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Diet composition of syntopically breeding falcon species *Falco vespertinus* and *Falco tinnunculus* in south-western Slovakia

Zloženie potravy syntopicky hniezdiacich druhov sokolov *Falco vespertinus* a *Falco tinnunculus* na juhozápadnom Slovensku

Filip TULIS, Roman SLOBODNÍK, Vladimír LANGRAF, Michal Noga, Zuzana KRUMPÁLOVÁ, Zbyšek ŠUSTEK & Anton KRIŠTÍN

Abstract: The red-footed falcon and Eurasian falcon represent two syntopical falcon species. While the Eurasian falcon is considered a common and numerous species in Slovakia, the red-footed falcon population has undergone a considerable decline during the past few decades. Nowadays it nests in a single locality in Slovakia, the Sysľovské polia Special Protection Area, which forms the northern and fragmented border of the species distribution area in Europe. By analysing prey remains from 9 nests (from 1998, 2001, 2013, 2014 and 2016), we identified 433 prey items belonging to 35 taxa and 9 orders. Every year, invertebrates made up the major part of the diet spectrum, in which *Calosoma auropunctatum*, *Tettigonia viridissima*, *Zabrus tenebrioides*, *Anisoplia aegetum* and *Rhizotrogus* sp. were the most frequent species of prey. Of the vertebrates, *Microtus arvalis* was the most hunted prey species. By supplementary analysis of 21 photos, we extended our knowledge on the diet by other 6 taxa. The peak of the *M. arvalis* population growth in 2014 did not manifest itself in the red-footed falcon diet composition. In 1998, 2014 and 2016 we also studied the diet of a syntopical species, the Eurasian kestrel. By analysing prey remains in 22 nests, we identified 1,151 prey items belonging to 37 taxa and 7 orders. In 1998 and 2014 vertebrates predominated, especially the common vole, however in 2016 invertebrates prevailed. This fact could be a reaction to the *M. arvalis* population peak in 2014 and its decline in 2016. These results suggest that this variability in the foraging behaviour of the Eurasian kestrel, an opportunistic predator, during the hunting of invertebrates increases the diet similarity and overlapping of the food niche of both studied falcon species.

Abstrakt: Sokol kobcovitý a sokol myšiar predstavujú dva syntopicky sa vyskytujúce druhy sokolov. Kým sokol myšiar je na Slovensku považovaný za bežný a početný druh, populácia sokola kobcovitého zaznamenala v posledných dekádach značný pokles. V súčasnosti tento druh hniezdi na Slovensku na jedinej lokalite – Chránenom vtáčom území Sysľovské polia, ktorá predstavuje severnú a fragmentovanú hranicu rozšírenia druhu v Európe. Analýzou potravných zvyškov z 9 hniezd (z rokov 1998, 2001, 2013, 2014 a 2016) sme tam determinovali 433 kusov koristi prislúchajúcich 35 taxónom a 9 radom. Bezstavovce tvorili každoročne majoritnú časť potravy, kde najčastejšie zastúpenými druhmi boli *Calosoma auropunctatum*, *Tettigonia viridissima*, *Zabrus tenebrioides*, *Anisoplia segetum*, *Rhizotrogus* sp. Zo stavovcov bol najčastejšie lovený druhom hraboš poľný. Doplnkovou analýzou 21 fotografií sme spektrum potravy rozšírili o ďalších 6 taxónov. Vrchol gradácie hraboša poľného v roku 2014 sa na zložení potravy sokola kobcovitého neprejavil. V rokoch 1998, 2014 a 2016 sme tiež sledovali potravu syntopického druhu – sokola myšiara. Analýzou potravných zvyškov 22 hniezd sme zistili 1151 zvyškov koristi, ktoré patrili 37 taxónom zo siedmych radov. V rokoch 1998 a 2014 v potrave dominovali stavovce, najmä hraboš poľný, v roku 2016 však prevažovali bezstavovce, čo môže byť reakciou na vrchol gradácie hraboša poľného v roku 2014 a pokles jeho populácie v 2016. Výsledky naznačujú, že táto variabilita potravného správania u oportunistického predátora sokola myšiara, lovom bezstavovcov zvyšuje podobnosť potravy i prekryv potravných ník oboch sledovaných druhov sokolov.

Key words: red-footed falcon, Eurasian kestrel, foraging, insectivory, central Europe

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Introduction

Worldwide agriculture is one of the main factors influencing the general decline in biodiversity as well as bird species. Effective conservation strategies depend on the type of relationship between biodiversity and land-use intensity, and on knowledge of foraging chains in this system (Ursua et al. 2005, Kleijn et al. 2009). Raptors are top predators in agroecosystems, but their foraging and food niches have been evaluated only partially there. Many papers have focused on the diet composition and foraging ecology of falcons, predominantly the myophagous Eurasian kestrel (*Falco tinnunculus*) (cf. review in Korpimäki 1985, 1986, Riegert et al. 2007, 2009). Less is known about the red-footed falcon (*Falco vespertinus*) diet, where insects predominate and are sometimes substituted with small vertebrates (see review in Szövényi 2015). There are differences however in the importance of particular taxa in the diet of both species in different parts of their breeding range (Keve & Szijj 1957, Riegert et al. 2007). Some of these differences have natural character, e.g. site effect and habitat quality (Haraszthy et al. 1994, Purger 1998, Riegert et al. 2009, Szövényi 2015), or age of nestlings (Fülöp & Slivka 1988), while some others can result from different methods of diet assessment (Tryjanowski et al. 2003). We have only scarce data on the similarity of diet composition and trophic niches in congeneric falcon species living together in the same habitats, and in the same period. Furthermore, there is less knowledge on inter-annual variability of the diet composition in the red-footed falcon.

The first data on the red-footed falcon diet from Slovakia were published by Balát & Bauer (1955), from the colony in Strekov (47°53.284' N, 18°25.602'E, Balát 1971), which does not exist anymore. Since that time more relevant data on the variability of the red-footed falcon diet in Slovakia are lacking. Only preliminary reports on the red-footed falcon diet have been published in Slovakia (Tulis et al. 2016).

The Eurasian kestrel is a vole-eating specialist in northern and central Europe, but it is also able to consume other prey, such as bats, birds, lizards or insects (Korpimäki and Norrdahl 1991, Riegert et al 2007, 2009). Around the Mediterranean and in Africa, insects may even predominate (del Hoyo et al. 1994). In Slovakia the Eurasian kestrel diet has been studied mainly in urban habitats (Darolová 1989, Kečkéšová & Noga 2008, Mikula 2012, Mikula et al. 2013), where the proportion of vertebrates and invertebrates varies significantly between localities and years.

The objectives of this study were therefore as follows: (i) to analyse the red-footed falcon diet in SW Slovakia in 1998, 2001, 2013, 2014 and 2016; (ii) to compare the diet composition of red-footed falcons in different areas of its Pannonian population; (iii) to analyse the diet composition of syntopically breeding Eurasian kestrels in 1998, 2014 and 2016; and (iv) to compare the diet composition of red-footed falcons and Eurasian kestrels breeding at the same site and in the same years (1998, 2014 and 2016).

Material and methods

Studied species

The red-footed falcon is a long-distance migratory species, staying in the Pannonian region from April to October (Cepák et al. 2008, Béltekiné et al. 2010). It breeds mostly in colonies and occupies empty nests in rookeries (Purger & Tepavcevic 1999, Purger 2001, Lebedeva & Ermolaev 2012). It may also breed solitarily (i.e. individually), mainly in the nests of magpies or rooks. In the last few decades it has also been known to occupy man-made nestboxes (Béltekiné et al. 2010, Kotymán et al. 2015, Slobodník et al. 2016). Whilst in Hungary the red-footed falcon population has grown during the last 10 years (Béltekiné et al. 2010), in Slovakia and throughout most of its distribution range its population has undergone a considerable decline during recent decades (Palatitz et al. 2015, Slobodník et al. 2014, 2016). The Sysľovské polia locality is not only the last breeding site in Slovakia, but it also represents its northernmost boundary of distribution in the Pannonian region. Nowadays it is considered a Near Threatened species (NT) in Europe and Vulnerable in EU 27 in the IUCN Red List (BirdLife International, 2016a), and listed in ANNEX I of the EC Birds Directive 79/409/EEC.

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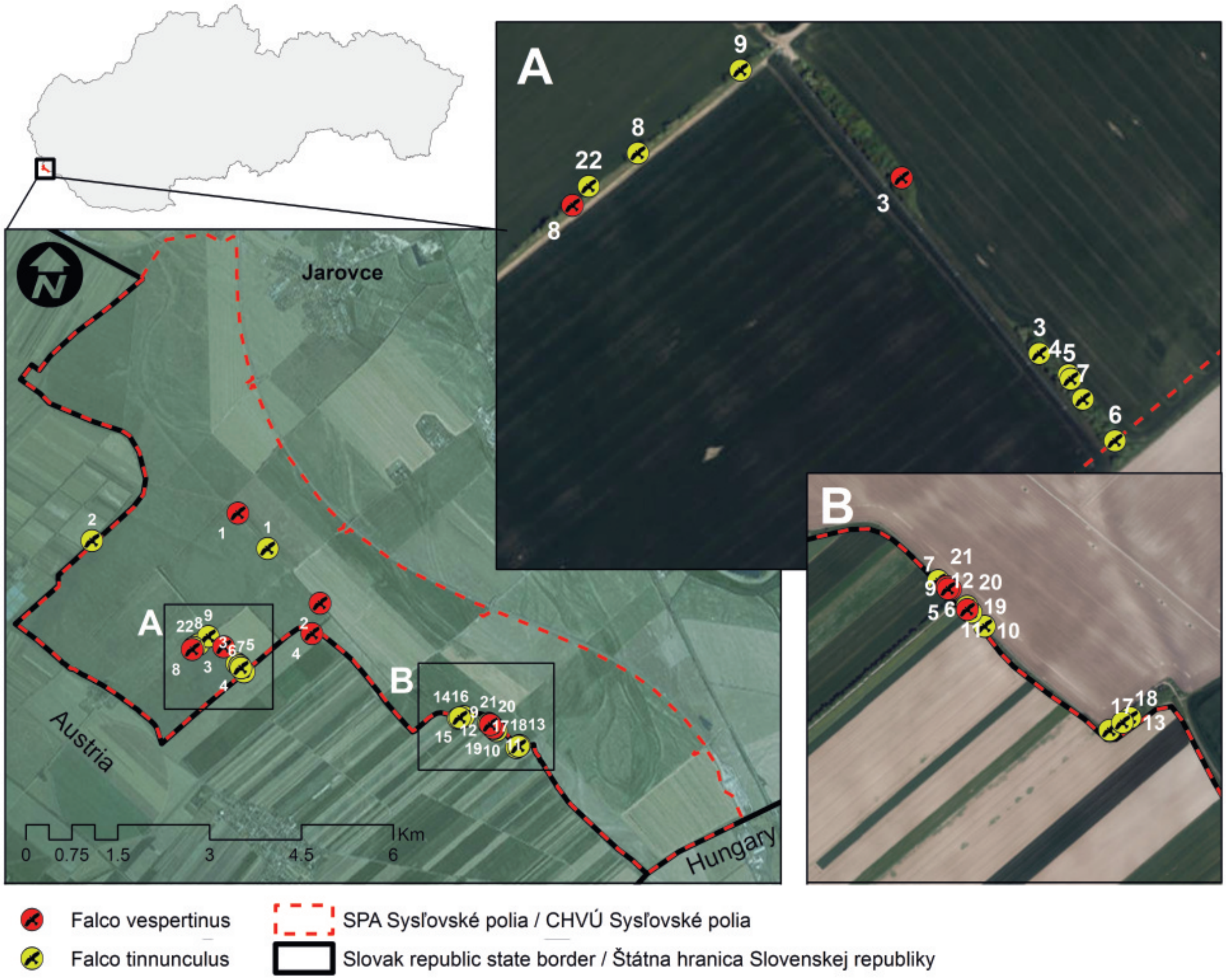

Fig. 1. Special protection Area Sysľovské polia. Study area with localisation of red-footed falcon and Eurasian kestrel nests.
Obr. 1. Chránené vtáčie územie Sysľovské polia. Študijná plocha s lokalizáciou hniezd sokola kobcovitého a sokola myšiara.

Nowadays, the Eurasian kestrel is a mainly short-distance migratory species in central Europe (Cepák et al. 2008), and breeds solitarily (Horváth 1975, del Hoyo et al. 1994). It also occupies empty nests in rookeries (Horváth 1975) and man-made nestboxes (Fargallo et al. 2001). Its population is numerous and stable, and in the IUCN Red List for Europe it is considered a Least Concern (LC, BirdLife International, 2016b). Its population density varies greatly between years, closely following the fluctuating spring densities of its main prey (Village 1982, Korpimäki & Norrdahl 1991), namely the common vole (*Microtus arvalis*). Characteristic for this rodent population are the several-year fluctuation cycles in our environmental conditions (Jacob & Tkadlec 2010, Jacob et al. 2013).

Study area

All the analysed samples of the red-footed falcon and Eurasian kestrel diets were collected in the Sysľovské polia Special Protection Area (SPA) (SW Slovakia, 48°01´N, 17°06´E), which is the last known locality of red-footed falcon breeding in Slovakia in the last six years. The locality (of 1,776 hectares, see Karaska et al. 2015 for more details) is situated near the Danube, in the environs of the village of Rusovce at the Slovak-Austrian border. The foraging territories are composed of extensive high-yield fields with multiple windbreaks and farmyards on the Slovak side and heterogeneous narrow small fields on the Austrian side (Fig. 1). The windbreaks, in which the nests are located, consist of 30 to 60 year old black locust (*Robinia pseudoacacia*), ash

(*Fraxinus* sp.), common oak (*Quercus robur*) and tree of heaven (*Ailanthus altissima*) with an overall length of 7.6 km in the locality.

Food analyses and prey items identification

In five separate years (nesting seasons of 1998, 2001, 2013, 2014 and 2016) (collection months: September–October) we processed 9 nest linings of red-footed falcons and 22 nest linings of Eurasian kestrels from the Sysľovské polia SPA (Tab. 1). The food remains were hand-separated from the nest linings and put dry into PVC bags. Mammals were identified by means of the key by Baláž et al. (2013). Birds, anurans and reptiles were identified using reference collections to the species level (except for *Mus* sp. because of the missing identification characteristics).

Invertebrates in food remnants were later identified using a microscope (Nikon) with 6–50x magnification. Each sample was processed on a Petri dish by separating paired and unpaired prey body parts (e.g. heads, mandibles, legs) to make an estimation of the numbers of individuals for each sample (Rosenberg & Cooper 1990, Nuhlíčková et al. 2016). We identified food remnants to the highest possible accuracy of taxonomic level using a comparative collection of arthropods (cf. Pechacek & Krištín 2004). The prey items and prey sizes were identified according to Chinery (1987) and other references relevant to particular invertebrate groups (e.g. Giljarov 1964). The remnants of insects were identified in a similar way, with the numbers of individuals based on unpaired body parts (head, pronotum), paired organs (elytra divided by two) and leg parts (divided by six)

Additionally, we also analysed 21 photos of a red-footed falcon bringing its prey to the studied nests, which it got from the locality of Sysľovské polia SPA in 2007–2016.

Tab. 1. Characteristics of the analysed red-footed falcon and Eurasian kestrel nests from the Special Protection Area Sysľovské polia. Upper index = the same nest box / tree.

Tab. 1. Charakteristika analyzovaných hniezdných výsteliek sokola kobcovitého a sokola myšiara z Chráneného vtáčieho územia Sysľovské polia. Horný index = totožná búdka / hniezdny strom.

nest box / nest / búdka / hniezdo	year / rok	nesting tree / hniezdny strom	height of nesting (m) / výška hniezdenia
red-footed falcon			
nest box	1998	*Robinia pseudoacacia*	8
nest box	1998	*R. pseudoacacia*	7
nest box	2001	*Ailanthus altissima*	9
nest box	2001	*R. pseudoacacia*	9
nest box	2013	*R. pseudoacacia*	5
nest	2014	*R. pseudoacacia*	8
nest box	2014	*R. pseudoacacia*	7
nest box	2016	*R. pseudoacacia*	7
nest box	2016	*Fraxinus* sp.	6
Eurasian kestler			
nest box	1998	*R. pseudoacacia*	10
nest box	1998	*R. pseudoacacia*	9
nest box	1998	*R. pseudoacacia*	7
nest box	1998	*Fraxinus* sp.	8
nest box	1998	*R. pseudoacacia*	10
nest box	1998	*Fraxinus* sp.	9
nest box	1998	*Fraxinus* sp.	8
nest box	1998	*Fraxinus* sp.	7
nest box	1998	*R. pseudoacacia*	9
nest box^{1}	2014	*Fraxinus* sp.	7
nest box^{2}	2014	*Fraxinus* sp.	7
nest box^{3}	2014	*R. pseudoacacia*	7
nest box	2016	*Fraxinus* sp.^{1}	12
nest box	2016	*R. pseudoacacia*	5
nest box	2016	*Fraxinus* sp.	9
nest box	2016	*Fraxinus* sp.	5
nest box	2016	*R. pseudoacacia*	4
nest box	2016	*Fraxinus* sp.^{1}	5
nest box^{1}	2016	*Fraxinus* sp.	7
nest box^{2}	2016	*Fraxinus* sp.	7
nest box^{3}	2016	*R. pseudoacacia*	7
nest box	2016	*R. pseudoacacia*	9

Statistical analyses

Bearing in mind the different methods and times of material collection, dissimilarities between the red-footed falcon diet in Slovakia in particular years and also between the diet of red-footed falcons in Vojvodina from 1991 (locality in the vicinity of Melenci village, northern Serbia; sample size = 302 specimens from 4 nests) (Purger 1998) and in Hungary from 1994 (locality in the vicinity of Kunmadaras and Nagyiván villages in the Hortobágy National Park; sample size = 764 specimens from 47 nests) (Haraszthy et al. 1994) were compared and estimated using the Jaccard dissimilarity index. The species were then clustered using Ward's minimum variance clustering method to the Jaccard dissimilarity matrix (Borcard et al. 2011). The validity of the cluster results was evaluated using the cophenetic correlation coefficient (Legendre & Legendre 1998, Kreft & Jetz 2010), where K indicates the means clustering optimization, which was used to determine the optimal number of classes. Analysis of similarities

(ANOSIM) was used to test for statistically significant differences between groups of sampling units.

The diet data of both falcon species were ln (x+1) transformed to suppress the influence of dominant taxa. Samples containing fewer than 3 individuals were excluded from the analysis. Non-metric Multidimensional Scaling (NMDS; Cox & Cox, 2001) on Bray-Curtis distances was used to visualize the patterns in diet composition of both falcon species in particular years. To run NMDS, the function "metaMDS" ("vegan" package) was used. Only taxa recorded in at least three samples were included in the analyses, and only taxa with a significant linear fit ("envifit" function) with the ordination ($P < 0.05$) were displayed in the resulting ordination diagram. Indexes of dissimilarity, cluster dissimilarity analyses and Non-metric Multidimensional Scaling analyses were imptlemented into R software v. 3.2.5 (R Core Team (2016), using the 'vegan' (Oksanen et al. 2013) package.

Food niche overlap was measured with Pianka's index (Pianka 1973), where the index varies between 0 (total separation) and 1 (total overlap).

Results

Diet variability in red-footed falcon nests: inter-annual and site effects

By analysing 9 nest linings (in 5 years; 1998, 2001, 2014 and 2016 = two nests, 2013 = one nest) we recorded 433 prey items belonging to 35 taxa and 9 orders (Tab. 2). Invertebrates (almost exclusively insects) accounted for 76.2% of the overall diet, among which the most frequent species were *Calosoma auropunctatum* (27%), *Tettigonia viridissima* (11.8%), *Zabrus tenebrioides* (10.4%) and *Anisoplia segetum* (4.7%). Vertebrates accounted for 23.8%, among which mammals predominated (22.6%). The most frequently hunted vertebrate was the common vole (*M. arvalis*) (18.5%).

Even in the inter-annual comparison of the diet composition, invertebrates always prevailed over vertebrates (Fig. 2). Whilst in 1998, 2011, 2013 and 2016 the Coleoptera prevailed in the diet, in 2014 the share of Orthoptera in the diet increased. Diet diversity varied, reaching the highest values in 2013 and 2016.

After evaluating the dissimilarity of the diet composition from the large-sized fields in south-western Slovakia between the individual years and the diet of the species from Vojvodina (foraging habitat composed

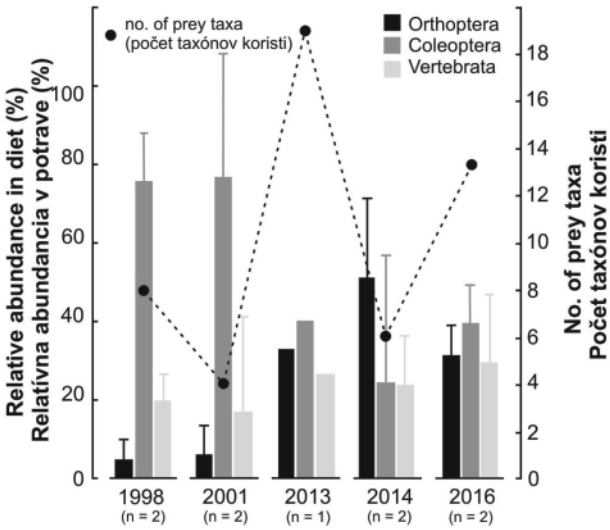

Fig. 2. Inter-annual differences in the relative abundance (mean value ± SD) of diet groups (Orthoptera, Coleoptera and Vertebrata, left Y-axis) and no. of taxa in diet (mean value; right Y-axis) at the Special Protection Area Sysľovské polia (n = number of nests).

Obr. 2. Medziročné rozdiely v relatívnej abundancii (priemerná hodnota ± SD) skupín potravy (Orthoptera, Coleoptera a Veretebrata na ľavej osi Y) a počte taxónov koristi (priemerné hodnoty; na pravej osi Y) v Chránenom vtáčom území Sysľovské polia (n = počet hniezd).

of agricultural land with small fields) in 1991 (Purger 1998) and from Hungary (foraging habitat composed of a close-to-nature puszta biotope covered with low grasses) in 1994 (Haraszthy et al. 1994), three main clusters were created (Fig. 3). The first group involves the diet of falcons in Slovakia from 1998, 2001, 2013 and 2016 for which the presence of *Apodemus sylvaticus* and *Calosoma auropunctatum* was typical. In addition, because of its size (length 20–30 mm, average dry weight 1.6 g, Šustek 1994, 2009), usually considerable abundance in arable land (Varvara et al. 2010) and easy visibility, *C. auropunctatum* can represent even a considerable contribution to the food offer for the falcons. In the second group, the analysis of dissimilarity singled out the red-footed falcon diet from Hungary in 1991, for which the occurrence of several species of insects (e.g. *Agriotes lineatus*, *Gryllotalpa gryllotalpa*, *Geotrupes mutator* or *Harpalus affinis*) or anurans (*Rana esculenta* and *Bufo bufo*) was typical. The third group was composed of the red-footed falcon diet from Slovakia in 2016 and from Vojvodina in 1991, in which the common vole was missing and in contrast the occurrence of

Tab. 2. Diet composition of the red-footed falcon during 5 years in 9 nests at the Special Protection Area Sysľovské polia SPA, Slovakia (n = number of prey items, g.sp. = unidentified genus and species, sp. = unidentified species).
Tab. 2. Zloženie potravy sokola kobcovitého v 9 hniezdach v Chránenom vtáčom území Sysľovské polia, Slovensko, počas 5 rokov (n = počet objektov potravy, g.sp. = neurčený rod a druh, sp. = neurčený druh).

breeding season / hniezdna sezóna	**1998**		**2001**		**2013**	**2014**		**2016**		**∑**	
taxa / food samples **taxón / vzorka potravy**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**n**	**%**
Invertebrates										330	76.2
Diplopoda											
Julus sp.					1					1	0.2
Odonata											
Odonata g.sp.					2					2	0.5
Orthoptera											
Tettigonia viridissima	4		3		15	14	1	3	11	51	11.8
Platycleis veyselii								2	1	3	0.7
Decticus verrucivorus					5	3			1	9	2.1
Calliptamus italicus	1	1			4	7	1	3	2	19	4.4
Chorthippus oschei								2		2	0.5
Chorthippus sp.								6		6	1.4
Stenobothrus sp.					1					1	0.2
Coleoptera											
Coleoptera g.sp.					2					2	0.5
Carabidae g.sp.									1	1	0.2
Zabrus tenebrioides	39	1			2	3				45	10.4
Pterostichus sp.		7			2	3		6		18	4.2
Calosoma auropunctatum	1	58	12	6	17	20		1	2	117	27.0
Cerambycidae g.sp.								1		1	0.2
Staphylinidae g.sp.								1		1	0.2
Scarabaeidae g.sp.								11		11	2.5
Cetonia aurata									10	10	2.3
Protaetia cuprea		4								4	0.9
Anisoplia segetum	1		2	1	10	5			2	21	4.8
Rhizotrogus sp.									3	3	0.7
Xylodrepa quadripunctata					1					1	0.2
Alleculides sp.					1					1	0.2
Mammalia										98	22.6
Rodentia											
Microtus arvalis	11	10	5		18	9		24	3	80	18.5
Apodemus sylvaticus	1		2		1				1	5	1.2
Apodemus microps					1					1	0.2
Mus sp.	1	2	2		1			1	1	8	1.8
Micromys minutus							1			1	0.2
Soricomorpha											
Crocidura leucodon						1				1	0.2
Crocidura suaveolens	2									2	0.5
Aves											
Passeriformes											
Sturnus vulgaris									1	1	0.2
Turdus merula								1		1	0.2
Passer domesticus					1					1	0.2
Reptilia											
Squamata											
Lacerta agilis									1	1	0.2
Amphibia											
Anura											
Pelobates fuscus					1					1	0.2
No. of taxa / počet taxónov	**9**	**7**	**6**	**2**	**19**	**9**	**3**	**13**	**14**	**35**	
∑	**61**	**83**	**26**	**7**	**86**	**65**	**3**	**62**	**40**	**433**	

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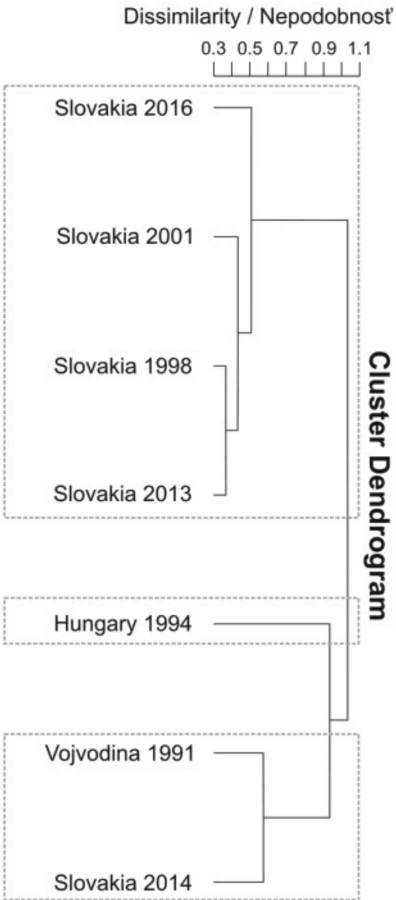

Fig. 3. Dendrogram of the dissimilarities between the red-footed falcon diets in four years in Slovakia, in Vojvodina (Serbia) in 1991 (Purger 1998) and in Hungary in 1994 (Haraszthy et al. 1994).
Obr. 3. Dendrogram nepodobnosti zloženia potravy sokola kobcovitého počas 4 rokoch na Slovensku, vo Vojvodine (Srbsko) v roku 1991 (Purger 1998) a v Maďarsku v roku 1994 (Haraszthy et al. 1994).

Pterostichus sp. was typical. Among the individual groups of clusters we recorded significant differences in the diet dissimilarity (R = 0.97, P = 0.014).

Diet of red-footed falcons in photos

In analysing the photos, we identified 21 items of red-footed falcon prey belonging to 11 taxa and 3 classes (Fig. 4). Mammals represented the most frequent class of prey (76.2 %), in case of insects it was 19%, and

Tab. 3. Prey composition of red-footed falcons identified in 21 photos taken at the Special Protection Area Sysľovské polia in 2007–2016 (* prey not found by food remains analysis in nests; g.sp. = unidentified genus and species, sp. = unidentified species).
Tab. 3. Zloženie potravy sokola kobcovitého zistené z 21 fotografií z lokality Chránenom vtáčom území Sysľovské polia v rokoch 2007 – 2016 (* druh koristi nebol zistený analýzou potravných zvyškov na hniezdach; g.sp. = neurčený rod a druh, sp. = neurčený druh).

taxa / taxón	n
*Apodemus flavicollis**	1
Apodemus sylvaticus	1
Apodemus sp.	2
Microtus arvalis	3
Microtus sp.	5
Rodentia g.sp.	4
*Gryllus campestris**	1
*Hydrous piceus**	1
Lumbricus sp.*	1
*Ruspolia nitidula**	1
*Stetophyma grossum**	1

Clicelatta made up to 4.8% of the diet. With this method we extended the diet spectrum of the species in the locality of Sysľovské polia by 6 prey species (1 species of mammal, 4 insect species and 1 Clicelatta), which had not been identified by means of analysis of the nest linings. In total, with both these diet study methods we identified 42 prey species within 495 prey items of the red-footed falcon.

Diet variability of the Eurasian kestrel: inter-annual variability

In analysing 22 nest linings (in 3 years: 1998 = 9 nests, 2014 = 4 nests, 2016 = 10 nests) of the Eurasian kestrel, we recorded 1,151 items belonging to 37 taxa and 7 orders (Tab. 4). Vertebrates represented 56%, among which the mammals prevailed (53.8%). The common vole was the most frequently hunted mammal species with 51.4%. Invertebrates (though exclusively insects) represented 44% of the diet. The most frequently and abundantly hunted taxa were Carabidae g.sp. (16.5%) and Curculionidae g.sp. (7.2%).

In the inter-annual comparisons we can see the predominance of vertebrates over invertebrates during 1998 and 2014 (Fig. 5). In 2016 however we recorded a change. There was then significant predominance of invertebrates over vertebrates, which showed itself in increased diet diversity.

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Fig. 4. Male red-footed falcon with hunted mouse (*Apodemus* sp.) (A) and common field-cricket (*Gryllus campestris*) (B) in locality Sysľovské polia.

Obr. 4. Samec sokola kobcovitého s ulovenou ryšavkou (*Apodemus* sp.) (A) a svrčkom poľným (*Gryllus campestris*) (B) na lokalite Sysľovské polia.

Diets of *Falco vespertinus* and *Falco tinnunculus* in the same habitat

NMDS analysis of the diet dissimilarity of both studied falcon species revealed high similarity of the Eurasian kestrel diets in 1998 and 2014. In that time it was *Microtus arvalis*, *Lacerta agilis* and *Anisoplia segetum* which influenced its diet. In 2016 *Rhizotrogus* sp. and *Pterostichus* sp. influenced its diet, which was different in comparison with the other studied years. The red-footed falcon diet evinced a constant similarity in 1998, 2013 and 2014. The diet of these samples was influenced mainly by *Tettigonia viridissima*. In 2016 the red-footed falcon diet partially differed from the other studied years, in which *Calliptamus italicus* had an impact on the diet composition. The red-footed falcon diet shows small similarity with the diet of the Eurasian kestrel across the studied years (Fig. 6).

Tab. 4. Diet of the Eurasian kestrel during 1998, 2014 and 2016 at the Special Protection Area Sysľovské polia site. Legend, see Table 2.
Tab. 4. Potrava sokola myšiara v priebehu rokov 1998, 2014 a 2016 v Chránenom vtáčom území Sysľovské polia. Legenda – viď Tab. 2.

breeding season / hniezdna sezóna	1998									2014			2016										Σ	
taxa / nest samples/ taxón / hniezdna vzorka	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	n	%
Insecta																							507	45.9
Orthoptera																								
Tettigonia viridissima																	1	1					2	0.2
Decticus verrucivorus																1	1						2	0.2
Calliptamus italicus																	3	1					4	0.3
Coleoptera																								
Coleoptera g.sp.								9					15					9		5	11		49	4.3
Carabidae g.sp.													1	1		6	1	2	61	55	58	5	190	16.5
Carabus coriaceus													1										1	0.1
Carabus scheidleri	1								1														2	0.2
Zabrus tenebrioides		1										1											2	0.2
Pseudoophonus calceatus										1													1	0.1
Pterostichus sp.			1		1						1		10		1						29		43	3.7
Pterostichus marginalis				1																			1	0.1
Calosoma auropunctatum			1		1						1		2						1	1	2	3	12	1.0
Curculionidae g.sp.													11	1		2	1	1	8	9	46	4	83	7.2

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Tab. 4. Continuation.
Tab. 4. Pokračovanie.

breeding season / hniezdna sezóna					**1998**						**2014**							**2016**					**∑**	
taxa / nest samples/ taxón / hniezdna vzorka	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**n**	**%**
Elateridae g.sp.													13		2	7	6	1				3	32	2.8
Scarabaeidae g.sp.																1							1	0.1
Cetonia aurata													1					2	1	1	2	2	9	0.8
Potosia aeruginosa	1		1										4										6	0.5
Protaetia cuprea													1										1	0.1
Anisoplia segetum	8		1							1	10	1		2			1	13	1	1	2	0	41	3.6
Rhizotrogus sp.					1								3	2				1				14	21	1.8
Onthophagus coenobita																		2					2	0.2
Dorcus parallelipipedus																		1	1				2	0.2
Mammalia																							619	53.8
Rodentia																								
Microtus arvalis	4	12	8	15	12	12	9	19	9	8	99	61	47	9	16	37	2	24	17	56	2	114	592	51.4
Clethrionomys glareolus				1																		1	2	0.2
Apodemus sylvaticus											1		1					1					3	0.3
Apodemus microps											1												1	0.1
Mus sp.				1		1			1		2			1	2			1	1	0	0	1	11	1.0
Soricomorpha																								
Crocidura leucodon													1									1	2	0.2
Crocidura suaveolens		1			1											1			1				4	0.3
Sorex araneus																						1	1	0.1
Sorex minutus		1																	1	1			3	0.1
Aves																							13	1.8
Passeriformes																								
Sturnus vulgaris													1									2	3	0.3
Passer domesticus			5											9									14	1.2
Passer montanus	1			1																			2	0.2
Alauda arvensis	2																						2	0.2
Reptilia																							3	0.3
Amphibia																								
Lacerta agilis			1								1											1	3	0.3
Amphibia																							1	0.1
Anura																								
Pelobates fuscus	0										1												1	0.1
No. of taxa / počet taxónov	**6**	**4**	**7**	**5**	**5**	**2**	**1**	**2**	**3**	**3**	**9**	**3**	**15**	**7**	**4**	**7**	**8**	**14**	**10**	**8**	**8**	**13**	**37**	
∑	**17**	**15**	**18**	**19**	**16**	**13**	**9**	**28**	**11**	**10**	**117**	**63**	**112**	**25**	**21**	**55**	**16**	**60**	**93**	**129**	**152**	**152**	**1151**	**100.0**

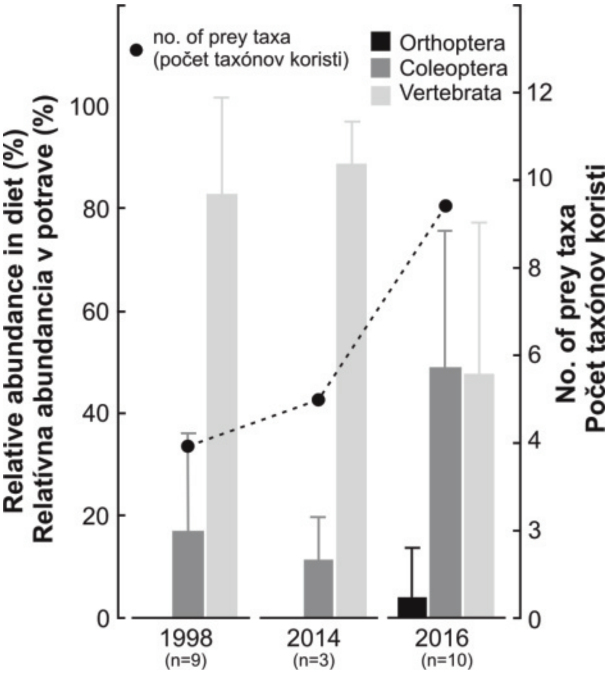

Fig. 5. Inter-annual differences in the relative abundance (mean value ± SD) of prey groups (Orthoptera, Coleoptera and Vertebrata in left Y-axis) and no. of prey taxa (mean value; right Y-axis) in Eurasian kestrel at the Special Protection Area Sysľovské polia (n = number of nests).
Obr. 5. Ročné zmeny v relatívnej abundancii (priemerná hodnota ± SD) skupín potravy (Orthoptera, Coleoptera a Vertebrata na ľavej osi Y) a počte taxónov koristi (priemerná hodnota; pravá os Y) sokola myšiara v Chránenom vtáčom území Sysľovské polia (n = počet hniezd).

Pianka´s index shows relatively low overlapping of the food niche between the two studied species in 1998 (Pianka´s index = 0.32) and in 2014 (Pianka´s index = 0.33). However in 2016, we recorded an increase in the food niche overlapping between both studied species (Pianka´s index = 0.67).

Discussion

Factors affecting prey variability in the case of the red-footed falcon

As we expected, invertebrates, especially insects, accounted for the major part of the red-footed falcon diet during the whole studied period. This is in accordance not only with the known works from the territory of Slovakia (Balát & Bauer, 1955) but also with the rest of the species occurrence area, e.g. from Germany (Bezzel & Hölzinger 1969), Vojvodina (Purger 1998) or Hungary (Keve & Szijj 1957, Haraszthy et al. 1994). Szövényi (2015) also described the hunting technique of the red-footed falcon as being effective just for the hunting of insects. The predominance of two species of insects *T. viridissima* and *C. auropunctatum* together with the high representation of common vole (as the most frequently hunted vertebrate) in Slovakia suggests that the red-footed falcon gets the major part of its diet in agricultural land with enough trees and scattered green vegetation. Analysis of its foraging habitat selection has shown that the red-footed falcon prefers hunting in grasslands and fallow lands; it has a neutral attitude towards the alfalfa and cereal fields and it avoids hunting over intertilled crops, water surfaces, woods and artificial surfaces (Palatitz et al. 2011).

The common vole in the natural conditions of Slovakia is typical for population fluctuations of several years' duration (Jacob & Tkadlec 2010, Jacob et al. 2013). In our studied nesting locality, the Sysľovské polia SPA, growth in the population of the common vole culminated in summer 2014 (Krištín et al. 2017), however this culmination did not manifest itself in the red-footed falcon diet, and we did not even record a single instance of common vole in its diet in that year. By contrast, Bezzel & Hölzinger (1969) recorded an increased representation of common voles in the red-footed falcon diet just in the time of the culminating populations of common vole and field vole (*Microtus agrestis*). Vertebrates are commonly considered the minority part of the red-footed falcon diet (Balát & Bauer, 1955, Bezzel & Hölzinger 1969, Purger 1998, Haraszthy et al. 1994, Szövényi 2015, this study). Nevertheless, short-term changes in the hunting strategy and diet preference may occur, e.g. during cold and damp days when it was found that the red-footed falcon hunts common spadefoots (*Pelobates fucscus*) more, whilst during clear warm days the most frequent prey species were orthopterans (Horváth 1963, using direct observations). Haraszthy et al. (1994) also recorded by direct observation more long-term changes in the hunting preference, when the common vole prevailed in the diet during a dry year whilst during the following wet and rainy year it was the common spadefoot that prevailed. The results of several other works based on direct observation (Horváth 1964, Bezzel & Hölzinger 1969) further suggest that vertebrates may play a more important role in the red-footed falcon diet than is suggested by the results of food remains and pellets analysis

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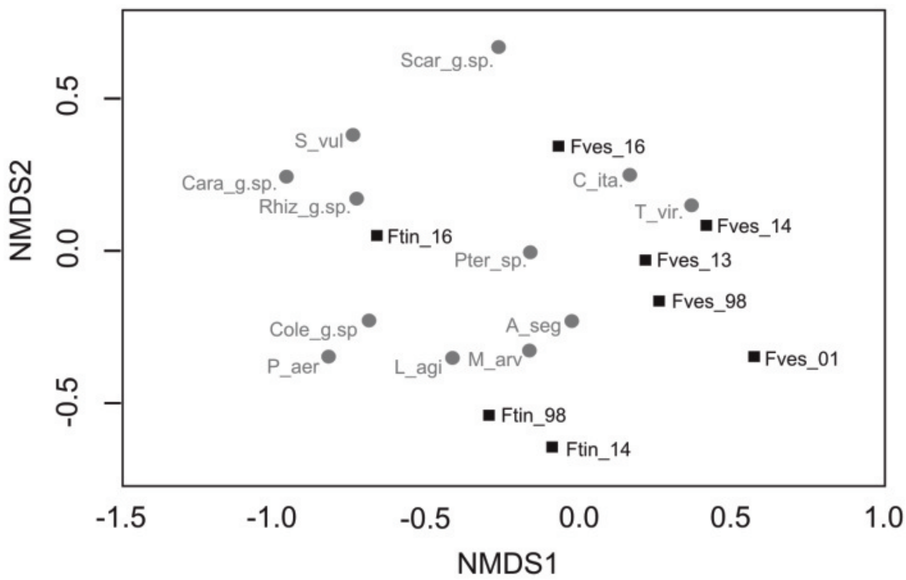

Fig. 6. The NMDS ordination diagram showing Bray-Curtis dissimilarity between the diets of red-footed falcon and Eurasian kestrel during the studied years; square – diet of both Falcon species, circle – significant prey taxa (P < 0.05); (Fvesp_98 – *Falco vespertinus* 1998 etc., Ftinn_98 – *Falco tinnunculus* 1998 etc.; T_vir – *Tettigonia viridissima*, C_ita – *Calliptamus italicus*, Cara_g.sp. - Carabidae g.sp., S_vul – *Sturnus vulgaris*, Rhiz_g.sp., Rhizotrogus g.sp., Scar_g.sp. – Scarabaeidae g.sp., P_aer – *Potosia aeruginosa*, Cole_g.sp. – Coleoptera g.sp, L_agi – *Lacerta agilis*, Pter_sp. – *Pterostichus* sp., M_arv – *Microtus arvalis*, A_seg – *Anisoplia segetum*.

Obr. 6. NMDS ordinačný diagram zobrazujúci Bray-Curtisovu nepodobnosť potravy sokola kobcovitého a sokola myšiara; štvorec – potrava oboch druhov sokolov počas sledovaných rokov; krúžok – významný taxón koristi (P < 0.05); (Fvesp_98 – *Falco vespertinus* 1998 atď., Ftinn_98 – *Falco tinnunculus* 1998 atď.; T_vir – *Tettigonia viridissima*, C_ita – *Calliptamus italicus*, Cara_g.sp. – Carabidae g.sp., S_vul – *Sturnus vulgaris*, Rhiz_ sp – *Rhizotrogus* sp., Scar_g.sp. – Scarabaeidae g.sp., P_aer – *Potosia aeruginosa*, Cole_g.sp. – Coleoptera g.sp, L_agi – *Lacerta agilis*, Pter_sp. – *Pterostichus* sp., M_arv – *Microtus arvalis*, A_seg – *Anisoplia segetum*.

(Balát & Bauer, 1955, Purger 1998, our study). Horváth (1964) also points out that the nestlings are fed only with vertebrates. According to Haraszthy et al. (1994) it is evident that vertebrates leave fewer traces in nest linings, possibly because they are eaten whole and are usually completely digested by the falcons. In any case, to know the red-footed falcon diet in as much detail as possible, this researcher recommends a combination of multiple research methods. By means of supplementary analysis of photos of the food from the studied locality, we confirmed a higher share of vertebrates in the diet, and we extended the diet composition by 6 taxa compared with the analysis of the food remains in nests (Tab. 3).

Comparison of the diet composition of the red-footed falcon from southwestern Slovakia (representing the northern boundary of the Pannonian population) with published data on the red-footed falcon diet from the central part of the Pannonian population, creates three main clusters with provably distinct diet composition. The red-footed falcon diet in Slovakia from 1998, 2001, 2013 and 2016 creates a separate branch excepting the year 2014, which showed a similarity with the falcons' diet in Vojvodina from 1991 (Purger, 1998). The red-footed falcon diet in Hungary from 1994 (Haraszthy et al. 1994) also forms a separate branch. These distinctions may be a manifestation of not only dissimilar prey availability in different foraging habitats, but also a different methodology of sample/data collection and analysis. In the surroundings of the nesting site in Vojvodina there was agricultural land with small fields, just as in the Austrian part of the territory near the Sysľovské polia SPA. In contrast, the nesting site in Hungary is situated in a puszta biotope typical for its high portion of short grasslands.

Factors affecting prey variability in the case of the Eurasian kestrel

In northern and central Europe, the Eurasian kestrel is considered as a species hunting mostly common voles and to a lesser extent invertebrates (Korpimäki 1985, Masman et al. 1986, Kochanek 1990, Zmihorski & Rejt 2007), which our results from 1998 and 2014 fully correspond with. It is also well known that in the southern parts of this species distribution area this ratio changes gradually and invertebrates predominate (Fattorini et al. 1990, del Hoyo et al. 1994). However, in 2016 we found a lower proportion of vertebrates in Slovakia as well, and invertebrates thus represented a major part of the diet. It was just the year 2016 that was characterized by a decrease in the number of common voles in the studied locality when compared to 2014 (Krištín et al. 2017), and the decrease in common vole availability could thus have been compensated by increased predation of invertebrates. This type of functional response, by which in reaction to a decrease in the number of common voles the Eurasian kestrel is able to switch to hunting insects, has been described by several researchers (Holling 1965, Korpimäki 1985). Changing meteorological conditions are a factor that may also affect the diet composition of the Eurasian kestrel. Decreasing temperature in the non-breeding period leads to alternative food, i.e. insects being replaced with birds and mice (Holling 1965, Korpimäki 1985). Furthermore, analysis of the Eurasian kestrel diet in an urbanized environment illustrates that the kestrel is able to broaden its diet spectrum opportunistically depending on the specific diet range in the environment, e.g. with bats, swifts and other birds or lizards (Darolová 1989, Romanowski 1996, Zmihorski & Rejt 2007, Mikula et al. 2013). Constantini et al. (2005) further noted that though the hunting area character determines the diet composition, and there may be a bigger proportion of more available prey species in the diet, on the other hand the Eurasian kestrel diet reflects a high degree of individual feeding behaviour, i.e. individual preferences or abilities to hunt some species of prey regardless of their actual availability. This knowledge may explain the variability in the diet dissimilarity between the nesting pairs which we analysed during the individual years. It follows from the above that the decreased availability of the common vole did not necessarily make a change in the representation of vertebrates and invertebrates in the diet explicitly in 2016.

Prey similarity in two syntopically breeding falcons

Our comparison of the diet composition of both studied species showed low diet similarity, however whilst in the red-footed falcon diet (found by analysing the food remains in nests) invertebrates prevailed, in the Eurasian kestrel diet in 1998 and 2014 vertebrates predominated (mainly common vole). Thus the overlapping of the food niche between both syntopic species was minimal in this period. The Eurasian kestrel is considered as an opportunistic predator which hunts locally-available prey (Village 1990), and as explained above, it is able to respond flexibly to changing prey availability, and to adapt its hunting technique. In 2016, when the common vole availability was lower in the studied locality and in the Eurasian kestrel diet, invertebrates prevailed (as it was in the case of heterospecific falcon species), so the diet similarity and overlapping of the food niche of both studied species increased. These results suggest that mainly in the years of low abundance of common vole, the Eurasian kestrel may be considered a prey rival for the red-footed falcon. However, more comprehensive analyses of the Eurasian kestrel biology indicate that the increasing number of insects in the diet correlates negatively with the number of breeding pairs of Eurasian kestrel (Itämies & Korpimäki1987), and that the abundance of common voles is the main factor influencing its population dynamics (Korpimäkki 1984). The assumption of possible competition or antagonistic behaviour is also disproved by Horváth (1975) who, based on the behavioural study of both syntopically occurring species, described the Eurasian kestrel as a peaceable and tolerant species with regard to the red-footed falcon.

Conclusion

This study presents the very first comprehensive data on the diet composition of the red-footed falcon from its single nesting locality in Slovakia, which currently represents the northern border of the species distribution area in the Pannonian lowlands. In the diet in each of the five studied years, invertebrates predominated and the culmination of the common vole population in 2014 had no impact on the diet composition. In comparison with other regions, there was prevalence of *Alphitobius diaperinus*, a facultative nidicolous detritophage and store pest (Dinev 2013) and *Calasoma auropunctatum*, a characteristic component of Carabid assemblages in different field crops in warm central and south-eastern European lowlands (Šustek, 1994, Varvara et al. 2010).

We also recorded *Alphitobius diaperinus* in the nest linings of red-footed falcons. In contrast, in the Eurasian kestrel diet in the "vole year" 2014 we recorded a decrease in otherwise predominating vertebrates and their replacement through the increased consumption of invertebrates. These results suggest that with increased consumption of invertebrates, there is consequently increased diet similarity and overlapping of the food niche of both studied species. Some easily visible beetles, like *Anisoplia segetum* or *Zabrus tenebrionides*, can be hunted just as well on cereal spikes as on the ground, in places with a sparse herbage layer or without it.

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