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Diet of the European ground squirrel (*Spermophilus citellus*) in the southern Pannonian plain

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Abstract: Overwinter survival of hibernators is directly influenced by the fat reserves accumulated during the active season. The European ground squirrel, *Spermophilus citellus*, an endangered flagship species of the open grasslands of central and southeastern Europe, is no exception. Considering anthropogenic changes affecting its habitats in northern Serbia, we studied the species' feeding habits by subjecting its feces to microhistological examination. In addition to identifying plant remains in the feces, we examined the vegetation of the four study sites located inside a local mosaic of steppe and saline pastures. Our findings indicate that these remaining European ground-squirrel sites are diverse and stable grasslands covered by native flora that represents a complete dietary base for the species. The diet is dominated by a small number of plant species, specifically *Achillea millefolium*, legumes and grasses, with sporadic contributions from a number of other species. The diet of *S. citellus* also differs by location and season in that grasses dominate during the early season, while *A. millefolium* takes precedence later in the year. This dietary information is essential for the development of future species and habitat management strategies. In light of the predicted impact of climate change on grasslands in northern Serbia, our findings will be instrumental for translocations and conservation actions in the future.

Keywords: grasslands; dietary preferences; hibernators; microhistology; habitat management

INTRODUCTION

Because the feeding habits of various species shed light on different ecological processes, such as niche allocation, competition, nutrient cycling and energy pathways, they have been the subject of extensive ecological [1,2], population [3], habitat preference [4] and conservation studies [5]. Considering the wide range of long-term and stochastic events that can influence the availability of feeding resources, a better understanding of an animal's feeding habits is an indispensable tool for population and habitat management. For small mammals to obtain the same amount of nutrients relative to their size as a large mammal, herbivores in particular have to consume high-quality plant tissues due to physiological constraints imposed by their digestive systems [6]. This is demanding for hibernators such as ground-dwelling squirrels due to relatively short active periods (usually 4 to 6 months) [7,8]. As the hibernation period is spent in torpor, their overwinter survival depends on the fat reserves accumulated during the active season [9-11]. Hence, for ground squirrels, nutritious and abundant food resources are essential for the survival of individuals and local populations [12].

The European ground squirrel, *Spermophilus citellus*, is a small diurnal rodent endemic to central and southeastern Europe, with an active season that starts in March/April and ends in September/October, depending on the altitude, latitude and annual environmental conditions [13,14]. The species is a short grass specialist, inhabiting a range of natural, semi-natural and artificial grassland habitats [15]. Through food web centrality, it has multiple ecological functions in grassland ecosystems, while also influencing ecological processes and

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diversity patterns. For example, the species' activities influence plant composition and soil characteristics, and it is considered one of the main prey targets for top predators, including birds and mammals. Moreover, its burrows provide a refuge for many invertebrate and vertebrate species, including some rare ones [16-19]. Formerly widely distributed, the species is now considered endangered throughout its range and is categorized as endangered (EN) on the IUCN Red List [20]. The latest assessment emphasizes land conversion and infrastructural development, along with the abandonment of traditional management practices, as the main drivers of its habitat fragmentation and consequent population decline. Based on the latest studies, these adverse conditions are also found in Serbia, and demand immediate conservation actions [15,21-24].

The majority of European ground squirrel populations are located in the northern Serbian province of Vojvodina, inhabiting salt steppe, steppe and sandy habitats, while a small number of populations remain in the mountainous regions of eastern and southeastern Serbia [22]. The species' range in Vojvodina has shrunk by 70% compared to the available historical data, and about half of the populations presently reside outside the protected area network [23]. To halt and potentially reverse the local population decline caused by anthropological activities and environmental variability, adequate habitat management plans and programs need to be established [24]. Detailed studies regarding habitat conditions and feeding habits are an important structural component of local habitat management plans and programs. Information regarding the species' feeding habits within the available habitats in Serbia, as well as other parts of its range, is scarce. The only regional study conducted to date was carried out in 1950 at the Deliblatska Peščara Sands Nature Reserve [25]. Consequently, no data pertaining to the steppe/saline part of the species' range in Vojvodina exists. The species is considered herbivorous, feeding mostly on green plant parts, as well as flowers, seeds and underground parts [2, 25, 26]. *S. citellus* shows a dietary preference for dicots over monocots [2] and seasonally shifts the preferred food group [2,25]. Although invertebrates – mostly insects – are an important protein source for *S. citellus*, its diet also includes smaller lizards and bird eggs [25,27]. Considering the dramatic changes that have taken place in Vojvodina in the last 70 years, such as intensification of agriculture, loss of natural grasslands, infrastructure development and changes in environmental conditions, the present study focused on the characteristics of steppe and saline vegetation at four study sites in order to quantify food availability. In addition, the noninvasive method involving microhistological analysis of fecal samples was employed to (i) determine and quantify the types of food resources exploited by *S. citellus*; (ii) to assess the effects of season and location on the feeding habits; (iii) to identify the patterns of consumption of plant species, and (iv) to provide recommendations regarding the possibility of exploiting the established feeding habits to fine-tune habitat management measures on a local scale.

MATERIALS AND METHODS

Study area

The study was conducted on 4 European ground squirrel sites in the northern Serbian province of Vojvodina. Vojvodina represents the southern-most part of the Pannonian Plain and the southern edge of the western section of the geographic distribution of *S. citellus*. The sites were located near the villages of Melenci (MLC) and Kumane (KMN) in the Banat region, east of the Tisza river, and near the villages Manđelos (MNS) and Neradin (NRD) located on the southern slopes of the Fruška Gora mountain, in the Srem region south of the Danube River. The Banat sites are part of a larger salty steppe, while Fruška Gora pastures represent some of the last remaining preserved steppe fragments in Vojvodina. All 4 sites are part of a local ecological corridor comprised of saline soils, salt steppe and steppe grasslands [28], which provide protection to the species, plant communities and sites (IBA, IPA, Emerald, and Ramsar) [29]. The Fruška Gora sites are also within the Fruška Gora National Park perimeters. All sites are surrounded by arable land and are used for cow and sheep grazing

Experimental design

Vegetation samples

The field study phase of this investigation was performed during the spring and summer of 2015, starting in April and ending in September, thus covering the entire active season of *S. citellus*. Fieldwork was conducted during each month of the sampling period. A survey of herbaceous vegetation was conducted to determine the vegetation composition. Using the quadrat method, the abundance of plant species inside 5 randomly chosen 1-m^2 plots was recorded. Plots were located around the central part of the area with open burrows. Along with the vegetation survey, samples of plant species were collected from the plots and used for generating a tissue reference collection. The collection consisted of dried plant material preserved in a herbarium and leaves preserved in alcohol, which were subsequently microphotographed to serve as a reference for plant fragments found in the dietary samples. Microphotographs were made using a LEICA DFC320 camera mounted on an Olympus BX51 microscope after chemically treating leaf fragments and mounting them on slides. The same chemical procedure (described below) was used for preparing the slides for the dietary (fecal) samples.

Dietary samples

Alongside the vegetation survey, fresh fecal pellets of *S. citellus* were collected from burrow entrances that were at least 20 m apart to ensure that all samples originated from different individuals. Samples mostly consisted of multiple pellets. The pellets collected from one burrow entrance were considered as one sample. To minimize any disturbance, sampling was usually conducted around noon to coincide with the period of low activity [7]. As this is a rare species and its population numbers differed across study sites, the number of available fecal samples in the field varied considerably throughout the sampling period (min: 1, max: 41). The highest number of samples was collected at the Neradin (NRD) site (min: 21, max: 41), while the lowest number was consistently found at the Kumane (KMN) site (min: 1, max: 23). As expected, the number of available samples across all sites was the highest during the summer months (June, July, and August), as this is the peak period of species activity. Upon collection, the fecal samples were labeled and air-dried for two days before being placed in the freezer until further analyses.

Prior to analysis, 15 samples were randomly selected from each month, including all samples for sites where less than 15 were collected, i.e. 3 samples (in August) from Melenci (MLC) and Manđelos (MNS), and 11 samples (in May) from Kumane (KMN). As only one sample was available for Kumane in September, it was excluded from further analyses. For this study, the active season of *S. citellus* was divided into 3 phases, based on the reproduction and activity of different age classes [8, 30]. The early season (April-May) covered the period between emergence from hibernation and the appearance of young aboveground organisms; the middle season (June-July) marks the period when all age classes were active above ground; the late season (August-September) marks the pre-hibernation period, which starts when adult individuals, especially males, start entering hibernation, and lasts until all individuals do the same.

Microhistological technique

To determine the plant composition of the dietary samples, the microhistological method of fecal analysis was used as it has been successfully applied in previous herbivore [31,32] and ground squirrel [2,8,33,34] studies. Despite the differences in digestibility and potential accuracy issues of this approach, microhistological techniques remain an invaluable tool for gaining a better understanding of the feeding habits of rare and endangered species without disturbing them. Moreover, studies conducted on ground squirrels indicate that this method has the same diagnostic power as stomach content analysis [35]. The method is based on a microscopic examination of plant material, usually epidermal cells, which are resilient to digestive processes and can be identified to a certain taxonomic level in the fecal material based on their specific morphological characteristics.

Using one pellet from each of the randomly chosen 15 (or less as in cases explained above) individual samples, monthly samples were formed for each month during the sampling period. A similar methodological approach has already been applied in herbivore diet studies [32]. The pellets were mixed with small amounts of water to defrost the contents before boiling in 20% nitric acid until discoloration. The resulting material was segregated into 20 subsamples that were mounted onto microscopic slides [2]. Within every subsample, we identified 20 plant/animal fragments. Identification and quantification of plant remains was done to the lowest possible taxonomic level by comparison with microphotographs in the plant reference collection. Most of the remains were identified to the species level, some to the genus level, and some remained unidentified. Other plant parts, such as seeds, roots and flowers were counted, but were not identified further. Animal remains were identified to higher taxonomic levels.

Statistical analysis

Dominance values for species in plant communities found at the study sites were calculated as follows: eudominant (10-100%), dominant (5-10%), subdominant (2-5%), precedent (1-2%) and subrecedent (<1%) [36].

The abundance of plant species in the feeding samples was expressed as the relative frequency of plant species in each sample using the expression below:

$$\frac{number\ of\ plant\ species\ fragments}{total\ number\ of\ plant\ fragments} \times 100\ (\%)$$

Diversity of vegetation and the dietary samples was measured using the inverse of the Simpson Index, *Ds*, calculated as:

$$Ds = \frac{1}{\sum_{i=1}^{s} p_i^2}$$

where p_i is the proportion of the *i*th resource in the sample. *Ds* increases with the number of items in the sample and the evenness of their utilization [37]. For our study, evenness was calculated using the Shannon-Wiener biodiversity index, *H'*, as follows:

$$E = \frac{H'}{H_{max}} \qquad H_{max} = log_2 S$$

where *S* indicates the maximum possible diversity in the sample. Evenness measures the homogeny of the distribution of species in a sample and ranges from 0 to 1 (values higher than 0.5 indicate high evenness).

To assess the food choice of *S. citellus* with regard to "supply" in the vegetation and the differences between the dietary samples, the Jaccard similarity index was adopted:

$$Ja = \frac{S_{12}}{S_1 + S_2 - S_{12}}$$

where S_1 is the number of species in Sample 1, S_2 is the number of species in Sample 2, and S_{12} is the number of joint occurrences of species in the two samples. The *Ja* values range from 0 to 1 and higher values indicate a higher degree of similarity.

The effect of season on the variations in the dietary samples was assessed by ANOVA and the pairwise Mann-Whitney test. Principal components analysis (PCA) was conducted to check for differences in samples based on location. All statistical analyses were executed using ComEcoPac and PAST.

RESULTS

Vegetation

Analysis of vegetation at the 4 study sites resulted in 134 vascular plant taxa from 24 families (including one undetermined taxon) and Bryophyte entities (Supplementary Table S1). The species list was largely dominated by forbs (75.2%), followed by grasses (16.5%), shrubs (6.8%) and graminoid species (1.5%). Species abundance, however, provided a different picture, as grasses were predominant in all areas irrespective of season. The mean grass cover was 59.05% (min: 44.85%, max: 75.05%). Legumes (Fabaceae) were the second most abundant plant family with a mean cover value of 12.95%. Overall, the cover percentage was mostly above 90% (Table 1).

The average number of plant taxa per site per season was 46.25, with greater diversity noted for the 2 sites from Fruška Gora (*mean*=55.66 taxa) relative to those from Banat (*mean*=39.16 taxa). Across all sites, the number of species increased during the middle season (Table 1). The pairwise Mann-Whitney test differentiated the Fruška Gora from the Banat sites based on the species composition during the middle (NRD:KMN $P<0.05$; MNS:KMN $P<0.001$, MNS:MLC $P<0.05$) and late (MNS:KMN $P<0.005$, MNS:MLC $P<0.005$) season. Despite the presence of a large number of species at the sites, only 11 taxa (mostly grasses) comprised more than 5% of the vegetation at any site or season, including *Achillea millefolium*, *Cirsium* sp., *Trifolium repens*, *Bromus hordeaceus*, *Cynodon dactylon*, *Cynosurus cristatus*, *Festuca pseudovina*, *F. rupicola*, *Lolium perenne*, *Poa annua* and *P. pratensis* (Supplementary Table S1). The complete set of dominance values is given in Table 1.

Table 1. Plant species dominance, richness, % cover, evenness and diversity of the vegetation in the early (E), middle (M) and late (L) season at the 4 study sites.

	NRD			MNS			KMN			MLC		
	E	M	L	E	M	L	E	M	L	E	M	L
S_E	2	4	2	3	2	2	1	3	3	2	2	3
S_D	5	0	2	1	5	2	5	1	4	3	3	1
S_Sd	7	6	8	10	5	7	8	2	3	9	4	5
S_R	4	4	4	6	8	7	7	8	3	7	7	8
S_Sr	29	46	28	29	53	43	21	24	19	14	28	13
N_E	31	66.55	43.5	46.6	22.7	36.8	22.5	67.6	52.7	30.55	43.55	60.575
N_D	30.5	0	14.8	5.5	39.08	11.55	34.21	4.96	22.5	24.33	23.15	6.1625
N_Sd	21.73	19.555	19	29.4	13.78	20.8	23.88	6.1	8.65	29.53	9.9	16.125
N_R	5.06	5.4125	4.65	6.83	11	8.55	8.75	11.6	3.8	8.68	8.8	11.8
N_Sr	9.72	7.48	6.6625	8.05	9.44	10.5	5.28	6.98	5.5	4.56	7.85	5.1625
Number of taxa in the sample	47	60	44	49	73	61	42	38	32	35	44	30
% cover of plant species	98.11	97.81	93.3	96.38	98.1	89	96.47	96.69	92.35	97.15	92.95	91.45
E	0.763	0.610	0.663	0.739	0.720	0.699	0.764	0.615	0.684	0.803	0.665	0.721
Ds	13.463	7.813	7.426	12.014	17.209	10.201	11.836	5.63	7.135	13.76	7.267	7.797

NRD – Neradin, MNS – Manđelos, KMN – Kumane, MLC – Melenci, S_E - number of eudominant species, S_D – number of dominant species, S_{Sd} – number of subdominant species, S_R – number of recedent species, S_{Sr} – number of subrecedent species, N_E – abundance for eudominant species, N_D – abundance for dominant species, N_{Sd} – abundance for subdominant species, N_R – abundance for recedent species, N_{Sr} – abundance for subrecedent species (Tischler's scale), E – Evenness, Ds – inverse of the Simpson index

Diet composition

The diet of the European ground squirrel in Vojvodina proved to be diverse. The feces samples contained leaves of 65 plant taxa from 14 families, 52 (80%) of which were identified to the species level. The samples also contained animal material as well as other plant parts, such as flowers, seeds, roots and the seed coat. Most of the samples contained small amounts of material (on average less than 1% per sample) that could not be identified (Table 2). Contrary to the species abundances in the vegetation, forbs dominated the diet over grasses, shrubs and graminoids with 70%, 25%, 3.1%, and 1.55%, respectively.

Table 2. Diversity, evenness and relative frequencies of plant species in the European ground squirrel dietary samples in the early (E), middle (M) and late (L) season at the 4 study sites.

Species	**NRD**			**MNS**			**KMN**			**MLC**		
	E (*n*=30)	M (*n*=30)	L (*n*=30)	E (*n*=30)	M (*n*=30)	L (*n*=18)	E (*n*=26)	M (*n*=30)	L (*n*=3)	E (*n*=30)	M (*n*=30)	L (*n*=30)
Achillea millefolium	11.75	6.875	33.75	12	19.125	23.875	2	18.5	32	6.75	12.375	43.75
Centaurea jacea	2.25	0	0	0	0	0	0.375	0	0	0.375	0	0.875
Other Asteraceae	0.125	0.375	0	0	0	0.5	0.375	0	0	0.25	0.75	1.625
Total Asteraceae	**15.125**	**10.5**	**33.75**	**12**	**19.125**	**27.75**	**2.375**	**19**	**32**	**7.375**	**13.125**	**46.25**
Echium italicum	0	0.125	0	1.75	3.5	3	0.125	0	0	0	0.125	0.75
Other Boraginaceae	0	0	0	0.125	0.625	0	0.75	0	0	0.125	0	0
Total Boraginaceae	**0**	**0.125**	**0**	**1.875**	**4.125**	**3**	**0.875**	**0**	**0**	**0.125**	**0.125**	**0.75**
Cerastium pumilum	0	0	0	2.25	0	0	0	0	0	0	0	0
Cerastium sp.	0	0	0	0.625	2.125	0.125	0.125	0	0.25	0	0	0.25
Other Caryophyllaceae	0	0	0	0	0	0.125	0	0.875	0	0	0	0
Total Caryophyllaceae	**0**	**0**	**0**	**2.875**	**2.125**	**0.25**	**0.125**	**0.875**	**0.25**	**0**	**0**	**0.25**
Carex sp.	0	0.5	0	0	0	0	2.125	1.875	0	0	0.25	0
Total Cyperaceae	**0**	**0.5**	**0**	**0**	**0**	**0**	**2.125**	**1.875**	**0**	**0**	**0.25**	**0**
Astragalus onobrychis	1	3.25	7	0	0	3.5	0	0.5	0	0	0	0
Lotus corniculatus	1.125	0.5	0.75	0	0	0.25	0.625	0.125	2.75	2	0.375	0.75

Table 2 continued

Medicago lupulina	16.125	8.625	8.75	4	3.875	3.5	1.25	6	3.5	1.5	1.875	0
Medicago minima	16.25	13.5	8.125	17.25	8.75	9.625	11	17	14.25	4.125	2	0.375
Medicago sativa	0	4.375	0.75	2.875	2.375	2.125	0	0.25	0	0	0	0
Medicago sp.	0.5	2.875	0.125	0	0	0.125	0	0	0	0	0.5	0.125
Trifolium campestre	1.75	1.875	0.5	0.375	0.125	0.125	9	0.875	0	7.875	0.5	0
Trifolium fragiferum	0	0	0.25	0	0	0	0	0	0	0	0.625	5.125
Trifolium pratense	5.125	2.75	2.75	0.5	0.125	0.25	12.25	3.375	5.75	12.5	6.875	0.125
Trifolium repens	4.75	12.625	6	3.25	3.125	2.375	27.25	19.125	2.5	15.75	16.25	0.875
Trifolium sp.	0.25	2.5	0.5	0	0	0.125	0.125	0	0	0.25	0.875	0.125
Other Fabaceae	0	0	0	0	0	0	2.125	0.625	0	1.875	1	0
Total Fabaceae	**45.875**	**49.625**	**28.5**	**28.25**	**18.375**	**18.5**	**63.625**	**47.375**	**28.75**	**45.875**	**30.875**	**7.5**
Total Geraniaceae	**0**	**0.125**	**0**	**0.125**	**0.375**	**0**	**0**	**0**	**0**	**0.125**	**0**	**0**
Total Lamiaceae	**0**	**0.625**	**0**	**1**	**1.875**	**0.25**	**0.125**	**0.625**	**0**	**0**	**0**	**0**
Total Malvaceae	**0.75**	**0.375**	**0.5**	**0.5**	**0.625**	**0.25**	**0**	**0**	**0**	**0**	**0**	**0**
Plantago lanceolata	0	0.875	0.125	2	2.125	2.5	0.125	1.625	1.75	0	0.875	3.25
Veronica persica	0	0.625	1.25	0.125	0.625	1.125	0	0	0	0	1.25	4.25
Veronica arvensis	0	9.625	4.875	0.125	3.375	0.75	0	2.375	0.75	0.875	10.75	14.125
Other Plantaginaceae	0.125	0.25	0.75	0	0	0	0	0	0	0	1.4	0.375
Total Plantaginaceae	**0.125**	**11.375**	**7**	**2.5**	**6.125**	**4.375**	**0.125**	**4**	**2.5**	**0.875**	**14.5**	**22**
Bromus commutatus	0.625	0	0	5	0	0.125	0.375	0	0	2.375	1	0
Dactylis glomerata	4	0.25	0.75	13.75	0.625	0.875	1.25	0.625	0.75	9.75	0.375	0.375
Festuca pseudovina	1.125	1.5	1.375	1.375	1	1.375	3.375	1	1.75	0	0.25	0.75
Festuca rubra	1	3.375	1.5	0.25	3.5	1.75	0.625	0.625	1.5	0.75	0.625	0.125
Festuca rupicola	6.125	2.25	4.25	3.25	3.125	2.75	1	3	3	5.5	3.125	1.875
Festuca sp.	0.625	0.25	0.125	0	0	0	0	0	0	4.875	1.75	0.125
Poa annua	2.5	5.25	3.875	2.625	6.625	1.625	2	9.5	15.5	1.75	14.25	8.25
Poa compressa	0.75	0	0.25	0	0	0	3.125	0	0	1.375	0.25	0.25
Poa pratensis	4.625	1.375	1.625	12.25	6.125	1.875	12.25	4.125	10.75	3.375	2.625	3.75
Poa sp.	8.25	1.375	0.125	0	0.25	0	0	0	0	11.25	5.875	3.375
Other Poaceae	0.875	1.25	1.75	0.375	2.125	0.75	0.125	0.125	0.25	1.125	1.625	1
Total Poaceae	**30.5**	**16.875**	**15.375**	**38.875**	**23.375**	**11.125**	**24.125**	**19**	**33.5**	**42.125**	**31.75**	**19.875**
Total Polygonaceae	**0.25**	**0**	**0.125**	**0**	**0.125**	**0.25**	**0**	**0**	**0**	**0**	**0.125**	**0**
Agrimonia eupatoria	0.5	0	0	1.375	8.875	2.375	0.125	0.125	0.25	0	0.25	0
Potentilla argentea	0	0	0	0	0	0	0	2.125	0.75	0	0	0
Other Rosaceae	0	0	0	0	0	0	0	0	0	0	0.125	0
Total Rosaceae	**0.5**	**0**	**0**	**1.375**	**8.875**	**2.375**	**0.125**	**2.25**	**1**	**0**	**0.375**	**0**
Total Rubiaceae	**0**	**0**	**0**	**0**	**0.125**	**0.125**	**0**	**0**	**0**	**0**	**0.25**	**0**
Total Violaceae	**0.125**	**0**	**0**	**0**	**0**	**0**	**0.125**	**0**	**0**	**0**	**0**	**0**
Flower	0	3.5	0.625	0	4.875	2.25	0	0.25	0	0	0.25	0
Seed	0	2.125	0.375	0.5	3.125	2.5	0	0.625	0	0	0.375	0.25
Other plants parts	0	0	0	0.125	0.25	0	0	0	0	0	1.125	0
Total other plant parts	**0**	**5.625**	**1**	**0.625**	**8.25**	**4.75**	**0**	**0.875**	**0**	**0**	**1.75**	**0.25**
Insecta	3.25	3	5.375	10.25	3.625	24.375	5.625	3	1.75	3.25	5.75	1.5
Other animal material (Gastropoda)	0	0	0	0	0	0.125	0	0	0	0	0	0
Total animal material	**3.25**	**3**	**5.375**	**10.25**	**3.625**	**24.5**	**5.625**	**3**	**1.75**	**3.25**	**5.75**	**1.5**
Unidentified material	**0.75**	**0.125**	**1**	**0.25**	**0.5**	**0.5**	**0**	**0.5**	**0**	**0.25**	**0.875**	**0.625**
Number of taxa in the sample	**34**	**37**	**34**	**30**	**36**	**39**	**29**	**28**	**19**	**29**	**44**	**32**
Ds	**11.856**	**16.284**	**7.149**	**11.236**	**14.438**	**7.618**	**8.021**	**8.954**	**6.296**	**13.221**	**12.469**	**4.459**
E	**0.772**	**0.821**	**0.716**	**0.774**	**0.815**	**0.695**	**0.719**	**0.749**	**0.741**	**0.810**	**0.753**	**0.614**

Species present in the samples with more than 1% are presented (species with lower relative frequencies are compiled in the category “Other”). *n* – number of analyzed samples, NRD – Neradin, MNS – Manđelos, KMN – Kumane, MLC – Melenci, Ds – inverse of the Simpson index, E – Evenness.

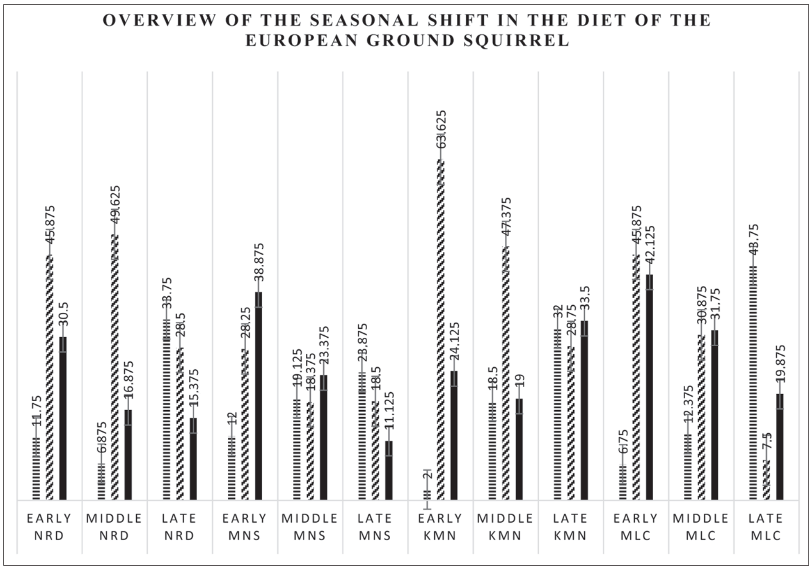

Fig. 1. Overview of the early, middle, and late seasonal shift in the consumption of *Achillea millefolium* (horizontally lined column), Fabaceae (diagonally lined column) and Poaceae (black column) by European ground squirrel on 4 study sites. NRD – Neradin, MNS – Manđelos, KMN – Kumane, MLC – Melenci.

Despite a relatively large number of food categories, only 14 accounted for more than 5% of the diet at any site or season (Table 2), as follows: *Achillea millefolium*, *Medicago lupulina*, *M. minima*, *Trifolium campestre*, *T. fragiferum*, *T. pratense*, *T. repens*, *Veronica arvensis*, *Bromus commutatus*, *Dactylis glomerata, Poa* sp., *P. annua* and *P. pratensis*. Insects accounted for more than 5% of the diet (Table 2). Moreover, only 11 taxa (mostly grasses) appeared in the diet at every site during every season, including *Achillea millefolium*, *Medicago minima*, *Trifolium pratense*, *T. repens*, *Dactylis glomerata*, *Festuca pseudovina*, *F. rubra*, *F. rupicola*, *Poa annua*, *P. pratensis*, and Insecta. On average, *A. millefolium*, legumes and grasses accounted for 78.5% of food in the samples (53.5-94.75%). Fig. 1 shows the seasonal preferences of ground squirrels for *A. millefolium*, legumes and grasses. Even though different taxa dominated different samples, towards the end of the active period, *A. millefolium* consumption increased (with the exception of the middle-season sample from Neradin), and that of legumes and grasses decreased (with the exception of the late-season sample from Kumane, possibly due to the small sample size). Insects proved to be an important protein source for *S. citellus*, occasionally making up a quarter of the monthly food consumption (Table 2).

Samples contained on average 32.5 taxa (19-44). Species richness was the highest during the middle season, except in Manđelos, where the late-season sample contained the highest number of species. According to the inverse of the Simpson index, the diet of ground squirrels was most (least) diverse during the middle (late) season (Table 2). ANOVA revealed significant seasonal variations only in samples originating from Neradin (early vs late: F=1.7724, P=0.018641) and Melenci (early vs late: F=3.0239, P<0.001; middle vs late: F=2.889, P<0.001). PCA analysis successfully distinguished the samples based on location, whereby PC1 separated Fruška Gora from Banat samples gathered during the early and late season, while middle season samples were mixed (Fig. 2).

Jaccard index values illustrating the similarity between the dietary samples ranged from 0.151 to 0.469 (Table 3). These relatively low values along with high evenness values (Table 2) suggest that, even though a small number of same plants was present in samples in high percentages and was accompanied by a large number of other species in small percentages, the exact plant species compositions of samples were not very similar.

Food selection

Food selection quantified using the Jaccard index marked *S. citellus* as picky eaters, considering the dietary samples and the vegetation composition which showed a low level of similarity, especially during the middle season when all age classes are active. The Jaccard index values are as follows: Neradin: early: 0.219, middle: 0.12, late season: 0.233; Manđelos: early: 0.175, middle: 0.119, late season: 0.159; Kumane: early: 0.25, middle: 0.215, late season: 0.305; Melenci: early: 0.3, middle: 0.186 and late season: 0.208.

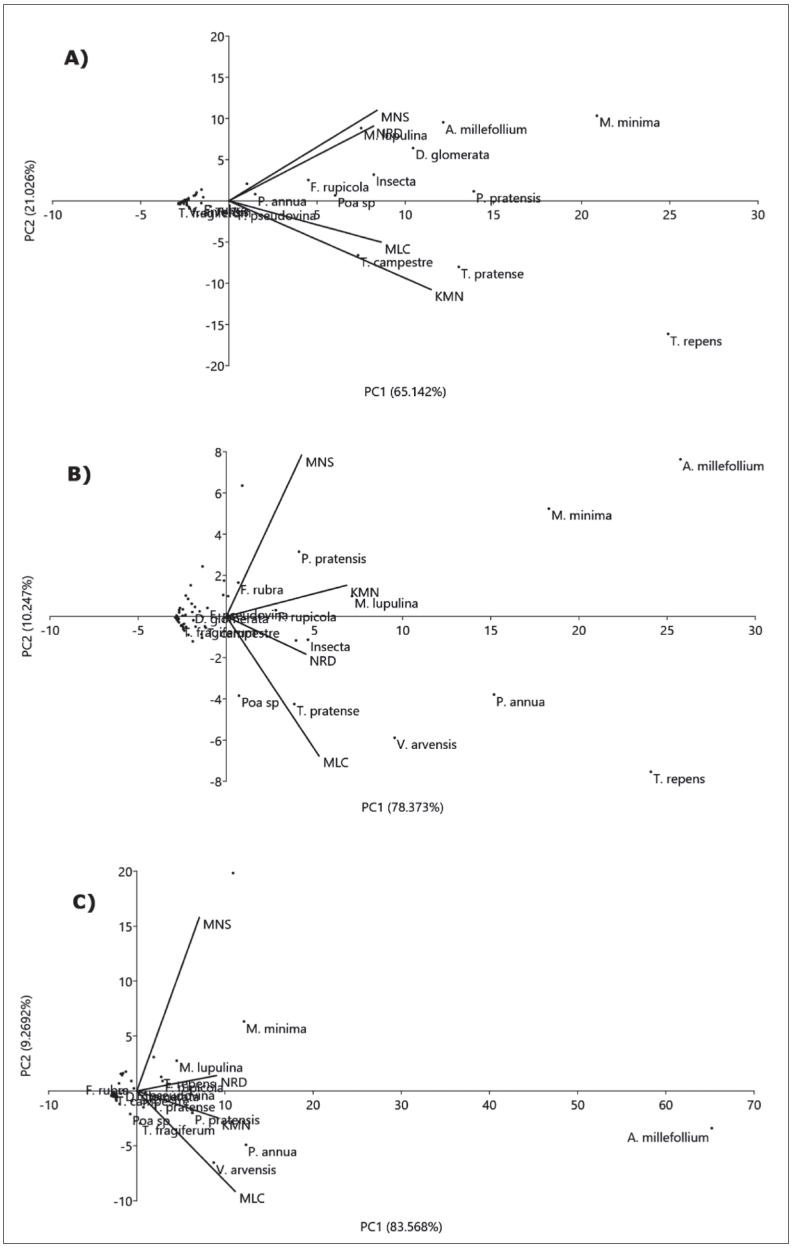

Fig. 2. PC plot of (**A**) early, (**B**) middle and (**C**) late season analysis results showing the dietary samples differentiation by location. NRD – Neradin, MNS – Manđelos, KMN – Kumane, MLC – Melenci. The plot only shows names of species present in the samples with more than 2%, but all species were included in the analysis.

DISCUSSION

In open grassland areas of agricultural landscapes, the local plant composition and its seasonal characteristics differentially modify the diet of the diurnal and endangered European ground squirrel. The species' diet is dominated by forbs, especially *Achillea millefolium* and legumes, while grasses, the group which predominates in the vegetation of habitats, presents a less-preferred but still important nutritional resource. Our survey of herbaceous vegetation revealed a high percentage cover of native plant species at all study sites. This finding further suggests that these are stabilized native grasslands known to be preferred by ground squirrels [38].

Despite a high number of available plants, the *S. citellus* diet is dominated by a small number of species present in high percentages, while most of the other identified species are consumed only occasionally. The available data from sandy-steppe habitats in Serbia indicate that although 31 plant species are consumed by the ground squirrels, only 8 of these are present in their diet during the entire active season and comprise most of the food intake [25]. In southern Austria, squirrel diet was shown to consist of about 60 plant species, about half of which appeared in the diet only occasionally [27], while in Hungary, *Achillea* sp., *Festuca* sp. and legumes dominated the diet [2]. A similar pattern has been reported for other species in the group [38,40-42]. That *S. citellus* does not follow patterns of species abundances in the vegetation was confirmed by the low Jaccard index values, indicating a low level of similarity between the diet and vegetation composition, not only in the number of species present in the samples, but in the relative frequencies of species as well.

Independently of habitat type, *S. citellus* in Vojvodina primarily feed on *Achillea millefolium*, legumes and grasses. Our analyses indicate that their preference shifts from grasses and legumes to *A. millefolium* throughout the season. Considering the relative frequencies of the three categories in the vegetation and food, it is evident that *S. citellus* actively seeks legumes during the entire active season. Similarly, there is

Table 3. Jaccard dissimilarity index (Ja) values of pairwise assessments of dietary samples from the early, middle and late season at the 4 study sites

Ja	NRD middle	NRD late	MNS early	MNS middle	MNS late	KMN early	KMN middle	KMN late	MLC early	MLC middle	MLC late
NRD early	0.245	0.283	0.207	0.207	0.197	0.312	0.265	0.325	0.369	0.218	0.2
NRD middle		0.315	0.196	0.303	0.288	0.222	0.3	0.302	0.245	0.227	0.190
NRD late			0.207	0.296	0.281	0.26	0.265	0.359	0.26	0.219	0.2
MNS early				0.32	0.254	0.204	0.261	0.289	0.204	0.156	0.170
MNS middle					0.339	0.204	0.306	0.309	0.204	0.176	0.193
MNS late						0.193	0.264	0.288	0.193	0.169	0.183
KMN early							0.325	0.371	0.349	0.177	0.151
KMN middle								0.469	0.295	0.2	0.176
KMN late									0.371	0.235	0.244
MLC early										0.281	0.173
MLC middle											0.187

NRD – Neradin, MNS – Manđelos, KMN – Kumane, MLC – Melenci

positive selection for *A. millefolium*. *Achillea* leaves are characterized by high antioxidant and cytoprotective activity [43], while its seeds contain notable amounts of α-linoleic and linolenic acid [44]. Both chemicals are polyunsaturated fatty acids (PUFAs) known to enhance torpor in hibernators and impact growth and gonadal development in male juvenile European ground squirrels [14, 45-47]. Because nutrition is highly influential on hibernation and overwinter survival, regardless of habitat type, *Achillea millefolium* is an important dietary category for *S. citellus*.

Our findings indicate that forbs are the preferred food resource of the European ground squirrel in Vojvodina. Studies of the its diet in Hungary similarly revealed the presence of 37 plant species in its diet, 31 of which were dicots [2], and a comparable pattern was reported for the American species of ground squirrels [4,34,35,48]. There are multiple reasons ground squirrels prefer forbs over grasses. For example, forbs are 30% to 50% more digestible than grasses because of slower foliage growth, which makes it tender for longer and renders it more palatable for animals [49,50]. Furthermore, forbs contain more water than grasses [51] and can contain up to 40% more protein, phosphorus, sodium and calcium [49,50,52]. On the other hand, grasses, although important, appear to be easy to digest, are readily accessible, but are not an actively sought-after food type, except during the early season, probably because other plants start their active phases later. It is also worth noting that the predominance of grasses in ground squirrel diet has been linked to habitat degradation [38]. Our results, therefore, possibly point to an already visible impact of a changing climate on the vegetation of grassland sites in the southern Pannonian plain in early spring, which is a crucial period for hibernators. Nevertheless, the abundance of grasses at the study sites makes them easily accessible, shortening the time needed for foraging and thus maximizing energy intake. This is especially important immediately after emergence from hibernation when energy reserves are low, and as a way to limit encounters with predators. Grasses also contain fewer secondary metabolites and thus require less energy for detoxification [50].

A high abundance of seeds has been reported in several ground squirrel food studies [33,40-42]. In line with the results reported in [8], our findings suggest that seeds and flowers are not a major constituent of ground squirrel diet. Furthermore, these items were consumed mostly during the middle season, possibly as a fat source for the young and females after reproduction. On the other hand, insects proved to be an important protein source throughout the season. Coleoptera, Lepidoptera, Orthoptera, and Odonata are known to be present in the diet of *S. citellus* [25,27,38,53]. However, it is worth noting that the relatively high percentage of insects in our study might be an overestimation, as chitin is almost indigestible, making it easier to detect insects in feces compared to plant remains [54]. Nevertheless, in a study conducted in 1927, insects were found to be the preferred food type of the thirteen-lined ground squirrel (*Ictidomys tridecemlineatus*), contributing up to 55% of their food intake [55].

Considering the differences in *S. citellus* diet at different times of the active season, open grassland sites in the agricultural setting should have a preserved ground-level vegetation layer composed of grasses and forbs, especially Fabaceae and *Achillea millefolium*, ensuring a complete dietary base throughout the active season. Restoration of European ground squirrel habitats should thus focus on low-level vegetation, whereas tall grasses should be avoided, as they affect their predator detection ability among other reasons [56-58]. Moreover, given the observed differences in food consumption between animals originating from different study sites (stemming from a large number of plant species present in samples in small percentages), their diet should be considered when developing management plans and programs, e.g., when assessing localities for repatriation and translocation activities. It is also worth considering that, according to data from Hungary, sites grazed by cows are richer in dicots than those grazed by sheep, resulting in greater dicot consumption by squirrels at the former sites [2]. As all sites examined in this study are grazed by both sheep and cows, limiting the number of cattle in the future should be considered.

As the feeding habits of herbivores are directly influenced by environmental conditions, open grassland habitat quality is a decisive factor in the survival of individuals and even populations [11]. Annual weather variations have been shown to exert a significant influence on the diet of *S. citellus* [53]. Considering the predicted loss of grassland plant diversity due to ongoing climate change [59,60], studies such as this one are an important first step in successful habitat management of existing populations.

As the dynamics and structure of *S. citellus* populations were not investigated in the present study, this could be a topic for further studies. It would be beneficial to examine the impact of environmental disturbances on a species highly dependent on local habitat vegetation as a food resource, at both population and individual levels. Despite the aforementioned limitations, we believe that our work has demonstrated the importance of plant species composition and percentage distribution to measure the overall availability of food resources for the European ground squirrel in different grassland habitats.

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Supplementary Material

The Supplementary Material is available at: http://www.serbiosoc.org.rs/NewUploads/Uploads/Arok%20et%20al_6110_Supplementary%20Material.pdf