

Seasonal changes in Tawny Owl (*Strix aluco*) diet in an oak forest in Eastern Ukraine

Yehor YATSIUK^{1*}, Yuliya FILATOVA²

¹National Park "Gomilshanski Lis", Kharkiv region, Ukraine

²Department of Zoology and Animal Ecology, Faculty of Biology, V.N. Karazin Kharkiv National University, Kharkiv, Ukraine

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Abstract: We analyzed seasonal changes in Tawny Owl (*Strix aluco*) diet in a broadleaved forest in Eastern Ukraine over 6 years (2007–2012). Annual seasons were divided as follows: December–mid-April, April–June, July–early October, and late October–November. In total, 1648 pellets were analyzed. The most important prey was the bank vole (*Myodes glareolus*) (41.9%), but the yellow-necked mouse (*Apodemus flavicollis*) (17.8%) dominated in some seasons. According to trapping results, the bank vole was the most abundant rodent species in the study region. The most diverse diet was in late spring and early summer. Small forest mammals constituted the dominant group in all seasons, but in spring and summer their share fell due to the inclusion of birds and the common spadefoot (*Pelobates fuscus*). Diet was similar in late autumn, before the establishment of snow cover, and in winter. The relative representation of species associated with open spaces increased in winter, especially in years with deep snow cover, which may indicate seasonal changes in the hunting habitats of the Tawny Owl.

Key words: Trophic ecology, Tawny Owl, *Strix aluco*, seasonal diet changes, small mammals, pellet analysis, Ukraine

1. Introduction

The Tawny Owl (*Strix aluco* L.) is adapted mainly to temperate deciduous forests (Petty and Saurola, 1997; Butyev et al., 2005), and is a well-studied example of a sedentary rodent-eating predator with a generalized feeding strategy (Petty, 1999; Newton, 2002). Bank voles (*Myodes glareolus* Schreber) and wood mice (*Apodemus* sp.) dominate the Tawny Owl diet throughout the main part of its range (Cramp, 1985; Galeotti, 2001). These rodent species show noncyclic fluctuations in their numbers (Jedrzejewsky et al., 1996; Petty, 1999) but they are rather abundant in temperate forests. This allows the Tawny Owl to reach maximal densities in temperate broadleaved forests (Southern, 1970; Galeotti, 2001) and in broadleaved forests of the Mediterranean region (Salvati and Ranazzi, 2002).

The Tawny Owl has the most diverse diet among all owls of the Western Palearctic (Cramp, 1985). A sedentary way of life promotes quick seasonal and annual diet changes in response to prey availability. It is well known that seasonal changes in Tawny Owl diet are driven by changes in snow cover and the development of ground vegetation, which alter the availability of different prey (Southern, 1954; Galeotti, 2001).

Tawny Owls use their roosting hollows in winter more consistently than in spring. This results in a substantial number of winter pellets found under winter roosting sites, while summer pellets are widely distributed between numerous hollows and perches used for roosting in summer time. As a result, the summer diet of the Tawny Owl is less known than the winter diet (Southern, 1970). Furthermore, very few pellets are usually found under their breeding hollows during the breeding season (Yatsiuk, 2009).

Our work is based on regular seasonal checking of Tawny Owl roosting places (both nest boxes and hollows) in the study region. Using data for six consequent years we analyzed the share of different prey types, with special attention to their habitat preferences and persistence of observed diet shifts between years.

2. Materials and methods

Tawny Owl pellets were collected in the territory of Gomilsha Forest (49°36'N, 36°19'E), National Park "Gomilshanski Lis" (Kharkiv region, Ukraine) (Figure 1). This forest is located at the southern border of the forest-steppe zone, and is one of the largest broadleaved forests in the region with total area of 10,000 ha. The study plot covered an area of 750 ha. Mean Tawny Owl density during

* Correspondence: yatsjuk.e@gmail.com

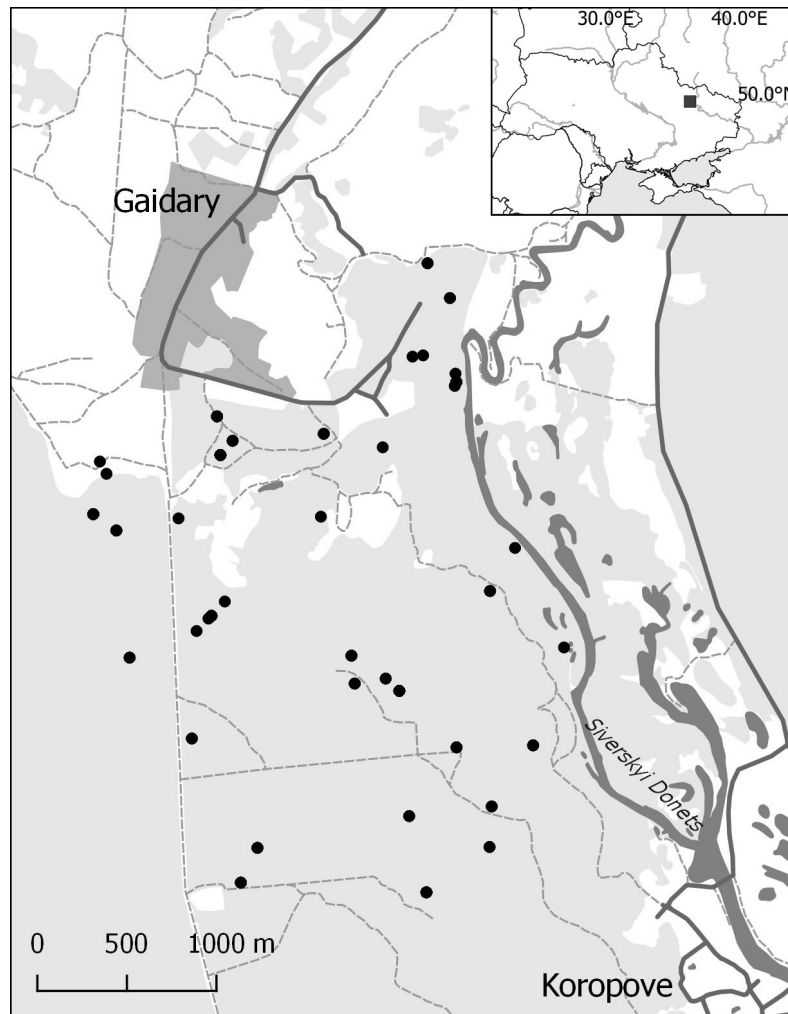


Figure 1. Location of the study area with indication of pellet collection points.

the six-year study was 2.5 pairs/km². According to census data, 8 territories of Tawny Owl are adjacent to human settlement areas and open spaces, 4 more territories adjoin open spaces only, and the last 7 are situated more than 500 m from both human settlements and open spaces (personal data, unpublished).

Forest stands are dominated by the pedunculate oak (*Quercus robur* L.) with the European ash (*Fraxinus excelsior* L.), small-leaved linden (*Tilia cordata* Mill.), and Norway maple (*Acer platanoides* L.). The average stand age is between 80 and 120 years. The northern part of the study plot is located in close proximity to settlements interlaced with meadows and limited by the Siverskyi Donets river valley to the east.

All known Tawny Owl shelters and hunting perches in each of 18 known territories were checked three times per year. Seasons were divided in accordance with pellet collection periods: mid-April (these samples reflect winter diet, from December to early April), beginning

of July (from April to June), and late November or early December (from mid-summer to autumn before snow cover was established). Autumn collections were divided into pellets found under and over the leaf litter. Since the most intense defoliation occurs in the second half of October, the composition of pellets found under the litter reflects Tawny Owl diet from July to October, while the composition of pellets found over the litter corresponds to the period from late October to early December. Thus, we compared diet over four annual periods figuratively named as follows: winter-spring, early summer, late summer-early autumn, and late autumn. In total we analyzed the contents of 1648 pellets collected from 43 localities in 2007–2012.

November and December in the studied region are characterized by inconsistent snow cover with frequent thaws. During the study period continuous snow cover was generally established between mid-December and the first half of January. Snow cover lasted for about 90–100 days until the end of March, with a mean maximal snow

depth of 20–30 cm in March. The start of egg incubation in the Tawny Owl occurred on about 25th March (personal data, unpublished).

Collected pellets were macerated in water, then the wool/fur of prey was removed, and the bones and remains of chitin were collected and dried (Novikov, 1949). Pellets from each locality were processed together, without separate analysis of each pellet.

Prey species were identified following the taxonomic keys (Nebogatkin, 1987; März, 2007; Voronetsky and Kuzmenko, 2013). The maximal number of individuals for each vertebrate prey species was determined as the maximal number of upper and lower jaws. The presence of beetles (Coleoptera) and other arthropods in the diet was recognized by residues of chitin in pellets, but they were not identified to species level. All measurements were performed using calipers with an accuracy of up to 0.1 mm.

Not all bird remains were identified to species level and so they were grouped together as Aves in calculations. All remains of *Microtus "arvalis"* (s.l.) voles were treated as the East European vole (*Microtus levis* Miller) in accordance with previous karyological studies in the studied region (Zagorodniuk, 1993, 2008). All remains of wood mice in our samples were identified as the Ural field mouse (*Apodemus uralensis* Pall), although there were some records of the wood mouse (*A. sylvaticus* L) in the study region (Naglov, 1996). When it was impossible to identify some prey to species level (for wood mice *Apodemus* sp. and *Microtinae*), individuals were assigned to similar species in the same proportion as these species occurred in the identified part of a particular sample (according to Balčiauskienė et al., 2006).

Proportion and biomass were calculated for each prey species or group of species. Data for the weight of each species were taken from online databases (<http://genomics.senescence.info/species/>) and the literature (Southern, 1954), as well as from our own data. The mean weight of young specimens was used for big prey, such as the brown rat (*Rattus norvegicus*) (Morris, 1979).

Prey species were grouped into the following categories: forest rodents (forest dormouse (*Dryomys nitedula* Pall), Ural field mouse, yellow-necked mouse (*Apodemus flavicollis* Melchior), bank vole, European pine vole (*Microtus subterraneus* Selys-Longchamps)), rodents and lagomorphs of open habitat (steppe mouse (*Mus spicilegus* Petenyi), house mouse (*Mus musculus* L), striped field mouse (*Apodemus agrarius* Pall), harvest mouse (*Micromys minutus* Pall), East European vole (*Microtus oeconomus* Pall)), large rodents and lagomorphs (brown rat, water vole (*Arvicola terrestris* L), European hare (*Lepus europaeus* Pall)), carnivores and insectivores, bats, birds, reptiles and amphibians, and invertebrates.

Diversity of the food spectrum was assessed with the Shannon index (H') and food niche breadth index (B) (Levins, 1968). To determine main and alternative prey species, we used Spearman correlations between a share of certain species, and Shannon and FNB indices with the assumption that the food spectrum becomes more diverse when the share of the main species is decreasing (Tome, 1994). For comparison of prey shares in different seasons, a Yates corrected chi-square test was used as 2×2 tables with $df = 1$ (Statsoft, 2014).

3. Results

In total, 3911 vertebrate and approximately 119 invertebrate prey specimens were found in Tawny Owl pellets. Vertebrates were represented by 36 species (Table 1), with 25 mammal species, at least 8 bird species, one reptilian (probably a grass snake (*Natrix natrix* L.)), and at least two amphibian species. The list of identified bird remains included the Grey-headed Woodpecker (*Picus canus* Gmelin), woodpeckers (*Dendrocopos* spp.), the Eurasian Jay (*Garrulus glandarius* L.), the Song Thrush (*Turdus philomelos* Brehm), tits (Paridae), the Common Chaffinch (*Fringilla coelebs* L.), the European Goldfinch (*Carduelis carduelis* L.), the Eurasian Siskin (*Spinus spinus* L.), the Hawfinch (*Coccothraustes coccothraustes* L.), and the Eurasian Bullfinch (*Pyrrhula pyrrhula* L.).

Small rodents dominated both in the number of specimens and in the biomass. The mean weight of vertebrate prey ranged from 6 to 120 g. Mean weight of prey was 22.7 g. The heaviest prey (brown rat, water vole, juvenile European hare, and Eurasian jay) occurred in pellets only occasionally.

The bank vole was the most numerous species detected among Tawny Owl prey in most seasons. The exception was a period from autumn 2010 to summer 2012 when the average share of the yellow-necked mouse was 1.4 times higher than that of the bank vole.

Among the two most abundant prey species, only the share of the yellow-necked mouse showed a significant negative correlation with diversity indices (Table 2). On the other hand, the share of the striped field mouse, lesser white-toothed shrew (*Crocidura suaveolens* Pall), and common spadefoot (*Pelobates fuscus*) positively correlated with diversity indices.

The share of certain species showed a positive correlation with each other. For species of open habitat: harvest mouse ($r_s = 0.55$, $P < 0.05$ for striped field mouse, $r_s = 0.51$, $P < 0.05$ for East European vole, $r_s = 0.57$, $P < 0.05$ for root vole), East European vole ($r_s = 0.55$, $P < 0.05$ for striped field mouse, $r_s = 0.51$, $P < 0.05$ for root vole). Shrews also had a significant positive relationship with a number of species: common shrew (*Sorex araneus* L.,)

Table 1. Numbers (n) and percentages (%) of Tawny Owl prey taxa in different seasons.

Season	Winter–spring		Early summer		Late summer–early autumn		Late autumn		Total	
	n	%	n	%	n	%	n	%	n	%
<i>Apodemus agrarius</i>	84	2.84	2	0.74	4	0.64	4	2.16	94	2.33
<i>Apodemus flavicollis</i>	437	14.79	72	26.77	159	25.56	51	27.57	719	17.84
<i>Apodemus uralensis</i>	206	6.97	2	0.74	51	8.20	30	16.22	289	7.17
<i>Micromys minutus</i>	36	1.22	1	0.37	1	0.16	1	0.54	39	0.97
<i>Mus spicilegus</i>	7	0.24	0	0.00	0	0.00	2	1.08	9	0.22
<i>Mus musculus</i>	4	0.14	0	0.00	0	0.00	1	0.54	5	0.12
<i>Dryomys nitedula</i>	14	0.47	11	4.09	30	4.82	1	0.54	56	1.39
<i>Microtus levis</i>	54	1.83	0	0.00	5	0.80	1	0.54	60	1.49
<i>Microtus subterraneus</i>	285	9.65	17	6.32	41	6.59	10	5.41	353	8.76
<i>Microtus oeconomus</i>	23	0.78	0	0.00	0	0.00	0	0.00	23	0.57
<i>Myodes glareolus</i>	1346	45.57	67	24.91	216	34.73	60	32.43	1689	41.91
Bats	9	0.29	8	2.97	3	0.48	0	0	20	0.49
<i>Talpa europea</i>	6	0.20	0	0.00	1	0.16	0	0.00	7	0.17
<i>Crocidura suaveolens</i>	59	2.00	0	0.00	7	1.13	3	1.62	69	1.71
<i>Sorex araneus</i>	124	4.20	2	0.74	6	0.96	5	2.70	137	3.40
<i>Sorex minutus</i>	53	1.79	1	0.37	4	0.64	2	1.08	60	1.49
Other mammals	6	0.19	0	0	0	0	0	0	6	0.13
Aves	108	3.66	24	8.92	17	2.73	4	2.16	153	3.80
Reptilia/Amphibia	58	1.96	31	11.52	34	5.47	0	0	123	3.05
Invertebrates	35	1.18	31	11.52	43	6.91	10	5.4	119	2.94
Total specimens	2954	100.00	269	100.00	622	100.00	185	100.00	4030	100.00
Number of pellets	1131		131		280		106		1648	
Mean prey mass	22.5		23.0		23.4		23.2		22.7	
Mass per pellet	58.7		47.3		51.9		40.5		55.5	
Shannon H'	2.04		2.10		1.97		1.92		2.11	
Levins B	4.03		5.90		4.82		4.66		4.45	
Number of prey species	36		14		16		13		36	

($r_s = 0.50$, $P < 0.05$ for striped field mouse, $r_s = 0.76$, $P < 0.01$ for harvest mouse, $r_s = 0.55$, $P < 0.05$ for East European vole, $r_s = 0.58$, $P < 0.05$ for pygmy shrew (*Sorex minutus* L.)), pygmy shrew ($r_s = 0.61$, $P < 0.01$ for harvest mouse, $r_s = 0.82$, $P < 0.01$ for East European vole, $r_s = 0.56$, $P < 0.05$ for root vole).

The bank vole and yellow-necked mouse were the most frequent species recorded as prey throughout the year.

During the transition from winter–spring to early summer seasons there was a significant increase in proportions of the forest dormouse ($\chi^2 = 37.3$, $P < 0.01$, number of observations shown in Table 1), Ural field mouse ($\chi^2 = 14.8$, $P < 0.01$) birds ($\chi^2 = 16.1$, $P < 0.01$), and the common spadefoot ($\chi^2 = 93.3$, $P < 0.01$), while the share of the yellow-necked mouse and bank vole declined significantly ($\chi^2 = 25.7$, $P < 0.01$ and $\chi^2 = 41.9$, $P < 0.01$ respectively).

Table 2. Relation between the diversity indices and shares of main prey species in Tawny Owl pellets.

Species	Shannon H'		Levins B	
	r _s	P-value	r _s	P-value
<i>Dryomys nitedula</i>	0.02	0.929	0.03	0.907
<i>Apodemus agrarius</i>	0.24	0.352	0.26	0.317
<i>Apodemus uralensis</i>	0.14	0.583	0.17	0.522
<i>Apodemus flavicollis</i>	<u>-0.49</u>	<u>0.047</u>	-0.43	0.082
<i>Micromys minutus</i>	0.27	0.301	0.25	0.326
<i>Myodes glareolus</i>	-0.40	0.107	-0.43	0.086
<i>Microtus levis</i>	<u>0.53</u>	<u>0.030</u>	0.43	0.086
<i>Microtus subterraneus</i>	0.11	0.666	0.17	0.504
<i>Microtus oeconomus</i>	0.21	0.409	0.17	0.519
<i>Nyctalus noctula</i>	0.03	0.904	-0.03	0.900
<i>Sorex araneus</i>	0.10	0.713	0.08	0.749
<i>Sorex minutus</i>	0.47	0.059	0.40	0.115
<i>Crociodura suaveolens</i>	0.47	0.060	<u>0.51</u>	<u>0.035</u>
Aves	0.48	0.053	0.38	0.136
<i>Pelobates fuscus</i>	0.62	0.008	0.51	0.035
Coleoptera	0.07	0.798	0.09	0.719

Species with number of individuals more than 10 are shown. Spearman r_s indices are given, indicators with P ≤ 0.05 are underlined.

In the late summer–early autumn, the share of the Ural field mouse in prey remained increased significantly again ($\chi^2 = 17.4$, $P < 0.01$), and the share of the bank vole also increased ($\chi^2 = 7.9$, $P < 0.01$), while proportions of birds and the common spadefoot decreased ($\chi^2 = 15.9$, $P < 0.01$ and $\chi^2 = 10.0$, $P < 0.01$ respectively). The share of the Ural field mouse continued to increase during the late autumn season ($\chi^2 = 9.3$, $P < 0.01$) (Table 1), but decreased significantly between late autumn and winter–spring seasons ($\chi^2 = 20.1$, $P < 0.01$), as did the yellow-necked mouse ($\chi^2 = 20.7$, $P < 0.01$). By contrast, the share of the bank vole increased over this period ($\chi^2 = 11.6$, $P < 0.01$).

Although small forest rodents dominated in prey remains in all seasons, their share decreased significantly in early summer ($\chi^2 = 28.0$, $P < 0.01$) and increased in late summer–early autumn ($\chi^2 = 28.1$, $P < 0.01$). The share of rodents of open habitat was significantly higher in the winter–spring season than in early summer ($\chi^2 = 13.2$, $P < 0.01$), and also increased in early autumn ($\chi^2 = 5.2$, $P < 0.05$). A significant decline in early summer was

also observed in insectivores, including a weasel (*Mustela nivalis* L.) that was assigned to this group ($\chi^2 = 16.9$, $P < 0.01$). Bats ($\chi^2 = 28.9$, $P < 0.01$), birds ($\chi^2 = 16.1$, $P < 0.01$), invertebrates ($\chi^2 = 126.0$, $P < 0.01$), and amphibians ($\chi^2 = 80.4$, $P < 0.01$) increased significantly in early summer. Bats, birds ($\chi^2 = 15.0$, $P < 0.01$), amphibians ($\chi^2 = 9.3$, $P < 0.05$), and invertebrates ($\chi^2 = 4.7$, $P < 0.05$) decreased in late summer–early autumn (Figure 2).

The highest diet diversity was observed in early summer (Table 1). Diet diversity in the winter–spring period was comparatively high because of the presence of prey species that were indistinctive for winter (invertebrates, reptiles, bats) but became active in the early spring.

4. Discussion

Our analysis has shown that in Gomilsha Forest, similar to most other studies, small rodents make up the main part of the Tawny Owl diet. The most frequently recorded species were the bank vole (41.9%) and the yellow-necked mouse (17.8%). The proportions of these two species were nearly

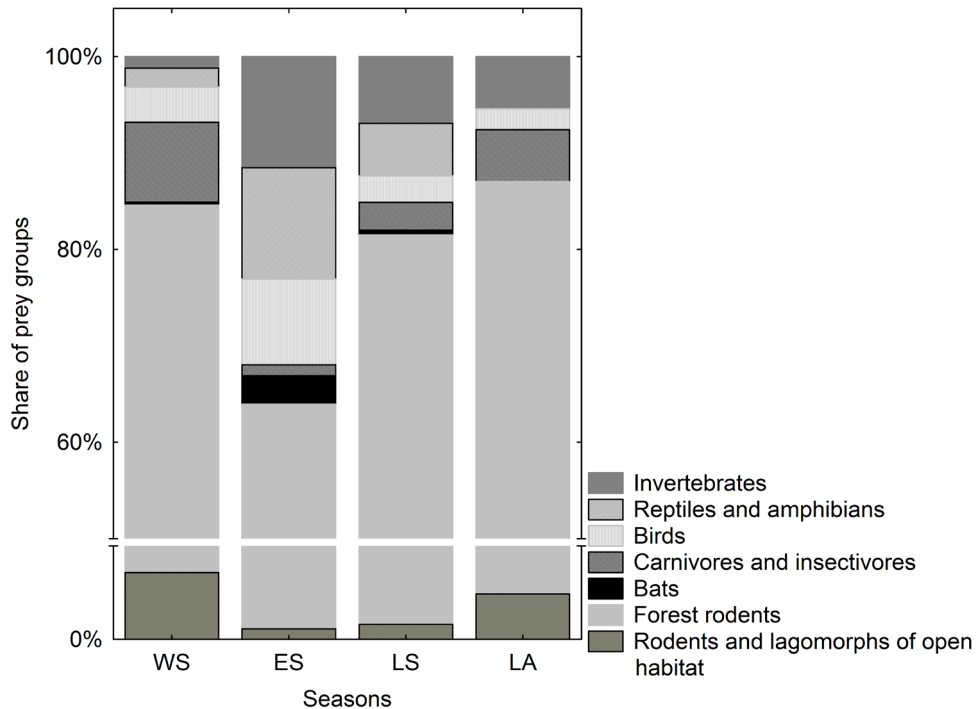


Figure 2. Proportion of prey groups in Tawny Owl pellets in different seasons. Note break of y axis between 10% and 50%. Abbreviations for seasons: WS – Winter-spring, ES – Early summer, LS – Late summer and early autumn, LA – Late autumn.

identical to those obtained during trapping in this region (48.3% for the bank vole and 17.4% for the yellow-necked mouse) (Naglov, 1996). The same situation takes place elsewhere, where proportions of main small mammal prey species are very similar to their share in the small mammal community (Southern, 1954; Jedrzejewski et al., 1994). *Microtus* voles are the other important prey group; they are more important in study areas with a large proportion of open spaces and also in the northern part of the Tawny Owl range (Petty, 1999; Sunde et al., 2001; Balciauskiene et al., 2005, 2006). Although more than half of the bird pairs in the studied territory had access to open spaces outside the forest, *Microtus* voles made up only a relatively small part of the diet. The only woodland representative of this genus, the European pine vole, formed a significant share of Tawny Owl prey here.

Seasonal changes in Tawny Owl diet mainly depend on hunting conditions: the importance of small rodents in temperate forests is maximal in winter and early spring (Southern, 1954; Gruzdev and Likhachev, 1960; Galeotti, 2001), but in late spring and summer the diet diversity increases, and different alternative types of prey can become more frequent (Cramp, 1985). Alternative prey can be represented by larger mammals, such as rabbits (*Oryctolagus cuniculus* Lilljeborg) and moles (*Talpa europaea* L.) (Southern, 1954), shrews (*Sorex* sp.) (Gruzdev

and Likhachev, 1960; Delmee et al., 1978; Petty, 1999), or birds (Kirk, 1982; Jedrzejewski et al., 1994). In our case, the East European vole, lesser white-toothed shrew, and common spadefoot were alternative prey in spring and summer. The composition of alternative prey appears to depend on local conditions without any geographical trend.

Southern (1969) noted that a switch between the winter and summer diet occurs in a very short period, driven by the rapid growth of ground vegetation, about 7–8 May. It is possible that another switch can occur at the beginning of April, shortly after snow melt, resulting in an increasing share of amphibian and, possibly, invertebrate prey. However, it should be noted that our spring collections of pellets, reflecting winter and early spring diet, were made mainly in mid-April, about two weeks after the snow melt.

Tawny Owl diet in the second half of summer can also be different from that of the breeding season. The share of small rodents is usually minimal in July–August (Southern, 1954; Jedrzejewski et al., 1994). Birds can be more numerous in autumn while shrews are more numerous in summer (Gruzdev and Likhachev, 1960). In our case, Tawny Owl diet in July–October was similar to the late autumn and winter diet. This may reflect specific changes in rodent abundance in summer, for example, when owls can catch them in dense oak stands with uneven ground

vegetation but plenty of potential food for voles and mice. However, the Tawny Owl is known to use tree hollows very rarely during summer, and to do so more often in September, well before autumn leaf fall (Southern, 1954). This can mean that pellets collected in autumn under tree hollows below fallen leaves may reflect the early autumn diet rather than the second half of summer.

The positive correlation between different species inhabiting open spaces indicates changes in hunting habitats of the Tawny Owl rather than fluctuations in some species numbers. Snow cover was shown to adversely affect the probability of catching bank voles in Białowieża Forest in Poland (Jędrzejewski et al., 1994). Our previous results showed that the Tawny Owl catches more rodents of open habitat in winters with deep snow cover (Yatsiuk, 2011). Similar trends of *Microtus* voles (associated mainly with open spaces) domination in winter, and bank voles in summer and spring, have been noted in broadleaved forests of the Tula region in Russia (Gruzdev and Likhachev, 1960). The tawny owl is a sedentary species occupying its territory throughout the year (Cramp, 1985).

According to census results, all prey have been caught in plots not bigger than 600 m around each roosting place. This probably means that about a half of our studied population had access to open spaces, with the use of this habitat increasing from November to March.

The mean depth and duration of snow cover in winter become important factors for the Tawny Owl in Eastern Europe, as well as in Northern Europe (Francis and Saurola, 2004). With a great degree of between-year winter weather fluctuations characteristic for the studied region, access to open habitats such as meadows or fields can be very important for local populations of Tawny Owl. It may be important to assess whether birds inhabiting territories situated inside big forests and near fields and meadows would have different reproduction success and long-term survival.

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References

- Balčiauskienė L, Jovaišas A, Naruševičius V (2006). Diet of Tawny Owl (*Strix aluco*) and Long-eared Owl (*Asio otus*) in Lithuania as found from pellets. *Acta Zoologica Lituanica* 16: 37-45.
- Balčiauskienė L, Juškaitis R, Atkočaitis O (2005). The diet of the Tawny Owl (*Strix aluco*) in south-western Lithuania during the breeding period. *Acta Zoologica Lituanica* 15: 13-20.
- Butyev VT, Zubkov NI, Ivanchev VP, Koblik YA, Kovshar AF, Kotyukov YV, Luleeva DS, Nazarov YN, Nechayev VA, Priklonsky SG et al., eds. (2005). Birds of Russia and adjacent regions. Volume 6: Strigiformes, Caprimulgiformes, Apodiformes, Coraciiformes, Upupiformes, Piciformes. Moscow, Russia: KMK Publishing House (in Russian).
- Cramp S, ed. (1985). Handbook of the Birds of Europe, the Middle East and North Africa. Vol. IV. Terns to woodpeckers. Oxford, UK: Oxford University Press.
- Delmée E, Dachy P, Simon P (1978). Quinze années d'observations sur la reproduction d'une population forestière de Chouettes hulottes. *Gerfaut* 68: 590-650 (in French).
- Francis CM, Saurola P (2004). Estimating components of variance in demographic parameters of Tawny Owls, *Strix aluco*. *Animal Biodiversity and Conservation* 27: 489-502.
- Galeotti P (2001). *Strix aluco* Tawny Owl. Birds of Western Palearctic, Update 3: 43-77, Oxford, UK: Oxford University Press.
- Gruzdev LV, Likhachev GN (1960). Contribution to feeding habits of *Strix aluco* in the Tula Zaseki. *Zoologicheskii Zhurnal* 39: 624-627 (in Russian with English summary).
- Jędrzejewski W, Jędrzejewska B, Szymura A, Zub K (1996). Tawny Owl (*Strix aluco*) predation in a pristine deciduous forest (Białowieża National Park, Poland). *Journal of Animal Ecology* 65: 105-120.
- Jędrzejewski W, Jędrzejewska B, Zub K, Ruprecht AL, Bystrowski C (1994). Resource use by Tawny Owls *Strix aluco* in relation to rodent fluctuations in Białowieża National Park, Poland. *Journal of Avian Biology* 25: 308-318.
- Kirk DA (1982). Diet changes in breeding Tawny Owls (*Strix aluco*). *Journal of Raptor Research* 26: 239-242.
- Levins R (1968). *Evolution in Changing Environments*. Princeton, NJ, USA: Princeton University Press.
- März R (2007). *Gewöll- und Rupfungskunde*. Reprint der 3. Auflage. Wiebelsheim, Germany: Aula-Verlag (in German).
- Morris PA (1979). Rats in the diet of the Barn Owl (*Tyto alba*). *Journal of Zoology London* 189: 540-545.
- Naglov VA (1996). Small mammals associations in dry valley Oak forests of the Eastern Ukraine. Communication 1. Specific composition and association structure. *Vestnik zoologii* 30: 46-52 (in Russian with English summary).
- Nebogatkin IV (1987). Express-key of mammals (informational-methodological letter). Kyiv, Ukraine: Main Sanitary and Epidemiological Bureau (in Russian).
- Newton I (2002). Population limitation in Holarctic owls. In: Newton I, Kavanagh R, Olson J, Taylor I, editors. *Ecology and conservation of owls*. Collingwood, Victoria, Australia: CSIRO Publishing, pp. 3-29.

- Novikov GA (1949). Field research in the ecology of terrestrial vertebrate animals. Moscow, USSR: Sovetskaya nauka (in Russian).
- Petty SJ (1999). Diet of Tawny Owls (*Strix aluco*) in relation to field vole (*Microtus agrestis*) abundance in a conifer forest in northern England. *Journal of Zoology London* 248: 451-465.
- Petty SJ, Saurola P (1997). Tawny owl *Strix aluco*. In: Hagemeyer WJM, Blair MJ, editors. The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance. London, UK: Poyser, pp. 410-411.
- Salvati L, Ranazzi L (2002). Changes in density and territory size of the Tawny Owl *Strix aluco* along an altitude gradient: the effect of forest types and wood cover. *Acta Zoologica Cracoviensia* 45: 237-243.
- Southern HN (1954). Tawny Owls and their prey. *Ibis* 96: 384-410.
- Southern HN (1969). Prey taken by Tawny Owls during the breeding season. *Ibis* 111: 293-299.
- Southern HN (1970). The natural control of a population of Tawny Owls (*Strix aluco*). *Journal of Zoology London* 162: 197-285.
- StatSoft, Inc. (2015) Electronic manual on statistic. <http://www.statsoft.ru/home/textbook/default.htm>.
- Sunde P, Overskaug K, Øien IJ (2001). Living at the limit: ecology and behaviour of Tawny Owls *Strix aluco* in a northern edge population in central Norway. *Ardea* 89: 495-508.
- Tome D (1994). Diet composition of the Long-eared Owl in Central Slovenia: seasonal variation in prey use. *Journal of Raptor Research* 28: 253-258.
- Voronetsky VI, Kuzmenko SV (2013). Key to Bird Pellets and Their Content. Study Guide. Moscow, Russia: Moscow State University Publishing House (in Russian).
- Yatsiuk YA (2009). Using of nest boxes by the Tawny Owl in the elevated Oak forest, Eastern Ukraine. In: Volkov SV, Sharikov AV, Morozov VV, editors. Owls of the Northern Eurasia: Ecology, Spatial and Habitat Distribution. Moscow: pp. 138-143 (in Russian with English summary).
- Yatsiuk YA (2011). Variability of the Tawny Owl (*Strix aluco*) winter and spring diet in a forest-steppe Oak forest. *Zoologicheskii Zhurnal* 90: 1483-1491 (in Russian with English summary).
- Zagorodniuk IV (1993). Taxonomy and distribution of the gray voles (Rodentiformes: Arvicolini) in Ukraine. In: Mammals of Ukraine. Kyiv, Ukraine: Naukova Dumka, pp. 63-76 (in Russian with English summary).
- Zagorodniuk IV (2008). Voles (Rodentia: Arvicolidae) in the Siversky Donets Basin: habitat preferences, changes of geographical ranges, and species identification. *Visnyk of Karazin Kharkiv National University (Series Biology)* 7: 74-93 (in Ukrainian with English summary).