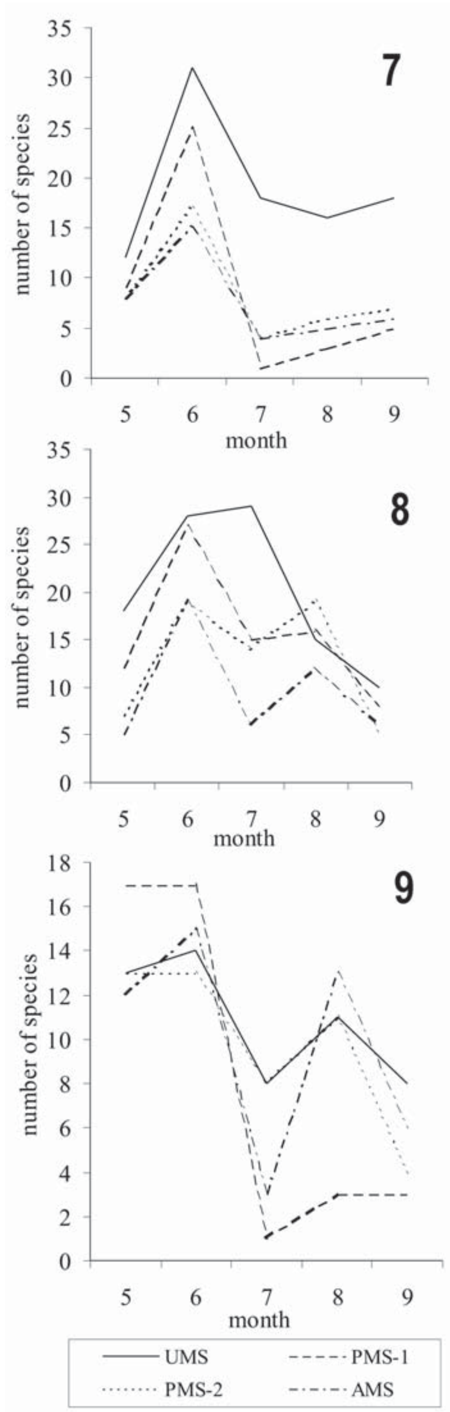


Рис. 7–9. Сезонная динамика видового богатства пауков на степных участках с различным режимом сенокошения. Сокращения в тексте. 7 — 'Стрелецкая Степь', 8 — 'Ямская Степь', 9 — 'Михайловская Целина'.

Figs 7–9. Seasonal dynamics of spider species richness in steppe plots under different management regimes. Abbreviations as in the text. 7 — 'Stereletskaya Steppe', 8 — 'Yamskaya Steppe', 9 — 'Mikhailovskaya Tselina'.

The above conclusion concerns the herb and low-mobile litter dwellers, rather than mobile litter dwelling spiders which demonstrated different habitat preferences. In early May, their densities in all the plots were the same (7.5–8.0 ind./10 trap-days). At the end of May the active density was higher in PMS (15.8 ind./10 trap-days) due to the abundance of *Pardosa palustris* (35%) and *P. riparia* (39%). In June it increased in UMS because of the great number of *P. prativaga* (46%), which was rare in the mowed steppe, and *P. riparia* (35%) penetrated from PMS to UMS. These three lycosid species comprised the bulk of wandering spiders. During the season the average active density was highest in UMS and lowest in AMS (Table). *P. riparia* dominated in all the sampling plots (30–39%), but in 1999 it was evenly distributed over the plots (16–22% of the total number of all specimens collected in the reserve), whereas in 1998 this species was more abundant in UMS (39%) than in PMS and AMS (17–23%). *P. prativaga* strongly predominated in UMS (93–95%), while *P. palustris* predominated in the mowed site (21–38%; but 2–8% in UMS). Among the less common species, *Alopecosa trabalis* and *Pardosa pullata* preferred UMS (46–52% and 56%, respectively), *Haplodrassus signifer*, *Xysticus bifasciatus* and *X. lineatus* preferred PMS and AMS (22–27, 33–67, and 50%, respectively). No regularities in the distribution of *Trochosa terricola* or *Alopecosa cuneata* were identified. The results of previous studies [see Pichka, 1984] differ from our data. *P. riparia* and *X. bifasciatus* were more abundant in UMS, whereas *T. terricola, Alopecosa aculeata* and *A. pulverulenta* were not found in the mowed steppe at all. Perhaps, this may be explained by changes in the vegetation and microclimatic conditions over the last 17 years.

The 'Yamskaya Steppe' Reserve

In the 'Yamskaya Steppe' the same regularities as above were observed in the spider assemblages, but the steppe fauna was richer (108 species). A number of forest species not mentioned before were present in UMS (*Enoplognatha latimana*, *Ceratinella brevis*, *Gonathium paradoxum*, *Minicia marginella*, *Agroeca brunnea*, *Philodromus cespitum* and others); on the contrary, *F. bucculenta* and *L. hortensis* were not recorded. Twenty-five species were not registered in the mowed steppe. Most of them were rare, and only *Gonathium patadoxum, P. cespitum*, *Sibianor aurocinctus* and *Heliophanus auratus* can be considered typical for this plot. The species composition of PMS-1's spiders was richer, as the nine species (viz., *Cercidia prominens*, *Cyclosa conica*, *Euryopis flavomaculata*, *Pardosa lugubris*, *Cheiracanthium punctorium*, *C. erraticum*, *Evarcha arcuata*, *Misumena vatia* and *Misumenops tricuspidatus*), which in 'Streletskaya Steppe' occurred only in the forest and UMS, were rather common in this plot. The plain faunas of PMS-2 and AMS were poorest (51 species altogether; I analyzed both plots together, as during the last years of study the regularity of mowing was broken). Many species found in most biotopes of the reserve (*Micaria formicaria*, *Zelotes subterraneus*, *Zora spinimana*, *Micrommata roseum*, *M. vatia*, *M. tricuapidatus*, *Xysticus ulmi*, *P. lugubris*, etc.) were absent from here. By contrast and in spite of annual mowing, the ravine steppe spider assemblages contained forest species, such as *Micaria formicaria*, *Trematocephalus cristatus* and *Heliophanus cupreus*, which were not reported from the steppe anywhere else, or those like *Neriene clathrata*, *Larinioides patagiatus*, *Dictyna uncinata*, *Agroeca lusatica* and *Ballus chalybaeus*, which were restricted to UMS. *Pachygnatha degeeri,* common in other reserves, in the 'Yamskaya Steppe' was found exclusively at the bottom of the ravine; this site, despite its small size, contained a somewhat unique and rich spider fauna consisting of 60 species.

In the herbage, dominant assemblages of different plots consisted of the same species but in different ratios. *Micrommata roseum* predominated in UMS (56% of all the collected specimens of this species), though in PMS-1 it represented only 17% and was absent in the remaining mowed plots (PMS-2 and AMS). *Agalenatea redii* (37–55%), *Tibellus oblongus* (both 35%), *Marpissa pomatia* (31–49%) were also more abundant in UMS. *X. cristatus* and *X. striatipes* were counted together because their juveniles cannot be distinguished reliably. Their combined numbers were highest in PMS-1 (40%) and lowest on the plain AMS and UMS (11 and 12.7% respectively). The decrease of these spiders in AMS was because they tended to avoid the plot after mowing in July–August (Figs 4, 8), the time when their juveniles are most common. The spatial distribution of the adults of *X. cristatus* and *X. striatipes* follows the same pattern, i.e., their maximum abundance was in PMS-1 (37 and 56% respectively) and the minimum was in UMS (13–14.5 and 0–4%, respectively).

The majority of spiders in all the sampling plots consisted of *Neoscona adianta*, *Araneus qudratus*, *Argiope bruennichi* and *Dictyna arundinacea*. The latter preferred UMS and PMS-1 (26.5–29.5%), i.e., the plots with numerous dry steams, where it spins its webs. The young of *N. adianta* and *A. quadratus* were counted together because earlier instars are poorly distinguishable. Both species preferred UMS (30–33%), but were less abundant in PMS-1 (17%) and especially in PMS-2 (8%). The correlation between the adults of *N. adianta* and *A. quadratus* depended on the relief, rather than on haymaking. In 2001, the ratio of their abundance changed as follows: 25:11 in UMS, 31:18 in PMS on the flat interfluve, and 11:16 on the ravine slope, respectively. At the bottom of the ravine *N. adianta* was not found. In the hotter and drier 2002, *A. quadratus* was very rare in the flat interfluve and common only in the ravines. The average seasonal number of spiders in the herbage of PMS and UMS was similar, naturally decreasing in the plots mowed during the year of study (Table).

Based on the litter samples studied, UMS was dominated by *Neottiura bimaculatum* (in different years 7–15%), *Zora spinimana* (13–17%), *Microlinyphia pusilla* (10%), *Stemonyphantes lineatus* (12%), *Clubiona neglecta* (10–15%), immatures of *Tibellus* (6–15%) and *Micrommata* (5.6–10.4%). In the mowed steppe the spider density was low even in PMS-1, nearly all species were recorded as singletons (Table). It is interesting to note that *N. bimaculatum* and *M. pusilla* are typical litter dwellers in the true steppe habitats, though in many other biotopes they occur on herbage.

In the pitfall samples the most numerous species was *Alopecosa trabalis*, reaching 71–80% in May. Then its abundance reduced to 34% in June and 16% in July. In June–July, the dominant species were *Drassodes pubescens* (15%), *Haplodrassus signifer* (13%), *Ozyptila atomaria* (18%); once (in 2002) they were accompanied by *Pardosa lugubris* (27%) and *Xysticus robustus* (14%). In August *Trochosa terricola* (24%) and the juveniles of *Alopecosa* spp. (mainly *A. trabalis*) (51%) predominated. Contrary to UMS, *A. trabalis* was not overwhelmingly dominant among wandering spiders (only 24–33% in May) in PMS. The following species: *A. aculeata* (11%), *Haplodrassus signifer* (25–44%, the abundance differed in different years and plots) and *Drassylus pusillus* (11%), occurred along with *A. trabalis*. In 2002 *A. trabalis* was not found in AMS and was replaced by *Pardosa palustris* (22%). In June–July *A. sulzeri* (15%) and *Xysticus robustus* (29–54%) appeared amongst the above-mentioned dominants. The effectiveness of pitfalls and the spider active density in PMS as a whole, and regardless of a period of mowing, were much lower than those in UMS (Table). Contrary to the patterns observed above, the mowed plot at the bottom of the ravine stood separately, with its spider active density approaching that of UMS (13 ind./10 trap-days). Despite annual mowing, it is the preferred habitat of *Pardosa palustris, Xerolycosa miniata* and *Alopecosa pulverulenta.*

The species diversity reached its peak in June and gradually decreased until autumn (Fig. 8). The two year seasonal dynamics of spider abundance did not show other regularities apart from a drop after mowing (Figs 3, 4).

The 'Michailovskaya Tselina' Reserve

The araneofauna of this reserve was the poorest (69 species), probably because of its small size. Seven species recorded in UMS (viz., *Crustulina guttata*, *Enoplognatha ovata*, *Centromerus sylvaticus*, *Diplocephalus picinus*, *Pocadicnemis pumila*, *Araniella cucurbitina* and *Clubiona lutescens*) were common to, and likely migrated from forest shelterbelts and the ravine, and they did not occur in the mowed plots. Not counting occasional findings (i.e., isolated specimens of a species), no species restricted to UMS was found in this reserve. *Drassodes pubescens*, *Haplodrassus signifer*, *Zelotes electus* and *O. scabricula* were found in the mowed plots only. The species composition of the herb dwelling spiders of UMS and PMS-1 were not significantly different. These plots were dominated by *Dictyna arundinacea* (71–75% of the spiders collected in May), *Erigone atra* (11% in May), *Cheiracanthium punctorium* (17% in July–August), *Larinioides patagiatus* (22% in August) and *Evarcha arcuata* (16% in August). The last three species were absent or rare after haymaking in PMS-2. In common with the other reserves, *X. cristatus* was more abundant in the mowed steppe (18% in June). In the litter the dominant assemblages consisted of *Meioneta rurestris* (9–11%), *Pachygnatha degeeri* (8–12%), and *Zora spinimana* (12–15%) throughout, although *Microlinyphia pusilla* (10–11%) was also found in PMS. As the PMS plots were mowed in turn, within two years they had identical spider assemblages, similar to those of UMS. In 1985 (before haymaking) the spider abundance of PMS-1 was close to that of UMS, whereas the species richness was even higher than in AMS (see Fig. 9). There was no similarity between the active herpetobiont spiders. This group preferred the mowed steppe, especially the year following mowing (*Alopecosa cuneata* — 57% of all the collected specimens of this species, *A. trabalis* — 63%); *P. palustris* was numerous in both PMS-1 and PMS-2 (49–50%). In May, *Alopecosa pulverulenta* was more numerous in PMS (33%, but only 5% in UMS), and in June it preferred UMS (31% and 8.8%, respectively). *Trochosa terricola* (24–29%) and *Pachygnatha degeeri* (21–28%) were distributed more or less evenly. Unlike the abovementioned two reserves, wandering species preferring only UMS were not found, and the active density in PMS was higher than in UMS (Table).

The seasonal dynamics of species richness had two peaks, one in May–June and the other in August with a small decrease in July (Fig. 9). A number of spiders in the herbage and the litter had increased by August and decreased in September. After haymaking, which broke that curve dramatically, the richness recovered gradually, regaining the June values only in September (Figs 5, 6).

Since the AMS plot was situated in a wet ravine, the dynamics of its spider community were different. The density of individuals (counted using a quadrat) and trapability (= active density) were even higher than in UMS. In addition, this spider community consisted virtually of the same steppe species mentioned above for PMS, with only four additional species: *Dicymbium nigrum*, *Pardosa prativaga*, *P. amentata* and *Pachygnatha clercki*. After the plot was mowed, lots of Linyphiidae, Lycosidae and Tetragnathidae remained there, and in August the density peaked and was the highest in the nature reserve. The herbage was also inhabited by spiders more quickly than that of the flat interfluve (Figs 5, 6).

Discussion

The microclimatic conditions of completely preserved (as compared to mowed) steppe differ in being more moist, in having lower average diurnal soil and air temperatures within the vegetation, as well as reduced flucuations in the overall diurnal temperature variation, and in being subject to lower wind effects [Semenova-Tian-Shanskaya, 1966]. The thick litter layer, accumulated in the absence of hay-mowing, not only determines the microclimate, but also serves as a substrate inhabited by many invertebrates. Spider species richness is much higher here than in the mowed plots. However, this phenomenon results from penetration by the photophilous and mesophilous forest species from neighbouring habitats, rather than resulting from true steppe dwellers. I have found no species associated only with UMS; usually they inhabit the adjacent forests and/or forest shelterbelts. In the mowed steppe, only three stenotopic species (*Steatoda phalerata*, *Agyneta saxatilis* and *Ozyptila praticola*) were recorded. They do not belong to the steppe dwellers *sensu stricto*, as in the steppe zone they occur in all habitats and/or intrazonal sites. In the forest-steppe, the conditions of the mowed steppe are most likely optimal for them.

The number of spiders in the herbage and their density in the litter were constantly highest in UMS. If the steppe was not mowed for at least one year, the structure of the spider community came close to that of UMS. The dominant assemblages, excluding wandering forms, consisted of the same species though in different ratios. The majority of wandering species preferred the mowed plots, but in total their active density may have been either higher or lower than that in UMS.

Hay-mowing constitutes a dramatic stress for the entire steppe community. In drier habitats greater changes occur. In the flat interfluve, in the spring following hay-mowing many species, viz., *Dictyna arundinacea*, *Agalenatea redii*, *Mangora acalypha* and *Theridion bimaculatum*, were absent or rare in the herbage; this resulted in the mono-dominance of juvenile Araneidae (up to 80%), which later may be accompanied by *X. cristatus*. In June the spider communities started restoring themselves, but if the steppe was mowed again in July it was only possible to find some juvenile specimens of *Xysticus*, *Tibellus*, *Hypsosinga*, *Pardosa* or *Alopecosa* on the ground. As spiders are mobile animals, the presence of a refugium, i.e., the UMS plots, makes possible the immediate colonization of the mowed areas. This process was much faster in the litter than in the herbage. It happened at different rates in the different nature reserves. In the northernmost 'Streletskaya Steppe', the spider abundance remained low until the end of the season. In the 'Yamskaya Steppe', the litter spider density had regained its June value by August, and exceeded it in September. In the 'Mikhailovskaya Tselina' Reserve it had risen by September.

In steppe ravines, even under the annual hay-mowing, the spider assemblages were diverse and abundant, with many mesophilous forest species also occurring there. In the AMS of the 'Mikhailovskaya Tselina' and 'Yamskaya Steppe' reserves, the spider richness was higher than that of the plain PMS-2 plots (Table; AMS and PMS-2), but not significantly so. In the 'Streletskaya Steppe', where all sampling plots were situated in the flat interfluve, the opposite pattern was observed: AMS species richness was lower than in PMS-2. The density of litter spiders in the ravine of the 'Mikhailovskaya Tselina' Reserve was even higher than that of UMS, and the dynamic density was higher than in PMS-2 (Table). The same data regarding the 'Yamskaya Steppe' Reserve were not incorporated into the Table (see Appendix); data for the flat interfluve are discussed above. As discussed earlier, the active density of spiders in the ravine of 'Yamskaya Steppe' approached that of AMS and exceeded that of PMS. This in not the case for low-mobile forms in the litter and herbage, for which their abundance was low, as in the other mowed sites.

In moister grassy habitats, specifically the meadows neighbouring the steppes, a greater resistance of the spider population to the impact of haymaking was observed. Thus, in the floodland meadows of Kharkov region, lots of Linyphiidae, Thomisidae and Araneidae were found shortly after hay-mowing. The *Pardosa* density reached 9 ind./m^2, and furthermore the five species found were numerous (*P. lugubris*, *P. amentata*, *P. paludicola*, *P. agrestis* and *P. palustris*). According to Nyffeler [1982], in the cultivated meadows of Switzerland the number of spiders after hay-mowing decreased by only 50% in the herbage and by 40% in the litter. According to my data, in the 'Mikhailovskaya Tselina' Reserve the number of hortobiont spiders decreased by 7.5 times in the flat interfluve and by 4.1 times in the ravine, whereas that of litter dwellers decreased by 7.6 and 5.2 times respectively. As this occurred, all the parameters in the ravine remained higher that those of the flat interfluve (Fig. 8). As indicated by the observations in the 'Streletskaya Steppe' Reserve, regardless of the original number of specimens in the plain sampling plot before hay-mowing, the sample following the hay-mowing was 2–3 ind./m^2 (Fig. 1). Therefore, the richness of PMS-1 decreased by a factor of 12, while that of PMS-2 and AMS decreased by only 2.3 and 4 times respectively. In the 'Yamskaya Steppe' Reserve, the richness of spiders decreased by 3.3–3.7 times in the herbage and 6.0–6.5 times in the litter regardless of orographic position. In the true steppes, I found an even greater difference between the spider densities before and after hay-mowing, from 15 to 1 ind./m^2, i.e., a decreased by a factor of 15. All these facts seem to suggest an intense effect of hay-mowing on spider assemblages, which also depends on microclimatic conditions and, in the majority of cases an orographic factor plays a leading role.

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Appendix
Приложение

Species composition of spiders and the changes resulting from the mowing regime of the nature reserves of the central forest-steppe.

Abbreviations: SST = 'Streletskaya Steppe', KST = 'Kazatskaya Steppe', YST = 'Yamskaya Steppe', MTS = 'Mikhailovskaya Tselina', 1 = strictly protected steppe, 2 = periodically mowed steppe, 3 = annually mowed steppe.

Видовой состав пауков и его изменение в зависимости от режима сенокошения в степных заповедниках Центральной лесостепи.

Сокращения: ССТ = 'Стрелецкая степь', КСТ = 'Казацкая степь', ЯСТ = 'Ямская степь' МЦ = 'Михайловская целина', 1 = абсолютно заповедная степь, 2 = периодически косимая, 3 = ежегодно косимая.

Species	**SST**			**KST**		**YST**			**MTS**		
	1	2	3	1	2	1	2	3	1	2	3
ATYPIDAE											
Atypus muralis Bertkau, 1980					+						
MIMETIDAE											
Ero cambridgei Kulczyński 1911	+										
E. furcata (Villers, 1789)	+			+		+	+				
E. tuberculata (De Geer, 1778)									+	+	
THERIDIIDAE											
Achaearanea simulans (Thorell, 1875)						+					

Appendix (continued).
Приложение (продолжение).

Crustulina guttata (Wider, 1834)	+					+			+		
C. sticta (O. Pickard–Cambridge, 1861)							+				
Dipoena tristis (Hahn, 1833)						+					
Enoplognatha latimana (Hippa et Oksala, 1982)						+					
E. ovata (Clerck, 1758)	+					+			+		+
Episinus angulatus (Blackwall, 1836)	+	+			+	+					
Euryopis flavomaculata (C.L. Koch, 1836)	+					+	+	+			
Neottiura bimaculata (Linnaeus, 1767)	+	+	+	+	+	+	+	+	+	+	+
Robertus arundineti (O. Pickard–Cambridge, 1871)						+					
R. lividus (Blackwall, 1836)						+	+				
Steatoda phalerata (Panzer, 1801)		+	+		+		+	+			
Theridion impressum L. Koch, 1881	+	+		+	+	+	+	+	+	+	
T. mystaceum L. Koch, 1870						+					
T. pinastri L. Koch, 1872						+					
LINYPHIIDAE											
Araeoncus humilis (Blackvall, 1841)	+										
Centromerus incilium (L. Koch, 1881)						+					
C. sylvaticus (Blackvall, 1841)	+								+		+
Ceratinella brevis (Wider, 1834)						+					
Dicymbium nigrum (Blackwall, 1834)	+		+								
Diplocephalus picinus (Blackwall, 1831)						+			+		
Diplostyla concolor (Wider, 1834)	+										
Entelecara flavipes (Blackwall, 1834)	+					+			+		
Erigone atra Blackwall, 1833									+	+	+
E. dentipalpis (Wider, 1834)	+	+				+			+	+	+
Floronia bucculenta (Clerck, 1758)	+			+							
Gonatium paradoxum (L.Koch, 1869)						+					
Gongylidiellum latebricola (O. Pickard–Cambridge, 1871)									+		
G. murcidum Simon, 1884									+		
Gongylidium rufipes (Linnaeus, 1758)				+		+					
Hylyphantes nigritus (Simon, 1881)											
Linyphia hortensis Sundevall, 1830	+			+							
L. triangularis (Clerck, 1758)	+			+		+					
Lophomma punctatum (Blackwall, 1841)										+	
Meioneta rurestris (C.L. Koch, 1836)	+	+	+	+	+	+	+	+	+	+	+
M. saxatilis (Blackwall, 1841)		+					+				
Metopobactrus prominulus (O. Pickard–Cambridge, 1872)				+							
Microlinyphia pusilla (Sundevall, 1830)	+	+	+	+	+	+	+	+	+	+	+
Microneta viaria (Blackwall, 1841)	+					+					
Minicia marginella (Wider, 1834)						+					
Neriene clathrata (Sundevall, 1830)						+					+
Oedothorax apicatus (Blackwall, 1850)						+				+	
Pocadicnemis pumila (Blackwall, 1841)	+			+					+		+
Porrhomma convexum (Westring, 1851)									+		+
Stemonyphantes lineatus (Linnaeus, 1758)	+	+	+	+		+	+		+	+	
Tapinopa longidens (Wider, 1834)		+									
Trematocephalus cristatus (Wider, 1834)								+			
Tapinocyboides pygmaeus (Menge, 1869)									+		
Walckenaeria antica (Wider, 1834)	+										
W. atrotibialis O. Pickard–Cambridge, 1878						+					
Micryphantinae sp. 1						+	+				
TETRAGNATHIDAE											
Metellina segmentata (Clerck, 1758)						+					
Pachygnatha degeeri Sundevall, 1830	+	+	+	+	+			+	+	+	+
ARANEIDAE											
Agalenatea redii (Scopoli, 1763)	+	+	+	+	+	+	+	+			
A. diadematus Clerck, 1758				+		+	+	+			
A. quadratus Clerck, 1758	+	+	+	+	+	+	+	+	+	+	+
Araniella cucurbitina (Clerck, 1758)									+		
Argiope bruennichi (Scopoli, 1772)	+	+	+	+	+	+	+	+			
Cercidia prominens (Westring, 1851)	+			+		+	+	+			
Cyclosa conica (Pallas, 1772)	+					+	+	+			

Appendix (continued).
Приложение (продолжение).

C. oculata (Walckenaer, 1802)						+	+				
Hypsosinga pygmaea (Sundevall, 1831)	+	+		+		+	+				
H. sanguinea (C.L. Koch, 1844)	+	+				+	+	+	+	+	
Larinioides suspicas (O. Pickard–Cambridge, 1876)									+	+	
L. patagiatus (Clerck, 1758)				+		+		+	+	+	+
Mangora acalypha (Walckenaer, 1802)	+	+		+		+			+	+	+
Neoscona adianta (Walckenaer, 1802)	+			+	+	+	+	+	+	+	+
Singa hamata (Clerck, 1758)	+	+		+							
LYCOSIDAE											
Alopecosa aculeata (Clerck, 1758)		+		+		+	+	+			
A. cuneata (Clerck, 1758)	+	+	+	+	+				+	+	+
A. pulverulenta (Clerck, 1758)	+	+		+	+	+	+	+	+	+	+
A. sulzeri (Pavesi, 1873)							+				
A. trabalis (Clerck, 1758)	+	+	+	+	+	+	+	+	+	+	+
Lycosa singoriensis (Laxmann, 1770)		+	+		+						
Pardosa agrestis (Westring, 1861)		+	+								+
P. lugubris (Walckenaer, 1802)	+			+		+	+	+	+	+	+
P. nigriceps (Thorell, 1856)	+										
P. palustris (Linnaeus, 1758)	+	+	+	+		+	+	+	+	+	+
P. prativaga (L. Koch, 1870)	+	+	+	+					+		+
*P. pullata (*Clerck, 1758)	+	+	+	+	+		+				
P. riparia (C.L. Koch, 1847)	+	+	+	+	+						
Tricca lutetiana (Simon, 1876)						+	+	+			
Trochosa ruricola (De Geer, 1778)	+	+	+		+	+		+			
T. terricola Thorell, 1856	+	+	+	+	+	+	+	+	+	+	+
Xerolycosa miniata (C.L. Koch, 1834)	+	+	+	+	+	+	+	+	+	+	+
PISAURIDAE											
Pisaura mirabilis (Clerck, 1758)	+	+	+			+	+				
AGELENIDAE											
Agelena gracilens C.L. Koch, 1841						+	+	+	+	+	
A. labyrinthica (Clerck, 1758)						+	+	+			
DICTYNIDAE											
Dictyna arundinacea (Linnaeus, 1758)	+	+	+	+	+	+	+	+	+	+	+
D. uncinata Thorell, 1856						+			+		
LIOCRANIDAE											
Agroeca brunnea (Blackwall, 1833)				+		+					
A. cuprea Menge, 1873	+	+	+			+	+	+			
A. lusatica (L. Koch, 1875)	+	+				+		+			
Phrurolithus festivus (C.L. Koch, 1835)				+							
MITURGIDAE											
Cheiracanthium erraticum (Walckenaer, 1802)	+					+	+	+			
C. punctorium (Villers, 1789)	+					+	+		+	+	+
CLUBIONIDAE											
Clubiona caerulescens L. Koch, 1867	+										
C. diversa O. Pickard–Cambridge, 1862				+			+	+			
C. lutescens Westring, 1851									+		+
C. neglecta O. Pickard–Cambridge, 1862	+			+		+	+	+	+	+	+
GNAPHOSIDAE											
Drassodes pubescens (Thorell, 1856)	+		+	+	+	+	+	+		+	
D. praeficus (L. Koch, 1866)	+	+	+	+	+	+	+	+			
D. pusillus (C.L. Koch, 1833)	+	+	+	+	+	+	+	+			
Drassylus lutetianus (L. Koch, 1866)				+	+						
Gnaphosa taurica Thorell, 1875							+				
Haplodrassus signifer (C.L. Koch, 1839)	+	+	+			+	+	+		+	
H. silvestris (Blackwall, 1833)											
Micaria formicaria (Sundevall, 1831)						+	+	+			
M. romana L. Koch, 1866		+									
M. pulicaria (Sundevall, 1831)	+			+						+	
Zelotes apricorum (L. Koch, 1876)	+	+	+	+			+				
Z. electus (C.L. Koch, 1839)							+	+		+	
Z. latreillei (Simon, 1878)	+	+		+		+	+		+	+	
Z. longipes (L. Koch, 1866)		+						+	+		+
Z. subterraneus (C.L. Koch, 1833)	+				+	+	+	+	+	+	+

Appendix (continued).
Приложение (продолжение).

ZORIDAE											
Zora armillata Simon,1878	+	+									
Z. spinimana (Sundevall, 1832)	+	+	+	+	+	+	+	+	+	+	+
HETEROPODIDAE											
Micrommata roseum (Clerck, 1758)	+	+		+	+	+	+	+	+	+	+
PHILODROMIDAE											
Philodromus cespitum (Walckenaer, 1802)						+			+	+	+
Thanatus arenarius Thorell, 1872		+	+	+			+				
T. formicinus (Clerck, 1758)			+	+	+						+
T. striatus C.L. Koch, 1845				+					+		
Tibellus oblongus (Walckenaer, 1802)	+	+	+	+	+	+	+	+	+	+	+
THOMISIDAE											
Misumena vatia (Clerck, 1758)	+			+	+	+	+	+	+	+	+
Misumenops tricuspidatus (Fabricius 1775)	+			+	+	+	+		+	+	+
Ozyptila atomaria (Panzer, 1801)	+	+	+	+		+	+	+			
O. scabricula (Westring, 1851)		+	+				+	+		+	+
O. trux (Blackwall, 1846)			+								+
Thomisus albus (Gmelin, 1789)										+	+
Xysticus bifasciatus C.L. Koch, 1837	+	+	+	+	+						
X. cristatus (Clerck, 1758)	+	+	+	+	+	+	+	+	+	+	+
X. kochi Thorell, 1872									+	+	+
X. lineatus (Westring, 1851)	+	+		+	+						
X. luctuosus (Blackwall, 1836)		+	+								
X. robustus (Hahn, 1832)		+	+	+			+	+			
X. striatipes L. Koch, 1870						+	+	+			
X. ulmi (Hahn, 1831)	+	+		+		+	+	+	+		+
SALTICIDAE											
Ballus chalybaeus (Walckenaer, 1982)						+		+			
Euophrys frontalis (Walckenaer, 1802)				+		+			+		
Evarcha arcuata (Clerck, 1758)	+			+	+	+	+	+	+	+	+
E. falcata (Clerck, 1758)											
E. laetabunda (C.L. Koch, 1846)						+	+	+			
Heliophanus auratus C.L. Koch, 1835				+	+	+	+	+	+		
H. cupreus (Walckenaer, 1802)				+				+			
H. flavipes (Hahn, 1832)	+	+		+	+	+	+	+			
Marpissa pomatia (Walckenaer, 1802)	+	+		+	+	+	+	+			
Neon valentulus (Falckonaer, 1912)									+		
Phlegra fasciata (Hahn, 1826)								+			
Sibianor aurocinctus (Ohlert, 1865)	+		+			+					
Talavera aequipes (O. Pickard–Cambridge, 1871)		+					+				
Number of species: 156	77	58	41	66	40	89	69	60	57	45	44