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Responses of the long-eared owl *Asio otus* diet and the numbers of wintering individuals to changing abundance of the common vole *Microtus arvalis*

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Abstract: Opportunistic predator like the long-eared owl is able to respond to population fluctuations of its main prey. The composition of the winter diet of this owl species was investigated during the period of 13 winters (1992–2000, 2006–2011) in agricultural areas in Slovakia. In total, we found 23 mammal species and 33 bird species ($H' = 0.82$) in pellets. The frequency of the dominant prey species, the common vole, varied from 57.7% to 92.4%. Our data show that the abundance of the common vole: (i) had biggest impact on the food niche breadth of the long-eared owl; (ii) when in decline, it was significantly compensated by the increase in the amount of 15 other accessory species (subject to the specific diet offered during the study winters); (iii) was positively correlated with the number of owls in the winter-roost, which varied during the 13 studied winters.

Key words: long-eared owl; prey, pellets; winter-roost; common vole fluctuation

Introduction

Food abundance and availability are important factors in habitat quality and have a strong influence on the population dynamics of a species (Klok & de Roos 2007). Birds of prey are well known for their dependence on the availability of prey, which may be affected by several factors. Structure of vegetation (Aschwanden et al. 2005), height of the vegetation cover (Sheffield et al. 2001; Šálek & Lövy 2012) and agricultural practices at the end of summer (which destroy rodents' sheltered habitats and expose them to higher risk of predation) (Huitu et al. 2004) belong to the most important factors increasing or decreasing the prey effectiveness of raptors. Weather conditions, mainly precipitation, are also known factor that often correlates with total food abundance or prey species structure (Rubolini et al. 2003; Romanowski & Żmihorski 2008; Sharikov & Makarova 2014). The abundance of some prey species may also be affected by their fluctuations (Korpimäki & Norrdahl 1991; Huitu et al. 2004), which may be synchronal over hundreds of square kilometres (Norrdahl & Korpimäki 1996, Sundell et al. 2004).

Overall the effect of diet availability is obvious not only in breeding density (Sergio et al. 2008), reproductive success (Korpimäki 1992; Kouba et al. 2014), or spatial activity of fledglings (Kouba et al. 2013) and adults birds (Galeotti et al. 1997), but also in the synchronization of numerical responses of wintering raptors to fluctuation of prey density (Norrdahl & Korpimäki 1996).

The long-eared owl *Asio otus* (L., 1758) is a nocturnal hunter, which prefers open lands (Galeotti et al. 1997; Hagemeijer et al. 1997), and its abundance is negatively affected by greater proportion of the forested land (Żmihorski et al. 2012). During the winter, the individuals spend daytime on communal roosting sites. These winter-roosts are often located in groups of coniferous trees, and formed from August – September to March – April (Wijnandts 1984). The winter-roosts are partially formed by closely related individuals (Galleoti et al. 1997).

The long-eared owl is an opportunistic predator (Tome 1991; Bertolino et al. 2001; Shao & Liu 2006), whose preferred prey is the common vole *Microtus arvalis* (Pallas, 1778) in most of Europe (reviewed by Birrer 2009). Populations of the common vole characteristically fluctuate over several years (Jacob et al. 2013). While population outbreaks of the Common vole are cyclical in Western Europe and Fennoscandia (Lambin et al. 2006), populations in other regions of Europe seem to fluctuate irregularly (Jacob & Tkadlec 2010). These fluctuations lead the owls to relocate to areas with a higher density of their preferred prey. Birds of prey like the long-eared owl, which are specialized in hunting a fluctuating prey, are ordinarily nomadic and able to move to more plentiful prey areas (Andersson 1980). The number of wintering long-eared owls is thus strongly affected by the abundance of the common vole (Sharikov et al. 2013) and decreases in the years of the common vole population collapse.

The pattern of the vole's population fluctuation is also reflected in the proportion of this species in the diet of the long-eared owl (Wijnandts 1984; Korpimäki & Norrdahl 1991; Korpimäki 1992). However, the majority of published papers regarding the winter diet of the long-eared owl present findings from the time periods shorter than one vole cycle (Tome 2003) and only few publications deal with long-term diet data sets. These studies found 3-year periods of fluctuations (Schmidt 1975; Bethge 1982; Wijnandts 1984) or 5 to 6-year fluctuations (Tome 2003). Low populations of the common vole are partially compensated by the amount of subdominant species (most often mice of the genus *Apodemus*) in the owl diet (Obuch 1989).

In this study we investigated the composition of the winter diet of the long-eared owl. We analyzed osteological material obtained from owl pellets during 13 winters with different proportion of the common vole in the diet.

The aims of this study were to evaluate: (i) responses of long-eared owl winter diet composition to the availability of the common vole; (ii) responses of long-eared owl numbers to changing availability of the common vole in diet during 13 winters.

Material and methods

Study area

The study was conducted in the western part of the Prievidzská kotlina basin in central Slovakia. The winter-roost of owls was located in spruce trees (*Picea* sp.) situated in the Bojnice-Spa area (48°46′ N, 18°34′ E, 317 m a.s.l.). In the vicinity of winter-roost, there were extensively exploited fields and meadows. The winter climate is characterized by cold weather with average temperatures of 1.3 °C and precipitation of 40.7 mm/month.

Diet analyses and counting of owls

The winter-roost location in Bojnice-Spa was monitored over the winters 1992–1993 to 1999–2000 and 2006–2007 to 2010–2011. Pellets were collected once per winter (at the end of winter) during the first two winters. From the winter 1994–1995 till the end of the study the collections were gathered in monthly periods (54 collections). Pellets 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 Veselovský et al. (2012). Bird bones were identified using a reference collection. The determination of birds was based on bills (rostrum), tarsometatarsi (tarsometatarsus), humeral (humerus) and metacarpal bones (metacarpus). The number of individuals of identified prey was estimated as the minimal number of individuals, which we were able to identify according the same anatomical parts of bones (Klein & Cruz-Uribe 1984).

The long-eared owls on the winter-roost were counted once a year (in January) during first two winters (1992–1993 and 1993–1994) on the winter-roost and once a month during their departure from the roost in the evening from the winter 1994–1995 till the end of the study (54 controls). The owls were counted by cooperation of two persons in the same day as pellets were collected.

Statistical analyses

The breadth of food niches (FNB) of owls during all particular controls was estimated using the formula by Levins (1968): $B = 1/\Sigma p_i^2$, where p_i is the proportion of the prey category in the total biomass of the owl's diet. Species biomass was calculated as the number of individuals of each species multiplied by the average body mass. The body mass of small mammal species was taken from Korpimäki & Sulkava (1987), Baláž & Ambros (2006) and Baláž et al. (2013) and the body mass of birds was taken from Hudec et al. (2005). The above-average and below-average preyed species were evaluated using Marked differences from the mean method – MDFM (Obuch 2001) in the ZBER software application (Šipöcz 2004). Levels of deviations for each item are represented by number before sings "+" for above-average deviation or "– "for below-average deviation from the mean. Samples in real values are placed in contingency table, sorted according to their similarity and the ordering is adjusted so that determining species with positive MDFM values are arranged in columns and blocks. Less abundant species are given below the table. Shannon diversity indices (H') were used for trophic diversity and given in the bottom row of the table.

STATISTICA 8.0 portable software (StatSoft Inc. 2007) was used for Spearman rank correlation analysis between the proportions of the common vole in diet and (i) number of long-eared owls on winter-roost; (ii) number of above-average preyed species in diet; (iii) width of the food niches. A discriminant function analysis was used to define accessory prey species from 11 winter seasons (except 1992–1993 and 1993–1994, due to the absence of results obtained by monthly monitoring in this time).

Results

Altogether, 11,555 pellets of long-eared owl were collected over the 13 non-breeding seasons. From these, 32,884 prey individuals were identified, formed by 23 mammalian species and 33 bird species. In relative numbers, the diet was comprised of 95.4% mammals and 4.6% birds. The common vole was the most dominant prey species found during all studied winters, constituting more than 84% of the prey items by both, number and mass (Table 1). Its frequency varied from 57.7 to 92.4%. Two declines of common vole were observed in winters 1996–1997 and 2006–2007.

The number of owls in the winter-roost location varied during the 13 studied winters (mean 12 ± 6.6 SD, range: 5–28 per winter, Coefficient of variation = 54.6%). The number of wintering owls during the common vole decline was six in 1996–1997 and five in 2006–2007. Based on monthly controls, the number of owls correlated positively with the relative abundance of the common vole in the diet (Spearman rank correlation: $r_s = 0.75$, $n = 56$, $P < 0.001$; Fig. 1).

Relatively large differences were found in diet composition of the owls during the study winters (Discriminant analysis: F (290.17) = 2.59 $P < 0.001$; Fig. 2).

Table 1. Diet composition of wintering long-eared owls, given as prey number and prey mass.

Prey	Prey items		Prey mass	
	No.	%	g	%
Microtus arvalis (Pallas, 1778)	27720	84.1	26.3	84.6
Microtus subterraneus (de Sélys-Longchamps, 1836)	284	0.9	18.7	0.6
Clethrionomys glareolus (Schreber, 1780)	104	0.3	23.0	0.3
Apodemus flavicollis (Melchior, 1834)	1036	3.2	33.0	4.0
Apodemus. sylvaticus (L., 1758)	1168	3.6	24.9	3.4
Nyctalus noctula (Schreber, 1774)	57	0.2	26.5	0.2
Mus musculus (L., 1758)	102	0.3	15.0	0.2
Micromys minutus (Pallas, 1771)	753	2.3	8.0	0.7
Rattus norvegicus (Berkenhout, 1769)	14	0.0	258.0	0.4
Passer domesticus (L., 1758)	781	2.4	32.0	2.9
Passer montanus (L., 1758)	100	0.3	23.0	0.3
Carduelis chloris (L., 1758)	54	0.1	30.0	0.2
Turdus merula (L., 1758)	62	0.2	106.5	0.8
Other prey items (frequency < 0.1%)				
No. of prey items	649	2.0		1.6
No. of species	46			
$\sum$	33.884	—	862.4 (kg)	–

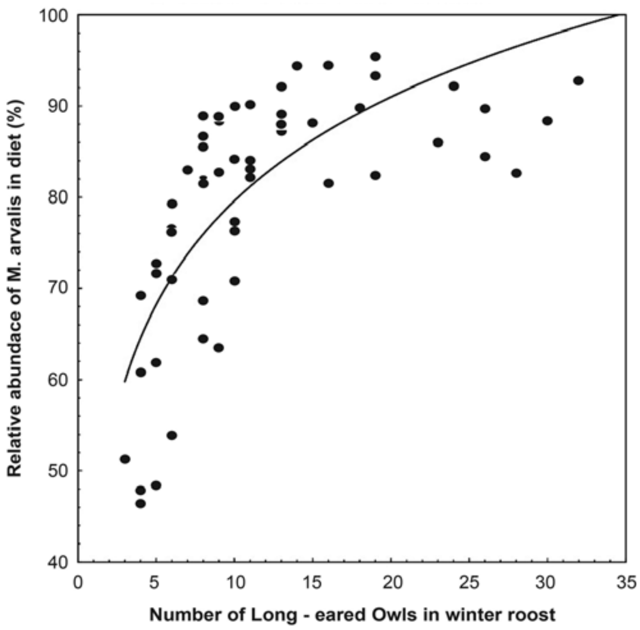

Fig. 1. Relationship between the proportion of *Microtus arvalis* in diet and number of long-eared owl on winter-roost based on monthly counts.

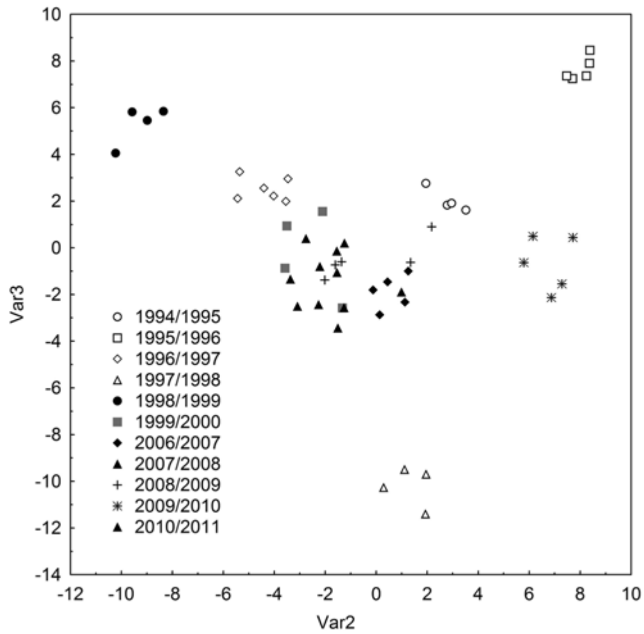

Fig. 2. Differences between diet compositions of long-eared owls during study winters based on monthly pellets collection.

Variation of the common vole was not the only factor responsible for the differences between seasons. Fifteen other species were characterized as species with significant impact on food composition (Table 2).

The lower abundance of the common vole in the diet led to the hunting other prey species and had an impact on the food niche breadth of long-eared owl (Fig. 3) that varied from 1.09 to 3.79. There was a negative significant relationship between the common vole abundance in the diet and the long-eared owl food niche breadth (Spearman rank correlation: $r_s = -0.99$, $n = 56$; $P < 0.001$).

The number of above-average preyed species in studied winters varied from zero to 12 and was negatively correlated with dominance of the common vole in the prey of the study winters (Spearman rank correlation: $r_s = -0.84$; $n = 13$ $P < 0.001$). The most common prey species in winters with lower abundance (1996–1997, 2006–2007) of the common vole were flock bird species such as tits (Paridae), sparrows (Passeridae), and cardueline finches (Fringilidae). The long-eared owls preyed more often on yellow-necked mouse *Apodemus flavicollis* (Melchior, 1834), bank vole *Clethrionomys glareolus* (Schreber, 1780) or on the harvest mouse

Table 2. The accessory prey species in winter diet of Long-eared owl during studied winters.

Species	Wilks' Λ	F-remove	Toler.	*P*
Microtus subterraneus (de Sélys-Longchamps, 1836)	3.68 E-07	3.74	0.103	< 0.05
Clethrionomys glareolus (Schreber, 1780)	4.05 E-07	4.25	0.103	< 0.01
Apodemus flavicollis (Melchior, 1834)	6.91 E-07	8.32	0.040	< 0.001
Mus musculus (L., 1758)	3.16 E-07	2.99	0.151	< 0.05
Micromys minutus (Pallas, 1771)	5.36 E-07	6.12	0.233	< 0.001
Sorex minutus (L., 1766)	4.22 E-07	4.50	0.033	< 0.01
Passer domesticus (L., 1758)	4.04 E-07	4.25	0.066	< 0.01
Passer montanus (L., 1758)	3.01 E-07	2.78	0.050	< 0.05
Carduelis carduelis (L., 1758)	5.28 E-07	6.00	0.078	< 0.01
Carduelis spinus (L., 1758)	3.29 E-07	3.18	0.120	< 0.05
Coccothraustes coccothraustes (L., 1758)	2.85 E-07	2.56	0.047	< 0.05
Parus ater (L., 1758)	4.23 E-07	4.51	0.029	< 0.01
Sitta europaea (L., 1758)	3.01 E-07	2.78	0.097	< 0.05
Erithacus rubecula (L., 1758)	2.97 E-07	2.72	0.100	< 0.05
Turdus merula (L., 1758)	4.25 E-07	4.55	0.091	< 0.01

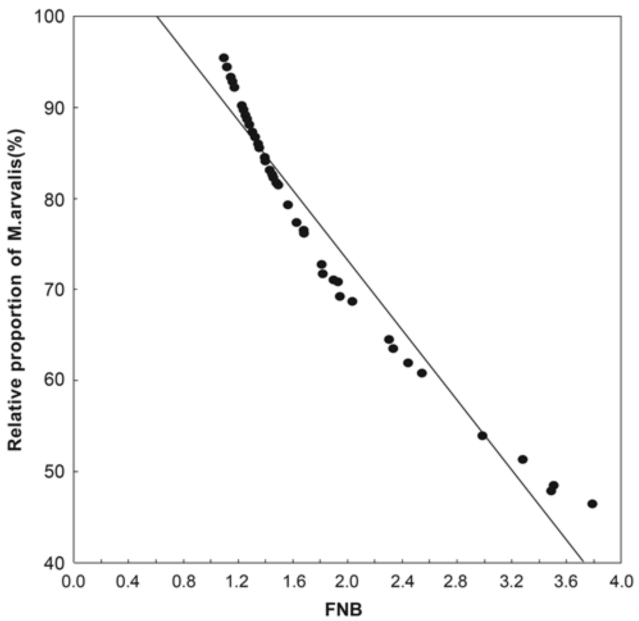

Fig. 3. Variation in the relative abundance of common vole and variation in food niche breadth (FNB) of the long-eared owls during 13 winters.

Micromys minutus (Pallas, 1771) during these winters (Appendix 1).

Discussion

In general, the main source of owl diet are those prey species that are the most numerous in the occupied habitat (Mikkola 1983). The long-eared owls are adapted to hunt in open fields where they mainly hunt the common vole (e.g., Obuch 1982; Wijnandts 1984; Tome 2003; Romanowski & Żmihorski 2008; Kitowski 2013, Sharikov et al. 2013). In synthesis of 312 studies of the long-eared owl diet, Birrer (2009) found the dominance of the common vole in Central Europe with the average representation of 81.6%. These findings are in accordance with our results from the locality where farmland was the predominant habitat, in the 5-kilometre radius from the winter-roost location. The mean proportion of the common vole in the diet was 84.1% with two distinct declines (57.7% and 59.3%) in winters with low numbers of observed owls in roost location. Correlation between proportion of the common vole in diet and number of owls in the winter-roost is fully in accordance with the theory of synchronization of numerical responses of wintering raptors to fluctuation of prey density (Galushin 1974; Korpimäki & Norrdahl 1991).

Proportionate declines of the common vole in the long-eared owl diet can be explained by the well-known fluctuation of the common vole population (Wijnandts 1984; Korpimäki & Norrdahl 1991; Korpimäki 1992; Tome 2003). Explosive increases of numbers followed by dramatic declines are mostly repeated in several years' fluctuations of voles (Jacob et al. 2013). Although the common vole fluctuations have affect to diet irrespective of their regularity and region (Schmidt 1975; Bethge 1982; Wijnandts 1984; Korpimäki 1992; Tome 2003), the weather conditions may also be influencing the diet composition in winter. The snow cover can decrease availability of voles but also increase availability of mice (Romanowski & Żmihorski 2008; Sharikov & Makarova 2014). Similarly, higher rainfall amounts can contribute to higher proportion of preyed birds as an alternative diet of owls (Sharikov & Makarova 2014).

Overall, the low availability of the common vole leads the long-eared owls to change hunting habitats (Romanowski & Żmihorski 2008) and to hunting other species that represent only marginal part of the diet in years with a higher abundance and availability of the common vole (Schmidt 1975; Bethge 1982; Obuch 1989; Tome 2003). Owls in present study most probably changed hunting habitats to forest edges and parks where they mainly hunted murids, tits and sparrows. We found significant negative correlation between the number of common vole and the number of above-average preyed species and between the dominance of this rodent species and the long-eared owl food niche breadth. These findings are in accordance with other studies (Bethge 1982; Schmidt 1975; Tome 2003;

Sharikov & Makarova 2014), in which the decline of the common vole was compensated by other species. The mice of the genus *Apodemus*, mainly the wood mouse *Apodemus sylvaticus* (L., 1758) are the most common substitute prey species. In addition, the lower availability of the common vole is sometimes reflected in higher proportion of birds in long-eared owl diet (Bethge 1982; Obuch 1989; Sharikov & Makarova 2014). In the present study mainly five bird species compensated lower abundance of the common vole (Appendix 1).

To conclude, the long-eared owl can exploit a wide range of food sources and change its diet according to the local food base (Lesiński 2010; Pirovano et al. 2000). We examined more than 50 mammalian and bird species preyed by wintering long-eared owl in the study location during 13 winters. Fifteen of them were classified as species with significant impact on total diet composition. The low density of voles was primarily compensated by hunting higher amounts wood mouse, yellow-necked mouse, harvest mouse, house sparrow *Passer domesticus* (L., 1758), and great tit *Parus major* (L., 1758). The other prey species, of which the abundance increased only in some winters, represented only a temporary alternative prey. Diet of most of the winters varied from year to year. This was likely caused by the fact that as opportunistic predators, the long-eared owls hunted the most available prey, which varied during the study seasons (except the common vole).

Among interesting findings were the detections of the juvenile common hare *Lepus europaeus* (Pallas, 1778), white-breasted hedgehog *Erinaceus roumanicus* (Barret-Hamilton, 1900), common dormouse *Muscardinus avellanarius* (L., 1758) and common noctule *Nyctalus noctula* (Schreber, 1774). Common hare is an unusually big prey species for the long-eared owl and white-breasted hedgehog and common dormouse belong to hibernating species with limited activity during winter. However, some information about common dormouse presence in the winter diet of the long-eared owls are known (Galeotti & Canova 1994; Tome 1994; Cecere et al. 2013). Common noctule was detected as an alternative prey species with relatively high dominance (8.8%) during the winter 2006–2007. Bats are generally considered a rare prey of the long-eared owl. From the more than 26,000 food items found, only 0.003% of those ones were related to bats (Schmidt & Topal 1971; Obuch 1998). Their increased occurrence in long-eared owl diet usually correlates with the low numbers of rodents and the clustered occurrence of bat groups around long-eared owls roosting places (García et al. 2005).

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Appendix 1. Winter diet of long-eared owl during 13 winters evaluated by MDFM method.

Species \ Winter	92/93	93/94	94/95	95/96	96/97	97/98	98/99	99/00	06/07	07/08	08/09	09/10	10/11	Total	%
Microtus arvalis	673	1222	2604	6794	1- 1601	2120	4015	1849	1- 301	759	1795	2278	1709	27720	84.13
Carduelis chloris	1+ 7		2	18	5	2	1- 1	2	5	1	2	5	4	54	0.17
Parus ater		1	2+ 15	1- 1	4	2	1			1	1	1		27	0.08
Sitta europaea			1+ 7	4	5			1		2	1		2	22	0.07
Carduelis spinus			1+ 6	3	3	1	3				1			17	0.05
Turdus merula	4	1	1+ 14	1- 6	1+ 15	1- 1	1- 1	3	1	1	2	7	7	62	0.19
Parus major	1	6	2+ 49	1- 26	1+ 27	14	1- 10	1- 5	1+ 8	1+ 11	1- 1	1- 9	9	176	0.54
Coccothraustes coccothr.		1		1+ 9	2	2							1	15	0.05
Microtus subterraneus	1- 2	2- 0	3- 0	1+ 100	33	19	32	14	2	4	18	33	1+ 27	284	0.88
Parus caeruleus		4	6	11	1+ 11	3	1- 3	2	2	3	2	9	6	62	0.19
Sorex minutus			1	1	1+ 9						1	1		13	0.04
Crocidura suaveolens		1	5	2- 1	2+ 35	1- 1	7	7		3		5	1+ 18	83	0.26
Apodemus sylvaticus	25	40	118	2- 105	2+ 293	99	1- 94	1- 58	12	1- 21	50	1+ 194	1- 59	1168	3.60
Apodemus uralensis			4	1- 1	1+ 8		1				3	1+ 7	1	25	0.08
Apodemus flavicollis	1- 8	2- 6	94	214	2+ 311	1- 68	1- 58	1+ 85	1+ 41	38	2- 10	1- 67	1- 36	1036	3.19
Passer domesticus	1+ 27	28	67	1- 144	2+ 231	1- 44	1- 64	1- 25	2+ 54	19	1- 23	1- 29	1- 26	781	2.40
Passer montanus	1	1	6	18	1+ 18	9	8	3	1+ 8	2	8	11	7	100	0.31
Mus musculus	2	6	5	1- 9	1+ 28	1+ 22	1- 4	4	4		4	12	1- 2	102	0.30
Micromys minutus	2- 3	3- 2	76	2- 62	1+ 85	2+ 294	3- 16	2- 8	10	1+ 29	42	1- 42	1+ 84	753	2.28
Clethrionomys glareolus	2	1	1- 4	17	11	8	15	1+ 17	1+ 7	1	1	1- 3	1+ 17	104	0.32
Nyctalus noctula			1- 0	2- 0	1- 0	1- 0	1- 0		4+ 45	1	5	6		57	0.18
Carduelis carduelis				7	5	3	3	1	2		3		4	28	0.09
Regulus sp.		2		5	2	2	2		1			2	1	17	0.05
Erithacus rubecula	1			3	2	1	1		4		2	1	1	16	0.05
Emberiza citrinella	2	2	1	3	4	1				1				14	0.04
Rattus norvegicus	1	1	2	7	2		1							14	0.04
Turdus pilaris	1			1	5	1								8	0.04
Fringilla coelebs	1	1	2	3					1		1		3	12	0.04
Troglodytes troglodytes			1	2	1	2	1	1			2	1	2	12	0.04
Muscard. avellanarius				1	2	3				1	3	1	1	12	0.03
Carduelis cannabina				4	4					1				9	0.03
Galerida cristata				5		1						1		7	0.02
Mammalia	716	1280	2913	7317	2420	2635	4243	2046	422	858	1933	2653	1957	30 711	95.40
Aves	46	50	1+ 186	1- 279	2+ 356	1- 93	1- 101	1- 45	2+ 86	43	1- 51	1- 84	78	1481	4.60
Total	762	1330	3099	7596	2776	2728	4344	2091	508	901	1984	2737	2035	32 192	100
Diversity index H'	0.60	0.45	0.80	0.59	1.60	0.93	0.43	0.60	1.55	0.78	0.61	0.81	0.80	0.82	

Other species (winter-quantity): *E. roumanicus* (09/10-1), *T.europaea* (99/00-1), *S. araneus* (95/96-1; 09/10-1; 10/11-2), *N.anomalus* (10/11-1), *R. hipposideros* (95/96-1), *L.europaeus* (95/96-1; 97/98-1; 08/09-1), *G. glis* (93/94-1), *A. terrestris* (95/96-3; 09/10-1), *M. nivalis* (99/00-1), *D. medius* (96/97-1), *D. urbica* (96/97-1), *M. alba* (93/94-1), *M. cinerea* (96/97-1), *S. communis* (95/96-1; 96/97-2), *Sylvia* sp, (96/97-1; 98/99-1; 09/10-1), Sylviidae sp, (95/96-1), *P. ochruros* (96/97-1), *T. torquatus* (09/10-1), *T. iliacus* (95/96-1), *T. philomelos* (08/09-2), *A. caudatus* (95/96-2; 96/97-1), *P. paustris* (93/94-2; 94/95-1; 07/08-1; 09/10-2), *F.montifringilla* (94/95-4; 95/96-1; 10/11-1), *P.pyrrhula* (94/95-2; 99/00-1), *S.serinus* (92/93-1), Fringillidae sp, (95/96-1; 97/98-4; 98/99-2), Passeriformes sp, (94/95-3; 95/96-1; 10/11-2), *S. vulgaris* (96/97-4), *M. agrestis* (97/98-1; 99/00-2; 07/08-1; 09/10-1)