Theriologia Ukrainica, **30**: 142–151 (2025)
p-ISSN 2616-7379 • e-ISSN 2617-1120
DOI: 10.53452/TU3015

SEASONAL VARIATION IN RED FOX (*VULPES VULPES*) DIET ACROSS AGRICULTURAL AND FOREST HABITATS IN CENTRAL HUNGARY

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Key words

food availability, food choice, food supply, opportunistic predator, seasonal changes, spatial differences

doi

http://doi.org/10.53452/TU3015

Article info

submitted 12.09.2025
revised 29.10.2025
accepted 30.12.2025

Language

English, Ukrainian summary

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Abstract

We investigated how seasonal and site-specific differences in food abundance affect the feeding habits of the red fox (*Vulpes vulpes*). To address this question, we analysed 356 scats collected over three years at four localities of central Hungary, representing distinct habitat types. This design enabled us to evaluate how temporal fluctuations and habitat heterogeneity influence feeding ecology. Food availability was assessed by estimating prey density with complementary methods. Small-mammal populations were surveyed by the capture-mark-recapture method, while the relative abundance of larger mammals was estimated through track counts. These data provided a background against which dietary preferences and flexibility could be assessed. We examined both the occurrence and the volume ratio of major diet categories by site and season. Overall, the red fox diet was dominated by mammals (about 51.1%), followed by plants (~22.1%), insects (~14.8%), birds (~11.7%), while reptiles and amphibians occurred in negligible amounts (~0.3%). At one locality, dietary data were directly compared with prey availability to test whether diet composition reflected resource abundance. Results revealed pronounced seasonal shifts: small rodents, especially *Microtus arvalis* (~15.6%) and *Sylvaemus sylvaticus* (~18.6%), were the staple food throughout the year, yet other resources gained importance in different seasons. In summer, insects were frequently consumed, while in autumn fruits and other plant materials became dominant. These changes closely followed the natural fluctuations of resource availability. Site-related differences were also detected. At the three localities dominated by juniper and poplar, dietary composition showed remarkable similarity, whereas the site dominated by oak presented distinct patterns, suggesting the role of vegetation structure and prey communities. A striking case was recorded at one locality where a goose farm was present: bird feathers occurred frequently in scats during this period but decreased sharply after farming ceased. Overall, the findings emphasise the opportunistic nature of the red fox. Its ability to adjust diet composition to both temporal and spatial changes in food supply underlines its ecological flexibility, which enhances survival in dynamic and human-modified landscapes.

Cite as

Zhelitski, I. 2025. Seasonal variation in red fox (*Vulpes vulpes*) diet across agricultural and forest habitats in central Hungary. *Theriologia Ukrainica*, **30**: 142–151. [In English, with Ukrainian summary]

Сезонні зміни у живленні лисиці рудої (*Vulpes vulpes*) в аграрних та лісових місцевостях центральної Угорщини

Іштван Желіцькі

Резюме. Ми досліджували вплив сезонних та локальних відмінностей кормової бази на харчові звички лисиці рудої (*Vulpes vulpes*). Для цього було проаналізовано 356 зразків екскрементів, зібраних протягом трьох років у чотирьох локалітетах центральної Угорщини, що представляли різні типи оселищ. Такий підхід дав змогу оцінити, як сезонні зміни та гетерогенність оселища впливають на живлення виду. Доступність кормових ресурсів оцінювалася за допомогою різних методів. Чисельність дрібних ссавців визначалася методом відлову-мітки-повторного відлову, тоді як відносна чисельність великих ссавців визначалася шляхом обліку слідів. На основі отриманих даних ми могли порівняти доступність потенційних здобичей з фактичним складом раціону. Порівняли частоту трапляння та об'ємне співвідношення основних категорій їжі за сезонами та локалітетами. Загалом, у раціоні лисиці переважали ссавці (близько 51,1 %), за ними рослини (≈22,1 %), комахи (≈14,8 %), птахи (≈11,7 %), тоді як рептилії та амфібії зустрічалися у незначних кількостях (≈0,3 %). В одному із місць дослідження результати безпосередньо порівнювалися з доступністю ресурсів, щоб з'ясувати, наскільки раціон відображає кормову базу. Результати показали виражені сезонні зміни: дрібні гризуни, зокрема *Microtus arvalis* (≈15,6 %) та *Sylvaemus sylvaticus* (≈18,6 %), залишалися основною здобиччю протягом року, проте інші ресурси набували значення залежно від сезону. Влітку важливу роль відігравали комахи, восени переважали плоди та інші рослинні компоненти. Такі зміни відображали природні коливання у доступності їжі. Було виявлено й відмінності між місцями дослідження. У трьох локалітетах, де домінували тополево-ялівцеві ліси, склад раціону був подібним, тоді як у ділянці з домінуванням дуба виявлено відмінності, що вказують на вплив рослинності та складу кормових угруповань. Цікавий випадок зафіксовано там, де була гусяча ферма: пір'я птахів часто траплялися у зразках саме в той період, коли вона існувала, але різко зменшилося після припинення господарської діяльності. Отже, результати підтверджують, що лисиця є типовим опортуністичним хижаком. Її здатність змінювати склад раціону відповідно до сезонних і просторових змін у доступності корму підкреслює екологічну гнучкість та забезпечує виживання у мінливих і антропогенно трансформованих ландшафтах.

Ключові слова: доступність їжі, вибір їжі, кормова база, опортуністичний хижак, сезонні зміни, просторові відмінності.

Introduction

Predator–prey interactions are key ecosystem processes affecting population density of both parties [Blackwell *et al.* 2001; Bishop & Wear 2005]. Shortage of food generated by natural changes may suppress predators focusing on a single prey type, and therefore monophagy is seldom among mammalian predators. Opportunistic carnivores such as cougar (*Puma concolor*), culpeo (*Pseudalopex culpaeus*), South American grey fox (*P. griseus*), Molina's hog-nosed skunk (*Conepatus chinga*), and Geoffroy's cat (*Oncifelis geoffroyi*) are able to switch to alternative preys with the greatest proportions in the available biomass [Novaro *et al.* 2000]. Similar results have been found in Europe for the golden jackal (*Canis aureus*) [Najar *et al.* 2024], the European wildcat (*Felis silvestris*) [García *et al.* 2025], and the Eurasian lynx (*Lynx lynx*) [Buzan *et al.* 2024]. Pampas foxes (*Pseudalopex gymnocercus*) showed a diet abundant in mammals, insects, and fruits as the main food items, whereas the less available birds, reptiles, and carrion (cattle and fish) were consumed in low proportion, suggesting that pampas foxes use the resources opportunistically [García & Kittlein 2005].

The red fox (*Vulpes vulpes*) is a widespread predator present on all continents except South America and Antarctica. Several studies showed this species being flexibly adapted to the local conditions, which is also reflected by its feeding habits [Contesse *et al.* 2004; Dell'Arte & Leonardi 2005; Sidorovich *et al.* 2006]. Many authors found that the red fox consumes mostly mammals (predominantly rodents), while feeding on insects, fruits, birds, and reptiles are less widespread [Lewis *et al.* 1993; Lanszki & Heltai 2002; Lenain *et al.* 2004], or their use is restricted to certain seasons.

Site-specific composition of red fox diet was demonstrated in a number of studies [Heltay 1989; Geffen *et al.* 1992; Padial *et al.* 2002; Russell & Storch 2004]. Such geographic differences could stem from variations in local prey density and availability [Sidorovich *et al.* 2006]. For instance, foxes consume poultry wherever they are available [Heltay 1989]. Thus, the presence or absence of a diet item can be related to human related factors, such as vicinity of human settlements, hunting activity, and others.

The feeding habit of the red fox also shows seasonal changes [Padial *et al.* 2002; Contesse *et al.* 2004], which is usually explained by the seasonal change in the availability of food sources [Lenain *et al.* 2004; García & Kittlein 2005; Mellado *et al.* 2005]. In other studies, the most important factor was the prey abundance [Donadio *et al.* 2010; Kidawa & Kowalczyk 2011]. Fox feeding on insects, fruits, birds, and reptiles is restricted to certain seasons [Lanszki & Heltai 2002; Lenain *et al.* 2004; García & Kittlein 2005]. Seasonal change also appears in the diet of the slightly larger golden jackal (*Canis aureus*) inhabiting the same area [Lanszki *et al.* 2002].

There is a fair amount of site-specific work on red fox diets, but long-term studies that compare habitats—such as forests and grasslands—through different seasons are much less frequent [but see Sidorovich *et al.* 2006]. In this study, we set out to explore how the feeding habits of this generalist predator respond to local and seasonal changes in food availability in areas that have not been studied before.

Materials and Methods

Study sites

The feeding habits of the red fox was studied at four sites in Hungary (Fig. 1), three of which (Bócsa, Bugac, and Orgovány) are pristine juniper–poplar forests within the Kiskunság National Park, while the fourth site is an oak wood near Nagykovácsi within the Duna–Ipoly National Park.

Fig. 1. The four study sites on the map of Hungary. The three nearby sites south of the capital Budapest represent juniper–poplar forests within the Kiskunság National Park, while the fourth site near Nagykovácsi is a protected oak forest (source: ArcGis, with modifications).

Рис. 1. Чотири досліджені місцезнаходження на карі Угорщини. Три близько розташовані локації на південь від столиці Будапешт — ялівцево-осиковий ліс у межах Національного парку «Кішкуншаг», а четверте місцезнаходження, Надьковачі — заповідний дубовий ліс (створено від ArcGis).

According to our data the three sites of the Kiskunság National Park have mainly shrubland vegetation dominated by common juniper (*Juniperus communis* Linnaeus, 1758) and white poplar (*Populus alba* Linnaeus, 1758).

The fauna comprises a wide spectrum of mammals including the red fox (*Vulpes vulpes* Linnaeus, 1758), European hare (*Lepus europaeus* Pallas, 1778), roe deer (*Capreolus capreolus* Linnaeus, 1758), red deer (*Cervus elaphus* Linnaeus, 1758), fallow deer (*Dama dama* Linnaeus, 1758), wild boar (*Sus scrofa* Linnaeus, 1758), European badger (*Meles meles* Linnaeus, 1758), western polecat (*Mustela putorius* Linnaeus, 1758), pine marten (*Martes martes* Linnaeus, 1758), European mole (*Talpa europaea* Linnaeus, 1758), common vole (*Microtus arvalis* Pallas, 1779), field vole (*M. agrestis* Linnaeus, 1761), European wood mouse (*Sylvaemus sylvaticus* Linnaeus, 1758), yellow-necked wood mouse (*S. flavicollis* Melchior, 1834), striped field mouse (*Apodemus agrarius* Pallas, 1771), common shrew (*Sorex araneus* Linnaeus, 1758), pygmy shrew (*S. minutes* Linnaeus, 1766), and northern white-breasted hedgehog (*Erinaceus roumanicus* Barrett-Hamilton, 1900).

Human settlements are sporadic here and keeping poultry in farms is widespread, although this activity was ceased due to a serious H5N1 bird flu viral outbreak in the study period.

According to our data, the fourth site near Nagykovácsi has different flora and fauna. The hills surrounding Nagykovácsi have mountain forest vegetation dominated by oaks (*Quercus* sp. Linnaeus, 1753), with patches of common hornbeam (*Carpinus betulus* Linnaeus 1953), European beech (*Fagus sylvatica* Linnaeus 1753), sporadically interspersed with wild cherry (*Prunus avium* Linnaeus, 1755), lime (*Tilia* sp. Linnaeus 1753), and common ash (*Fraxinus excelsior* Linnaeus 1753). Potential fox prey here include the red deer, roe deer, wild boar, red fox, mouflon (*Ovis musimon* Schreber, 1782), pine marten, beech marten (*Martes foina* Erxleben, 1777), wild cat (*Felis sylvestris* Schreber, 1777), European badger, European wood mouse, yellow-necked wood mouse, harvest mouse (*Micromys minutes* Pallas, 1771), European edible dormouse (*Glis glis* Linnaeus, 1766), common shrew, European mole, northern white-breasted hedgehog, and red squirrel (*Sciurus vulgaris* Linnaeus, 1758). As Nagykovácsi is a suburb of the capital, poultry keeping is restricted to households and farming is less common.

Fox scat collection

Fresh fox scats were collected at the four study sites in the middle of each season (January, April, July, October) during 2003–2006. Previous experience and statistical analyses of major diet items indicated that seven independent scats (collected the same day and at least 100 m apart from each other) is a sufficient sample size for describing the local fox diet at the genus level. For avoiding interference with the social system of the foxes, only one half of a scat was removed from the place. The time and location of scats were recorded on the collection boxes. After collection, samples were dried in a Sigma Systems Ventilated Safety Cabinet at room temperature for 2 days.

Microhistological analysis of scat content

The fox diet composition was determined by microhistological analysis of the individual scat samples treated as sample units. Samples were soaked in alcohol for 24 hours. Then each sample was loosened by pincers and thoroughly washed for 20 minutes in flowing warm water through two sieves with mesh sizes of 2 mm and 1 mm. This way the samples were cleaned from excreta that can disturb the analysis. The 2 mm sieve captured large amorphous items like plants and insects, while the finer sieve captured mostly hairs of mammals. After drying of washed samples, the contents of sieves were put to separate bags for later identification of the food remnants.

For the analysis, the remnants from both sieves were dispersed with pincers in Petri dishes. Following Ciucci *et al.* [2004], the point-frame method was used to identify 50 pieces of remnants from the 2 mm sieve, and 100 pieces of remnants from the 1 mm sieve. The pieces were identified under a binocular microscope at a magnification of 200x. Additionally, cuticular and medullar preparations of hairs were made following Teerink [1991]. Food items were identified to genus.

Statistical analyses

The proportion of diet components was estimated by methodology of Katona & Altbäcker [2002] and calculated for each scat using the formula N_i / N_t x 100, where N_i is the number of identifiable food item *i* (e.g., hairs, bones, feathers, or insect remains), and N_t is the total number of identified items from that scat. This variable is an indicator of the actual diet composition of that particular individual for the day before the scat was deposited.

For major food types, the occurrence (%) was calculated for each type by dividing the number of scats in which the given food type was present (O_i) by the total number of scats (O_t) collected for that period (O_i / O_t x 100) [Zabala & Zuberogoitia 2003]. This gives a rough estimate of how evenly that food is present in the diet of different individuals. When the frequency distribution of diet types estimated either by their proportion or occurrence were associated, the Chi-square test of homogeneity was used.

Scat composition was also tested for significant differences between study sites and seasons. For major food types, their percent volume in the diet was analysed using two-way ANOVA, treating the study site as an independent factor, the scat as a random factor, and seasons within years as a repeated measures factor. Two- or three-way interactions among the site, season, and year of observation were also included in the model.

The statistical tests were carried out in Statistica by StatSoft.

Food availability

The relationship between food abundance and feeding habits was only investigated at the Bugac juniper–poplar forest site. The yearly fluctuation of food supply was determined by live trapping of small rodents, and by track count estimate for large mammals. For the capture-mark-recapture estimation of small prey density, 49–49 live traps were used in two 60 x 60 m grids at Bugac, with a 10 m distance between the traps. To estimate the relative density of large mammals we used the methodology of Fonseca *et al.* [2007] and Funston *et al.* [2010], the tracks of mammals crossing the freshly ploughed sandy surface were counted on 5 sample routes, 350 m each, seasonally at the time of scat collection. The frequency distribution of scat remnants to prey density, separately for small and large mammals, was compared using the Chi-square test of homogeneity.

Scat counts were used to estimate fox density [Webbon *et al.* 2004]. The relative fox density (R) was calculated as $R = S / L$, where S is the number of scats, L is the walking distance covered from start point to the locality of the last (most often of the time the seventh) sample.

Results

The food diversity in the fox scats was the richest at Nagykovácsi, where 16 mammal species were present, followed by Orgovány, Bugac, and Bócsa with 14, 9, and 7 species of mammals, respectively (Table 1).

The main food items were mammals, birds, insects, and plants at all sites. Reptiles were present in small quantities at Bócsa only; we found frog remnants in the scats twice, in the spring of 2004 and the summer of 2006. The volume % and occurrence % variables were highly correlated (r = 0.86, p = 0.01). Mammals were present in two-thirds of the scats, and scat composition was dominated by mammalian remnants if mammals were present. High values of both variables indicate that foxes readily consumed mammals wherever it was possible. Plants were also frequently present at all sites in the scats, but their proportion was low indicating that plants are less optimal foods but may have other functions such as controlling parasites. Birds and insects were both present and constituted a medium percent of remnants (see: Table 1).

Comparing the proportion of mammals in the scats we found differences in the fox diet (Fig. 2), both among the sites (RM ANOVA $F(3, 24) = 3.21$, $p = 0.04$), years ($F(2, 48) = 4.65$, $p = 0.01$), and seasons ($F(3, 72) = 18.99$, $p = 0.00$), as well as a significant interaction between sites and seasons ($F(9, 72) = 2.38$, $p = 0.02$), and between sites, years, and seasons ($F(18, 144) = 2.07$, $p = 0.00$).

Table 1. Composition of red fox scats at the four study sites. Both the proportion percentage by volume (Vol) of main diet types within the scats and their percentage of occurrence (Occ) in the seasonal samples are shown. The data for mammalian food items are given by species, whereas other foods are summarised at levels of higher taxa

Таблиця 1. Вміст послідів лисиці рудої з чотирьох досліджених місцезнаходжень. Показано частки (Vol) основних об’єктів живлення у посліді та частки їх трапляння (Occ) за сезонами. Дані ссавців подано за видами, а інших об’єктів — на рівні вищих таксонів

Taxa of prey items	Juniper–poplar						Oak forests		Mean of sites	
	Bócsa		Bugac		Orgovány		Nagykovácsi			
	Vol	Occ	Vol	Occ	Vol	Occ	Vol	Occ	Vol	Occ
Sylvaemus sylvaticus	7.9	16.6	15	22.6	21.7	28.5	29.9	60.7	18.6	32.1
Canis familiaris	0.4	3.5	2.2	4.7	0.1	1.2	0.4	4.7	0.8	3.5
Capreolus capreolus	5.6	10.7	4.8	10.7	4.3	11.9	0.9	7.1	3.9	10.1
Cervus spp.	–	–	7.1	11.9	3	5.9	1.2	3.5	2.8	5.3
Felis spp.	–	–	0.1	1.2	–	–	–	–	0.1	0.6
Glis glis	0.3	8.3	–	–	1.3	3.5	3.7	19	1.3	7.7
Lepus europaeus	9.9	22.6	1.2	4.7	4.4	4.7	1.7	7.1	4.3	9.8
Martes spp.	–	–	–	–	–	–	0.3	1.2	0.1	0.3
Meles meles	–	–	–	–	–	–	0.2	1.2	0.1	0.3
Micromys minutus	–	–	–	–	0.1	2.3	1.3	4.7	0.4	1.8
Microtus arvalis	21.4	32.1	19.6	32.1	19.4	30.9	2.1	3.5	15.6	24.7
Mustela spp.	–	–	–	–	0.9	2.3	1.1	3.5	0.5	1.5
Myotis spp.	–	–	–	–	–	–	0.1	1.2	0.0	0.3
Ondathra zybethicus	–	–	–	–	0.2	1.2	–	–	0.1	0.3
Rattus norvegicus	–	–	–	–	0.7	1.2	0.2	1.2	0.2	0.6
Sciurus vulgaris	–	–	–	–	1.1	1.2	0.1	3.5	0.3	1.2
Sus scrofa	–	–	2.3	3.5	1.4	8.3	3.2	14.2	1.7	6.5
Vulpes vulpes	0.2	19	0.2	16.6	0.5	27.3	0.7	30.9	0.4	23.5
Mammals	45.7	66.6	52.5	77.3	59.1	82.1	47.1	80.9	51.1	76.7
Birds	26.9	45.2	11.7	27.3	3.6	15.4	4.5	13	11.7	25.2
Reptiles	1.1	2.3	–	–	–	–	–	–	0.3	0.6
Insects	8.9	27.3	18.4	30.9	12.2	32.1	19.8	50	14.8	35.1
Plants	20.6	64.2	16.5	69	23.8	77.3	27.6	80.9	22.1	72.9

Among the mammals, the most important preys were rodents. The proportion of rodents varied between the years ($F(2, 48) = 16.23$, $p = 0.00$), seasons ($F(3, 72) = 7.72$, $p = 0.00$), and the interaction of years and sites was also significant ($F(6, 48) = 2.19$, $p = 0.05$).

Among the rodents, the proportion of meadow voles *Microtus arvalis* was low (2.1%) at the forested site of Nagykovácsi, while they were consumed in tenfold higher ratios (20.93%) in the three juniper–alder forests of the Kiskunság National Park surrounded by meadows, so the vegetation type nearby to the forests has an impact on food composition. The consumption of *M. arvalis* was affected by sites ($F(3, 24) = 5.47$, $p = 0.00$) and years ($F(2, 48) =11.87$, $p = 0.00$), with a significant interaction between years and sites ($F(6, 48) = 2.84$, $p = 0.01$), seasons and sites ($F(9, 72) = 3.20$, $p = 0.00$), and years, seasons, and sites ($F(18, 144) = 4.77$, $p = 0.00$).

The proportion of *Sylvaemus sylvaticus* also differed among the sites. They were more important (29.9%) at Nagykovácsi than at the other sites ($F(3, 24) = 6.35$, $p = 0.00$). Among the other mammal species, only the proportions of *Cervus spp.* and *Capreolus capreolus* showed differences, whereas other species were too sporadic for a detailed analysis. The scat content ratio of *Cervus* spp. differed among the seasons ($F(3, 72) = 5.06$, $p = 0.00$), sites ($F(3, 24) = 5.84$, $p = 0.00$), with a significant interaction ($F(9, 72) = 2.77$, $p = 0.00$). The ratio of roe deer in the scat remnants significantly differed by seasons ($F(3, 72) = 2.87$, $p = 0.04$), but not by sites ($F(3, 24) = 1.52$, $p = 0.23$), and their interaction was also not significant ($F(9, 72) = 0.78$, $p = 0.63$).

Birds were also important food items in the diet of foxes at some localities and in certain seasons (Fig. 3). We found differences among the sites (*F*(3, 24) = 8.72, *p* = 0.00), and significant interactions between seasons and sites (*F*(9, 72) = 2.48, *p* = 0.01) and years and seasons (*F*(6, 144) = 3.09, *p* = 0.00). Seasonal differences (*F*(3, 72) = 1.62, *p* = 0.19) and the interaction between years, seasons, and sites (*F*(18, 144) = 1.57, *p* = 0.07) turned out to be insignificant.

The quantity of insects (*Grillus* spp., *Tettigonia* spp.) in the fox scats (Fig. 4) was dependent on the site (*F*(3, 24) = 6.60, *p* = 0.00), years (*F*(2, 48) = 5.53, *p* = 0.00), and seasons (*F*(3, 72) = 29.71, *p* = 0.00), while the interaction between years and sites (*F*(6, 48) = 2.77, *p* = 0.02), seasons and sites (*F*(9, 72) = 3.21, *p* = 0.00), and years and seasons (*F*(6, 144) = 2.82, *p* = 0.01) were also significant.

The proportion of plants (Fig. 5) was different among the sites (*F*(3, 24) = 3.70, *p* = 0.02), seasons (*F*(3, 72) = 10.20, *p* = 0.00), with a significant interaction between seasons and sites (*F*(9, 72) = 5.98, *p* = 0.00) and years and seasons (*F*(6, 144) = 3.07, *p* = 0.00).

When we compared the density of large mammals estimated from track counts to their proportion in the fox scats, we found a certain similarity in their pattern. The *Capreolus capreolus* track density and its proportion in the scats were positively correlated at all sites (*r* = 0.38–0.53). The density of *Lepus europaeus* tracks also correlated with their ratio in the fox diet (*r* = 0.31–0.41), but only at Bócsa and Orgovány.

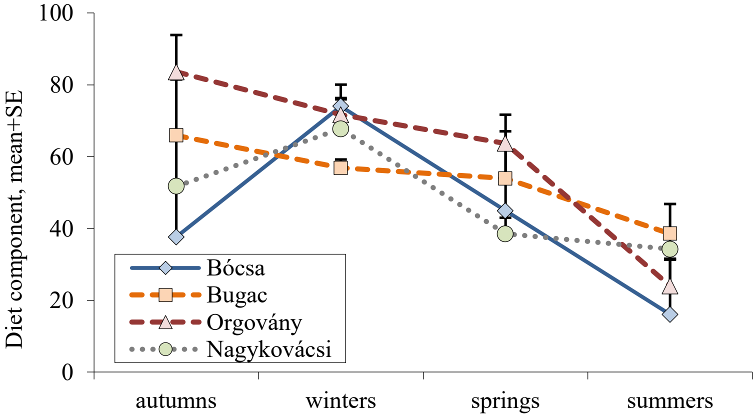

Fig. 2. Seasonal changes in the proportion of mammals in the red fox diet determined from scats. For each season, data calculated as means + SE of the three study years are shown. For each site, year, and season, values were calculated from 7–7 independent scats (*N* = 336).

Рис. 2. Сезонні зміни частки ссавців у живленні лисиці рудої за результатами аналізу вмісту послідів. Для різних пір року дані обчислені як середнє арифметичне + стандартна похибка за три роки досліджень. Для кожного місцезнаходження, року та пір року показники обчислено за 7 окремими послідами (*N* = 336).

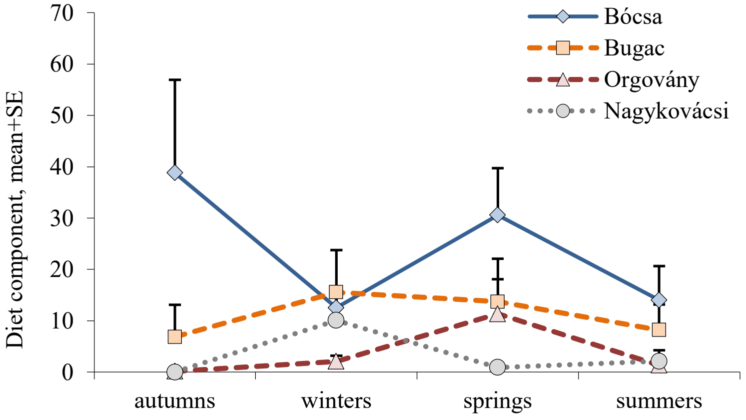

Fig. 3. Seasonal changes in the proportion of bird remnants in the red fox scats. For each season, data calculated as means + SE of the three study years are shown. For each site, year and season, values were calculated from 7–7 independent scats (N = 336).

Рис. 3. Сезонні зміни частки птахів у живленні лисиці рудої за результатами аналізу вмісту послідів. Для різних пір року дані обчислені як середнє арифметичне + стандартна похибка за три роки досліджень. Для кожного місцезнаходження, року та пір року показники обчислено за 7 окремими послідами (*N* = 336).

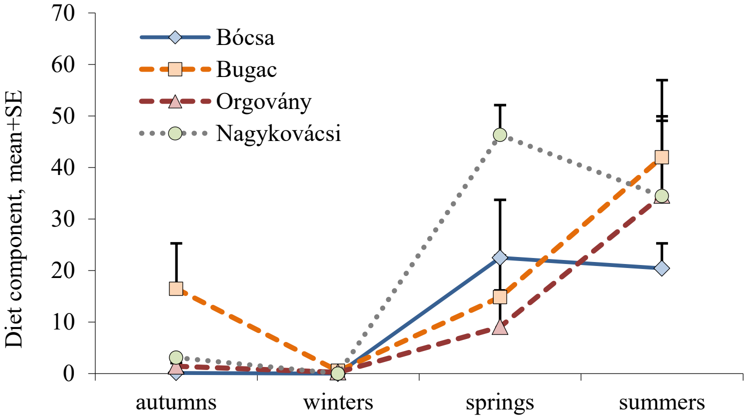

Fig. 4. Seasonal changes in the proportion of insects in the red fox diet. For each season, data calculated as means + SE of the three study years are shown. For each site, year and season, values were calculated from 7–7 independent scats ($N = 336$).

Рис. 4. Сезонні зміни частки комах у живленні лисиці звичайної за результатами аналізу вмісту послідів. Для різних пір року дані обчислені як середнє арифметичне + стандартна похибка за три роки досліджень. Для кожного місцезнаходження, року та пір року показники обчислено за 7 окремими послідами ($N = 336$).

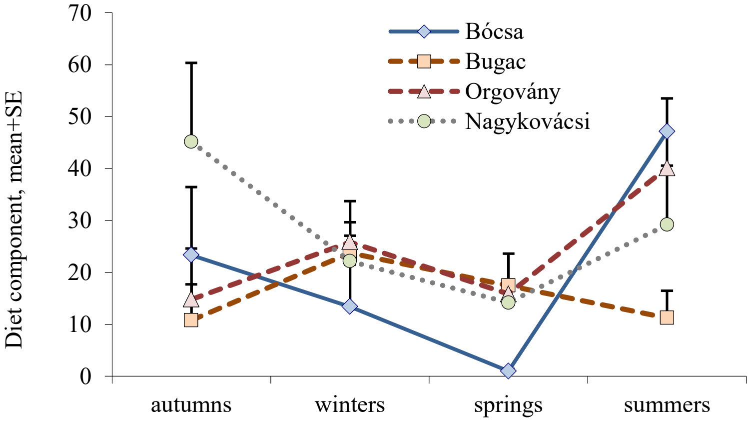

Fig. 5. Seasonal changes in the proportion of plants in the fox diet. For each season, data calculated as means + SE of the three study years are shown. For each site, year and season, values were calculated from 7–7 independent scats ($N = 336$).

Рис. 5. Сезонні зміни частки рослин у живленні лисиці звичайної за результатами аналізу вмісту послідів. Для різних пір року дані обчислені як середнє арифметичне + стандартна похибка за три роки досліджень. Для кожного місцезнаходження, року та пір року показники обчислено за 7 окремими послідами ($N = 336$).

The small rodent availability was estimated at Bugac and for two seasons only. The rodent community was dominated by *Microtus arvalis* in the open areas and *Sylvaemus sylvaticus* in the juniper–alder forest. The frequency distribution of small mammals and of consumed preys were significantly associated in both studied seasons ($\chi^2 = 111.11$, $p = 0.00$ in the summer of 2009 and $\chi^2 = 22.07$, $p = 0.00$ in the autumn of 2009).

The fox density was correlated with the proportion of *Cervus* sp. ($r = 0.30$), insects ($r = 0.45$), and plants ($r = 0.27$) only at Bugac ($r = 0.42$); with *Lepus* ($r = 0.34$) only at Nagykovácsi; and with *Microtus* sp. ($r = 0.26$–0.43) and birds at Bócsa and Nagykovácsi ($r = 0.25$–0.30).

Discussion

We investigated site-specific and seasonal differences in red fox feeding habits via scat analysis and found that the food composition was highly flexible showing site-specific fluctuations along the seasons and sometimes between years. By comparing the density of some prey types to the fox faecal content, we also found that prey availability affected food choice. Previous studies [Lenain *et al.* 2004; García & Kittlein 2005; Mellado *et al.* 2005] also found that availability is reflected in the diet composition of this species.

The red fox's feeding habit showed seasonal changes, which is in accordance with findings of other studies [Padial *et al.* 2002; Contesse *et al.* 2004]. Contrary to Sidorovich *et al.* [2006], the proportion of large mammals was low in our samples, which is most probably due to the low density of deer at our study sites. Based on their proportion in the scats, foxes sporadically consumed red deer, roe deer, wild boar, and even domestic dog, all of which were probably available as roadkill or hunting carcasses, since these species are considerably larger than foxes. The proportion of lagomorphs was generally low but their importance increased in certain periods. As density estimates suggest, small rodent availability increased twofold from summer to autumn while their proportion in the faeces increased by 12.5 times. So, temporal changes of both available species and food preferences are reflected in the fox diet.

We found differences among the investigated sites, similarly to other studies targeting geographic variation in diet composition [Padial *et al.* 2002; Russell & Storch 2004; Dell'Arte & Leonardi 2005]. Such locality-dependent difference is most probably related to food supply and availability [Sidorovich *et al.* 2006]. Wherever it was available, red fox consumed poultry [Heltay 1989] as we found from scats collected near Bócsa where a goose farm was established.

The fox diet was diverse containing over twenty species at each site. The main items in fox scats were mammals, followed by insects, plants (generally fruits), birds, and, occasionally, reptiles. The diet was dominated by rodents (mostly *Microtus* sp. and *Sylvaemus* sp.), similarly to previous findings [Lanszki & Heltai 2002; Russell & Storch 2004; García & Kittlein 2005]. The most diverse prey composition was found at Nagykovácsi, followed by Orgovány, Bugac, and Bócsa (see Table 1). This pattern is expected as Nagykovácsi has the most diverse vegetation cover among the sites, and such site-related differences are also reflected in the diet composition.

Insects, fruits, and other plants were present in the scats depending from the seasonal and site-specific availability. In a number of studies, birds and reptiles were found to be also frequently consumed [Lewis *et al.* 1993; Lanszki & Heltai 2002; Russell & Storch 2004]. The proportion of the main food in our study changed from season to season. When fruits were available, the proportion of plants increased and the other remains decreased in the diet. The relative fox density was slightly correlated with the abundance of some potential prey species in a site-dependent pattern. Besides, the proportion of consumed species in the scats did not necessarily correlate with their density.

So, abundance is not a crucial factor in determining the diet. Theoretically, scat density must increase when the abundance of high-quality food increases, because of the red fox individuals exploring for the high-quality patches. We found a positive relationship between fox faeces density and quantity of some food items in the scats, which may indicate a frequency-dependent food selection. When the fox population density is high, subordinate animals are probably forced to hunt in suboptimal areas or in periods when foraging is costly or less effective.

The red fox is considered to be an opportunistic, omnivorous predator, which predominantly feeds on small mammals [Padial *et al.* 2002; Lenain *et al.* 2004; Lanszki *et al.* 2023]. The fox diet at study sites was flexible as the animals followed availability to avoid food shortage and thus achieved a diverse food composition. It would be promising to investigate how food supply relative to fox population density affects the food choice depending on the status of individuals.

Acknowledgements

I am indebted to A. Miklósi, V. Altbäcker, K. Csatadi, P. Pongracz, I. Nemeth, O. Váczi and I. Hadnagy for their help in collecting samples. My thanks to the Kiskunság National Park for allowing to work in the protected areas.

Declarations

Funding. This study received no specific funding.

Conflict of interests. The author has no conflicts of interest to declare that are relevant to the content of this article.

Handling of materials. The study was conducted in compliance with the current legislation in regard to working in protected areas and with live animals.

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