

Weather conditions explain variation in the diet of Long-eared Owl at winter roost in central part of European Russia

Alexander Sharikov* & Tatiana Makarova

The Research Group of Avian Population Ecology, Zoology and Ecology Department, Moscow Pedagogical State University, Kibalchicha str. 6 – 5, 129164, Moscow, Russia.

** Corresponding author's e-mail: avsharikov@ya.ru*

Received 7 November 2012, accepted 6 February 2014

The influence of weather conditions on the winter diet of the Long-eared Owl was studied in 2005–2013 at one roost site in Moscow, Russia. Pellets were collected every week from November to March. The diet composition of the owls included 6 rodent species, 2 insectivore species and 18 bird species. Common Vole was by far the most frequent prey (70.0%), followed by Ural Field Mouse (10.8%) and Brown Rat (7.5%). Among bird prey (5.3%), House Sparrow, Great Tit, Bullfinch, Tree Sparrow and Blue Tit were the most numerous species. The winter diet showed marked interannual fluctuations. In terms of weather conditions, depth of snow cover appears to be the most important factor affecting the availability of the most frequent prey species and prey groups in the diet of the Long-eared Owl. Wind speed and precipitation do not play a significant role in predating on voles and mice. The proportion of bird prey was relatively low, but increased with precipitation, indicating the high importance of birds as an alternative prey for owls. The results thus suggest that specific features of behavior and activity of prey in different weather conditions explain their proportions in the diet of the Long-eared Owl.



1. Introduction

Diet composition of birds of prey is commonly determined by the abundance of their main prey species. At the same time, some significant changes in the diet might take place in response to environmental conditions, particularly weather, which affects availability of prey and the hunting success of the predator (Nilsson 1981, Wijnandts 1984, Rubolini *et al.* 2003, Birrer 2009). Winter seems to be the time when such an influence of weather on the diet might be the strongest.

The diet composition of Long-eared Owl (*Asio otus*) during the winter season has been a frequent

subject of investigations, mainly due to the relative ease of pellet collection. In Europe, many studies have been carried out in Italy (Canova 1989, Galeotti & Canova 1994, Pirovano *et al.* 2000, Rubolini *et al.* 2003) and in other parts of southern and eastern Europe, including Spain (Escala 2009), Greece (Alivizatos & Goutner 1999), Romania (Laiu & Murariu 1998, Sándor & Kiss 2008, Benedek & Širbu 2010), Slovenia (Tome 1994), and Bulgaria (Milchev *et al.* 2003), where the owls' aggregations in winter may be composed of tens to hundreds of individuals. There are also numerous studies from central and northern parts of Europe, for example from the Netherlands (Wijnandts

1984), Poland (Romanowski & Źmihorski 2008), and southern Sweden (Nilsson 1981). In the European part of Russia, the number of studies dealing with winter diet of the Long-eared Owl is relatively low, with the majority being made within the Moscow Region (Kalyakin 2009, Sharikov *et al.* 2009), Tula Region (Shvets 1998, Shvets & Novokhatka 2003) and Stavropol krai (Sharikov 2006).

However, very few studies analyzing seasonal changes in diet have focused on weather conditions (Nilsson 1981, Wijnandts 1984, Canova 1989, Bencová *et al.* 2006, Romanowski & Źmihorski 2008). A comprehensive study to reveal the role of weather in the diet changes of owls seems to be important for understanding their adaptation to harsh winter conditions. Therefore, the aim of the current study was to assess the relative contribution of weather conditions and its influence in the variability of the owls' diet composition during the winter.

2. Material and methods

2.1. Study site

The fieldwork was carried out in a parkland located in the southwestern part of Moscow city (55°41' N, 37°31' E), European Russia. The total area of the park was 68 ha, mostly spacious open green areas with groups of trees (birches, larches, spruces, pine trees), of which the study site, consisting of three groups of Norway spruces (*Picea abies*), covered about 11.9 ha. The park was surrounded by the built-up area. Owls occupied the same spruce trees throughout the studied years. The number of individuals at the roost site varied from 1 to 5 individuals. In some years the owls temporarily left the roosting site for 1–2 weeks.

2.2. Data collection

Long-eared Owl's pellets were collected at the daily roost once a week from November–December to February–March (depended on the roost duration) from 2005–2013. All pellets were examined using standard techniques (Galushin 1982). Prey remains were identified using taxonomic

keys (Gromov & Erbaeva 1995). Data on the twin-species Common vole (*Microtus arvalis* and *M. rossiaemeridionalis*) were pooled due to the difficulty of identification by skeleton remains. Bird remains were identified to the species level with the aid of the scientific ornithological collection of the zoology and ecology department of Moscow pedagogical state university.

Meteorological data used in the analysis were taken from the meteorological station # 27612 (55°50' N, 37°37' E) located 18.2 km north of the study site. Four weather variables – mean daily air temperature (°C), snow depth (cm), wind speed (m/sec) and amount of precipitation (mm) – averaged for the week before the day of roost inspection were used in the analyses.

2.3. Data analysis

Total proportions of different prey in the diet composition were calculated as the ratio between number of prey items of each species and the total number of identified prey items for the time interval studied. Proportions of bird species were pooled.

Variation in the diet of wintering owls was studied using a Generalized Linear Model (GLM) with logit link function and binomial error distribution (Zuur *et al.* 2009). To fit the model we used the *aod* package (Lesnoff & Lancelot 2012) in R (version 2.15.21; R Core Team 2012). For the analysis of the prey proportion of rodents and birds in a weekly pellet sample ($n = 110$), the number of an observed specific prey item and the total number of prey items, were used as response variables in models. Correlations between independent variables were tested, showing a high correlation between temperature and snow depth, and otherwise low correlations. To assess weather factors affecting the diet, we first simplified them with a Principal Component Analysis (PCA). The PCA produced one factor (Temp/Snow) with eigenvalues higher than 1 (which together explained more than 75% of the variance). Factor loadings of temperature and snow depth had high absolute values (more than 0.7) with alternative coefficients – positive for temperature and negative for snow. The effect of year was included in the model as a categorical variable accounting for that the samples from different years could not be regarded as independent.

Table 1. The proportion and number of more frequent prey species identified in Long-eared Owl pellets at the winter roost in Moscow.

Prey/Winter	Dietary percent by number (%)								Total	
	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	<i>n</i>	%
<i>Microtus arvalis s.l.</i>	43.3	85.2	80.7	62.9	61.9	89.1	91.5	56.7	2,637	70.0
<i>Apodemus uralensis</i>	17.5	6.9	5.7	9.3	14.0	5.4	1.9	20.5	408	10.8
<i>Apodemus agrarius</i>	15.2	1.4	3.7	1.6	6.4	–	–	3.6	142	3.8
<i>Rattus norvegicus</i>	10.3	4.1	4.6	18.4	7.3	2.0	1.4	7.3	282	7.5
<i>Mus musculus</i>	1.9	–	0.3	2.4	0.9	0.6	–	2.1	43	1.1
Other mammals	3.4	–	0.7	0.2	3.7	0.9	1.1	1.8	58	1.5
Mammalia	91.6	97.6	95.7	94.8	94.2	97.9	95.9	92.0	3,570	94.7
<i>Passer montanus</i>	0.8	0.5	1.2	0.3	0.9	0.6	0.3	1.5	32	0.8
<i>Passer domesticus</i>	0.4	–	0.2	1.2	1.4	–	1.4	2.8	42	1.1
<i>Parus major</i>	0.8	–	0.6	1.0	1.1	–	0.8	1.9	35	0.9
<i>Cyanistes caeruleus</i>	3.4	0.5	0.3	0.5	0.8	–	–	–	20	0.5
<i>Pyrrhula pyrrhula</i>	2.6	0.9	1.3	1.0	0.8	–	0.5	0.6	35	0.9
Other birds	0.4	0.5	0.7	1.2	0.8	1.5	1.1	1.2	36	1.0
Aves	8.4	2.4	4.3	5.2	5.8	2.1	4.1	8.0	200	5.3
Total number	263	217	680	582	642	348	366	672	3,770	100

To explain the relationship between the proportion of prey in the diet and various weather conditions we used the Akaike's Information Criterion (corrected for finite sample sizes, AICc; Burnham & Anderson 2002), generating a rank from the best to the least supported model. Competing models for the same response variable were evaluated by means of Akaike weights ranging from 0 to 1, with higher values signifying better models (Johnson & Omland 2004). Differences in AICc (Δ AICc) larger than 2 were considered to indicate relevant support in favor of the model with lower AICc (Burnham & Anderson 2002). Models were compared using the dredge function of the MuMIn (Bartoń 2013) package in R (version 2.15.21; R Core Team 2012).

3. Results

3.1. Diet variability

The total number of prey remains found within the pellets of Long-eared Owls at the local roost site amounted to 3,770. As expected, small mammal remains (94.7%) far exceeded those of birds. The prey spectrum of the owls in the study area in-

cluded 6 rodent species, 2 insectivore species and 18 bird species. Among mammals, Common vole (*Microtus* spp.) was by far the most frequent prey (70.0%) while among additional prey, the proportions of Ural field mouse *Apodemus uralensis* (10.8%) and Brown rat *Rattus norvegicus* (7.5%) were relatively high. Birds were found only in 64 of 110 samples. However, their total share in owls' winter diet (5.3%) was rather noticeable, mainly consisting of House Sparrow *Passer domesticus* (1.1%), Great Tit *Parus major* (0.9%), Bullfinch *Pyrrhula pyrrhula* (0.9%), Tree Sparrow *Passer montanus* (0.8%) and Blue Tit *Cyanistes caeruleus* (0.5%) (Table 1).

Species found occasionally at Long-eared Owls' roost sites were Bank vole (*Myodes glareolus*, *n* = 1), Common shrew (*Sorex araneus*, *n* = 2) and Lesser white-toothed shrew (*Crocidura suaveolens*, *n* = 10), Coal Tit (*Periparus ater*, *n* = 1), Northern Long-tailed Tit (*Aegithalos caudatus*, *n* = 1), Eurasian Nuthatch (*Sitta europaea*, *n* = 1), Eurasian Tree-Creeper (*Certhia familiaris*, *n* = 1), European Robin (*Erithacus rubecula*, *n* = 1), European Pied Flycatcher (*Ficedula hypoleuca*, *n* = 1), Fieldfare (*Turdus pilaris*, *n* = 3), White Wag-tail (*Motacilla alba*, *n* = 1), Common Chaffinch (*Fringilla coelebs*, *n* = 3), European Greenfinch

Table 2. Rank of generalized linear models depicting the relationship between the proportion of prey-species in the diet of Long-eared Owls, the effect of the year and weather factors that might have influenced on it based on Akaike's Information Criterion corrected for small sample size (AICc). Akaike's weight (ω_i) was presented for each model within $\Delta\text{AICc} < 2$ of the top-ranking model and the model contained all independent variables.

Model ¹	df	ΔAICc	ω_i
<i>Common vole</i>			
Year + Temp/snow ²	10	0.00	0.50
Year + Temp/snow + Precipitation	11	1.32	0.26
Year + Temp/snow + Precipitation + Wind	12	3.78	0.08
<i>Ural field mouse</i>			
Year + Temp/snow	10	0.00	0.44
Year + Temp/snow + Wind	11	0.90	0.28
Year + Temp/snow + Precipitation	11	1.88	0.17
Year + Temp/snow + Precipitation + Wind	12	3.49	0.08
<i>Brown rat</i>			
Year + Precipitation	10	0.00	0.20
Year	9	0.01	0.20
Year + Wind	10	0.08	0.19
Year + Wind + Precipitation	11	0.73	0.14
Year + Temp/snow	10	1.72	0.09
Year + Temp/snow + Precipitation + Wind	12	3.15	0.04
<i>Birds</i>			
Temp/snow + Precipitation	4	0.00	0.18
Temp/snow + Precipitation+ Wind	5	0.03	0.15
Precipitation+ Wind	4	0.43	0.14
Temp/snow	3	0.89	0.11
Wind	3	0.95	0.11
Intercept only	2	1.01	0.10
Precipitation	3	1.20	0.09
Temp/snow + Wind	4	1.65	0.08
Year + Temp/snow + Precipitation + Wind	12	9.00	0.002

1) AICc of top *Common vole* model = 622.4; of top *Ural field mouse* model = 478.2; of top *Brown rat* model = 395.6 and top *Birds* model = 376.3.

2) Temp/snow – a variable derived by the PCA and combined highly correlated temperature and snow cover depth.

(*Carduelis chloris*, $n = 2$), Common Redpoll (*Carduelis flammea*, $n = 2$) and Eurasian Siskin (*Carduelis spinus*, $n = 4$). Some individuals (45 rodents and 13 birds) remained unidentified.

3.2. Annual changes in the diet composition and influence of weather

Comparing all possible models predicting changes in the frequencies of the Common vole and Ural field mouse as prey of owls showed that all top candidate models included year and temperature/snow factor and the top-ranking model contained only year and temperature/snow factor (Table 2). Precipitation or wind were not included in the highest-ranking models. Models including

all variables showed that among weather conditions, temperature/snow factor was the most important predictor of changing the proportion of both Common vole and Ural field mouse, and the significance of year was much higher for Common vole (Table 3).

The top model for the Common vole predicted that relative frequency of catching that prey species by wintering owls was highly dependent on a certain year and was more likely to fall with decreasing temperature and increasing snow cover. For the Ural field mouse, the effect of year was also revealed, although not in all cases. Significant differences in proportions Ural field mouse were found only between sixth and seventh years of study. Unlike the Common vole, the relative frequency of the Ural field mouse was likely to rise

Table 3. Estimated effects and their standard errors (SE), from the model containing all variables.

Bolded numbers indicate statistically significant effects ($P < 0.05$).

Parameter	Estimate	SE	P
<i>Common vole</i>			
Intercept	-0.07	0.40	0.8
Temp/snow ¹	0.34	0.09	< 0.005
Wind	-0.06	0.22	0.77
Precipitation	-0.03	0.03	0.28
Year 1/2	1.72	0.39	< 0.005
Year 2/3	1.56	0.35	< 0.005
Year 3/4	0.64	0.31	< 0.05
Year 4/5	0.90	0.30	< 0.005
Year 5/6	1.82	0.36	< 0.005
Year 6/7	2.37	0.41	< 0.005
Year 7/8	0.36	0.31	0.28
<i>Ural field mouse</i>			
Intercept	-2.29	0.45	< 0.005
Temp/snow	-0.52	0.02	< 0.005
Wind	0.25	0.74	0.32
Precipitation	0.02	0.11	0.56
Year 1/2	-0.41	0.46	0.38
Year 2/3	-0.61	0.42	0.14
Year 3/4	-0.04	0.37	0.92
Year 4/5	-0.18	0.34	0.59
Year 5/6	-0.66	0.42	0.12
Year 6/7	-1.56	0.57	< 0.005
Year 7/8	0.46	0.33	0.16
<i>Brown rat</i>			
Intercept	-2.78	0.51	< 0.005
Temp/snow	-0.14	0.12	0.86
Wind	-1.15	0.27	0.15
Precipitation	-0.10	0.03	0.16
Year 1/2	-0.93	0.49	0.06
Year 2/3	-1.22	0.42	< 0.005
Year 3/4	0.58	0.33	0.08
Year 4/5	-0.24	0.35	0.48
Year 5/6	-1.69	0.53	< 0.005
Year 6/7	-2.34	0.67	< 0.005
Year 7/8	-0.41	0.35	0.25
<i>Birds</i>			
Intercept	-1.92	0.57	< 0.005
Temp/snow	-0.10	0.14	0.48
Wind	-0.45	0.33	0.18
Precipitation	0.07	0.03	< 0.05
Year 1/2	-1.17	0.61	0.06
Year 2/3	-0.55	0.44	0.21
Year 3/4	-0.33	0.42	0.43
Year 4/5	-0.62	0.42	0.13
Year 5/6	-0.75	0.49	0.12
Year 6/7	-0.88	0.52	0.09
Year 7/8	-0.21	0.39	0.59

1) See Table 2.

with decreasing temperature and increasing snow cover (Table 3).

All the top models for the Brown rat also included the effect of year, with or without any weather factors (Table 2). Estimated effects of the weather variables were all non-significant (Table 3). Thus, changes in the proportion of the Brown rat were more likely to depend on some annually changing conditions, but not on the studied weather variables.

Unlike the rodent species, the top candidate models for birds did not contain any effect of year. Lower-ranking models included other weather variables or even the model with an intercept only. The top model for birds predicted that their proportion in the diet probably depended on temperature, snow and precipitation (Table 2). However, comparing estimates from the model including all independent variables showed that only precipitation was significant (Table 3).

4. Discussion

Our findings on the diet composition of wintering owls at the study area were in line with both our earlier studies (Sharikov *et al.* 2009) and findings by other researchers in the Moscow Region (Voronetsky & Sokolov 1996, Kalyakin 2009). Small mammals were the core of owls' diet in winter. The common vole – one of the main prey species of Long-eared Owls in Europe (Mikkola 1983, Birrer 2009) – expectedly predominated, with Ural field mouse proportionally second. Unlike in other studies in Europe (Galeotti & Canova 1994, Bencová *et al.* 2006, López-Gordo *et al.* 1976 cited in Escala 2009), the proportion of Brown rats (7.5%) in our study was relatively high, but not very high compared to the Common vole and the Ural field mouse. Birds were widely represented in the diet of owls by 18 species. Nevertheless, most bird species were obviously occasional prey as their proportions were extremely low. Bullfinches, sparrows and tits were the most frequent bird prey, which most probably reflected their abundance within the park.

The ratio of the main rodent species in the diet of owls showed significant interannual changes that did not apply to the proportion of birds. Presumably the effect of the year was apparent only

for rodents, particularly for the Common vole, as they are known to have marked year to year fluctuations with peak numbers attained at intervals of three to four years (Korpimäki 1992). The proportion of the Common vole in the diet of owls, in its turn, highly depends on the abundance of this species in the owls' hunting habitat (Korpimäki 1992, Tome 1994). Bird populations are not cyclic, especially within the city and the frequency of catching them depends not on their abundance but on some other factors.

Weather conditions seem to influence the diversity of diet composition of Long-eared Owls through the accessibility of prey items. However, the main effective factor is probably different between geographical regions and depends on the local climate patterns. Thus, in southern Europe, with generally milder climate, the winter diet of owls is affected mostly by the amount of precipitation (Rubolini *et al.* 2003, Romanowski & Żmihorski 2008) and temperature (Rubolini *et al.* 2003), although the importance of snow cover was also pointed out (Canova 1989). At Moscow's latitude, the depth of snow cover is likely to be the most important factor for Long-eared Owls, because this has an impact on the availability of the Common vole (Elders *et al.* 1979, cited in Birrer 2009, Wijnandts 1984, Schmitz 1987, cited in Birrer 2009, Ancelet 1987, cited in Birrer 2009). Voles generally make tunnels under the snow layer (Jędrzejewska & Jędrzejewski 1998, Romanowski & Żmihorski 2008). Increasing the snow cover deeper than 10–15 cm might thus appreciably decrease their availability for the Long-eared Owl. Temperature obviously also affected the availability of rodent preys due to its profound effect on snow cover in winter. Unlike voles, wood mice often walk on the snow surface, being thus more exposed to owls, and frosts have little effect on their mobility (Rotshild 1956, Jędrzejewska & Jędrzejewski, 1998). When the snow is deep enough and probably compacts with ice crust, the availability of vole decreases and the Ural field mouse might become the general alternative prey species as we observed in this study. The same situation appears in other regions where the Ural field or Wood mice (*A. sylvaticus*) are abundant (Laiu & Murariu 1998). Meanwhile it should not be forgot-

ten that this is only a minor effect, as voles remain the major prey item even during heavy snow cover (Uttendörfer 1952).

Brown rats also compensated for a deficiency of voles caused by both interannual fluctuations of voles' population and weather conditions reducing their availability. Rats themselves did not depend on the weather as owls were likely to hunt for them closer to buildings where rats were more abundant and impact of weather was mitigated.

The proportion of birds in the diet composition of Long-eared Owl obviously varies widely. Thus, Sándor and Kiss (2008) and García and Cervera (2001) (cited in Escala *et al.* 2010) found birds to predominate in the diet, reaching up to 59.3% and 52.1%, respectively, and low abundance of rodents in these regions was supposedly the reason. In regions where rodents are available, the proportion of birds rarely exceeds 5% (Tome 1994, Sharikov 2006), although sometimes it can achieve the level of 10–13% (Alivizatos & Goutner 1999, Milchev *et al.* 2003). In the current study, the proportion of bird prey was rather low overall, but increased proportionally with increasing precipitation. Precipitation in view of worse audibility is likely to contribute to a failed hunting on rodents, as the Long-eared Owl is rather an acoustic than visual predator (Dooling 2002), and birds are easier to catch using vision only.

To conclude, the winter diet composition of Long-eared Owl in our study area with severe winters showed marked interannual fluctuations. The proportion of the main prey species depended first of all on its abundance and secondly on its availability due to snow cover and temperature. Shortage of the Common vole induces switching to substituting prey that is based on specific features of prey's behavior particularly its activity and habitat preferences. With such ecological plasticity, the Long-eared Owl is likely to successfully overwinter in relatively inclement conditions during prolonged northern winters.

Acknowledgements. We are grateful to the reviewers for important suggestions for improvement of the manuscript. We are also much obliged to Lidiya Nikitina and Roman Zakharov for their help in collecting pellets and deeply appreciated Dmitry Shitikov and Alan Sieradzki for providing valuable comments and advice on the manuscript.

Sääolosuhteet selittävät sarvipöllön saalistyyppien vaihtelua Moskovalaisessa talvehtimispaikassa

Tutkimme sääolojen vaikutusta sarvipöllön talviravintoon, perustuen Moskovalaisen päivehtimispaikan seurantaan vuosina 2005–2013. Oksenuspalloja kerättiin viikoittain marraskuusta maaliskuuhun. Pöllöjen saalislajeista 6 olivat jyrsijöitä, 2 hyönteissyöjiä ja 18 lintuja. Selvästi runsain saalis oli lajipari kenttämyyrä–idänkenttämyyrä (70,0 %), toiseksi runsain oli idänmetsähiiri (10,8 %) ja kolmanneksi rotta (7,5 %). Linnuista (5,3 %) yleisimmät saalislajit olivat varpunen, tali-tiainen, punatulkku, pikkuvarpunen ja sinitiainen. Talviravinnon koostumuksessa oli huomattavaa vuosien välistä vaihtelua. Säätekijöistä lumen paksuus näyttäisi olevan tärkein sarvipöllön ruokavalioon vaikuttava tekijä, vaikuttaen tyypillisimpien saalistyyppien pyydystettävyyteen. Tuulen nopeus ja sadanta eivät vaikuttaneet myyrien ja hiirien saalistukseen. Lintujen osuus saalismäärissä oli kohtalaisen matala, mutta nousi lisäytyneen sadannan myötä, mikä viittaa siihen, että linnut saattavat toisinaan olla tärkeää vaihtoehtoisravintoa pöllöille. Tulokset osoittavat sen, että tietyt piirteet saalislajien käyttäytymisessä ja aktiivisuudessa eri sääoloissa selittävät niiden osuuden sarvipöllön talvisessa ruokavaliossa.

References

- Alivizatos, H. & Goutner, V. 1999: Winter diet of the Barn Owl (*Tyto alba*) and Long-eared Owl (*Asio otus*) in Northeastern Greece: a comparison. — *Journal of Raptor Research* 33 (2): 160–163.
- Bartoň, K. 2013: MuMIn: multi-model inference. R package version 1.9.5. Available from: <http://CRAN.R-project.org/package=MuMIn>
- Bencová, V., Kašpar, T. & Bryja, J. 2006: Seasonal and interannual changes in diet composition of the Long-eared Owl (*Asio otus*) in Southern Moravia. — *Tichodroma* 18: 65–71.
- Benedek, A.M. & Șirbu, I. 2010: Dynamics of *Asio otus* L., 1758 (Aves: Strigiformes) winter–spring trophic regime in western plain (Romania). — *Travaux du Muséum National d’Histoire Naturelle «Grigore Antipa»* 53: 479–487.
- Birrer, S. 2009: Synthesis of 312 studies on the diet of the Long-eared Owl *Asio otus*. — *Ardea* 97 (4): 615–624.
- Burnham, K.P. & Anderson, D.R. 2002: Model selection and multimodel inference: a practical information-theoretic approach. — Springer, New York.
- Canova, L. 1989: Influence of snow cover on prey selection by Long-eared Owls *Asio otus*. *Ethology*. — *Ecology & Evolution* 1 (4): 367–372.
- Dooling, R. 2002: Avian Hearing and the Avoidance of Wind Turbines. — National Renewable Energy Laboratory, Technical Report, NREL/TP-500-3084: 1–84.
- Escala, C., Alonso, D., Mazuelas, D., Mendiburu, A., Vilches, A. & Arizaga, J. 2009: Winter diet of Long-eared Owls *Asio otus* in the Ebro valley (NE Iberia). — *Revista Catalana d’Ornitologia* 25: 49–53.
- Galeotti, P. & Canova, L. 1994: Winter diet of Long-eared Owls (*Asio otus*) in the Po Plain (Northern Italy). — *Journal of Raptor Research* 28 (4): 265–268.
- Galushin, V.M. 1982: Role of birds of prey in the ecosystems. Results of science and techniques. VINITI. — *Zoology of vertebrates* 11: 158–236. (In Russian).
- Gromov, I.M. & Erbaeva, M.A. 1995: Mammals of fauna of Russia and neighboring areas. Lagomorphs (Lagomorpha) and rodents (Rodenta). — Zoological Institute, Russian Academy of Science, Saint Petersburg. (In Russian).
- Jędrzejewska, B. & Jędrzejewski, W. 1998: Predation in vertebrates communities: the Białowieża Primeval Forest as a case study. *Ecological studies* 135. — Springer, Heidelberg.
- Johnson, J.B. & Omland, K.S. 2004: Model selection in ecology and evolution. — *Trends in ecology and evolution* 19: 101–108.
- Kalyakin, V.N. 2009: Diet of Long-eared Owl in the Moscow Region. — In: Volkov, S.V. (ed.-in-chief), Sharikov, A.V. & Morozov, V.V. (Eds.) *Owls of The Northern Eurasia: Ecology, spatial and habitat distribution*. Moscow: 70–74. (In Russian with English summary).
- Korpimäki, E. 1992: Population dynamics of Fennoscandian owls in relation to wintering conditions and between-year fluctuations of food. — The ecology and conservation of European owls. Joint Nature Conservation Committee (UK Nature Conservation, No 5), Peterborough, 1–10.
- Laiu, L. & Murariu, D. 1998: The food of the Long-eared Owl (*Asio otus* L.) (Aves: Strigiformes) in wintering conditions of the urban environment in Romania. — *Travaux du Muséum National d’Histoire Naturelle “Grigore Antipa”* 40: 413–430.
- Lesnoff, M. & Lancelot, R. 2012: aod: Analysis of Overdispersed Data. R package version 1.3. Available from: <http://cran.r-project.org/package=aod>
- Mikkola, H. 1983: *Owls of Europe*. — T & A D Poyster, London.
- Milchev, B., Boev, Z. & Toteva, T. 2003: Diet composition of the Long-eared Owl (*Asio otus*) during the autumn-winter period in the northern park of Sofia. — *Annual of Sofia University “St. Kliment Ohridski”*. Book 1. Zoology, 93–94: 49–56.
- Nilsson, I.N. 1981: Seasonal changes in food of the Long-

- ered Owl in southern Sweden. — *Ornis Scandinavica*, 12: 216–223.
- Pirovano, A., Rubolini, D., Brambilla, S. & Ferrari, N. 2000: Winter diet of urban roosting Long-eared Owls *Asio otus* in northern Italy: the importance of the Brown Rat *Rattus norvegicus*. — *Bird Study* 47(2): 242–244.
- R Core Team. 2012: R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available from: <http://www.R-project.org/>
- Romanowski, J. & Żmihorski, M. 2008: Effect of season, weather and habitat on diet variation of a feeding-specialist: a case study of the long-eared owl, *Asio otus* in Central Poland. — *Folia Zoologica* 57 (4): 411–419.
- Rotshild, E.V. 1956: Winter movements of small forest rodents. — *Zoologicheskii Journal* 35 (5): 758–769. (In Russian).
- Rubolini, D., Pirovano, A. & Borghi, S. 2003: Influence of seasonality, temperature and rainfall on the winter diet of the long-eared owl, *Asio otus*. — *Folia Zoologica* 52 (1): 67–76.
- Sándor, A.D. & Kiss, B.J. 2008: Birds in the Diet of Wintering Long-eared Owls (*Asio otus*) in the Danube Delta, Romania. — *Journal of Raptor Research* 42 (4): 292–294.
- Sharikov, A. V. 2006: Peculiarities of winter feeding in the Long-Eared Owl (*Asio otus*) in settlements of Stavropol krai. — *Zoological journal* 85 (7): 871–877. (In Russian with English summary).
- Sharikov, A.V., Kholopova, N. S., Volkov, S.V. & Makarova, T.V. 2009: Review of the owls' diet in the Moscow City and the Moscow Region. — In: Volkov, S.V. (ed.-in-chief), Sharikov, A.V. & Morozov, V.V. (eds) *Owls of The Northern Eurasia: Ecology, spatial and habitat distribution*. Moscow: 188–204. (In Russian with English summary).
- Shvets, O.V. & Novokhatka, A.D. 2003: Changes in the diet composition of the Long-eared Owls wintering in a town park. — Proceedings of II scientific-practical conference “Animals in the city”. Moscow: 171–172. (In Russian).
- Shvets, O.V. 1998: Winter diet of Long-eared Owls in the park of Tula. — Proceedings of the Third Conference on Raptors of Eastern Europe and Northern Asia. Part 1. Stavropol: 127. (In Russian).
- Tome, D. 1994: Diet composition of the Long-eared Owl in Central Slovenia: seasonal variation in prey use. — *Journal of Raptor Research*. 28(4): 253–258.
- Uttendörfer, O. 1952: Neue Ergebnisse über die Ernährung der Greifvögel und Eulen. *Vogelwartenbuch* 31. — Eugen Ulmer, Stuttgart.
- Voronetsky, V.N. & Sokolov, A.V. 1996: About winter diet of Long-eared Owl in the Botanical Garden of the Moscow state university. — *Ornithologia* 27: 305–307. (In Russian).
- Wijnandts, H. 1984: Ecological energetics of the Long-eared Owl (*Asio otus*). — *Ardea* 72: 1–92.
- Zuur, A.F, Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. 2009: *Mixed effects models and extensions in ecology with R*. — Springer, New York.