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Prey of Small Mammal-Eating Owls (*Strix nebulosa*, *Bubo bubo*) as a Source of Selective Accumulation of Palaeotheriological Material

N. G. Smirnov*, Yu. E. Kropacheva, and S. V. Zykov

Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia

**e-mail: nsmirnov@ipae.uran.ru*

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Abstract—The accumulation of prey remains in the pellets of the great gray owl in the winter and nesting periods was studied over a number of years at the contact of the taiga and northern forested steppe belts in the Trans-Urals. It is shown which of the characteristics of the hunting territory and the population of small mammals have the greatest effect on the composition and ratio of prey species. A comparison with the results of the feeding activity of the eagle owl was also made. Published information concerning four places of long-term nesting on rocks in the river valleys of the western slope of the Middle Urals in similar natural conditions was used as well. Selective accumulation of prey remains of these two owl species was revealed to lie in a small number of the main prey species, those mostly populating open habitats. In both owls, mammal species of closed forest (transitional) habitats served as concomitant (secondary) prey. The eagle owl was characterized by a large size range of prey. Special attention was paid to the indicator roles the concomitant prey play in paleoreconstructions.

Keywords: paleontological reconstructions, *Strix nebulosa*, *Bubo bubo*, diet, prey selection, nesting period, Middle Urals

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INTRODUCTION

Based on data on the current state of ecosystems and communities of animals and species, ideas about the past stages of their existence are generated (Sher, 1999). Over the past decades, paleontologists have made significant progress in uncovering the mechanisms of accumulation and transformation of animal bone remains in localities (Terry, 2010; Andrews, Fernández-Jalvo, 2018; Comay and Dayan, 2018). It is in taphonomy that knowledge about the present in the most explicit form is used by paleontologists for paleoecological reconstructions. The basis of these approaches in the domestic paleozoology of small mammals was laid by I.M. Gromov in the middle of the 20th century (1957). Owls are one of the main accumulators of bone remains of small mammals. This article discusses materials on the nutrition of two species of mammal-eating owls: the great gray owl (*Strix nebulosa* J.R. Forster 1772) and the eagle owl (*Bubo bubo* Linnaeus 1758). Attention is mainly paid to the study of the selective accumulation of their prey.

The main prey of the owl, the accumulator of the material, may not be the most numerous species in the natural community. It has been shown that, in the same species of owls in different parts of the range, depending on the availability of certain prey species, the main and alternative prey species differ (Mikkola, 1983; Pukinskii, 1993; Korpimäki and Marti, 1995; Zárybnická et al., 2009). The range of diet variation is the widest among universal predators. They prey on the most numerous and accessible prey of the preferred size (Korpimäki, 1986; Korpimäki and Marti, 1995; Rutz and Bijlsma, 2006; Zárybnická et al., 2009).

The great gray owl was chosen as the main object of the study. Due to the fact that this species is a specialized myophage, the analysis of its diet allows one to obtain a clearer picture of selectivity than when studying the diet of universal predators and to describe some of the mechanisms underlying the accumulation of bone remains in ornithogenic deposits.

The eagle owl is a universal predator; throughout its range, significant changes have been noted in the diet, which includes a very wide range of prey. For certain parts of the range, however, the most preferred prey have been distinguished, such as hares, water voles, mole voles, and gray voles (Mikkola, 1983; Shepel, 1992; Pukinskii, 1993; Karjakin, 1998; Tobajas et al., 2016). The eagle owl is the most frequent accumulator of bone material for small mammals on rock outcrops, which are widely represented in the Urals (Shepel, 1992; Smirnov and Sadykova, 2003).

The purpose of this work is to characterize the formation of the food range of the great gray owl and

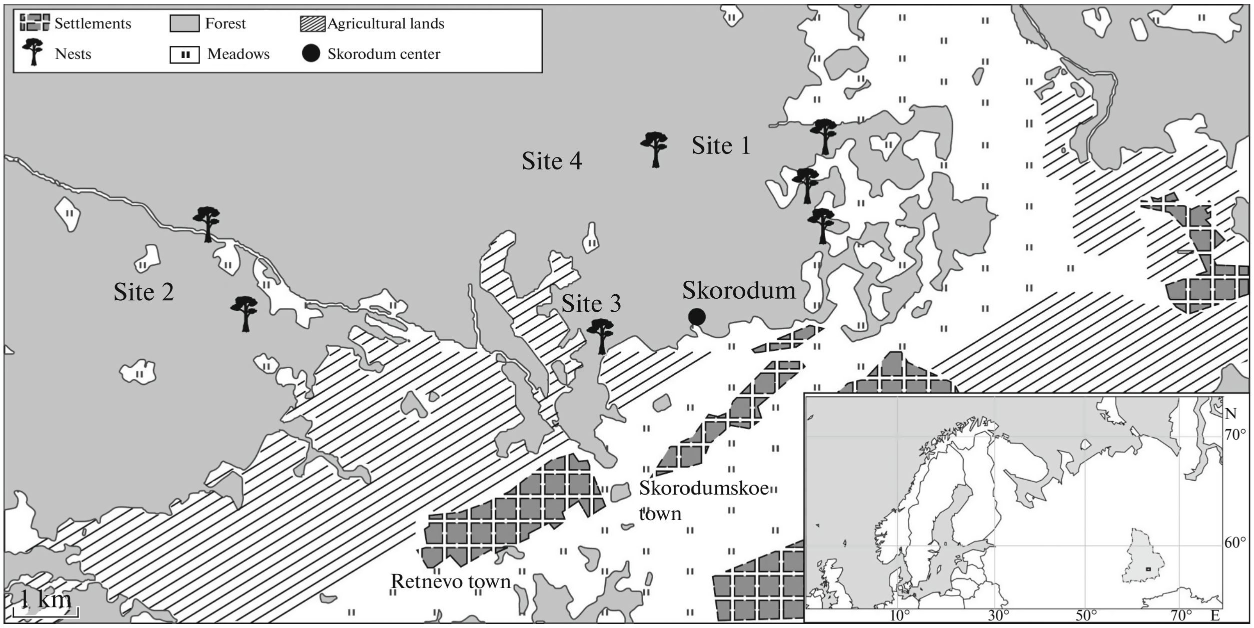

Fig. 1. Scheme of the location of the nests of the great gray owl in the study areas.

eagle owl as a source of selective accumulation of paleontological material. For its implementation, the following tasks were set: (1) to assess the differences in the diet of the great gray owl that occupied different nests, but within the boundaries of areas with the same biotopic characteristics, and estimate interannual nutritional variability; (2) to evaluate the differences in the diet of great gray owls in areas with different biotopic characteristics; (3) to assess the selectivity of the feeding of the great gray owl in the study area in comparison with the results of catches and source data on the fauna of the region; (4) to characterize the composition and structure of the eagle owl's prey from individual nests located in the same type of landscape environment, but with a specific ratio of biotopes; (5) to assess the selectivity of the eagle owl's feeding in the studied area in comparison with the source data on the composition of the fauna and structure of the population of the region; and (6) to evaluate the similarities and differences in the selective accumulation of the remains of the prey of the two species of owls.

MATERIAL AND METHODS

Study Areas

The work was carried out on the basis of field collections on the diet of the great gray owl and eagle owl in two regions of the Middle Urals located approximately at the same latitude of 57° N at a distance of 200 km from each other.

The study of the feeding of the great gray owl was carried out from 2015 to 2018 in the Irbit district of Sverdlovsk oblast (the eastern slope of the Urals) on the basis of the Skorodum scientific and practical center of biodiversity. In it, for these birds, G.N. Bachurin and V.N. Bachurin established artificial nests (Smirnov et al., 2015). The study area is located on the border of the forest and forest–steppe zones and is distinguished by a variety of biotopic conditions. The vegetation is represented by unevenly aged and heterogeneous forest areas with clear-cut areas and vast swampy areas interspersed with agricultural land (fields, meadows, pastures). A detailed description of the territory and the results of comparing the composition of pellets in 1978 and 2015 were published earlier (Smirnov et al., 2015). Inhabited nests were located in areas with different ratios of open and closed habitats. In accordance with the biotopic characteristics, four areas were identified (Fig. 1). Each site contains individual territories around nests with a diameter of 3 km. This area was chosen in accordance with the understanding of the size of the hunting territory of the great gray owl during the nesting period (Bull et al., 1988; Duncan and Hayward, 1994; van Riper and van Wagtendonk, 2006).

On site 1, the vegetation is represented by three categories: meadows (47% of the site area) with pine-birch groves (7%) and forest (46%). There are three nests on the site. Hereinafter, along with the number, this site will be called the "meadow." Site 2 is a forest (88%) with meadow areas (12%) (2 nests). The name "forest–meadow" will be used for it. Site 3 consists of cultivated and abandoned fields (47%) and forest (53%) (one nest); it will be called the "field." Almost the entire territory of site 4 is covered with forest (98%) with forest clearings (2%), and the nearest meadows are located at a distance of 1.5 km from the nest (one nest); it will be "forest." Winter pellets were collected under owls' perches at the territory of the Skorodum center and within the first kilometers around the center (Fig. 1).

The material on the feeding of eagle owls was collected in places of their long-term nesting (several decades) in karst shelters and grottoes of the Western slope of the Middle Urals. Here lies the border of the southern part of the taiga and the Krasnoufimsk insular forest–steppe. The investigated nests and perches are located on small areas on the ground and a rocky bed in the upper parts of high coastal limestone cliffs of the Serga (Filin, Starik and Bazhukovo) and Ufa (Sukhorechenskii) rivers (Smirnov et al., 1992; Smirnov, 1993; Sadykova, 2006, 2011). All these localities are of the same type in terms of the structure of the surrounding landscapes. On the opposite bank from the rocks with the nest, there is a strip of floodplain meadows' on the overlying terraces, there are mixed forests of different species with small meadows. Agricultural fields are located at some distance from the river valley (from hundreds of meters to the first kilometers). On the opposite bank, large areas (many kilometers) are occupied by continuous massifs of mixed and coniferous forests, with small areas of open spaces in the form of clearings, burnt-out areas and raised bogs. Despite the fact that the structure of the landscape is the same for all localities, they differ in the most important parameter, the distance to vast arable farmland. The fields are located literally in line of sight at a distance of less than one kilometer from the Sukhorechenskii nest. The owl's nest is located close to vast fields adjacent to the town of Arakaevo. The straight-line distance is slightly over 1 km. Open spaces near the Starik and Bazhukovo nests are represented only by floodplain natural meadows, hay meadows in the forest, and relatively small pastures around the junction of Bazhukovo and the town of Polovinka at a distance of several kilometers.

Analysis of the Food Range of the Great Gray Owl

Fresh pellets were collected under the perches near nests during the nesting period, until the birds left the nesting site. In 2016 and 2018, owls left their nests at the end of May without completing their nesting because of the decline in the number of rodents. In 2015 and 2017, nesting was successful. Data were obtained from an analysis of pellets collected during 13 nestings and 4 winters. The years of occupation of each nest are given in Table 1. Rodents were identified to a species on the basis of their molars (Borodin, 2009) and insectivores to a genus (Bol'shakov et al., 2000). The number of individuals is determined from the maximum number of remains of the same name (molars). Out of 525 pellets, 5080 remains from 2055 animals were identified. The prey species are grouped according to biotopic and systematic principles (Gromov and Polyakov, 1977; Bashenina, 1981; Bolshakov et al., 2000; Markova et al., 2017) taking into account data on their role in the foraging activity of owls. There are six such groups: (1) common voles (*Microtus arvalis* sensu lato) and narrow-headed voles (*M. gregalis*) living in open biotopes (meadows), (2) *Microtus* voles living in relatively open forest biotopes (root vole (*M. oeconomus*) and field vole (*M. agrestis*)), (3) Clethrionomys voles (northern red-backed vole (*Clethrionomys rutilus*), bank vole (*C. glareolus*), and gray red-backed vole (*C. rufocanus*)), and (4) Ural field mouse (*Sylvaemus uralensis*). Shrews (Soricidae) (5) and other prey (6) were distinguished into two separate groups, the remains of which in the pellets of the great gray owl are rare or scarce: muskrat (*Ondatra zibethicus*), wood lemming (*Myopus schisticolor*), water vole (*Arvicola terrestris*), red squirrel (Sciurus vulgaris), russet ground squirrel (*Spermophilus major*); northern birch mouse (*Sicista betulina*), least weasel (*Mustela nivalis*), and frog (*Rana* sp.).

The division of prey into main, alternative, and concomitant ones is based on the interaction of the characteristics of the predator and prey. The main prey are the stably dominant size-biotopic prey groups. Alternative prey with a decrease in the number of main prey supplements the diet (Korpimäki and Norrdahl 1991; Rutz and Bijlsma 2006; Zárybnická et al., 2009). Concomitant (secondary) preys are sporadically hunted and are represented in the pellet material by single specimens.

Estimation of the Abundance of Small Mammals in the Hunting Territory of the Great Gray Owl

Simultaneously with the collection of pellets in 2016–2018, small mammals were caught with live traps and returned to their habitat. The traps were placed for 2–4 days within 1 km^2 around the inhabited nests. The captures covered dry and swampy areas of the forest, forest edges, thickets of bushes, and meadows. The traps were set in a line at a distance of 10 m from each other. They were checked twice a day, in the morning and evening. Rodents were identified to species, insectivores to genus (Bol'shakov et al., 2000; Borodin, 2009). The number of animals per 100 trap-days (t/d) was calculated separately for forest and meadow catch lines. In total, 186 individuals were caught and identified, which, when describing the material, were combined into the same groups as when analyzing pellets.

To compare the diets of owls, as well as the nutrition of owls and catches, the method of correspondence analysis was used. The comparison includes groups of species that make up at least 10% of bone remains and captured animals. Mice were excluded from the comparison of the feeding of the great gray owls, as their remains were sporadic and were not present in all samples. The comparative analysis of the feeding of the gray owl and the eagle owl included the water vole and the hamster because in the eagle owl's diet, these species accounted for a significant propor-

Table 1. Proportions of prey in the pellets of great gray owls that inhabited different sites during the nesting period (1–4) and in their winter feeding, %

Prey group	Taxon/Nest, No.	Meadow (1)			Forest–meadow (2)		Field (3)	Forest (4)	Winter feeding
		1	2	3	4	5	6	7	
1	*Microtus arvalis* s. l.	26.3	17.5	20.4	65.4	48.1	0	5.2	14.1
	M. gregalis	42.0	35.9	24.1	0.4	0	34.2	1.3	41.1
2	*M. oeconomus*	21.7	17.9	33.6	11.9	22.2	9.8	26.1	12.4
	M. agrestis	6.2	12.7	14.1	10.4	18.0	2.4	25.4	6.9
3	*Clethrionomys rutilus*	0.4	3.3	2.6	1.7	0.8	4.9	0.4	4.9
	C. glareolus	0.8	2.1	1.3	1.7	1.9	7.3	1.7	2.6
	C. rufocanus	0	0	0	0	0	0	0	0.9
4	*Sylvaemus uralensis*	0.4	0.9	0.7	0	0	0	1.7	2.3
5	*Sorex* sp.	2.0	6.9	2.3	7.9	4.1	39.0	36.0	12.4
6	*Arvicola terrestris*	0	0.7	0.1	0	0	0	0.9	0
	Myopus schisticolor	0	0	0	0	0	0	0	1.7
	Sciurus vulgaris	0	0	0.3	0	0	0	0	0.6
	Spermophilus major	0	0	0	0	0	2.4	0	0
	Sicista betulina	0.5	0.8	0.3	0.7	4.5	0	0.4	0
	Ondatra zibethicus	0	0	0	0	0	0	0	0.3
	Mustela nivalis	0.4	0.7	0.1	0	0.4	0	0	0
	Rana sp.	0	0.5	0.1	0	0	0	0.8	0
Pellet collection years		2016, 2018	2016–2018	2015, 2017, 2018	2017, 2018	2017	2017	2016, 2017	2015–2018
Number of pellets		61	61	165	43	63	10	60	62
Number of prey individuals		250	243	534	194	266	41	179	348

tion, but shrews were excluded, since not all published works on the eagle owl contain information about this group (Smirnov et al., 1992; Smirnov, 1993; Sadykova, 2006; Sadykova, 2011). The relationship between the proportions of individual groups of prey in the diet and the proportion of meadow territories in the habitat was estimated using the Spearman's correlation coefficient. The data were processed using the Statistica 8.0 software package (StatSoft 2007).

RESULTS

General Taxonomic Composition of Prey and the Ratio of the Shares of Different Species in the Diet of Great Gray Owls

The remains of 16 taxa of mammals were found in pellets in the studied area as a whole for all the years of collection (Table 1). Prey belonging to other taxa (birds, amphibians, insects) were extremely rare. The vast majority of species were voles. Mice were present as single specimens. Several species have been found among insectivores. As follows from the list of prey, almost all species should be classified as small mammals with a body size of no more than 150 mm. This small range of variation in the size of prey and its taxonomic composition confirms the generally accepted conclusion that the great gray owl belongs to the category of specialized myophage predators.

In the proportion of individuals in the diet, the most important prey for the great gray owl is the *Microtus* voles (78%), which can be considered the main prey. Among them, the share of species characteristic of meadow biotopes is 47% (*M. arvalis* 25% and *M. gregalis* 22%); for forest habitats, 31% (*M. oeconomus* 19% and *M. agrestis* 12%). This is followed by shrews (14%), which are, obviously, alternative prey. Concomitant prey (12 taxa) accounts for 8%. *Clethrionomys* voles account for 5% (*C. glareolus* 2.5%, *C. rutilus* 2.5%, *C. rufocanus* < 1%), mice for 1%, and other species for 2%. Previously, we described the differences in the diet by years, nesting periods, and different numbers of prey in a special work (Kropacheva et al., 2019), and so they are not considered in detail in this paper.

Differences between Individual Nests of Great Gray Owls within Areas with the Same Biotopic Characteristics. Interannual Nutritional Variability

On the meadow site (1), significant interannual changes in the diet were recorded ($\chi^2 = 54.22$, df = 9, $p < 0.001$). In 2015, 2016, and 2018, in all samples, voles inhabiting meadow biotopes (*M. arvalis* and *M. gregalis*) predominated; in 2017, voles inhabiting forest habitats (*M. oeconomus* and *M. agrestis*) prevailed. If we compare the material accumulated over the same time interval, the differences between the samples turn out to be significant only for 2018 ($\chi^2 = 23.94$, df = 6, $p = 0.05$). If we summarize the material for 3 years for two nests and for 2 years for one nest, the differences between the samples prove to be significant ($\chi^2 = 44.42$, df = 6, $p < 0.001$). The diet of owls from two nests was dominated by voles inhabiting meadow biotopes (*M. arvalis* and *M. gregalis*), while the diet of owls from the third nest was dominated by gray voles inhabiting forest habitats (*M. oeconomus* and *M. agrestis*) (Table 1, Fig. 2). In the forest–meadow site (2), *Microtus* voles inhabiting meadow biotopes were predominant (*M. arvalis*), followed by the *Microtus* voles inhabiting forest habitats (*M. oeconomus* and *M. agrestis*). The differences between the samples from the two nests are significant ($\chi^2 = 18.72$, df = 3, $p = 0.005$); they mainly consist in different proportions of these biotopic groups of gray voles (Fig. 2). Interannual differences in the diets are not significant ($\chi^2 = 7.81$, df = 3, $p = 0.09$). On the field site (3), the shares of *Microtus* voles inhabiting open biotopes (*M. greralis*) and shrews were approximately equal. In the forest site (4), significant interannual differences in nutrition were recorded ($\chi^2 = 47.35$, df = 3, $p < 0.001$). In 2016, the diet of owls was dominated by shrews; in 2017, it was dominated by the *Microtus* voles inhabiting forest habitats (*M. oeconomus* and *M. agrestis*). In the winter diet, the *Microtus* voles inhabiting open biotopes (*M. arvalis* and *M. gregalis*) were absolute dominants, followed by the *Microtus* voles inhabiting forest habitats (*M. oeconomus* and *M. agrestis*), with an average of 10% each for *Clethrionomys* voles and shrews (Fig. 2).

Differences in the diets of great gray owls at different sites during the nesting period and in winter are significant ($\chi^2 = 428.29$, df = 12, $p < 0.001$). The diet of owls from forest and field plots was the most original. The diets of owls inhabiting meadow and forest–meadow areas and winter feeding turned out to be the most similar (Table 1; Figs. 2, 3). The proportion of *Microtus* voles in open habitats in the diet does not correlate with the proportion of meadow habitats in the area (Spearman rank correlations, $Sr = 0.14$, $P < 0.05$).

Estimates of the Number of the Great Gray Owl's Prey by Means of Catches with Live Traps

In the conducted catches, if we evaluate them in total, *Microtus* voles (49%) prevailed, of which a large share consisted of voles inhabiting meadow biotopes, 44% (*M. arvalis* 33% and *M. gregalis* 11%) and a much smaller proportion was voles inhabiting forest habitats, 5% (*M. oeconomus* < 1% and *M. agrestis* 5%). This was followed by mice, 31% (*Sylvaemus uralensis* 31%, *Apodemus agrarius* < 1%); *Clethrionomys* voles, 19% (*C. rutilus* 14%, *C. glareolus* 5%); and shrews, 1%. The share of prey groups in catches significantly differed from their proportions in pellets ($\chi^2 = 593.02$, df = 4, $p < 0.001$) (Fig. 4). During the years of research, different numbers of small mammals were observed. In

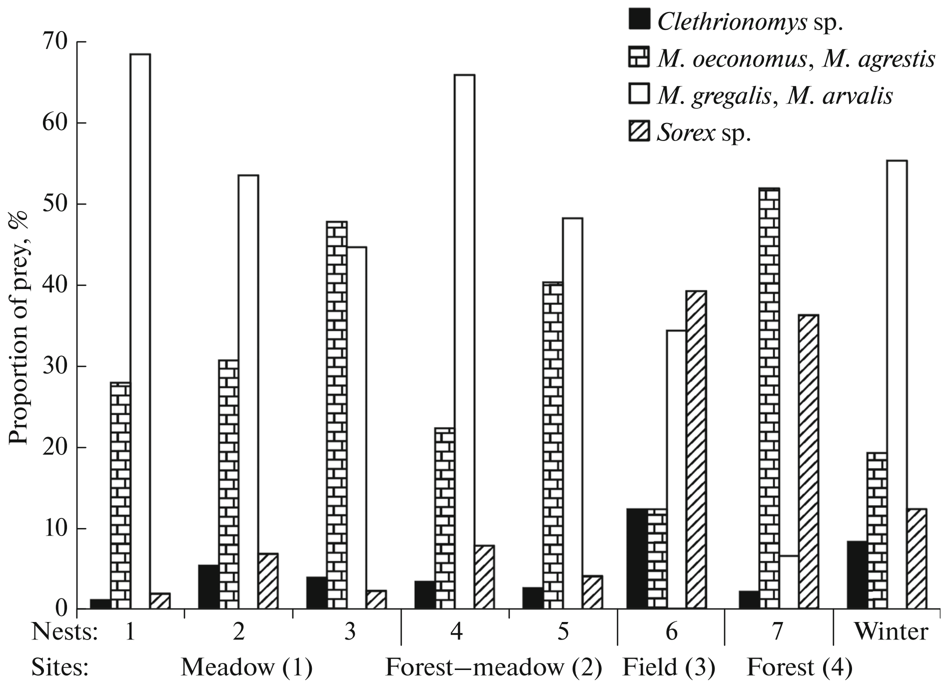

Fig. 2. Average values of the proportions of prey groups in the diet of great gray owls during the nesting and winter periods.

2016 and 2018, a depression in the number of rodents was recorded. In 2017, the abundance of 5.0 individuals/100 t/d was recorded in meadow biotopes, and 6.0 individuals/100 t/d in forest biotopes.

Ratio of the Proportions of Prey Species in the Eagle Owl Diet

In the diet of the eagle owl, 15 species of rodents were recorded (Table 2). Voles that inhabit the meadow biotopes of the study area predominate: *M. arvalis*, 39%, followed by *A. terrestris*, 29%. These species should be considered the main prey, accounting for 68% of the diet. Alternative prey includes the *Microtus* vole inhabiting forest habitats (mainly *M. oeconomus*) and the common hamster (*Cricetus cricetus*), because their share ranges from a few percent to 25% in different nests. Concomitant species (11 taxa) account for a total of 16%. The diets of the eagle owl and the great gray owl were significantly different ($\chi^2 = 585.66$, df = 4, $p < 0.001$) (Fig. 5).

Composition and Structure of Eagle Owl Prey from Individual Nests Located in the Same Type of Landscape Environment, but with a Specific Ratio of Biotopes

Differences between samples from localities formed by eagle owl pellets were significant ($\chi^2 = 88.19$, df = 12, $p < 0.001$). The deposits of the three studied localities were dominated by *M. arvalis*. In the Filin nest, this species was an absolute dominant; in the Sukhorechenskii locality, the remains of *A. terrestris* and *C. cricetus* were numerous; and, in the Starik nest, the dominance of *M. arvalis* was less pronounced, with comparable shares belonging to *A. terrestris* and *M. oeconomus*. In the Bazhukovo locality, the absolute dominant was *A. terrestris*; much smaller shares belonged to *M. arvalis* and *M. oeconomus* (Fig. 6).

DISCUSSION

The specificity of the owl diet was determined by the area of the hunting territory and which of the preferred hunting biotopes and the prey inhabiting them were represented on it.

Differences between Individual Nests of Great Gray Owls within Areas with the Same Biotopic Characteristics. Interannual Nutritional Variability

When summarizing the materials of all years for each nest, the differences between them were, apparently, determined by a set of factors: local biotopic conditions of the hunting grounds and the presence of interannual dynamics of the number of small mammals, as well as alternation in the population of different nests by birds over the years. The interannual dynamics, traced in the meadow site (1), consisted in fluctuations in the proportion of the main prey with consistently low proportion of alternative prey. In the forest site (4), in different years, an alternation of dominance of the main and alternative prey was observed. Thus, in sites with biotopes inhabited by two groups of main prey, the redistribution in dominance

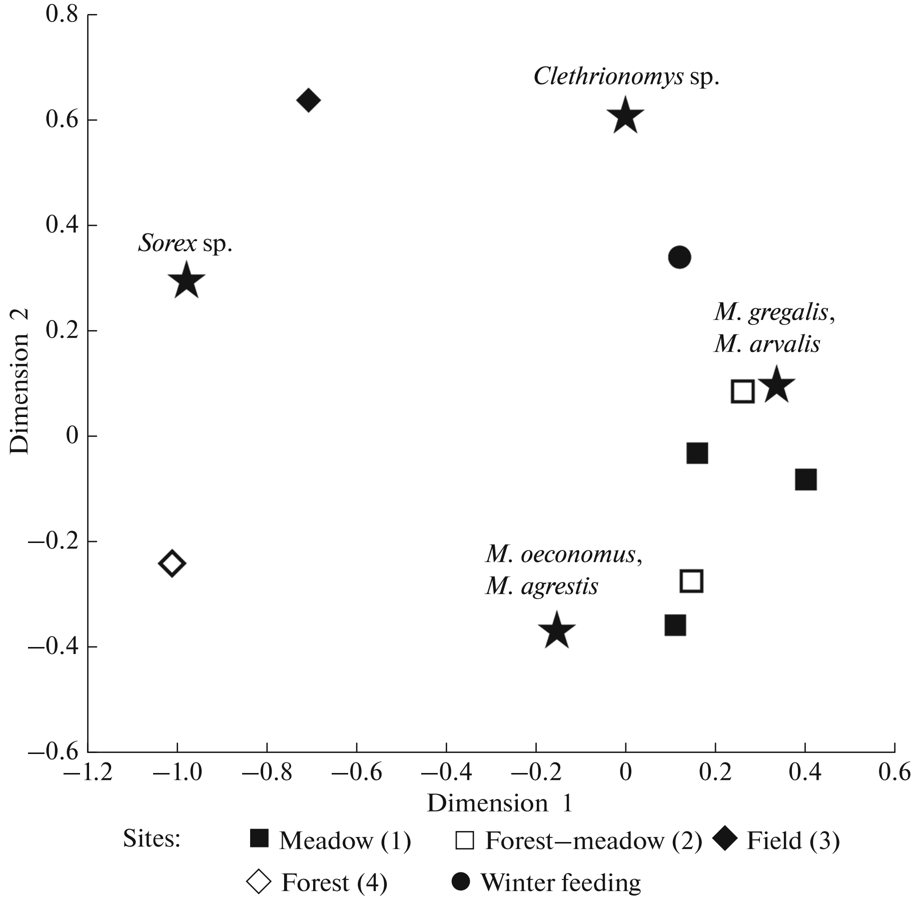

Fig. 3. Distribution of the proportions of groups of prey species by nests in different areas according to the results of the correspondence analysis.

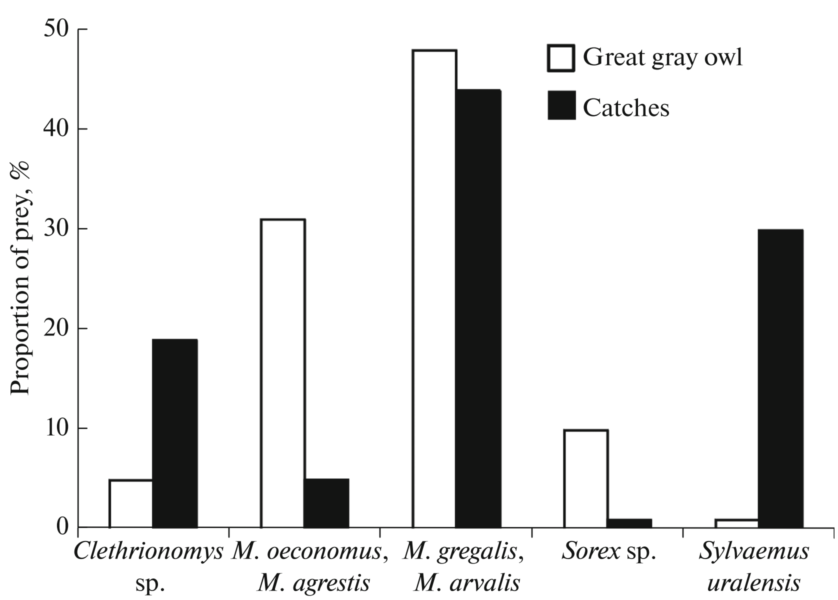

Fig. 4. Average values of the proportions of groups of species in the diet of the great gray owl and groups of the same species in the catches.

Table 2. Proportion (%) of prey in the eagle owl's diet

Taxon	Nest			
	Bazhukovo	Filin	Starik	Sukhorechenskii
Microtus arvalis s. l.	19.0	56.7	33.8	44.7
M. oeconomus	10.0	10.0	24.9	0.5
M. agrestis	6.0	2.4	4.6	2.8
Clethrionomys rutilus	0	0.9	2.1	0
Cl. glareolus	0	1.8	3.2	2.5
Cl. rufocanus	0	0	0.4	1.0
Clethrionomys sp.	7.0	4.3	0	0
Apodemus sp.	0.2	2.2	0.4	6.7
Arvicola terrestris	50.3	12.6	26.0	27.2
Cricetus cricetus	2.0	2.4	2.5	13.7
Myopus schisticolor	0.2	0.1	0	0
Ondatra zibethicus	0	1.9	0.4	0
Sciurus vulgaris	0.3	0.4	0.7	0.2
Rattus norvegicus	0	2.8	0	+
Pteromys volans	0.1	0.1	0	0.4
Sicista betulina	0.3	1.2	1.1	0
Quantity of teeth	23031	672	1376	1704

occurred between them. In the presence of biotopes on the site inhabited by only one group of the main prey, the redistribution of dominants occurred between the main and alternative prey.

There are a number of factors that do not allow the results of the analysis of the composition and structure of the remains of small mammals from multilayered deposits to be directly used to reconstruct the interannual dynamics of their abundance. The accumulation of pellet material occurs unevenly in different years. Burial of the bones of the prey and their transformation into subfossil remains is accompanied by their partial loss. During the formation of deposits, mixing of the remains can occur, as a result of which the cor-

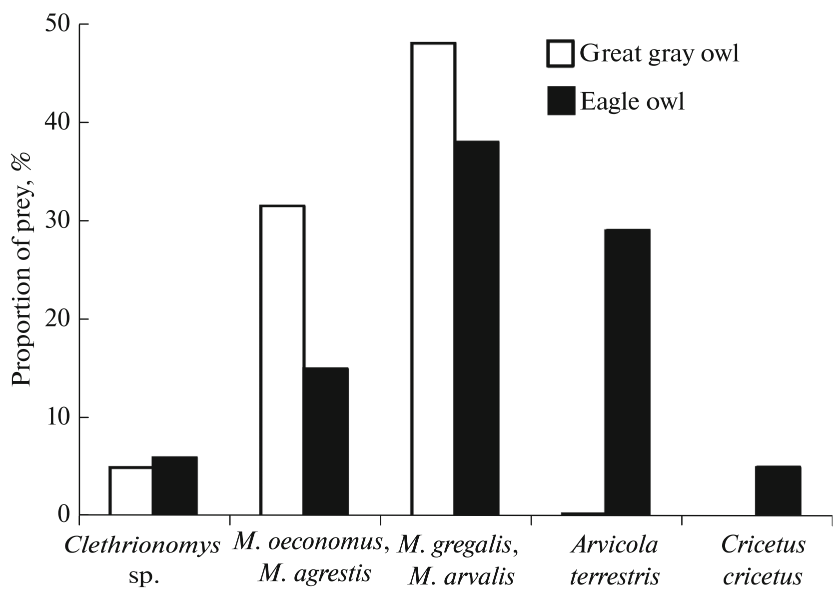

Fig. 5. Average values of the proportions of prey groups in the diet of the great gray owl and eagle owl.

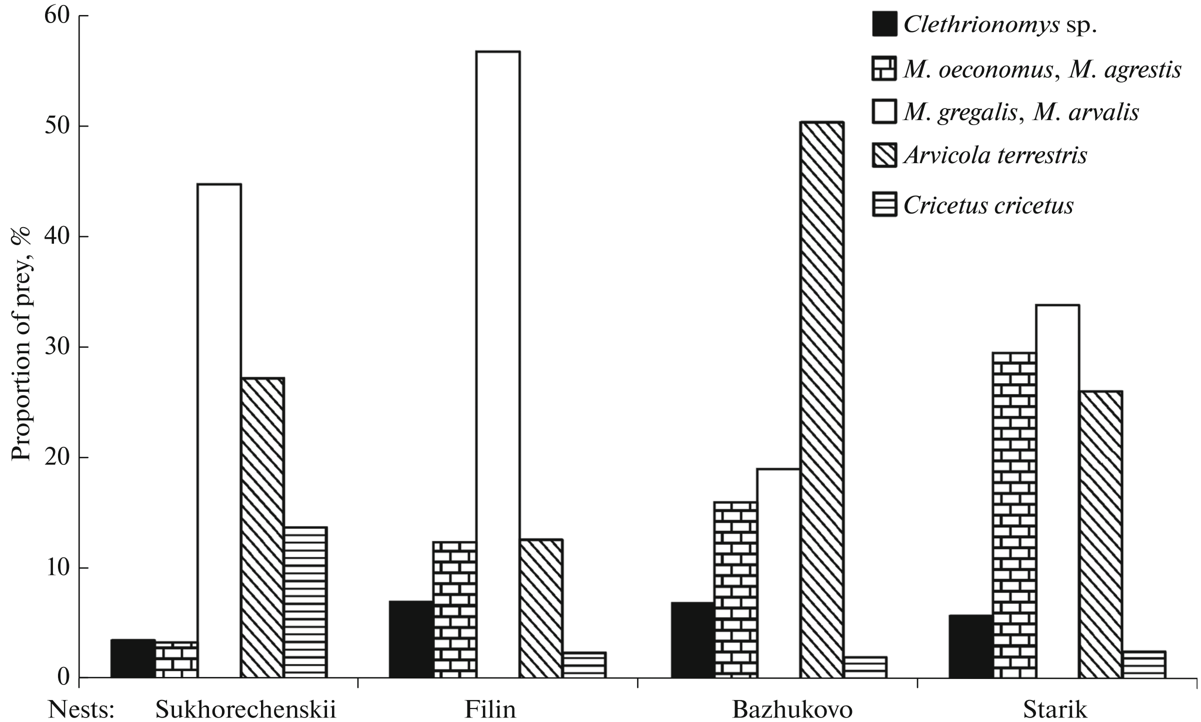

Fig. 6. Proportion of some groups of prey in the owl's diet.

rect stratigraphic sequence is disrupted. These processes lead to the averaging of data not only over individual years, but over tens and hundreds of years.

It can be assumed that in the presence of two and, possibly, more preferred species or biotopically similar groups of prey on the site, their shares become equal as a result of interannual dynamics. If there is a switch to alternative prey in the habitat in years with a low number of main prey, their share in the deposits increases due to accumulation over a number of such years.

Differences between the Diets of Great Gray Owls in Areas with Different Biotopic Characteristics

In the presence of meadows in the habitat (sites 1–3), regardless of their area and the number of species inhabiting them, the inhabitants of the meadows dominated in the diet of the great gray owl. On the meadow site (1), two species dominated, *M. arvalis* and *M. gregalis*; in the forest–meadow site (2), one species dominated in the hunting of the great gray owls, *M. arvalis*; and *M. gregalis* dominated in the field site (3). The great gray owl preferred to hunt voles inhabiting open biotopes in the winter season as well, when the size of the owl's hunting territory is much larger than during the nesting period (Bull et al., 1988; van Riper and van Wagtendonk, 2006). The next-most-abundant group of prey at sites 1 and 2 were *Microtus* voles inhabiting relatively open forest habitats (*M. oeconomus, M. agrestis*). On plot 3, shrews had a comparable proportion to voles in the diet of the owl. We have only one small sample from this site, and so its originality may be associated with both the volume of the material and the biotopic characteristics of the site.

The forest site (4) differed from the others in the low proportion of meadow species, despite its insignificant distance from the meadows (1.5 km). This characterizes the coverage of the territory, which may be reflected in the diet of this species during the nesting period. On this site, with a lower availability of meadow species, the diet was dominated by the *Microtus* voles inhabiting relatively open forest habitats (*M. oeconomus*, *M. agrestis*). The second largest group of prey at site 4 is the alternative prey, shrews.

Eating Selectivity of the Great Gray Owl. Specificity of the Diet in Comparison with Other Parts of the Range

In the pellets of the great gray owl, 15 species of rodents were registered. All of them have been recorded in the sources for this area (Bol'shakov et al., 2000). The flying squirrel, chipmunk, harvest mouse, and common hamster—rare species in the study area and everywhere in Sverdlovsk oblast—were absent in prey (Bolshakov et al., 2000). Of the particularly rare, but, within the main size group of prey, the forest lemming and the gray red-backed vole were noted in the pellets. In addition to rodents, the pellets also contained the remains of shrews, weasels, and frogs. Thus, the rodent fauna of the region is quite fully reflected in the diet of the owl. Many studies have shown that the analysis of owl pellets can be more effective in assessing the fauna than by capture (Andrews, 1990; Terry, 2010).

The feeding of the owl was dominated by species whose habitats were preferred for hunting by the birds (Bull et al., 1989; Duncan, Hayward, 1994; van Riper, van Wagtendonk, 2006): *Microtus* voles of meadow habitats (*M. arvalis* and *M. gregalis*). In our catches, this group of small mammals also dominated. The second most abundant group of prey was the *Microtus* voles inhabiting relatively open forest biotopes (*M. oeconomus, M. agrestis*). The share of these species in pellets significantly exceeded their share in the catches. The root vole prefers to settle in swampy and other humid biotopes. The field vole lives in clearings and burned-out areas, forest glades, and swamps. The study area has many biotopes suitable for these species. The listed species are the main prey of the great gray owl in other parts of its range as well. Thus, in the Ural region, *M. arvalis* sensu lato, which inhabits mainly agricultural landscapes, is abundant in the diet (Karjakin, 1998; Shepel, 2011). The field vole and, to a lesser extent, the root vole are the main prey of this owl species in Fennoscandia and Belarus (Mikkola and Sulkawa, 1970; Mikkola, 1981; Sulkava and Huhtala, 1997; Tishechkin, 1997). The root vole in northeastern Europe, as well as in the Urals, inhabits moist forest and floodplain habitats, while the field vole in Eastern Fennoscandia occupies a wide range of habitats, the most common of which are agricultural lands and the outskirts of settlements (Ivanter et al., 2013). Thus, the common vole inhabits a number of biotopes characteristic of the common vole in the Urals.

The proportion of shrews in the diet ranged from zero to dominance, and in our catches it was consistently low. Throughout the great gray owl's range, shrews were a constant element of prey (Mikkola and Sulkawa, 1970; Mikkola, 1981; Duncan and Hayward, 1994; Sulkava and Huhtala, 1997; Tishechkin, 1997; Karjakin, 1998; Pukinskii, 2005).

Clethrionomys voles were rare prey of great gray owls during the nesting period; their proportion increased in winter. In our catches, forest voles were the second most abundant group. Among them, *Cl. rutilus* prevailed. Literature data indicate that in other parts of the range, forest voles reached a significant proportion in the diet of the great gray owl; however, this group was represented by *Cl. glareolus* (Perm krai, Bashkiria (Karjakin, 1998), a number of localities in Fennoscandia (Mikkola, 1981)) and *Cl. rufocanus* (Murmansk oblast (Mikkola, 1981)). Compared to *Cl. glareolus* and *Cl. rufocanus*, *Cl. rutilus* occupies more closed habitats (Bashenina, 1981). The low proportion of *Clethrionomys* voles in the diet of the great gray owl in the study area may be associated with the low abundance of *Cl. glareolus* and, especially, *Cl. rufocanus*, as well as the less available *Cl. rutilus*, compared to these species. This assumption is supported by the higher proportion of forest voles in the winter diet, when, due to the lack of foliage, they become a more accessible prey than in the spring-summer period.

The findings of mice were single in pellets at all sites, despite their presence in nature. They made up a high proportion of our catches. The proportion of mice in the diet of the great gray owl is never high in other parts of the range (Mikkola, 1981; Korpimäki, 1986; Tishechkin, 1997). It may be that this group of prey is inaccessible for the great gray owl, as it prefers closed habitats and is characterized by high mobility.

Thus, in the diet of the great gray owl, in comparison with the data of trapping of small mammals in the study area, there was a comparable proportion of gray voles in open habitats, a large proportion of *Microtus* voles in relation to open forest habitats and shrews, and a smaller proportion of forest voles and mice.

Composition and Structure of Eagle Owl Prey from Individual Nests Located in the Same Type of Landscape Environment, but in Territories with Different Biotope Ratios

The general composition of prey in each locality fully reflects the composition of the regional fauna. The proportion of the remains of voles of three species of the genus *Clethrionomys*, which can be used to judge the presence of prey caught by eagle owls in closed forest biotopes, does not reach 10%. Other species (inhabitants of forest biotopes: squirrel, flying squirrel, forest mice, wood lemming) do not significantly change the idea about predominant species from open biotopes among the prey. The differences in the diet of eagle owls in the four localities used in this study are mainly determined by the composition of the dominant species. In two nests—Sukhorechenskii and Filin—the inhabitants of fields and meadows (common voles) are dominant; in Bazhukovo, more than 50% of remains are those of the water vole, while in the Starik nest there is no obvious dominant, and ~30% each fall on the remains of the water and common vole and of a group that includes the field vole and root vole. This specifics is easily explained by differences in the biotope characteristics of areas around the nests. As indicated above in the description of the studied region, the main difference is the distance from farmland. The Sukhorechenskii cove is the best example. It is located on the banks of the Ufa River, the right bank of which is occupied by the taiga forests of the Ufa plateau and the left bank is occupied by the Krasnoufimsk forest–steppe, which is almost fully utilized, with farmlands and settlements. Judging by the main prey of eagle owl in this nest, its main prey were caught in the open spaces of the forest–steppe, and the species from forest habitats were less than 7%. The size range of eagle owl prey was equally wide in all nests (from 50 to 350 mm), but the sizes of the main prey differed significantly depending on which of the dominants (water vole or common vole) played the main role in the prey. According to the share of caught individuals, the size group that includes relatively large rodents (muskrat, common hamster, water vole, gray rat, squirrel, flying squirrel) is 52.4% in the Bazhukovo nest, 29.6% in the Starik nest, and 43.5% in the Filin and Sukhorechenskii nests. It is difficult to accurately estimate the mass of prey of this group of species, but in percent this figure is clearly several times higher than the proportion of small prey.

Eagle Owl Feeding Selectivity in the Study Area Compared with Literature Data on the Fauna Composition and Population Structure of the Region

A correct quantitative assessment of prey selectivity of a predator compared with the fauna and prey population structure is possible provided that the scale of the study of the territory (local, regional, zonal) is strictly correlated with the area of the hunting area. Unfortunately, we have no information of this kind and have to use only the qualitative approach, limiting ourselves to preliminary results.

The taxonomic composition of small mammals in the eagle owl prey almost completely corresponds to the regional fauna, which excludes this aspect from the discussion of selectivity. This situation makes us consider the eagle owl of this region a universal predator. This characteristic is enhanced by the presence of bird remains in the deposits studied by us (Smirnov et al., 1992; Smirnov, 1993; Sadykova, 2006, 2011).

The size range of prey is very wide: from hares to small shrews and birch mice. The proportion of hunted individuals from the group of small prey ranges from half to two-thirds. These estimates, on the one hand, once again characterize the eagle owl as a universal, rather than specialized, predator, but, on the other hand, require characterization of selectivity in the choice of prey according to its size. It seems justified to consider jointly interrelated characteristics—the compositions of the size and biotopic groups of eagle owl prey. Two species form the basis of food: water vole and common vole. The first species forms the basis of the population of meadows in floodplains and, at the same time, this is the most abundant species in the size group of large rodents. The common vole is a mass species of the biotope of agricultural meadows and fields, and it actually determines the number of prey of the small size group. In the literature, there is an idea that predatory birds hunt any object available in size (from the corresponding range of habitat) that is within reach (Pyke, 1984). This view determines the possibility for the predator to choose only the time and place (biotope) for hunting in accordance with its physical capabilities and behavioral skills. Using this approach, it should be recognized that the selectivity of hunting for the main prey of eagle owls in the area in question consists in the choice between hunting in floodplains for water voles and hunting in the open areas of farmland for common voles.

Similarities and Differences in Selective Accumulation of Prey Remains for Two Species of Owls

The eagle owl and great gray owl have some common or similar traits, but other traits are specific. Both species are rather large, although the great gray owl is inferior to the eagle owl both in the body length and in mass. Another common feature is that when choosing the hunting grounds, they prefer open biotopes: meadows, fields, and wastelands. If the hunting grounds are forest regions, they choose relatively open regions such as swamps, burnt-out areas, and clearings (Mikkola, 1981; Bull et al., 1989; Duncan and Hayward, 1994; Pukinskii, 1993, 2005; Van Riper and van Wagtendonk, 2006).

The diet of the eagle owl more completely reflects the fauna of small mammals than that of the great gray owl due to large prey: the common hamster, flying squirrel, and gray rat. The most frequent prey is the open-space *Microtus* voles for both species. In the diet of the great gray owl, the second most abundant group is the *Microtus* voles inhabiting the relatively open forest biotopes. In the diet of the eagle owl, the water vole is common prey. In 1978, a significant proportion of voles of this species were noted in the diet of the great gray owl in the study area (Smirnov et al., 2015); therefore, they are available prey that are not being hunted at present, probably because of reduced abundance. In the diet of the eagle owl, the common hamster is present in noticeable proportion, but it is absent in the diet of the great gray owl. This species presently inhabits the study area, but its abundance is low.

An analysis of the composition of the concomitant prey shows that these are mostly the inhabitants of forest biotopes. This complements substantially the characteristics of the territory in which the studied nests are located.

Dependence of the Results of Prey Evaluation on the Scale of the Territory

According to our observations, the territory the population of which of small mammals was reflected in the feeding of the great gray owl was small, 7 km^2. Meadows as the main hunting biotopes determined the groups of the main prey inhabiting them. If these meadows were relatively close to the nest, there was no relationship between their area, and the proportion of species inhabiting open habitats. It is impossible to distinguish a community of small mammals of a forest area with an insignificant proportion of meadows from a community of a region where meadows make up almost half of the area. In both cases, the basis of prey was formed by the species of open biotopes. In the case with meadows located at a distance of 1.5 km from the nest, only a few remains of species of meadow habitats testified to their presence.

The area of the eagle owl's hunting territory during the nesting period is much larger than that of the great gray owl (Mikkola, 1981, 1983). In addition, there are localities formed not only at nesting sites, but also in places of perches. In these localities, pellets accumulate during all seasons. Outside of the nesting period, the hunting territory significantly expands; therefore, in such localities, the territory reflected in the diet is much larger.

The main prey serve as indicators of the preferred hunting habitats, while the concomitant species are caught by predators not only in these biotopes, but also during transit crossing of various habitats inconvenient for hunting by birds. From the viewpoint of obtaining data on the feeding of predators, the concomitant species do not play an important role, while for paleoreconstructions they are of great value as habitat indicators. The identification of this group of prey depends on both the spatial and temporal scales of consideration.

CONCLUSIONS

Consideration of the prey of myophage owl as a source of accumulation of paleotheriological materials leads to the conclusion that the most important aspect of selectivity is the choice of the hunting biotopes. It is in these biotopes that birds hunt for the main and alternative prey. This prey dominates in terms of the number of individuals, but, as a rule, belongs to a limited number of species. Most of the list of prey belongs to concomitant prey, which predators procure not only in the hunting, but also in transit territories. It is these species that act as indicators of the presence of such habitats in the surrounding landscape that are important for paleoreconstructions, but are secondary to the foraging activity of predators. The assessment of the reliability of use of concomitant prey as indicators of certain properties of the reconstructed communities appears to be quite acceptable from the methodological point of view. The key to the success of the application of the developed approach is the fact that the division of prey species into main, alternative, and concomitant ones is based on an objective characteristic: their share in the predator's diet. This trait, which is dynamic in time and space, belongs to the category that does not contradict the principle of disconformity, in contrast to a whole series of traits, which are indicators of environmental characteristics based on the ecological properties of small mammals (Markova et al., 2017).

Differences in the composition of the prey of the great gray owls that occupied the nests within the areas with the presence of two types of biotopes preferred for hunting and, accordingly, two groups of main prey, were insignificant and manifested themselves in fluctuations in the proportion of the main prey. Interannual nutritional variability exhibited the same manifestations. In the presence of biotopes on a site inhabited by only one group of the main prey, the redistribution of shares took place between the main and alternative ones. The feeding of owls in different areas was determined by the presence of open habitats. The proportion of *Microtus* voles from these habitats in the diet is not directly dependent on the proportion of meadow biotopes in the area.

In the diet of the great gray owls, in comparison with the catches carried out, a comparable proportion of *Microtus* voles in open habitats, a large proportion of *Microtus* voles relative to open forest habitats and shrews, and a smaller proportion of *Clethrionomys* voles and mice were observed. The composition and structure of the eagle owl's prey fully reflected the fauna of the region. According to the composition of the main prey, the food of birds from individual nests reflected the population of rodents inhabiting the preferred hunting biotopes. Eagle owl food selectivity consisted in the choice between hunting water voles and root voles in floodplain meadows and hunting common voles in agricultural lands. The similarity in the selectivity of prey in the two species of owls was that the diet was based on a small number of main prey species inhabiting mostly open habitats. In both species, the concomitant prey is species of closed forest (transit) biotopes. The differences lie in the larger size range of the eagle owl's prey.

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The authors declare that they have no conflict of interest. This paper does not contain any studies involving animals or human participants performed by any of the authors.

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