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Long-eared owls roosted in the forest, still hunted in open land

Myšiarky ušaté zimovali v lese, stále lovili v otvorenej krajine

Filip TULIS, Michal ŠEVČÍK & Ján OBUCH

Abstract: Long-eared owls' winter roosts located within forest, compared to their winter roosts in human settlements, often escape human attention. Only minimum information has been published about winter roosts located deep in the forest. During the years 2005 to 2016, we collected long-eared owl pellets at irregularly occupied forest winter roosts. Compared to the diet at winter roosts in human settlements, the long-eared owls roosting in the forest surprisingly significantly more frequently hunted the common vole. Moreover, we did not record higher consumption of forest mammal species in the diet of owls at forest winter roosts. Long-eared owls roosting in human settlements hunted significantly more birds. The results show that, despite the location of deep forest winter roosts, long-eared owls preferred hunting the common vole, i.e. hunting in open agricultural land. The study also points out the lack of knowledge about winter roosts located deep in the forest.

Abstrakt: Zimoviská myšiarok ušatých situované v lesoch v porovnaní so zimoviskami v blízkosti ľudských obydlí často unikajú ľudskej pozornosti. O zimoviskách hlboko v lese bolo dodnes publikovaných minimum informácií. V priebehu rokov 2005 až 2016 sme na nepravidelne obsadených lesných zimoviskách zbierali vývržky myšiarok ušatých. V porovnaní s potravou zo zimovísk v blízkosti ľudských obydlí, myšiarky zimujúce v lese lovili preukazne viac hraboša poľného. V potrave v lesných zimoviskách sme však nezaznamenali vyššiu konzumáciu lesných druhov cicavcov. Myšiarky zimujúce v blízkosti ľudských obydlí naopak lovili preukazne viac vtáky. Výsledky poukazujú, že aj napriek situovaniu zimovísk hlboko v lese, myšiarky preferovali lov hraboša poľného, teda lov v otvorenej poľnohospodárskej krajine. Práca tiež poukazuje na nedostatok informácii o zimovískách situovaných hlboko v lesných porastoch.

Key word: *Asio otus*, pellets, diet, winter roost, forest

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Introduction

Food availability and weather conditions are factors which affect over-wintering birds' survival (Lahti et al. 1998, Robinson et al. 2007). The selection of roosting-place plays an important role in protection against predators (Sunde et al. 2003) and minimisation of thermoregulation cost (Körtner & Geiser 1999). The localisation of birds' roosting-places does not strictly predict the localisation of their feeding sites (Caccamise & Morrison1988, Hill & Frederick1997).

Aggregation to communal winter roosts is a typical phenomenon for long-eared owls during the non-breeding season. The process of winter roost creation is still not quite clear. According to Wijnands (1984), in the beginning the roosts are formed by adult pairs and their juveniles. However molecular analyses have revealed that only some individuals in the wintering flock are closely related (Galeotti et al. 1997a). The number of wintering owls varies from several to dozens of individuals (Winjands 1984, Škorpíková et al. 2005, Noga 2007, Makarova & Sharikov 2015, a.o.). The largest winter roost of approximately 750 owls was recorded in 2009 in Serbia (Radišić 2010). The number of wintering owls in the conditions of central Europe is affected by the abundance of common vole *Microtus arvalis* (Grzędzicka 2014, Tulis et al. 2015a), the most frequently preyed species in this area (reviewed by Birrer 2009). The common vole is a typical inhabitant of open agricultural areas (Baláž 2010), and its abundance in central Europe changes irregularly in three to five-year fluctuations (Jacob & Tkadlec 2010, Jacob et al. 2013). These fluctuations lead to a functional response in the long-eared owl diet (Korpimäki & Norrdahl 1991, Tome 2003). The composition of their diet is also affected by land use or by quantitative relations of small mammals, which may vary regionally. Particular regions thus offer different prey availability, which on a small scale affects the proportion of prey species and diversity of the long-eared owl diet (Tome 2000, Noga 2007). On a larger scale it can affect regional-specific patterns, where for example the long-eared owl is considered as a specialist predator in northern Europe, but in southern Europe as a generalist predator (Kontogeorgos et al. 2019). Our study sites were localized in two regions where the diet of long-eared owls has been studied in the long term (Obuch 1982, Obuch 1989, Šotnár & Obuch 1998, Tulis et al. 2012, Benešová 2013, Tulis et al. 2015a). Comparison of these two different regions reveals long-term differences in the proportion of particular prey species and diet diversity. Occupation of human settlements by long-eared owls for roosting in the breeding season is common (e.g. Kiat et al. 2008, Riegert et al. 2009), and relatively common in forest. Several studies have also presented information about the diet of long-eared owls roosting in forest areas (Gawlik & Banz 1982, Bull et al. 1989, De Wavrin et al. 1991, Bodbijl 1997).

Similarly, during the non-breeding season long-eared owls´ winter roosts have regularly been recorded within human settlements (Škorpíková et al. 2005, Noga 2007, Zaňát et al. 2007, Ružič et al. 2010), where the proportion of synanthropic species in their diet increases with the rising level of urbanisation, but the common vole still represents these owls' main prey (Riegert et al. 2009, Sharikov & Makarova 2014, Mori & Bertolino 2015, Szép et al. 2018). However, several studies deal with winter roosts located in rural zones such as windbreaks and bushes within agricultural land or forest edges (Czarnecki 1956, Enriquez-Rocha et al. 1993, Smith & Devine 1993, Škorpíková et al. 2005, Zaňát et al. 2007) and some of them also deal with diet composition (Holt & Childs 1991, Cecere et al. 2013). Studies which deal with winter roosts located deeper inside compact forest (more than 500 m from the forest's edge) can be found only rarely (Armstrong 1958 in Holt (1997), Enriquez-Rocha et al. 1993, Škorpíková et al. 2005, Zaňat et al. 2007). Škorpíková & Křivan (2013) described one winter roost of long-eared owls in a patch of young spruces (5–8 m high) which was part of a larger coniferous forest complex. This winter roost was used for at least 17 years, and the owls moved several times from older and denser stands to younger and thinner ones. The nearest clear cut was 200 m away, and the edge of the forest was 500 m from this winter roost. The roost was occupied by 4–6 individual long-eared owls, and also at least two individual short-eared owls (*Asio flammeus*). Despite several studies mentioned above, data about the diet of long-eared owls wintering in the forest are still completely lacking.

This study presents the first data about the diet of long-eared owls from winter roosts situated within forest areas. The aims of this study were to: (i) investigate the diet ecology of long-eared owls from winter roosts located in the forest and (ii) compare the diet spectrum of these owls with the diet of long-eared owls from the nearest winter roosts situated within human settlements. We hypothesized that long-eared owls wintering in the forest hunted more forest small mammal species than those wintering within human settlements.

Material and methods

Study sites

All our study sites are located in the central part of Slovakia. Pellets were collected at two types of winter roosts (Fig. 1): (i) winter roosts situated within forest, and (ii) winter roosts situated within human settlements, which were used as control sites (Tab. 1).

Winter roosts situated within forest

Three forest winter roosts were situated in 20–30 year-old spruce or pine monoculture patches situated in mixed forest at various distances (≥ 800 m) from the edge of the forest (Tab. 1). Two winter roosts (nos. 1 and 2) were discovered accidentally. Winter roost no. 3 was discovered during telemetry study of long-eared owls, while tracking one individual which was caught and marked with a radio transmitter in the vicinity of winter roost no. 4 within human settlement, 1.5 km away from each other (Fig. 1). Next day after catching, the marked individual was found at a winter roost with another eight owls (Tulis 2013). The proportion of forest in a 3 km buffer zone around all forest winter roosts was greater than 35% (Fig. 2). Winter roost no. 1 (48°50'56.86" N, 18°44'44.30" E) was situated at Žiar Mts., winter roost

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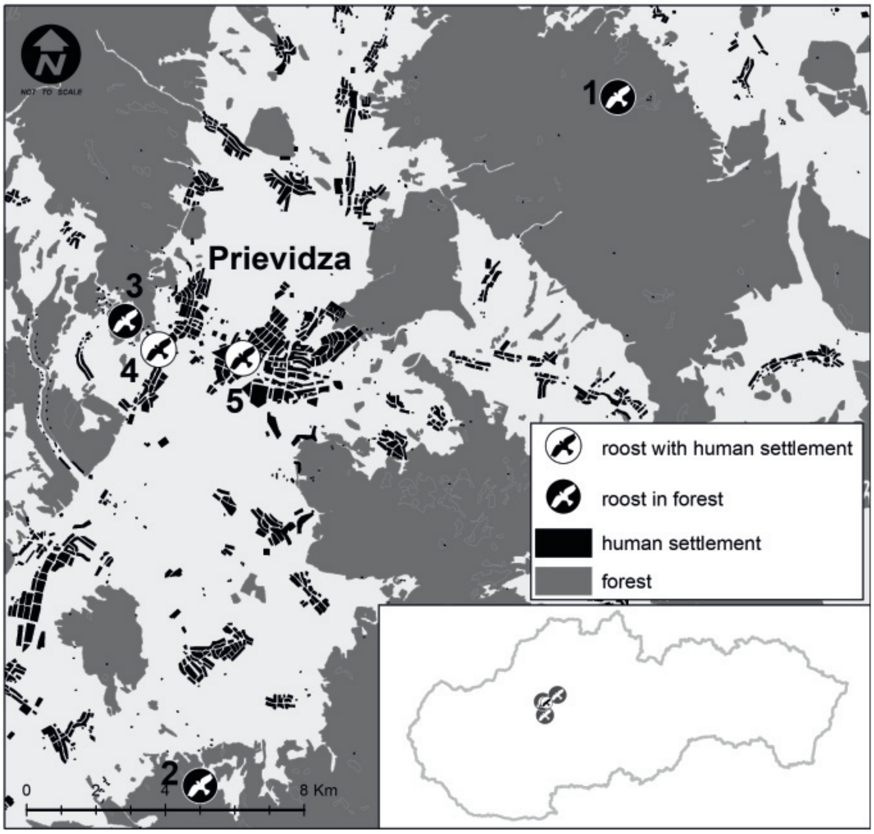

Fig. 1. Location of winter roosts (1 – Budiš, 2 – Lehota p. Vtáčnikom, 3 – Viglaš, 4 – Bojnice, 5 – Prievidza).
Obr. 1. Lokalizácia sledovaných zimovísk (1– Budiš, 2 – Lehota p. Vtáčnikom, 3 – Viglaš, 4 – Bojnice, 5 – Prievidza).

no. 2 (48°39'43.59" N, 18°36'14.61" E) was situated in the Vtáčnik Mts., and roost no. 3 (48°46'51.01" N, 18°33'36.09" E) was located in the Strážov Mts.

Winter roosts situated within human settlement

Two winter roosts no. 4 (48°46'26.80" N, 18°34'25.97" E) and no. 5 (48°46'25.53" N, 18°36'25.53" E) situated within human settlements were used as control sites in this study (Fig. 1). The diet data used for winter roost no. 4 were published in Tulis et al. (2015a). Winter roost no. 4 has not been used since 2014. Winter roost no. 5 was formed in winter 2016. For selection of control sites (winter roosts), two options were taken into consideration: (i) distance from the forest winter roost, using the nearest known winter roost; (ii) the same year of pellet collection as for the forest winter roosts. In this way we avoided the possible influence of different prey abundance.

Tab. 1. Studied winter roosts of long-eared owls (compared pairs of roosts are in the same row).
Tab 1. Sledované zimoviská myšiarky ušatej (dvojice porovnávaných zimovísk sú v rovnakom riadku).

ID	forest / les	winter / zima	DFE (km)	ID	settlement / sídlo	winter / zima	DBW (km)
1	Budiš	2005	1.6	-	-	-	-
2	Lehota p. Vtáčnikom	2007	1.3	4	Bojnice	2007	12.4
	Lehota p. Vtáčnikom	2009	1.3		Bojnice	2009	12.4
	Lehota p. Vtáčnikom	2013	1.3		Bojnice	2013	12.4
3	Viglaš	2011	0.8		Bojnice	2011	1.5
	Viglaš	2012	0.8		Bojnice	2012	1.5
	Viglaš	2016	0.8	5	Prievidza	2016	3.4

DFE – distance from forest edge / vzdialenosť od okraja lesa; DBW – distance between roosts / vzdialenosť medzi zimoviskami

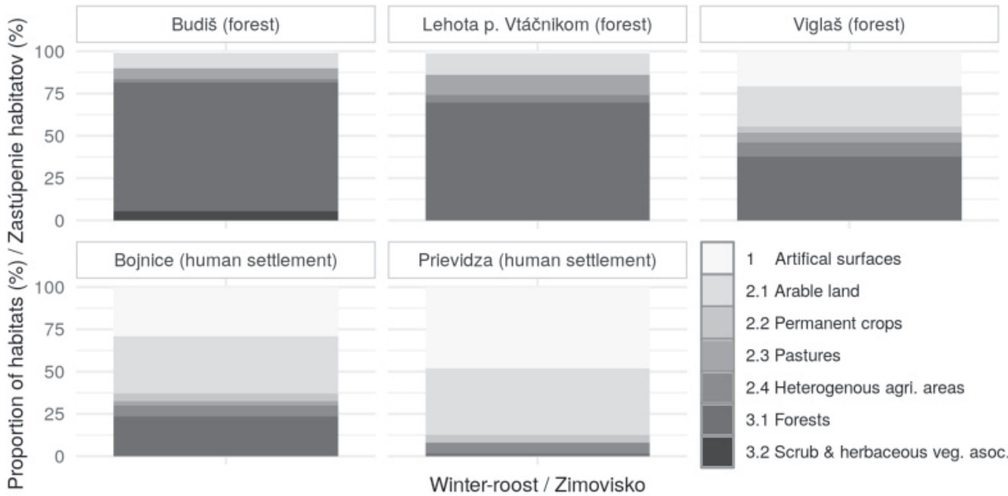

Fig. 2. Land cover in a 3 km buffer around winter roosts, (numbers before legend items represent their position in the hierarchy of land use according to the Corine legend; Heterogeneous agri. Areas = Heterogeneous agricultural areas, Scrub and herbaceous veg. association = Scrub and herbaceous vegetation association; parentheses after the names of winter roosts indicate their location: forest or human settlement).

Obr. 2. Krajinná pokrývka v 3 km rádiuse od zimovísk, (1 – zastavané územie, 2.1 – orná pôda, 2.2 – trvalé plodiny, 2.3 – pasienky, 2.4 – heterogénne poľnohospodárske plochy, 3.1 – lesy, 3.2 – kroviny a bylinná vegetácia; v zátvorkách za názvom zimoviska uvádzame jeho lokalizáciu: les alebo ľudské obydlie).

A circle of 3 km around the long-eared owls' roosting site was used to simulate the habitat use of the potential hunting area utilized by long-eared owls (Tulis 2013). The CORINE map from 2006 and 2012 was used as the background. As the legend for land use we used the proportion of: 1. Artificial surfaces (level 1), 2. Agricultural areas in detailed level 2, e.g. 2.1 Arable land, 2.2 Permanent crops, 2.3 Pastures, 2.4 Heterogenous agricultural areas and 3 Forest and seminatural areas in detailed level 2, e.g. 3.1 Forests, 3.2 Scrub and herbaceous vegetation association. In cases where pellets were collected over a longer period, we visualized both available time periods. The proportion of forest in a 3 km buffer zone around all forest winter roosts was greater than 35%, and the proportion of forest around winter roosts within human settlement was less than 20%, but the proportion of open land was greater than around forest roosts (Fig. 2).

Diet analyses

Pellets were collected at the end of the wintering period during March and April and were put into 5% solution of sodium hydroxide (NaOH), which dissolves all the undigested parts of prey except the bones. Mammals were identified by skull (maxilla) and jaw (mandibula) according to Anděra & Horáček (2005) and Baláž et al. (2013). Bird bones were identified using a reference collection. The identification of birds was based on beaks (rostrum), metatarsal (tarsometatarsus), humeral (humerus) and metacarpal bones (metacarpus). The number of individuals of identified prey was estimated as the least number of individuals which we were able to identify according to the same anatomical parts of bones (Klein & Cruz-Uribe 1984). Data for mammal and bird prey biomass were taken from Baláž & Ambros (2006), Baláž et al. (2013) and Hudec & Šťastný (2005).

Data analyses

The breadth of food niches (FNB) was estimated using the formula proposed by Levins (1968): $B = 1/\Sigma p^2_i$, where p_i is the proportion of the prey category in the total biomass of the owl's diet. Trophic niche overlap was measured with Pianka's index, using the percentage of biomass consumed of particular food items ($O_{jk} = \sum p_{ij}\, p_{ik} / \sqrt{\sum p_{ij}^2 \sum p_{ik}^2}$, where p_i is the percentage of prey item "i" in the diet of species "j" and "k") (Pianka 1973). Pianka's index varies between 0 (total separation) and 1 (total overlap). Diet diversity was evaluated with the Shannon diversity index. Overall diet diversity was compared by means of the Hutcheson t-test, which was developed as a method to compare the diversity of two community samples using the Shannon diversity index (Hutcheson 1970).

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For comparison of the food spectrum from forest roosts with roosts within human settlement, we grouped the components of the diet into five prey categories: common vole, other Cricetidae (including all voles except the common vole), Muridae, Soricidae and Aves. The yellow-necked mouse (*Apodemus flavicollis*) and bank vole (*Myodes glareolus*) were considered as typical forest species of small mammals. For forest winter roost no. 1 we did not find any winter roosts meeting the above-defined conditions for control site. For this reason we did not include this winter roost in the analysis.

For eliminating bias caused by different sample sizes (sampling effort), i.e. different numbers of analysed pellets, we used two approaches: in the first (proportional) approach, we used the ratio between the number of prey items of each species and the total number of identified prey items for each particular collection (roost). The relative proportions of diet items were arcsin transformed. This approach was justified by several studies (Varuzza et al. 2001, Charter et al. 2007, Sergio et al. 2008, Kross et al. 2018). Secondly, we used a control for sampling effort (Morand et al. 2015, McElreath 2016), where we regressed the number of long-eared owl prey items found against a number of pellets examined in logarithmic space. A number of diet components were affected by sampling effort (r^2 = 0.095, F = 7.19, P = 0.009). Original values of diet abundance were then replaced with their residual deviations from the regressions in log space and used in subsequent analyses. Differences in transformed diet items between the two kinds of roosts (from both approaches) were analysed by means of Monte Carlo permutation testing for paired individuals with 9999 permutations, for each prey category using the surveillance package (Meyer et al. 2017). All statistical analyses were performed using R software v. 3.2.5 (R Core Team 2018).

Regional comparison of diet was evaluated using the calculations of marked differences from the mean (MDFM, Obuch 2001) with comparison of published data from winter roosts within human settlements in the Hornonitrianska kotlina Basin (Tulis et al. 2015a) and Turčianska kotlina Basin regions (Benešová 2013). The samples in the adjusted results tables are sorted according to their similarity, and the ordering is adjusted so as to have the determining species with positive MDFM values arranged in columns and blocks. These blocks are enclosed in continuous line borders. Species without MDFM are arranged under a dashed line and ranked down according to total abundance. Calculations of the MDFM and contingency tables were carried out in the ZBER software application (Šipöcz 2004).

Results

Diet of owls in forest winter roosts

Altogether, 4995 prey items (129.7 kg of biomass) consisting of 16 mammal species and 10 bird species were identified in pellets from the forest winter roosts (Appendix 1). The common vole was the most frequent prey species in all forest winter roosts with average proportion of relative abundance (mean ± SD) 92.1 ± 5%, range: 82.1–96.6%. Relative abundance of forest mammal prey species (bank vole and yellow-necked mouse) was minimal (1.5 ± 2.4%, range: 0–9.7%).

Diet of owls in winter roosts situated within human settlements

Based on all pellets from winter roosts within human settlements, we identified 5,757 (151.5 kg of biomass) prey items consisting of 18 mammal and 24 bird species (Appendix 2). The common vole was the most frequent prey species in both winter roosts with average proportion (mean ± SD) 84.2 ± 3.6%, range: 79.6–88.9%. The proportion of forest mammal prey species was also minimal, and similar to the proportion in forest winter roosts (1.9 ± 1.5%, range: 0–4.3%).

Comparing the diets between winter roosts situated in forest and in human settlements

Comparing the diets, we recorded a statistically significant higher amount of common vole in the diet of long-eared owls wintering in the forest (Tab. 2). In contrast, the presence of birds was significantly higher in the diet of owls wintering in human settlements. Differences in the presence of other diet groups were not significant (Fig. 3). The results of both applied methods (proportional approach and CFC) were the same (Tab. 2).

Overall food diversity was higher in long-eared owls wintering in human settlements (Shannon index: forest roosts H´= 0.41, human settlements H´= 0.8, Hutcheson t-test: t = 12.7, P < 0.001). The differences in breadth of the food niche between the two winter roosts were minimal: (mean FNB in human settlements ± SD: 1.2 ± 0.2, range: 1.1–1.5; mean FNB in forest roost: 1.4 ± 0.3, range: 1.2–1.9). Pianka's overlap index then showed

Tab. 2. The comparison of prey categories proportion in diet of long-eared owls wintering in the forest and in human settlements using two methods (proportional approach and control for sampling effort approach).
Tab. 2. Porovnanie zastúpenia jednotlivých kategórii koristi myšiarok ušatých zimujúcich v lese a v blízkosti ľudských obydlí použitím dvoch metód (proporčný prístup – proportional approach a prístup kompenzujúci skreslenie, vplyvom rozličného úsilia zberu dát – control for sampling effort approach).

diet / method potrava / metóda	proportional		control for sampling effort	
	t	P	t	P
Microtus arvalis	0.007	0.016	0.009	0.014
other Cricetidae	0.113	0.074	0.177	0.204
Muridae	0.131	0.119	0.093	0.111
Soricidae	0.350	0.278	0.232	0.255
Aves	0.002	0.016	0.005	0.016

high match in the food spectrum between compared pairs of winter roosts (mean ± SD = 0.99 ± 0.003).

Regional differences in diets

Comparing the diets of long-eared owls using the MDFM method, we found regional differences between the diets in the Horná Nitra and Turiec areas. While the proportion of common vole in the diet in forest winter roosts was still higher than in human settlements in both regions, in the Turiec area the abundance of common vole in human settlements was higher (> 95%). In the region of Horná Nitra, the proportion of common vole was lower in human settlements due to higher consumption of various rodent species (Rodentia) and songbirds (Passeriformes). Long-eared owls had become specialized in hunting the common noctule (*Nyctalus noctula*) wintering in adjacent human settlements. Consequently, the diet diversity of winter roosts in the Horná Nitra region was higher in human settlements than in forest winter roosts. The lowest value of diet diversity was in the forest winter roosts in the Turiec region (Tab. 3).

Discussion

A higher proportion of common vole has been recorded in the diet of long-eared owls wintering in the forests. The preferred habitat of the common vole is open agricultural land (Tkadlec & Stenseth 2001, Baláž 2010). During the population peak the common vole sporadically penetrates more deeply into the forest habitat, but it is still linked only with small, open meadows and clear cuts (Zejda et al. 2002), where it survives only until other small mammals expel it as part of the succession process (Tichý 1978). In the Vtáčnik Mountains (where winter roost no. 2 is located), small isolated populations of common vole were confirmed, which survived in small, open areas at an altitude of 1,200 to 1,346 m a.s.l.

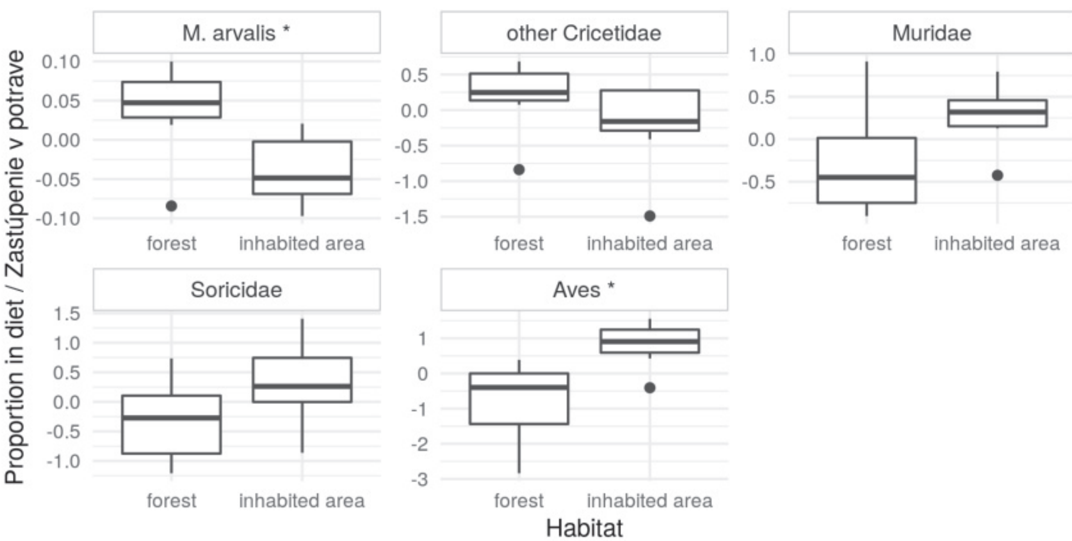

Fig. 3. Results of diet comparison between winter roosts in forest and within human settlements evaluated using the control for sampling effort approach (* = statisticaly significant difference; median, upper and lower quartiles, min–max (whisker) are presented).
Obr. 3. Porovnanie zloženia potravy medzi zimoviskami v lese (forest) a v ľudských obydliach (inhabited area) pomocou prístupu transformácie dát kompenzujúcich skreslenie, vplyvom rozličného úsilia zberu dát (* predstavuje štatisticky preukazný rozdiel; medián, horný a dolný kvartil, min–max sú prezentované v grafoch).

Tab. 3. Comparison of regional differences in long-eared owl diets between the regions of Horná Nitra and Turiec. Numerical data in the table are given in absolute values, and positive and negative deviations (e.g 1+, 2+, 1-, 2-) are marked deviations from the mean (MDFM, Obuch 2001) for the species in these samples (see Methods). H' – diversity index.

Tab. 3. Porovnanie regionálnych rozdielov v potrave myšiarky ušatej medzi regiónmi Horná Nitra a Turiec. Číselné hodnoty v tabuľke sú uvedené v absolútnych hodnotách, kladné a záporné odchýlky (1+, 2+, 1-, 2- a podobne) sú výrazné odchýlky od priemeru (MDFM, Obuch 2001) druhov vo vzorkách (pozri Metodiku). H' – index diverzity.

region / región	**Horná Nitra**			**Turiec**			
years / roky	**2007–14**	**2010–12**	**2007–14**	**2006–18**	**2004–05**		
roost / zimovisko	**setl. / sídlo**	**forest / les**	**forest / les**	**setl. / sídlo**	**forest / les**		
species/ locality	**1**	**2**	**3**	**4**	**5**	**∑**	**%**
Microtus arvalis (n)	8352	1352	2111	6150	1181	19,146	89.59
%	83.99	90.74	92.43	95.63	96.72		
Apodemus sylvaticus	1+ 410	39	1- 23	2- 51	1- 12	535	2.50
Apodemus microps	1+ 12		1	1- 0	1	14	0.07
Mus cf. *musculus*	1+ 30	5	1	1- 7		43	0.20
Terricola subterraneus	1+ 96	14	20	3- 2	1- 0	132	0.62
Nyctalus noctula	1+ 57		1- 0	3- 0		57	0.27
Crocidura suaveolens	1+ 29	4	2	1- 3		38	0.18
Passer domesticus	1+ 189	2- 0	1- 10	2- 14	2- 1	214	1.00
Passer montanus	1+ 40		4	1- 3		47	0.22
Parus major	1+ 78	3	10	2- 9	1- 1	101	0.47
Cyanistes caeruleus	1+ 29		3	1- 1	1	34	0.16
Carduelis chloris	1+ 20	1	3	1- 3		27	0.13
Turdus merula	1+ 20		1	4		25	0.12
Micromys minutus	1+ 231	1+ 37	2- 8	1- 41	1- 9	326	1.53
Apodemus flavicollis	1+ 216	22	1+ 64	2- 40	1- 9	351	1.64
Apodemus agrarius	2- 0			1+ 18		18	0.08
Myodes glareolus	37	11	11	39	4	102	0.48
Muscardinus avellanarius	12		3	2	1	18	0.08
Erithacus rubecula	9			6		15	0.07
Arvicola amphibius	3		2	8	1	14	0.07
Carduelis carduelis	9			1		10	0.05
Sitta europaea	7			1		8	0.04
Sorex araneus	5			2		7	0.03
Sorex minutus	3		1	3		7	0.03
Emberiza citrinella	3		2	2		7	0.03
Fringilla coelebs	6			1		7	0.03
Mammalia	**9501**	**1484**	**2250**	**6369**	**1218**	**20,822**	**97.44**
Aves	**1+ 443**	**2- 6**	**1- 34**	**2- 62**	**3- 3**	**548**	**2.56**
∑	**9944**	**1490**	**2284**	**6431**	**1221**	**21,370**	**100**
H'	**0.84**	**0.48**	**0.44**	**0.30**	**0.20**	**0.60**	

setl. – settlement; Locality / lokalita: 1 – Bojnice (Tulis et al. 2015a), 2 – Vigľaš (our study / naša práca), 3 – Lehota pod Vtáčnikom (our study / naša práca), 4 – Turiec (Benešová 2013), 5 – Budiš (our study / naša práca)

as a consequence of deforestation and grazing in the past (Ambros et al. 1994). These small, open areas represent only refugiums of its occurrence, in comparison to open agricultural land. These habitats are also covered with a compact snow layer during winter, and without snow cover these places can partially represent suitable hunting habitats for long-eared owls, mainly because of their closeness. However, the distance of hunting places from the winter roost does not strictly affect the owls´ preferences. During telemetry study, several individuals occupying winter roost no. 4 hunted every tracked night in a range from several hundreds to several thousand meters, but one individual preferred hunting places 5 km away from the winter roost (Tulis 2013). Long-eared owls search for prey during active flight at low levels (Voous & Cameron 1988), predominantly in open habitats with forest edges and network habitats such as edge banks and treelines (Galeotti et al 1997b, Henrioux 2000, Lövy & Riegert 2013). In our case, clear cuts and fallows can also play the role of open habitats with forest edges. In winter 2012, moreover, an individual from winter roost no. 3 similarly tracked by telemetry was seen avoiding contiguous forest immediately after leaving its winter roost, preferring hunting in open agricultural land and its along edges bordering the forest (Tulis 2013). Our results show a low proportion of forest mammal species in the diet of forest-roosting owls, which indicates that they did not go hunting in forest areas. All these findings point to the conclusion that despite the location of winter roosts in deep forest, the long-eared owls went hunting in the forest only minimally and preferred hunting in open agricultural landscape.

On the other hand, we noticed a significantly higher proportion of birds in the diet of long-eared owls wintering in human settlements. Flocks of songbirds wintering in human settlements are a suitable source of prey for long-eared owls (Moučka 1966, Ginter 1971, Bezzel 1972, Laiu & Murariu 1998, Mori & Bertolino 2015). In larger settlements we can even see an increase in the proportion of synanthropic species of prey for wintering long-eared owls, e.g. brown rat (*Rattus norvegicus*) (Laiu & Murariu 1998, Pirovano et al. 2000, Mori & Bertolino 2015). The incidence of common vole in the diet of both types of winter roosts was over 85%. This result fully correspondends to the diet ecology of the long-eared owl in this European region (reviewed by Birrer 2009). Korpimäki (1992) explains the overall preference for the common vole by the fact that the hunting habitats of long-eared owls are precisely the areas where common voles are numerous, and also due to the voles´ gregarious way of life. Colonies of common voles are thus subjected to greater predation risk than other solitary-living species of voles and mice. The high abundance of common voles, the food niche breadth and the low food diversity at all monitored winter roosts show that there was no decline in the availability of common voles during the monitored period. Data from winter roost no. 4 (but at a different time) confirm that the decrease in the availability of common voles led to a decrease in their diet proportion to under 60% (Tulis et al. 2015a). The natural extension of the food spectrum thus represents a functional response by long-eared owls to the long-term unavailability of common voles caused by fluctuation in their population (Jacob & Tkadlec 2010) or by cycles in their abundance (Lambin et al. 2006), or by short-term unavailability due to meteorological factors (Canova 1989, Tome 2000, Rubolini et al 2003, Romanowski & Zmihorski 2008, Sharikov & Makarova 2014). Extension of the food niche as a response to the decline in the main component of prey is known in several owl species, such as the barn owl (*Tyto alba*) (Horváth et al. 2018) or boreal owl (*Aegolius funereus*) (Korpimäki & Hakkarainen 2012). Our results also suggest regional differences in diets between the compared regions. Spatial heterogenity is often observed in the long-eared owl diet (Tome 2000, Noga 2007, Escala et al. 2009) and also in the diets of other owl species, such as the barn owl (Horváth et al. 2018), tawny owl (*Strix aluco*) (Żmihorski et al. 2008, Obuch 2011), or eagle owl (*Bubo bubo*) (Obuch 2014). This is a consequence of differing land use and regional differences in the quantitative relations of small mammals, which are then reflected in the dietary composition of owls (Horváth et al. 2005, Szűcs et al. 2014).

To date only a few data about the wintering of long-eared owls in deep forests have been published (Armstrong 1958 in Holt 1997, Enriquez-Rocha et al. 1993, Škorpíková et al. 2005, Zaňat et al. 2007). Czarnecki (1956), making reference also to the experience of other researchers in the first half of the 20th century, indicates that wintering colonies of long-eared owls can be found in forests no deeper than 60 to 80 m from their edges. In contrast, winter roosts in human settlements are a relatively common phenomenon nowadays. Škorpíková et al. (2005), moreover, identified the aggregation of long-eared owls in winter roosts in human settlements in this region as a less common phenomenon in the past. The possibility of overlooking a large number of pellets and a high number of owls in the immediate vicinity of human dwellings is hardly likely. The oldest found published information about winter roosts situated within human settlements began appearing at the end of the 19th (1884 in Ružič 2011) and beginning of the 20th century (Bread 1906, Knežourek 1910, Fischer 1919, Spiker 1933). According to Volkov et al. (2005), in the past long-eared owls tended to roost in forest or its margins. Saunders (1919) observed a group of long-eared owls occupying clumps of fir trees near a mountain meadow. Škorpíková et al. (2005) further contend that urban development has also played a major role in the last few decades. Potential reasons why long-eared owls utilize human settlements for their wintering may be the better microclimate and smaller predation risk (Noga 2007, Zvážal & Sviečka 2009, Sharikov et al. 2010). From this point of view, use of human settlements by long-eared owls for wintering, similarly as for nesting (Sharikov et al. 2010), appears to be a feature of synanthropisation, as previously described in the case of other birds of prey and owls (reviewed by Kettel et al. 2018).

After their discovery, all three monitored winter roosts were inspected yearly, but their occupancy was not repeated annually. Winter-roost no. 3 was even abandoned during one winter from December 20, 2011 to January 14, 2012 (Tulis et al. 2015b). From the discovery of winter roost no. 3 (November 22) to its abandonment on December 19, 2011), the average temperature was 1.5 °C, without presence of snow cover (www.ogimet.com). During the absence of the wintering group from December 20, 2011 to January 12, 2012, the average temperature was -2.3 °C and the average snow cover reached 4.9 cm. We do not know where the owls were during this interval. After this time, the weather became warmer and the snow cover melted away. On February 14, 2012, the wintering flock reappeared at the monitored winter roost, and was recorded again during every subsequent inspection until March 2012. Long-eared owls are also typical for their aggregation response to unavailability of prey, whereby during a decline in the vole population they are able to relocate into more plentiful prey areas (Village 1981, Korpimäki 1992, Norrdahl & Korpimäki 1996).

The application of two evaluation methods in our study revealed identical results. However, performing standardization based upon the number of pellets collected by several persons may be partially subjective. In future, it would be advisable to standardize the material based on the weight of analyzed dried pellets, which would seem to be more explicit.

To conclude, our study indicates a preference among long-eared owls for hunting in an open agricultural landscape, regardless of where the winter roost is located. The location of a winter roost in the forest did not lead to increased consumption of forest mammals. While relatively more is known about the winter roosts of long-eared owls situated in human settlements, we have minimal information about their winter roosts located deep in the forest. In any case, with regard to the difficulty involved in discovering them, we cannot say that winter roosts located deep in the forest are less common than those in human settlements. This lack of data points to the need for more intensive study of long-eared owls' winter roosts in forests.

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Appendix1. Diet of long-eared owl within roosts situated in forest.
Príloha 1. Potrava myšiarky ušatej na zimoviskách situovaných v lesnom poraste.

locality / lokalita	1			2			2			2			3			3			3			∑			
winter / zima	2005/2006			2007/2008			2009/2010			2013/2014			2011/2012			2012/2013			2016/17						
	items / kusy		mass / hmotn.	items / kusy		mass / hmotn.	items / kusy		mass / hmotn.	items / kusy		mass / hmotn.	items / kusy		mass / hmotn.	items / kusy		mass / hmotn.	items / kusy		mass / hmotn.	items / kusy		mass / hmotn.	
species / druh	n	%	%	n	%	%	n	%	%	n	%	%	n	%	%	n	%	%	n	%	%	n	%	b(kg)	%
M. arvalis	1181	96.6	96.9	1379	94.1	93.4	471	93.6	94.0	261	82.1	80.9	878	89.2	92.3	132	96.4	97.2	342	92.7	94.1	4644	92.6	122.2	85.2
M. subterraneus				11	0.8	0.5	6	1.2	0.8	3	0.9	0.7	12	1.2	0.9	2	1.5	1.0				34	0.7	0.6	0.5
M. glareolus	4	0.3	0.3	6	0.4	0.4	1	0.2	0.2	4	1.3	1.1	7	0.7	0.6				4	1.1	1.0	26	0.5	0.6	0.5
A. amphibius	1	0.1	0.6	2	0.1	0.9																3	0.1	0.5	0.4
M. minutus	9	0.7	0.1	3	0.2	0.1	3	0.6	0.1	2	0.6	0.1	35	3.6	0.6	1	0.7	0.1	1	0.3	0.1	54	1.1	0.2	0.2
A. flavicollis	9	0.7	0.9	30	2.0	2.5	3	0.6	0.8	31	9.7	12.1	15	1.5	2.0	1	0.7	0.9	6	1.6	2.1	95	1.9	3.1	2.4
A. sylvaticus	12	1.0	0.9	11	0.8	0.7	6	1.2	1.1	6	1.9	1.8	33	3.4	3.3	1	0.7	0.7	5	1.4	1.3	74	1.5	1.8	1.4
A. microps	1	0.1	0.1							1	0.3	0.2										2	0.1	0.04	0.1
M. cf. *musculus*							1	0.2	0.2				4	0.4	0.4				1	0.3	0.3	6	0.1	0.2	0.1
M. avellanarius	1	0.1	0.1	2	0.1	0.1	1	0.2	0.2													4	0.1	0.1	0.1
T. europaea				1	0.1	0.3	1	0.2	0.8													2	0.01	0.2	0.1
C. leucodon										1	0.3	0.1										1	0.01	0.01	0.1
C. suaveolens				2	0.1	0.1													4	1.1	0.2	6	0.1	0.03	0.1
S. minutus				1	0.1	0.1																1	0.01	0.01	0.1
T. merula				1	0.1	0.3																1	0.3	0.1	0.1
P. major	1	0.1	0.1	3	0.2	0.1	6	1.2	0.9	1	0.3	0.2							3	0.8	0.6	14	0.3	0.26	0.2
C. caeruleus	1	0.1	0.1	2	0.1	0.1	1	0.2	0.1													4	0.1	0.04	0.1
P. ater																			1	0.3	0.1	1	0.01	0.01	0.1
C. chloris				1	0.1	0.1	1	0.2	0.2	1	0.3	0.4							1	0.3	0.3	4	0.1	0.1	0.1
P. domesticus	1	0.1	0.1	4	0.3	0.3				6	1.9	2.3										11	0.2	0.3	0.2
P. montanus				3	0.2	0.2				1	0.3	0.3										4	0.1	0.09	0.1
P. pyrhulla																			1	0.3	0.3	1	0.01	0.02	0.1
E. citrinella				1	0.1	0.1	1	0.2	0.2													2	0.01	0.06	0.1
C. cinclus							1	0.2	0.5													1	0.01	0.06	0.1
Mammalia	**1218**	**99.7**	**99.8**	**1448**	**98.8**	**98.9**	**493**	**98.0**	**98.1**	**309**	**97.2**	**96.9**	**984**	**100**	**100**	**137**	**100**	**100**	**363**	**98.4**	**99.0**	**4952**	**99.1**	**129.7**	**99.2**
Aves	**3**	**0.2**	**0.2**	**15**	**1.0**	**1.1**	**10**	**2.0**	**1.9**	**9**	**2.8**	**3.1**							**6**	**1.6**	**1.0**	**43**	**0.9**	**1.1**	**0.8**
∑	**1221**			**1463**			**503**			**318**			**984**			**137**			**369**			**4995**		**130.8**	
Diversity (H´)		0.21			0.36			0.38			0.76			0.51			0.21			0.41			0.41		
FNB		1.06			1.15			1.13			1.49			1.25			1.17			1.05			1.14		

B(kg) – biomass (mass) in kilograms / biomasa v kilogramoch; **Localities / Lokality**: 1 – Budiš, Lehota p. Vtáčnikom, 3 - Viglaš; also in a case when the item proportion of mass (%) was less than 0.1 we used value 0.1 /aj v prípade ak proporcia položky potravy (%) bola menšia ako 0.1 použili sme hodnotu 0.1

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Appendix 2. Diet of long-eared owl within roost situated within human settlements.
Príloha 2. Potrava myšiarky ušatej na zimoviskách v ľudských obydliach.

locality / lokalita								**4**								**5**				**∑**		
winter / zima	**2007/2008**			**2009/2010**			**2011/2012**			**2012/2013**			**2013/2014**			**2016/2017**						
	items / kusy		**mass / hmotn.**	**items / kusy**		**mass / hmotn.**	**items / kusy**		**mass / hmotn.**	**items / kusy**		**mass / hmotn.**	**items / kusy**		**mass / hmotn.**	**items / kusy**		**mass / hmotn.**	**items / kusy**		**mass / hmotn.**	
species / druh	**n**	**%**	**%**	**n**	**%**	**%**	**n**	**%**	**%**	**n**	**%**	**%**	**n**	**%**	**%**	**n**	**%**	**%**	**n**	**%**	**B (kg)**	**%**
M. arvalis	759	84.2	86.1	2278	83.2	83.4	435	87.7	89.6	336	88.9	91.5	739	81.4	81.1	285	79.6	71.4	4832	83.6	127.2	83.7
M. subterraneus	4	0.4	0.3	33	1.2	0.9	7	1.4	1.0	2	0.5	0.4	4	0.4	0.3				50	0.9	0.9	0.6
M. glareolus	1	0.1	0.1	3	0.1	0.1				1	0.3	0.2	7	0.8	0.7				12	0.2	0.3	0.2
A. amphibius				1		0.2							2	0.2	1.5				3	0.05	0.5	0.4
M. minutus	29	3.2	0.5	42	1.5	0.2	4	0.8	0.1	7	1.9	0.3	13	1.4	0.2	16	4.5	0.6	111	1.9	0.4	0.3
A. flavicollis	38	4.2	5.4	67	2.4	3.1	6	1.2	1.6	5	1.3	1.7	13	1.4	1.8				129	2.2	4.2	2.8
A. sylvaticus	21	2.3	2.3	194	7.1	6.7	19	3.8	3.7	9	2.4	2.3	46	5.1	4.8	13	3.6	3.1	302	5.2	7.5	4.9
A. microps					0.3	0.2										1	0.3	0.2	8	0.1	0.2	0.1
M. cf. *musculus*				12	7	0.4	1	0.2	0.2	2	0.5	0.5	5	0.6	0.5	4	1.1	1.0	24	0.4	0.6	0.4
R. norvegicus																6	1.7	14.7	6	0.1	1.6	1.0
M. avellanarius	1	0.1	0.1	1						1	0.3	0.3	5	0.6	0.6				8	0.1	0.2	0.1
C. leucodon										3	0.8	0.2							3	0.05	0.02	0.01
C. suaveolens	3	0.3	0.1	5	0.2	0.1	1	0.2	0.1				2	0.2	0.1				11	0.1	0.1	0.1
N. noctula	1	0.1	0.1	6	0.2	0.2							1	0.1	0.1				8	0.1	0.2	0.1
T. merula	1	0.1	0.5	7	0.3	1.0							3	0.3	1.3	2	0.6	2.0	13	0.2	1.4	0.9
T. philomelos				1		0.1										2	0.6	1.3	3	0.1	0.2	0.1
P. major	11	1.2	0.9	9	0.3	0.2	15	3.0	2.2	4	1.1	0.8	21	2.3	1.6	8	2.2	1.4	68	0.1	1.3	0.8
C. caeruleus	3	0.3	0.1	9	0.3	0.1				2	0.5	0.2	5	0.6	0.2	3	0.8	0.3	22	0.1	0.3	0.2
P. palustris	1	0.1		2	0.1	0.1													3	0.05	0.03	0.02
C. chloris	1	0.1	0.1	5	0.2	0.2							3	0.3	0.4	1	0.3	0.3	10	0.1	0.3	0.2
P. domesticus	19	2.1	2.6	29	1.1	1.3	3	0.6	0.8	3	0.8	1.0	32	3.5	4.3	6	1.7	1.8	92	0.2	2.9	1.9
P. montanus	2	0.2	0.2	11	0.4	0.4	1	0.2	0.2				3	0.3	0.3	1	0.3	0.2	18	0.3	0.4	0.3
S. vulgaris				3	0.1	0.3													3	0.05	0.2	0.1
E. rubecula				1									2	0.2	0.1	3	0.8	0.5	6	0.1	0.1	0.1
G. cristata				1		0.1							1	0.1	0.2	1	0.3	0.4	3	0.1	0.1	0.07
Regulus sp.				2	0.1	0.1	1	0.2	0.1							1	0.3	0.1	4	0.07	0.01	0.01
S. europaea	2	0.2	0.2							2	0.5	0.5				1	0.3	0.2	5	0.09	0.1	0.08
Mammalia	**858**	**95.2**	**95.1**	**2653**	**96.9**	**96.0**	**473**	**95.4**	**96.2**	**367**	**97.1**	**97.5**	**838**	**92.3**	**91.5**	**325**	**90.8**	**90.9**	**5514**	**95.4**	**144.2**	**95.0**
Aves	**43**	**4.8**	**4.9**	**84**	**3.1**	**4.0**	**23**	**4.6**	**3.8**	**11**	**2.9**	**2.5**	**70**	**7.7**	**8.5**	**33**	**9.2**	**9.1**	**264**	**4.6**	**7.8**	**5.0**
Σ	**901**			**2737**			**496**			**378**			**908**			**358**			**5757**		**151.5**	
Diversity (H´)		0.78			0.81			0.61			0.61			1.06			0.93			0.8		
FNB		1.34			1.42			1.24			1.19			1.51			1.9			1.42		

B (kg) – biomass (mass) in kilograms; **Localities / lokality:** 4 – Bojnice, 5. Prievidza; Prey species occurred 1 time (species, locality, year) / Druh koristi s 1 výskytom(druh, lokalita, rok): *E. roumanicus* 4, 2009; *T. torquatus* 4, 2009; *C. cannabina* 4, 2007; *E. citrinella* 4, 2007, *T. troglodytes* 4, 2009; *Sylvia* sp. 4, 2009; *F. coelebs* 4, 2011; *C. coccothraustes* 5, 2017; Prey species occurred 2 times (species, locality, year) / Druh koristi s 2 výskytmi (druh, lokalita, rok): *M. agrestis* 4, 2007, 2009; *S. araneus* 4, 2009, 2012; *S. minutus* 4, 2009, 2013; *P. ater* 4, 2007, 2009; *P. pyrrhula* 4, 2011; *C. carduelis* 5, 2017; *C. spinus* 5, 2017; also in a case when the item proportion of mass (%) was less than 0.01 we used value 0.01 /aj v prípade ak proporcia položky potravy (%) bola menšia ako 0,01 použili sme hodnotu 0,01