Spatial and Temporal Dynamics of Owls Feeding and the Ornithogenic Deposits Formation

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Abstract—Deposits accumulated by raptors over long periods of time can record changes in small mammal populations. However, between the natural community and the paleocommunity of small mammals in the ornithogenic localities, a number of stages of the taphonomic process pass. The initial stage is associated with the selectivity and plasticity of the predator's diet. We have studied an accumulation of great gray owl (*Strix nebulosa*) pellets in order to better understand this process. For seven years, during the nesting period, 712 pellets were collected at four study sites containing 6328 identified remains (NISP) of 2350 individuals (MNI). Several years of pellet accumulation is not enough to form a complete list of all available prey. Prey ratios can be established in ornithogenic deposits during several phases of the small mammals' population cycle, but they depend significantly on the habitat conditions of the nesting area. A significant change in the diet structure during the nesting period from the stage of egg laying and incubation to the stage of nestling feeding was noted. Given that most of the remains accumulate in the second stage, the features of the diet that are characteristic of it are enhanced. The uneven remains accumulation of prey more and less preferred by the owl at different phases of the small mammals' population cycle was described. This should be taken into account in morphological studies, since many morphological characteristics of small mammals differ in different phases of the cycle.

Localities formed as a result of the food activity birds of prey (ornithogenic) consisting of subfossil and fossil bone remains are a key source of information about communities of small mammals (SM) of the past [1]. Bone remains from pellets are used for monitoring the populations of modern SM and their dynamics [e.g., 2–4]. Owls are the main accumulators of SM bones in paleontological localities [1].

Between the SM communities in wildlife and the ornithogenic paleocommunity, there are many stages of the taphonomic process, at which transformation and loss of information occur. There are three major stages in the taphonomic history of a pellet: transformation of the SM community as a result of the behavioral characteristics of the predator and the influence of local environmental conditions; bone fragmentation and loss of bone mass as a result of predator digestion; various diagenesis processes occurring after pellet regurgitation [5].

Recently, significant progress has been made in studies of SM taphocenoses formation. A research direction has been formed that studies various aspects of the transition of SM from objects of biocenoses to a subfossil state using recent data [e.g., 6–15]. The most

studied is the destruction of bones as a result of predator feeding behavior and digestion to determine the accumulators of bone remains [1, 16–21]. Researches of the community dynamics of SM over time are accompanied by determination of the main collectors of bone remains [e.g., 22–25]. A number of studies are also devoted to the processes that occur after the regurgitation of pellets [5, 26, 27].

Patterns of bone remains accumulation in relatively short time intervals, associated with the plasticity of the raptor's diet, still remain without due attention in taphonomic studies [28]. The study of this stage is closely intertwined with the study of the feeding behavior of birds and is possible only on the basis of recent data.

The species composition of prey may include all representatives of the mammalian fauna available to this species of owls [8, 10, 29–32]. However, the structure (ratio of species) of SM communities is significantly distorted due to the choice of optimal food habitats by predators and the vulnerability of different types of prey [33–35]. Even in the diet of opportunistic predators, the proportions of prey species are not identical to their proportions in the natural commu-

nity, although they can be well correlated [33, 36]. The more specialized the predator, the more obvious these differences are.

Ornithogenic localities are often formed at the nest site. During the nesting period, the size of the hunting territory is significantly smaller compared to the non-breeding season [37−39]. Thus, the ratio of prey in a given area is formed as a result of selective predation by a predator, but also reflects a rather small area community, corresponding to the size of the predator's foraging area. Part of this work is devoted to studying the influence of local nesting conditions on the composition and ratio of SM in the owl's diet.

Another part of this work is devoted to the study of the effect of predator diet plasticity on the formation of prey composition in a hypothetical locality. Birds of prey can vary their diet depending on the state of food supply [e.g., 40−45]. Both intraannual and long-term dynamics of the diet were noted, depending on the abundance and prey availability in foraging areas [e.g., 41, 44, 46−48]. The diet of SM bone-collecting owls changes along with the prey population structure. This fact is beyond doubt and underlies paleoecological reconstructions [e.g., 49−52]. Changes in the diet over short time intervals (during nesting and its interannual dynamics), coupled with a different amount of accumulated remains, creates the proportions of species that paleontologists subsequently work with. In this paper, we take a step towards greater detail in understanding the accumulation of remains in ornithogenic localities.

We aimed to describe the process of formation of the proportions of species and prey groups during the initial stages of ornithogenic deposits creation on a model object − great gray owl (GGO, *Strix nebulosa*). We have studied: (i) how the composition of GGO prey in the study area reflects the fauna of SM in the region (Sverdlovsk region); (ii) how the local features of habitats around the nest affect the composition and ratio of prey in the diet of GGO; (iii) how changes in diet (both during nesting and between years with different prey numbers) and the amount of accumulated remains affect the structure of a hypothetical subfossil community of SM.

MATERIAL AND METHODS

Study area. The study was conducted in the Irbitsky district of the Sverdlovsk region (eastern slope of the Urals, the preforest−steppe subzone of the taiga zone [53]) at the Scientific and Practical Center for Biodiversity "Skorodum" (57°34′ N, 62°42′ E). Artificial nests for owls were installed by the center's staff in 2007. The nests were located in territories with different proportions of open and closed habitats. Based on this characteristic, it was divided into plots consisting of separate territories around nests with a radius of 1.5 km. The area around the nest that an owl uses to hunt in during the nesting period rarely exceeds this value [37, 54, 55]. Figure 1 shows the locations of the nests in the study area. A total of 8 nests were studied. The distance between the most remote nests is 9 km. Using the SAS-planet service (https://sasplanet.ru), the areas of closed (forest) and open (meadow, field) territories were estimated for each plot. The vegetation on the meadow plot is represented by three categories: meadows (47% of the plot area), pine−birch groves (7%), and the forest (46%). In different years, four nests in this plot were inhabited. The meadow−forest plot is a forest area (88%) with the presence of meadows (12%). There are two nests in this plot. In the forest plot, almost the entire territory is covered in forest (98%) with small forest clearings (2%). The nearest meadows are located 1.5 km from the nest (one nest). The field plot is represented by cultivated and fallow lands (47%) and forest (53%) and contains one nest.

Samples. The material for the study was the GGO pellets collected during the nesting period. GGO has several preferred perches at a distance of no more than 100 m from the nest, which facilitates the collection of pellets, because the bulk of the material is concentrated under them. When searching for pellets, we also carefully examined the ground around all trees located at a distance of up to 180−200 m from the nest for the presence of single items. During the nesting period, several stages of collecting pellets were organized. The study covered the period from 2015 to 2021. A total of 712 pellets were collected containing 6,328 identified remains of 2350 SM. The minimum number of individuals (MNI) in the studied samples for each nest and nesting stage for the different years is presented in Table 1.

The remains of the prey were identified to species by molars and mandibles using guides [56−60] and reference collections of the Laboratory of Paleoecology at the Institute of Plant and Animal Ecology, Ural Branch of the Russian Academy of Sciences. MNI was calculated per pellet by the maximum number of the same craniodental element.

Estimation of the number of SM in the foraging area of the GGO. Live-trapping of SM was carried out synchronously with the collection of pellets in 2016−2021. The animals were returned to their habitat after marking. 200 traps were placed for 2−4 days within the hunting territories of birds with an interval of 10 m from each other in several trap lines. The traps were checked 4−5 times a day to avoid the death of the animals. The traps covered dry and swampy areas of the forest, forest edges, and thickets of shrubs and meadows. In total, 6594 trap-nights were performed, and 304 individuals were caught and identified. In cases where species identification by the exterior was difficult [61], we determined species by the occlusal surface shape of teeth using a non-traumatic intravital imprints method [56, 62, 63].
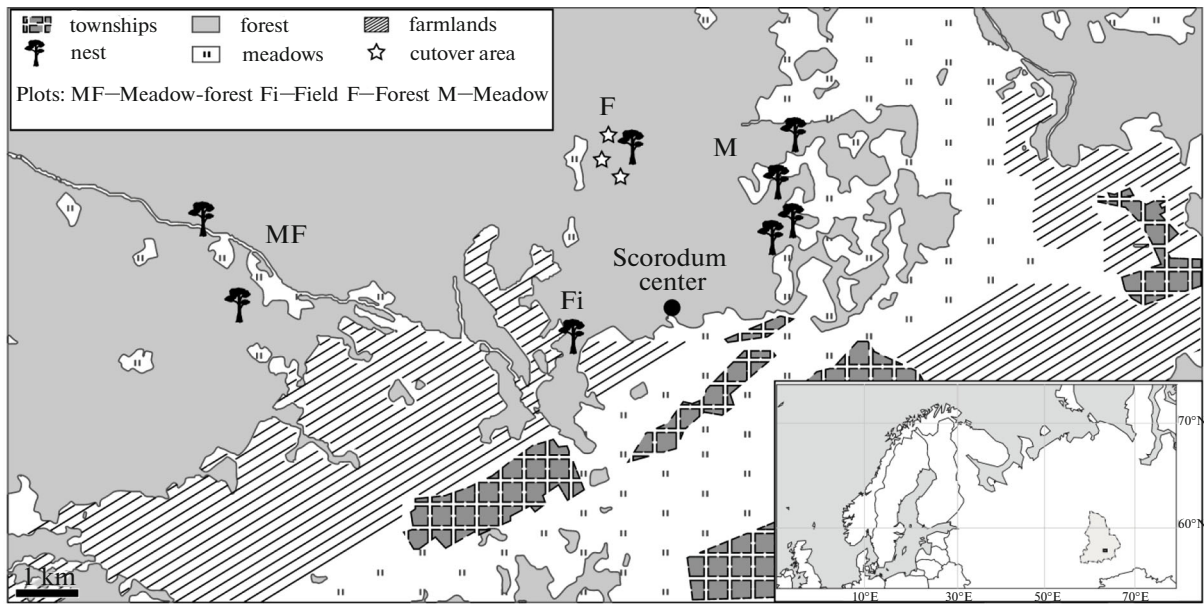
Fig. 1. Locations of owl nests in the study plots.

Data analysis. To analyze the diet and its dynamics, prey species were grouped according to their role in the diet of owls [45, 64, 65]. Categorization of prey groups is the link between the ornithological and paleoecological approaches. This approach makes it possible to correlate the structure of the diet of a predator accumulating bone remains in an ornithogenic taphocenosis with a community of SM. The main prey are the most preferred prey groups in terms of size and habitat. It consistently dominates the predator's diet. Alternative prey have a number of characteristics that make them less preferred by predators, e.g., they are smaller, live in less accessible habitats, and are more energy-intensive for the predator to catch [e.g., 44, 46, 66, 67]. Their proportion in the diet increases with the lack of the main prey, periodically reaching significant amounts [41, 45, 64]. For paleoenvironmental studies, it is proposed to single out the category of concomitant prey [65]. These species appear episodically in prey, are represented by single specimens, and do not play a significant role in the diet of owls [65]. In the paleontological data, it is possible to distinguish groups of prey by their ratio in the paleocommunity. The main prey dominates the community. Concomitant prey

Table 1. Minimum number of individuals (MNI) in the samples for each nest and nesting stage for the different years

Year	Plot	Meadow				Meadow-forest		Forest	Field
	Nest, No.	1	2	3	4	5	6	7	8
	Nesting stage								
2015	1			67					
2016	2	111	46					51	
2017	1		18	30		46	120	65	
	2		102	316		98	144	59	42
2018	1	20		52					
	2	115	9	19		13			
2019	1		63						
	2		80			52			
2020	1				203	40			
	2				126	49			
2021	1				89	24			
	2				64	17			

constitutes single finds. An intermediate position is occupied by alternative prey [65]. When identifying prey groups, we were guided by the abovementioned criteria, taking into account the data obtained both earlier [15, 68] and in the course of this study. From a statistical point of view, arranging species into groups reduces the problem of data sparseness with observed zeroes and increases the adequacy of chi-square-type statistics.

To illustrate the dynamics of prey groups during nesting, all samples used were arranged according to their collection dates for the year. For subsequent analysis, the data was grouped into two nesting stages. The first stage was considered the period of laying and incubation of eggs. All collections from April to the first decade of May are referred to as belonging to this stage. The onset of the second stage (feeding of nestlings) is marked by the egg shells and the droppings of nestlings in the female's pellets. In the years when the female left the clutch due to the lack of food supply, hatching did not occur. However, the birds stayed in the nesting areas for some time, leaving pellets. Therefore, even during these years, we attribute the collection of pellets, starting from the second decade of May, to the second stage of nesting.

Bone remains in the locality accumulate mainly before the nestlings leave the nests; therefore, the main characteristic of the nesting period in this study was its completeness. Nesting was considered completed when it continued until the nestlings left the nest and was considered uncompleted when the owls left the nests at the stage of laying eggs or feeding of nestlings.

For statistical modeling of the spatiotemporal features of a multinomial-dependent variable, which was the species of SM (or their pools, via collapsing species into groups), we used: 1) correspondence analysis [69] and 2) generalized linear models (GLM) [70] for discrete variables: multinomial and binomial logit regression and Poisson regression for the number of species and individuals (MNI). The predictors are: 1) the spatial factor — the plots (4) or nests (8); 2) the time factor — the phase of SM population cycle (Trough, Increase, Peak) or the year of observation (2015–2021), collection dates for the nesting period, and two stages of the nesting period (I — laying + incubation, II — feeding of nestlings). As a proxy measure for the SM density, we used a "catch index", which is the proportion of live-trapping success per 100 trap-nights, and transformed it to log-odds (logit), which makes the distribution of the trait symmetric. Statistical analysis was performed using the Statistica 7 package [71].

RESULTS

Composition and structure of the GGO diet in the study area. In the diet of the owls, 23 species of SM were identified (Table 2). The most numerous prey were *Microtus* voles, and they accounted for 87% of individuals. They are classified as the main prey. Based on the size and the biotopic characteristics of these species, we divided them into two groups: smaller open habitat species [the common vole (*Microtus arvalis*) and narrow-headed vole (*M. gregalis*)] and larger species from near-water and relatively open forest habitats [the root vole (*M. oeconomus*) and field vole (*M. agrestis*)].

Alternative prey include species whose proportion in the total sample (*n* = 2350) was 1−3% (at least 20 individuals). These include two species of *Clethrionomys* voles, *C. glareolus* and *C. rutilus*, and four species of shrews, *Sorex araneus*, *S. minutus*, *S. caecutiens*, and *S. isodon*. The assignment of these taxa to the category of alternative prey is supported by the fact that they periodically make up a significant proportion in the diet of owls in this study area [15, 68]. The proportion of this group was 10.2%.

Species represented in the diet by single individuals are classified as concomitant prey (13 species): *Sciurus vulgaris, Spermophilus major, Sicista betulina, Apodemus uralensis, Micromys minutus, Ondatra zibethicus, Arvicola terrestris, Myopus schisticolor, Neomys fodiens, Sorex daphaenodon, Sorex minutissimus, Sorex* cf. *tundrensis* and *Mustela nivalis*; the proportion of this group was 2.6%. In owl pellets, single remains of amphibians were also found, but we do not discuss them in this paper.

The maximum number of species identified per year for individual nests was 15. Poisson regression analysis showed that it depended on the number of individuals (MNI) (Table 3a). However, according to the total data for all years, 10−17 species were identified for the nests [an average of 56% (43−74%) of the prey list throughout the territory], and the number did not depend on MNI (Table 3b).

Diets of the owls from different plots. Canonical correspondence analysis using prey species and nests as factors in the contingency table factors showed high similarity of diet structure within the same plots and noticeable differences for different plots (Fig. 2a). For the meadow plot, the maximum number of species (*n* = 20) was detected (see Table 2). Here, *M. oeconomus, M. arvalis, M. gregalis* and *M. agrestis* dominated. In total, 16 species were found in the diet of owls from the forest meadow plot (see Table 2). Among the main prey, *M. arvalis* was the most dominant, followed by *M. oeconomus* and *M. agrestis*. The contrast between these plots in the ratio of *M. arvalis* and *M. gregalis* is estimated by the model using the main prey species and groups of other prey as factors (Fig. 2b). 14 species were found in the diets of owls from the forest plot. *M. oeconomus* and *M. agrestis* played the main role in the diet of GGO. Alternative prey constituted a high proportion of the diet. The remains of *M. gregalis* were single, and the proportion of *M. arvalis* was insignificant. In total, 10 species were identified for the field

Table 2. Composition and structure (%) of the diet of the GGO in the four plots (M—meadow, MF—meadow–forest, F—forest, Fi—field): a—species; b—prey groups

	Species and prey groups	Whole territory	Plots			
			M	MF	F	Fi
a						
Main prey	*Microtus arvalis*	31.53	23.33	61.53	7.43	0
	M. gregalis	14.77	21.5	0.33	1.14	33.33
	M. oeconomus	25.87	30.65	13.76	29.71	9.52
	M. agrestis	15.02	14.97	11.61	30.29	2.38
Alternative prey	*Sorex araneus*	3.15	1.18	3.65	13.14	26.19
	Clethrionomys glareolus	2.17	2.35	1.66	1.14	7.14
	C. rutilus	1.49	1.31	1.82	1.14	4.76
	Sorex minutus	1.32	1.44	0.66	2.29	2.38
	S. isodon	1.11	0.20	1.99	4.57	7.14
	S. caecutiens	0.98	0.72	0.83	2.86	4.76
Concomitant prey	*Apodemus uralensis*	0.64	0.33	1.16	1.71	0
	Sicista betulina	0.55	0.65	0.33	0.57	0
	Micromys minutus	0.38	0.52	0.17	0	0
	Neomys fodiens	0.26	0	0	3.43	0
	Arvicola terrestris	0.13	0.13	0	0.57	0
	Mustela nivalis	0.13	0.13	0.17	0	0
	Sorex daphaenodon	0.13	0.20	0	0	0
	Myopus schisticolor	0.09	0.07	0.17	0	0
	Sciurus vulgaris	0.09	0.13	0	0	0
	Sorex minutissimus	0.09	0.13	0	0	0
	Ondatra zibethicus	0.04	0.07	0	0	0
	Spermophilus major	0.04	0	0	0	2.38
	Sorex cf. *tundrensis*	0.04	0	0.17	0	0
b						
M. arvalis + *M. gregalis*		46.3	44.83	61.86	8.57	33.33
M. oeconomus + *M. agrestis*		40.89	45.62	25.37	60	11.90
Alternative prey		10.22	7.20	10.61	25.14	52.37
Concomitant prey		2.61	2.36	2.17	6.28	2.38
Number of individuals		2350	1530	603	175	42
Number of species		23	20	16	14	10
Number of nests		8	4	2	1	1

plot. *M. gregalis* and alternative prey dominated, *M. arvalis* was absent and *M. oeconomus* and *M. agrestis* accounted for a low proportion (Figs. 2a, 2b).

The diets of owls from the meadow and forest–meadow plots had the greatest similarity in terms of the ratio of prey groups (Fig. 2c). A high proportion of both main prey groups and a relatively low proportion of alternative and concomitant prey were typical for the feeding of owls from both plots. The differences between them were determined by the ratio of the two

groups of main prey, which formed the first canonical axis. The second dimension is the proportion of alternative and concomitant prey, which was numerous in the forest and field plots.

Variability of the GGO diet during the nesting period. Based on the different study durations for the plots and the similarities and differences in the owls' diet structure, we studied the variability of the diet during the nesting period and its long-term dynamics according to the data for meadow (M) and meadow–
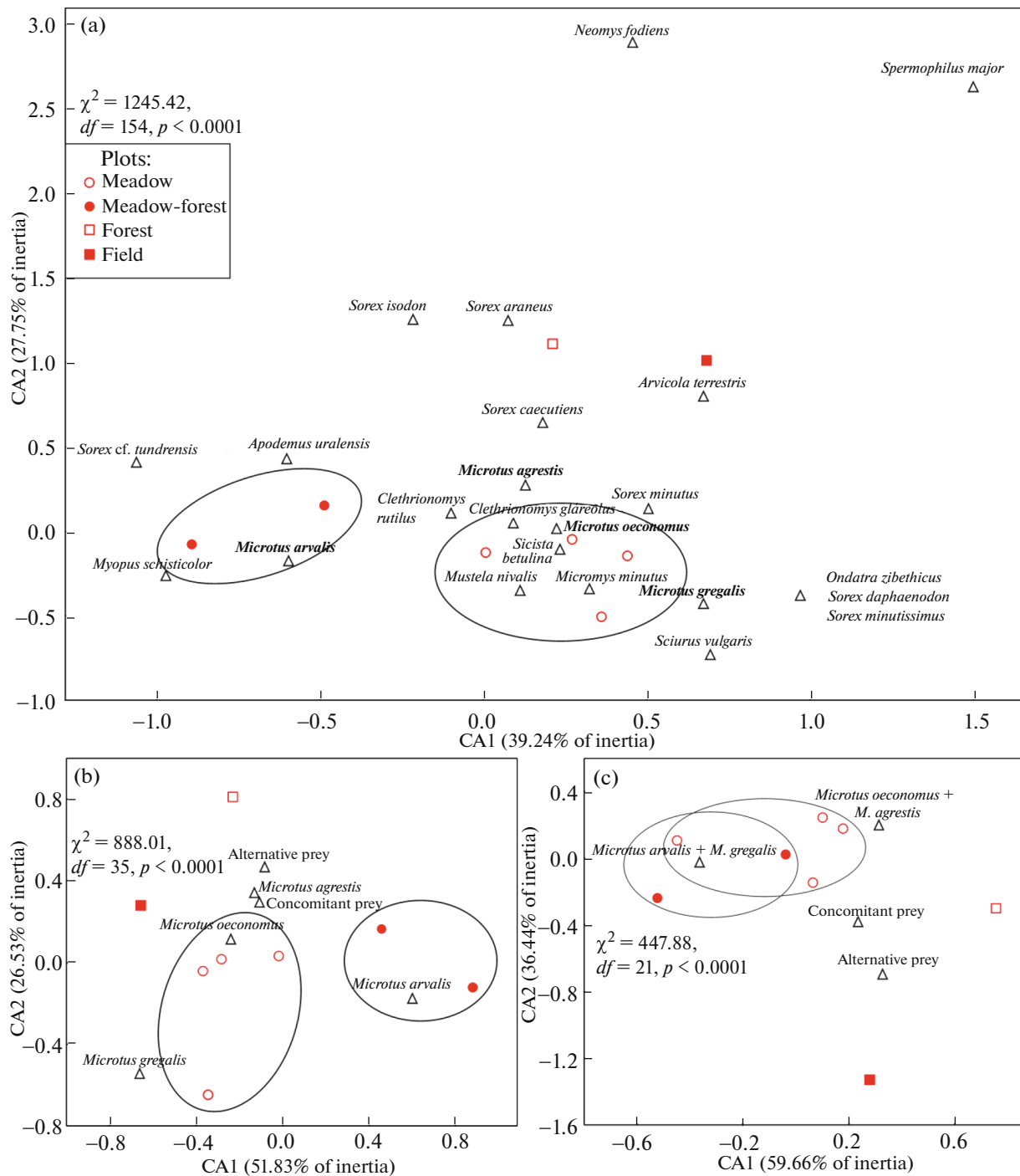
Fig. 2. Ordination of owl diets in the study area in the two canonical axes (CA) space: a − nests and prey species (main prey are indicated in bold); b − nests and four species of main prey and groups of other prey (alternative and concomitant); c − nests and four prey groups.

forest (MF) plots. The proportion of *M. arvalis* and *M. gregalis* in the diet decreases, while the proportion of *M. oeconomus* and *M. agrestis* increases during nesting. The similarity of the dynamics of the main prey species serves as a statistical basis for their collapse into pairs: *M. arvalis* + *M. gregalis* and *M. oeconomus* +

M. agrestis. During nesting, the proportions of alternative and concomitant prey increase (Fig. 3, Supplementary, Table 1).

Interannual variability in the diet structure of owls. The interannual variability of prey in the owls' diet was studied in relation to the dynamics of the abundance
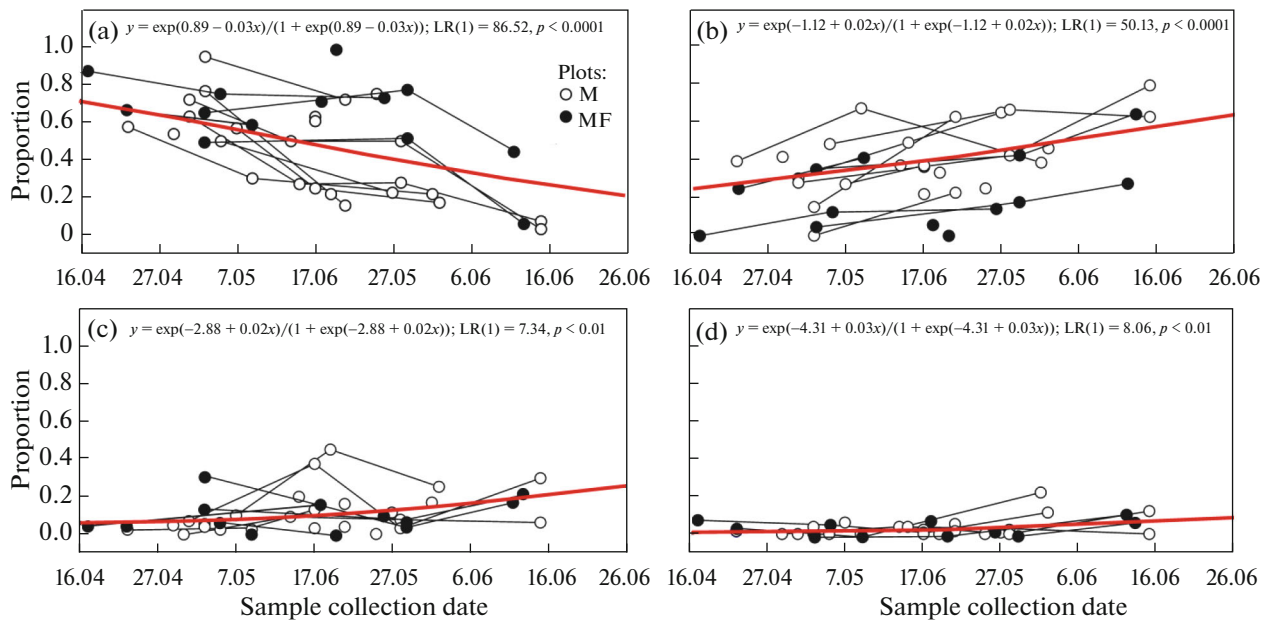
Fig. 3. Trajectories of changes in the proportions of prey groups in the owls' diets during nesting (days) during different years in the meadow (M) and forest−meadow (MF) plots: a − *M. arvalis* + *M. gregalis*; b − *M. oeconomus* + *M. agrestis*; c − alternative; d − concomitant. The thin lines connect the data within a year for each nest; the thick dotted line and the equation is the result of logit regression for all years and nests (see Online Resource 1).

of SM according to live traps (Fig. 4). Based on the results of logit regression to describe the odds of SM capture, the following phases of the population cycle were identified: 2016 and 2019 − growth, 2017 and 2020 − peak and 2018 and 2021 − trough (Table 4). For the study area, there was no data on the number of SM in 2015. The nearest place where monitoring studies of the number of SM were carried out in the study period was the Visimsky State Biosphere Reserve (southern dark coniferous taiga, Middle Urals). In 2016-2021, the phases of the SM population cycle observed there were the same as in the territory we studied. In 2015, there was a trough phase in the population cycle of SM [72−74]. Thus, it can be assumed that in 2015, there was also a trough phase in the study area. Nevertheless, the habitable burrows, plant bites, droppings, and the number of diurnal predators

observed by us this year suggest that the absolute abundance was not extremely low. Thus, our studies presumably cover two complete cycles: increase − peak − trough (2016−2018 and 2019−2021) and a hypothetical trough in 2015 (Table 4).

At the preliminary stage of assessing the dynamics of the diet structure of owls by years and phases of the population cycle of SM, a multinomial logit regression was used with the "prey group" as the dependent variable, and "year" (or "phase"), "plot", and "nesting stage" as predictors, taking into account the interaction of the factors of "year" (or "phase") and "plot" (Supplementary, Table 2). In general, similar patterns were revealed for the meadow and forest−meadow plots, but for the *M. arvalis* + *M. gregalis* (vs. other groups), interaction was significant for two years of observation. The model with the "phase" factor

Table 3. Poisson regression results: $\ln(\text{м}) \sim b_0 + b_1 * \ln(N)$ is used to describe the number of species as a function of MNI for individual nests: a—per year (20 cells, nest-year); b—for all years (8 nests)

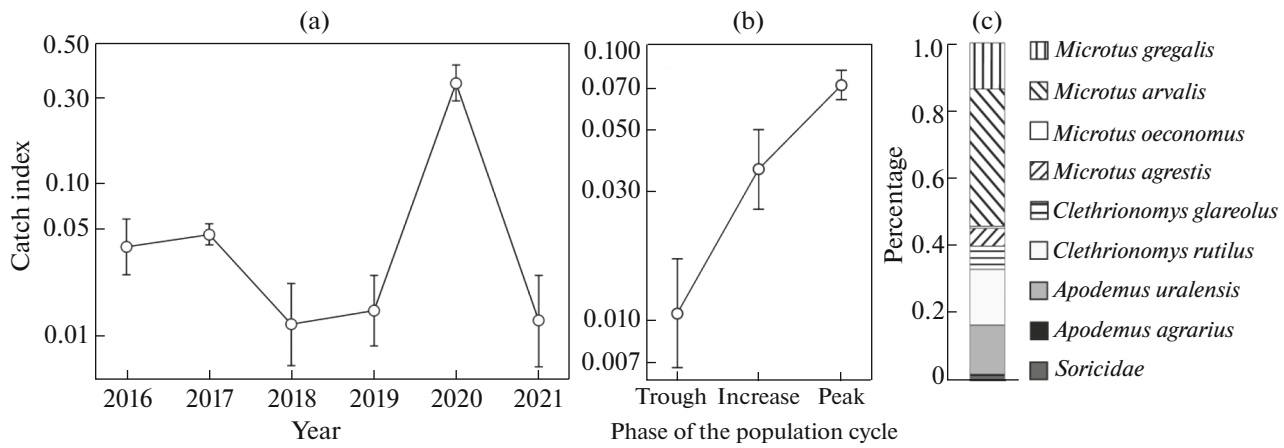| Predictors	B	SE	Wald $X^2(1)$	p	95% CI		Exp(b)	95% CI	
a. cell = nest-year, $n = 20$: $\ln(\text{м}) \sim b_0 + b_1 * \ln(N_{it})$, $LR(1) = 12.11$, $p < 0.001$									
b_0	0.86	0.41	4.33	<0.05	0.05	1.68	2.4	1.1	5.4
Ln (MNI)	0.30	0.09	11.38	<0.001	0.12	0.47	1.34	1.13	1.60
b. cell = nest, $I = 8$: $\ln(\text{м}) \sim b_0 + b_1 * \ln(N_i)$, $LR(1) = 0.63$, $p = 0.43$									
b_0	1.96	0.79	6.1	<0.05	0.40	3.51	7.1	1.5	33.4
Ln (MNI)	0.11	0.14	0.60	>0.05					

Fig. 4. The number of SM (catch index in logit scale) according to the live-trapping data during the nesting of owls (May−early June) (see Table 4 for logit regression results): a − long-term dynamics; b − dynamics by phase of the population cycle; c − the ratio of species in the trapping lines; whiskers − 95% CI.

revealed the interaction in one case. The proportions of prey groups in these areas varied (Table 2, Supplementary, Tables 1 and 3). Based on these results, we will use the data from these two plots in further models of dietary dynamics, introducing the "plot" factor.

The results of binomial logit regression with the factors "year", "plot", and "nesting stage" showed the interannual changes in the proportions of the two main prey groups. They were opposite to each other. The proportions of alternative and concomitant prey in the total food spectrum are low, and their changes are synchronous (Fig. 5a, Supplementary, Table 2 4).

Depending on the number of prey, both uncompleted and completed nestings of the owls were observed. In the years of the trough, only uncompleted nestings were observed (2018, 2021); in the years of increase, uncompleted (2016) and completed (2019) nestings were observed, and in peak years, only completed nestings were observed (2017, 2020).

In the gradient ranging from low SM abundance and uncompleted nesting to high SM abundance and completed nesting, the following structural changes in the diets of the owls can be distinguished: I. dominance of *M. arvalis* + *M. gregalis*, low proportion of other prey groups (2016 − increase phase, 2018 −

Table 4. Results of logit regression for describing the abundance of SM on the trapping lines (May vs. early June) for 2016−2021, with predictors a—"year" and "month of trapping" (b_0—May, 2021); b—"phase" and "month of captures" (b_0—trough, May)

| Predictors	b	SE	Wald $X^2(1)$	p	95% CI		Odds ratio		
							Exp (b)	95% CI	
a. LR(6) = 320.0, p < 0.0001									
b_0	−8.66	0.95	83.23	<0.0001	−10.52	−6.80			
June	0.97	0.17	33.34	<0.0001	0.64	1.30	2.64	1.90	3.68
2016	0.10	0.21	0.23	>0.05	−0.31	0.51	1.11	0.74	1.66
2017	0.30	0.12	6.18	<0.05	0.06	0.53	1.35	1.07	1.71
2018	−1.11	0.30	14.12	<0.001	−1.69	−0.53	3.04^{-1}	5.44^{-1}	1.70^{-1}
2019	−0.90	0.25	12.92	<0.001	−1.40	−0.41	2.47^{-1}	4.04^{-1}	1.51^{-1}
2020	2.68	0.17	245.62	<0.0001	2.34	3.01	14.56	10.42	20.35
b. LR(3) = 121.01, p < 0.0001									
b_0	−4.23	0.70	36.49	<0.0001	−5.60	−2.86			
June	0.14	0.12	1.24	>0.05	−0.11	0.38	0.14	0.90	1.47
Increase	0.18	0.15	1.47	>0.05	−0.11	0.47	0.18	0.90	1.60
Peak	0.90	0.11	71.48	<0.0001	0.69	1.11	2.46	1.99	3.03
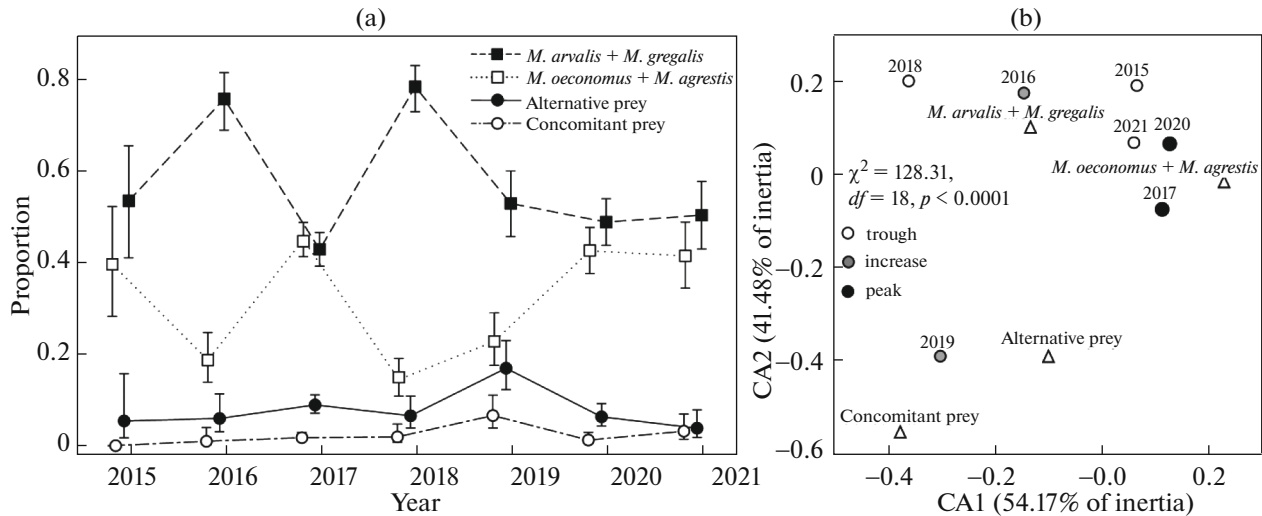
Fig. 5. Long-term dynamics of the owls' diet structure: a − results of binomial logit regression, b − canonical correspondence analysis.

trough phase, uncompleted nestings); II. a high proportion of *M. arvalis* + *M. gregalis*, but also a high proportion of alternative and concomitant prey (2019 − increase phase, completed nestings); III. a high proportion of *M. oeconomus* + *M. agrestis* and a low proportion of alternative and concomitant prey (2017, 2020 − peak phases, completed nestings) (Figs. 5a, 5b). The diets from 2015 (presumably, the trough phase; the number and completion of nestings are unknown) and from 2021 (the trough phase, interrupted nesting) show similarities with 2020 and 2017 in terms of the ratio of the main prey groups and with 2016 and 2018 in the low proportion of other prey (Figs. 5a, 5b).

Based on the similarity in the proportions variability of alternative and concomitant prey by cycle phases (Supplementary, Table 5), we combined these groups into the "other prey" group in subsequent models of the structure dynamics of the owls' diets. The results of the logit regression with the predictors: "phase", "nesting stage", and "plot" (b_0 − peak phase, first stage, MF) show that the odds of catching *M. arvalis* + *M. gregalis* in the trough phase and increase phase in the SM population cycle were higher, and the odds of catching *M. oeconomus* + *M. agrestis* were lower, when compared to the peak phase. The odds of catching "other prey" in the trough phase decreased, and in the growth phase increased compared to the peak phase (Fig. 6a, Table 5). Table 5 also shows differences in the odds of catching prey groups between plots and nesting stages. Canonical correspondence analysis with the factors "phase + plot" and "group of prey" showed differences between the plots in terms of the ratio of prey groups. Changes in diets according to the cycle phases in the meadow and meadow−forest plots occurred in a similar way (Fig. 6b).

Dynamics of prey numbers (MNI) in the GGO diet. The dynamics of total MNI over the years is in good agreement with the phases of the SM population cycle according to live trapping data. The maximum prey numbers were recorded in 2017 and 2020 (peak phases). The MNI of both groups of the main prey reflect the dynamics of the total MNI for the year. The maxima were noted at the peaks of the population cycles of the SM. The maximum numbers of alternative and concomitant prey were observed in 2017 and 2019 (Fig. 7a, Supplementary, Table 6).

Based on similar patterns of MNI changes over years (Fig. 7, Supplementary, Table 6) and cycle phases (Supplementary, Table 7), we can combine *M. arvalis* + *M. gregalis* and *M. oeconomus* + *M. agrestis* into one "main prey" group and combine alternative and concomitant prey into the "other prey" group. The Poisson regression model with the "phase" factor (b_0 − peak phase) showed that the total number of owls' prey far exceeded the number of prey in the trough and growth phases. The MNI of the main prey was comparable in the trough and growth phases and was much higher than these values in the peak phase. The number of "other prey" varied significantly less between the peak and growth phases (Table 6, Fig. 7b). The proportion of bone remains of the main prey accumulated during the trough, growth, and peak phases and averaged over the number of nests in the corresponding phase was 23, 22, and 56%. The ratio of bone remains of the other prey in these phases was 11, 40 and 49%, respectively. Thus, the remains of the main prey were mainly accumulated in the peak phase due to the large amount of bone remains in this phase. The other prey accumulated in the increase phase due to its relatively high proportion in the diet and in the peak phase due to the overall large amount of prey eaten.

Table 5. Logit regression results with the predictors of "nesting stage", "plot", and "phase" describing the probability of catching prey group by owls in different phases of SM population cycle (b_0: the first stage, MF, peak)

| Predictors	b	SE	Wald X^2	p	95% CI		Odds ratio		
							Exp(b)	95% CI	
M. arvalis + M. gregalis vs other groups LR(4) = 154.27, $p < 0.0001$									
b_0	1.22	0.12	107.99	<0.0001	0.99	1.45			
Stage 2	−0.56	0.1	33.88	<0.0001	−0.74	−0.37	1.75^{-1}	2.10^{-1}	1.45^{-1}
Plot M	−0.94	0.11	78.54	<0.0001	−1.15	−0.73	2.56^{-1}	3.14^{-1}	2.08^{-1}
Trough	0.29	0.08	14	<0.0001	0.14	0.44	1.33	1.15	1.55
Increase	0.22	0.08	6.88	<0.05	0.06	0.38	1.24	1.06	1.46
M. oeconomus + M. agrestis vs other groups LR(4) = 187.72, $p < 0.0001$									
b_0	−1.87	0.13	211.55	<0.0001	−2.12	−1.62			
Stage 2	0.49	0.1	24.19	<0.0001	0.29	0.68	1.63	1.34	1.98
Plot M	1.18	0.11	107.34	<0.0001	0.96	1.4	3.25	2.6	4.06
Trough	−0.15	0.08	3.28	>0.05	−0.3	0.01	1.16^{-1}	1.36^{-1}	1.01
Increase	−0.46	0.09	26.48	<0.0001	−0.64	−0.29	1.59^{-1}	1.89^{-1}	1.33^{-1}
Alternative and concomitant vs other groups LR(4) = 26.27, $p < 0.0001$									
b_0	−2.00	0.18	126.01	<0.0001	−2.34	−1.65			
Stage 2	0.24	0.16	2.30	>0.05	−0.07	0.55	1.27	1.07^{-1}	1.74
Plot M	−0.38	0.16	5.90	<0.05	−0.69	−0.07	1.47^{-1}	2.00^{-1}	1.08^{-1}
Trough	−0.36	0.13	7.12	<0.05	−0.62	−0.09	1.43^{-1}	1.86^{-1}	1.1^{-1}
Increase	0.49	0.12	16.68	<0.0001	0.25	0.72	1.63	1.29	2.06
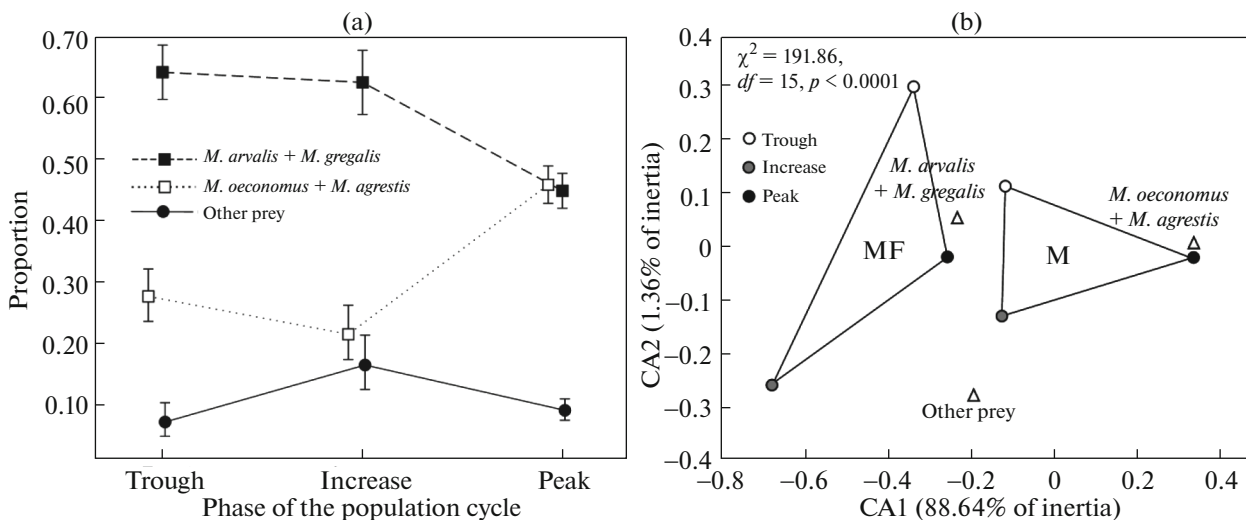
Fig. 6. Variability of the owls' diet structure according to population cycle phases of SM.
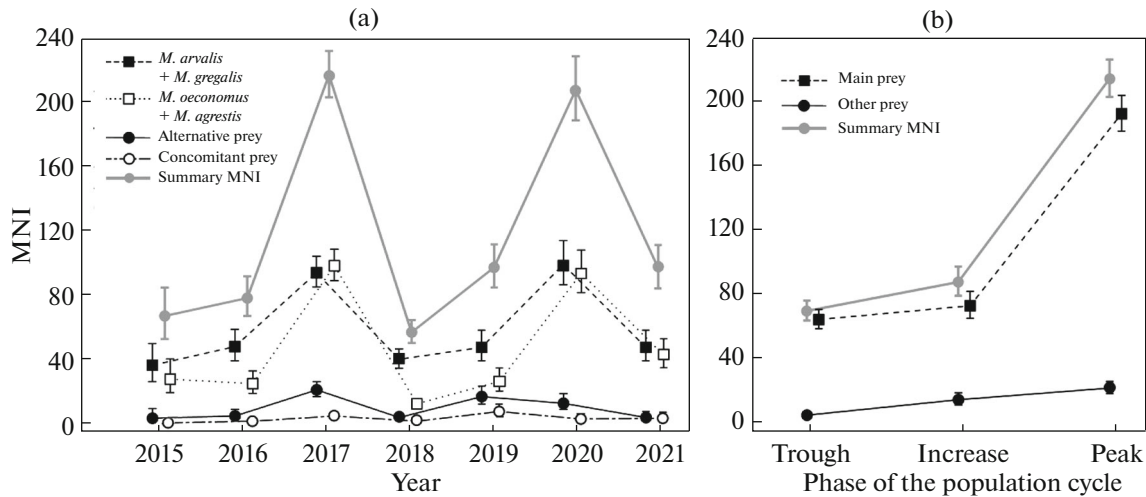
Fig. 7. Dynamics of MNI by years (a) and phases of the SM population cycles (b).

DISCUSSION

The list of GGO prey species obtained in all years of research corresponds to the faunal list of SM in the Sverdlovsk region, with some exceptions [61]. The study area is the northern edge of the range of the narrow-headed vole (*M. gregalis*) and the russet ground squirrel (*Spermophilus major*). The first species was found there precisely due to the analysis of the contents of the pellets of the GGO [75]. The russet ground squirrel was found in the pellet once. The wood lemming (*Myopus schisticolor*), a rare species with a mosaic range in the taiga zone, is difficult to detect in standard catches, but it was found in pellets. Additionally, in the pellets, remains of small rodents which are

difficult to catch by standard methods were found, including the harvest mouse (*Micromys minutus*) and the northern birch mouse (*Sicista betulina*). Shrew species, which are rare for the Middle Urals, were also found, including the Siberian large-toothed shrew (*Sorex daphaenodon*) and the tundra shrew (*Sorex* cf. *tundrensis*) [61, 76]. Previously, in the winter diet of owls, a species that is relatively rare for the eastern slope of the Middle Urals was found, i.e., the gray red-backed vole (*Clethrionomys rufocanus*) [15]. Among the prey of owls, a number of SM species included in the fauna of the Sverdlovsk region were not recorded. Species that are very rare in all habitats and, moreover, inaccessible to the GGO as prey due to their habitats (the Siberian flying squirrel (*Pteromys volans*), the

Table 6. Results of Poisson regression describing the number of owls' prey (MNI) in different phases of the SM population cycle (b_0—peak)

Predictors	b	se	Wald X^2	p	CI, 95%		Rate ratio		
							Exp(b)	CI, 95%	
MNI of all prey; LR(2) = 573.19, $p < 0.0001$									
b_0	4.70	0.03	35106.07	<0.0001	4.65	4.75	109.8	104.5	115.3
Increase	−0.22	0.04	31.08	<0.0001	−0.30	−0.14	1.25^{-1}	1.35^{-1}	1.15^{-1}
Trough	−0.45	0.04	156.04	<0.0001	−0.52	−0.38	1.57^{-1}	1.69^{-1}	1.46^{-1}
MNI of main prey; LR(2) = 516.97, $p < 0.0001$									
b_0	4.58	0.03	29184.69	<0.0001	4.53	4.63	97.4	92.4	102.6
Increase	−0.28	0.04	42.71	<0.0001	−0.37	−0.20	1.32^{-1}	1.44^{-1}	1.22^{-1}
Trough	−0.41	0.04	113.68	<0.0001	−0.48	−0.33	1.5^{-1}	1.62^{-1}	1.39^{-1}
MNI of other prey; LR(2) = 74.58, $p < 0.0001$									
b_0	2.45	0.08	1012.24	<0.0001	2.30	2.60	11.6	10.0	13.5
Increase	0.22	0.11	4.18	<0.05	0.01	0.43	1.25	1.01	1.54
Trough	−0.84	0.12	46.02	<0.0001	−1.09	−0.60	2.32^{-1}	2.97^{-1}	1.82^{-1}

Russian desman (*Desmana moschata*) and the Siberian chipmunk (*Tamias sibiricus*)) were absent from the study area. European mole (*Talpa europaea*) is a common species, but not available as a GGO prey. The striped field mouse (*Apodemus agrarius*) is probably inaccessible due to its high mobility and low abundance in the study area. The common hamster (*Cricetus cricetus*) was visually noted by us during our research. It is probably too large to be prey for the GGO, although in a number of locations in the Urals [77] it was noted in the diet. The absence of this species in the diet of *S. nebulosa* in the study area is probably also related to its low abundance here. In the diet of owls, the following synanthropic species were also not found: the house mouse (*Mus musculus*) and the Norway rat (*Rattus norvegicus*). For individual nests, 43−74% of the total number of species found in the diet of owls in the studied area was identified. The number of species of prey collected from individual nests was not influenced by the MNI. In cases where the collection size ranges from tens to thousands of MNI, the relationship between taxonomic richness and the abundance of prey can be established [8]. Apparently, at such short time intervals of bone remains accumulation as several years, when the collection size ranged from tens to several hundreds (MNI = 42−484), the number of species identified for a nest depended on the conditions of the habitat (number of prey in the foraging area and completion of nesting), and was also determined by the SM species composition in a relatively small hunting area around the nest. In another study, when comparing data on SM captures and data of different ages from a long-term nesting site of barn owl (*Tyto alba*) in a cave in northwestern Nevada, it was shown that the concentration of all known species in a locality would require a time span of centuries [10]. The maximum recorded distance flown by the great grey owl from its nest was 13.4 km [38]. It can be assumed that over a long period of time, for each nest, hypothetically, a complete list of species for the study area can be identified.

Thus, in pellets from all nests during the study period, almost all species available as prey for GGO living in the region (Sverdlovsk region) were identified. Our results are consistent with the opinion that the analysis of the food spectrum of owls can reveal a faunal list of SM in the region available to this species of owls, including rare species that require specific methods of trapping [e.g., 10, 29−32]. We also agree with the opinion that in order to obtain the most complete information about the fauna of the region from modern pellets of owls, a sufficiently large coverage of the territory for collecting pellets in various biotopes is necessary, taking into account the size of the hunting territory of the predator [32]. Concentrating the species richness of a particular area in each of the nests would require a much longer time interval.

The generalized food spectrum of the owls in the study area was dominated by *Microtus* voles (*M. arva-lis*, *M. gregalis*, *M. oeconomus*, *M. agrestis*), corresponding to data from the main part area [77−80]. The raptors' home range is significantly reduced during the nesting period, and, accordingly, the coverage of the territory, the population of which constitutes the food base of the predator, decreases [37−39]. The ratio of prey species is most similar in the diet of owls that occupied nests in the same plots. Diet dynamics during nesting and its interannual variations were observed between dominants (see below). Thus, it can be said that the ratio of species is formed already at the initial stages of the locality formation, but it strongly depends on the environmental conditions around the locality.

The GGO preference for open hunting habitats is reflected in their diet patterns [37, 38, 78−81]. If there were open spaces at the plot, regardless of their area (meadow − 47%, forest−meadow − 12%, field − 53%), the diet was dominated by the species inhabiting them, or they were part of the dominants. The meadow and forest-meadow plots had the greatest similarity in the ratio of prey groups in the diet. At the same time, the composition of dominant species among the inhabitants of meadow habitats was different: in the meadow plot, these were *M. arvalis* and *M. gregalis*, in the forest-meadow, only *M. arvalis*, and in the field, only *M. gregalis*. In the forest plot, in the absence of open habitats in the hunting area, among the dominant prey were species inhabiting relatively open forest and near-water habitats. Thus, species and prey groups ratio in each of the plots serves as an illustration of the importance of local conditions around the nest, namely preferred hunting habitats and the size of the hunting territory during the nesting period. The effect of local conditions around the nest and the structure of the hunting territory on diet has been shown in a number of studies on different owl species [32, 48, 82, 83]. The choice of hunting habitats of the eagle owl is shown in subfossil remains from a number of locations in the Urals. Only in the northern taiga, the main prey of the eagle owl included an inhabitant of forest biotopes − a red squirrel (*Sciurus vulgaris*). All other main prey species live in open and near-water habitats [65]. Significance of open habitats is shown in two localities of the Middle Urals, where the ratio of the two preferred prey species, the common and water vole, was determined by the presence or absence of meadows and farmlands near the locality [65].

Many aspects of raptors feeding behavior conform with the provisions of the optimal foraging theory [84, 85]: for an optimal diet, only the absolute abundance of preferred prey is important, and the relative abundance of non-preferred prey is irrelevant (Pulliam 1974); dietary diversity increases when the number of preferred prey decreases [84]. Our results are in good agreement with these provisions: if both groups of main prey (*M. arvalis* + *M. gregalis* and *M. oeconomus* + *M. agrestis*) dominated in the diet on a plot, then the proportion of alternative prey was low (meadow and

forest-meadow plots); in cases where the proportion of one of the groups of the main prey was low, a significant proportion was made up of alternative prey (forest and field plots).

Based on the provisions of the theory of optimal foraging [84, 85] and other research, we can surmise the significance of our results for interpreting the ratio of species and prey groups in ornithogenic deposits. Large owls, such as the GGO, require large numbers of prey to feed on. It is estimated that the GGO requires about 1400 voles per year [54], and the incubating female needs 60−80 g of prey per day [86]. Having enough preferred prey, owls do not prey on less preferred species [40−43, 45, 64]. Only a consistently high abundance of a species in a community can determine its high share in the owl's diet. Thus, the dominant species in the deposits (the main prey) most likely had a high proportion in the community of the past within the hunting territory of the owl. Their abundance was not necessarily proportional to the area of the respective habitats. The opposite interpretation is possible with caution: a low proportion of a species that, based on current data, is preferred, but is not a dominant species in the deposits of a locality, probably means that its proportion in the community was low. This is especially true for situations where only one of two (or, theoretically, several) species occupying similar habitats is well represented. For example, among a pair of species living in open spaces and preferred by the GGO (*M. arvalis* and *M. gregalis*), in the forest-meadow plot, the narrow-headed vole was occasionally noted in the diet of the owls, while the common vole was absent in the forest-meadow plot.

A relatively high proportion of species that, judging by current data, are less preferred prey (alternative prey) of the bone-accumulator owl indicates a high proportion of these species in the community of the past. In our case, *Clethrionomys* voles dominating the forest lines of live-trapping were in the category of alternative prey for owls. Other studies also show instances where alternative prey species were at the core of a SM community [64, 65, 87, 88]. A high proportion of alternative prey in the diet may indirectly indicate a shortage of main prey [6, 40−43, 45]. In our example, a high proportion of this group of prey in the diet of owls was observed in the field and forest plots, with a low proportion of one of the main prey groups. However, the low proportion of alternative prey in deposits says nothing about their abundance in the natural community of the past.

Concomitant prey make up a small proportion of the owl diet, regardless of their numbers in the community. In ornithogenic localities, these species make up no more than 1%. According to their findings, one can only judge their presence in the owl's hunting area. In our study, among the concomitant prey of the GGO was the Pygmy Field Mouse (*Apodemus uralensis)*, which is a common and even numerous inhabi-

tant of the forests of the Middle Urals [61] and was found frequently during our trapping. On the basis of subfossil remains accumulated by the eagle owl in the Urals, situations have been described where a rare species in the diet of an owl from the list of concomitant prey nevertheless occupies a dominant position in the rodent community judging by the number of captures [65, 87]. Identification of species from this category complements the understanding of the fauna composition. Some may be important for indicating certain habitats.

The non-detection of any species does not indicate its absence in the natural community of the past. This paleontological postulate was also confirmed by our research, since several species living in the studied area were not included in the composition of the prey due to their low availability for this species of owls.

The collection of pellets carried out several times during the nesting period for several years made it possible to trace the initial stages of remains accumulation in two areas (meadow and forest−meadow). During nesting, the proportions of different prey groups changed in the diet of the owls. During the second nesting stage, the proportion of smaller species inhabiting open spaces (*M. arvalis* and *M. gregalis*) decreased, whereas the proportion of larger prey inhabiting near-water and relatively open forest biotopes (*M. oeconomus* and *M. agrestis*) increased. During the second period, the proportion of alternative and concomitant prey, which, in general, are also forest dwellers, increased as well.

Changes in diet during different seasons and during stages of nesting have been described for many owl species. Among the reasons discussed for these variations are changes in food availability because of the reduction of snow cover, the development of vegetation, and an increase in the population density of more preferred prey [28, 46−48, 89]. Our annual surveys began when the snow cover was almost gone. Nevertheless, the pellets that we collected during the first rounds of collection probably accumulated under conditions when the snow cover was still partially preserved in the forests. The winter diet of the GGO in this area was dominated by voles inhabiting open spaces [15]. It can be assumed that the snow cover at the beginning of the nesting period limited the availability of forest inhabitants for owls. We observed the first changes in the proportions of prey as early as the end of April and the beginning of May, when the vegetation was just beginning to develop. Therefore, changes in vegetation were not the cause of the change in the owls' dietary characteristics.

Changes in the proportions of prey groups occurred in all years, including the years when the abundance of SM was high. Thus, the redistribution of hunting biotopes and the extraction of a larger number of inhabitants of forest and near-water habitats of *M. agrestis* and *M. oeconomus*, at least during years of

high abundance, were not associated with the depletion of the food supply in the fields. Nesting stages vary in the amount of food required [90]. For altricial birds, which include owls, the most energy-intensive stage of nesting is the stage of parental feeding of their young [90]. For a number of owl species, including the GGO and the eagle owl, it has been shown that the male brings larger-size prey to the nest than he usually eats [81, 91]. It is possible that the increase in the proportion of larger voles is associated with an increased need for food during nesting, as well as the increase in the availability of these prey due to their seasonal habitat changes.

Thus, in cases where raptor nesting covers the period from the snow season to the formation of a full-fledged vegetation cover, there are prerequisites for the changes in the availability of different prey groups, at least for phenological reasons. In ornithogenic deposits, a large proportion of the bone remains accumulate during the stage of feeding nestlings in the nest. Accordingly, the feeding features characteristic of this stage are enhanced by a more number of remains than in the previous stages.

During the study, interannual differences in the ratio of prey groups in the owls' diet were observed. The trough phase of the population cycle of SM is characterized by the dominance of *M. arvalis* + *M. gregalis* and a low proportion of other prey groups. *M. arvalis* + *M. gregalis* dominated the increase phase, but there was also a significant proportion of other prey (alternative and concomitant). Similar proportions of *M. oeconomus* + *M. agrestis* and *M. arvalis* + *M. gregalis* and a low proportion of other prey were observed during the peak phase. Thus, the voles living in open habitats, *M. arvalis* + *M. gregalis*, were the basis of the diet in the studied plots. Larger voles from near-water and relatively open forest habitats, *M. oeconomus* + *M. agrestis*, were likely important in rearing nestlings. Other prey were associated with trying to feed nestlings when the amount of main prey was low. The expansion of the food niche during the nesting period is a functional response to food shortages and is described by the theory of optimal foraging [40, 41, 64, 67]. This phenomenon is more typical for generalist predators, while specialist predators (like GGO), not having the ability to vary their diet as widely, more often resort to a numerical response — interruption of nesting [e.g., 40−42, 45, 64, 67]. In the trough phase of the population cycle, uncompleted nesting was observed. During the increase phase, both uncompleted and completed nesting was observed. During the peak phase, all nesting were completed.

The collection of pellets around the nests within a certain area allowed us to trace the dynamics of the number of individuals of prey under different nesting conditions. The largest amount of prey was obtained during the peak phase of the population cycle of SM, when it accumulated a high number of prey throughout the entire nesting period. Significantly fewer remains of prey were obtained during the increase phase; they accumulated a low number of prey during both uncompleted and completed nestings. The minimum amount of remains was obtained during the trough phase when the owls interrupted nesting due to limited food.

Accumulation of the remains of the main prey occurred during peak phases due to the large number of prey in pellets during these years, despite the pronounced dynamics of their proportions over the years and phases of the population cycle of SM. The remains of alternative and concomitant prey accumulated during peak phases due to a large number of prey, despite their low proportion in the diet during these years. During the increase phase, the remains of these prey accumulated due to their relatively high proportion in the diet when owls were trying to feed their nestlings under the conditions of low abundance of the main prey. Thus, completed nesting with a low availability of main prey contributed to the accumulation of remains of alternative and concomitant prey. This rule should be more pronounced for generalist predators than for specialist ones, such as GGO. Generalist predators have a higher nesting success rate during years of low SM abundance because they have more opportunities to hunt alternative prey [e.g., 42, 43, 45, 48]. Thus, during the formation of ornithogenic deposits due to the feeding activity of raptors, there may be uneven accumulation of different prey groups in different phases of the population cycle of SM. This should be taken into account in morphological studies because many morphological features of SM differ during different phases of the cycle. Firstly, the size of the animals varies; this phenomenon is known as the 'Chitty effect' and has been described in numerous studies (e.g. 74, 92]. There are also a number of papers showing variation in the frequency of fluctuating asymmetry and in certain molar morphotypes in a number of species of voles and shrews [93−96].

CONCLUSIONS

The ornithogenic locality does not always reflect the complete composition of the fauna of SM of the region due to the inaccessibility of certain species of prey for the owl. Several years of locality formation is not enough to form a complete list of available prey for the owl. In the first years, the number of species depends not so much on the amount of MNI as on the conditions for the locality formation more number of remains — habitat characteristics around the nest and the number of prey during nesting. To obtain the most complete information about the fauna of the region from recent pellets of owls, a sufficiently large coverage of the territory for collecting pellets in various habitats is necessary, taking into account the size of the hunting territory of the predator.

Prey proportions are established at the initial stage of formation of ornithogenic deposits, which includes different phases of the population cycle of small mammals. Population structure is reflected in the diet of owls according to the preferences of the owl for certain prey species inhabiting the most favorable hunting habitats within the hunting area. In order to correlate the structure of the diet of a predator accumulating bone remains in an ornithogenic taphocenosis with the community of small mammals, it is proposed to distinguish groups of prey in a similar way to how it is done in ornithological studies: the main prey are the most preferred prey, dominating the diet of owls and, accordingly, the ornithogenic taphocenosis, consisting of numerous members of the SM community. Less preferred species are alternative prey. Their ratio in the diet is determined primarily by whether the main prey is sufficient, and only secondarily by their abundance in the natural community. Concomitant prey are the single predation cases of owls, which for a number of reasons are the avoided or the least accessible species for this predator.

Accumulation of prey residues occurs unevenly during different nesting stages and different phases of the population cycle of SM. The ratio of prey in the diet of owls changes during nesting. It should be borne in mind that in ornithogenic deposits, the peculiarities of the diet are probably most pronounced during the feeding of nestlings, when the bulk of the boneremains accumulate. The remains of the most preferred prey (the main prey) accumulate in the sediments of ornithogenic localities during the peak phase in the abundance of SM due to the large amount of bone remains entering the sediments. The remains of less preferred prey (alternative and concomitant) accumulate both during the peak phase due to a large total amount of bone remains and in the increase phase in the number of SM, when, owing to the lack of the main prey, the ratio of less preferred prey increases in the diet. This heterogeneity in the accumulation of bone remains over time should be taken into account when conducting morphological studies because many morphological features of SM differ during different phases of the cycle.

SUPPLEMENTARY INFORMATION

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The authors of this work declare that they have no conflicts of interest.

REFERENCES

1. Andrews, P., and Cook, J., *Owls, Caves and Fossils: Predation, Preservation and Accumulation of Small Mammal Bones in Caves, with an Analysis of the Pleistocene Cave Faunas from Westbury-sub-Mendip*, Somerset, Chicago: Univ. of Chicago Press, 1990.

2. Contoli, L., Borre di Strigiformi e ricerca teriologica in Italia, *Nat. Montagna*, 1980, vol. 3, pp. 73—94.

3. Balčiauskienė, L., Analysis of tawny owl (*Strix aluco*) food remains as a tool for long-term monitoring of small mammals, *Acta Zool. Litu.*, 2005, vol. 15, pp. 85—89.

4. Lesiński, G., Romanowski, J., Gryz, J., et al., Small mammals of Kampinos National Park and its protection zone, as revealed by analyses of the diet of tawny owls *Strix aluco* Linnaeus, 1758, *Fragmenta Faunistica*, 2013, vol. 56, pp. 65—81.

5. Terry, R.C., Owl pellet taphonomy: a preliminary study of the post-regurgitation taphonomic history of pellets in a temperate forest, *Palaios*, 2004, vol. 19, pp. 497—506.

6. Andrews, P., Experiments in taphonomy, *J. Archaeol. Sci.*, 1995, vol. 22, pp. 147—153.

7. Behrensmeyer, A.K., Kidwell, S.M., and Gastaldo, R.A., Taphonomy and paleobiology, *Paleobiology*, 2000, vol. 26, no. S4, pp. 103—147.

8. Lyman, R.L., Power, E., and Lyman, R.J., Quantification and sampling of faunal remains in owl pellets, *J. Taphonomy*, 2003, vol. 1, pp. 3—14.

9. Terry, R.C., Modeling the effects of predation, prey cycling, and time averaging on relative abundance in raptor-generated small mammal death assemblages, *Palaios*, 2008, vol. 23, pp. 402—410.

10. Terry, R.C., On raptors and rodents: testing the ecological fidelity and spatiotemporal resolution of cave death assemblages, *Paleobiology*, 2010, vol. 36, pp. 137—160.

11. Fernández, F.J. and Montalvo, C.I., Actualistic taphonomy of small mammals from owl pellets in South America and its archaeological implication, *Global J. Archaeol. Anthropol.*, 2017, vol. 2, no. 1, pp. 1—4.

12. Comay, O. and Dayan, T., From micromammals to paleoenvironments, *Archaeol. Anthropol. Sci.,* 2018, vol. 10, pp. 2159—2171.

13. Denys, C., Stoetzel, E., Andrews, P., et al., Taphonomy of Small Predators multi-taxa accumulations: palaeoecological implications, *Hist. Biol.,* 2018, vol. 30, pp. 868−881.

14. Lopez, J.M., Actualistic taphonomy of barn owl pellet-derived small mammal bone accumulations in arid environments of South America, *J. Quat. Sci.,* 2020, vol. 35, no. 8, pp. 1057−1069.

15. Smirnov, N.G., Kropacheva, Y.E., and Zykov, S.V., Prey of small mammal-eating owls (*Strix nebulosa, Bubo bubo*) as a source of selective accumulation of palaeotheriological material, *Biol. Bull.,* 2021, vol. 48, pp. 118−131.

16. Terry, R.C., Inferring predator identity from skeletal damage of small-mammal prey remains. *Evol. Ecol. Res.,* 2007, vol. 9, pp. 199−219.

17. Fernández-Jalvo, Y., Andrews, P., Denys, C., et al., Taphonomy for taxonomists: Implications of predation in small mammal studies, *Quat. Sci. Rev.,* 2016, vol. 139, pp. 138−157.

18. Comay, O. and Dayan, T., Taphonomic signatures of owls: New insights into micromammal assemblages, *Palaeogeogr., Palaeoclimatol., Palaeoecol.,* 2018, vol. 492, pp. 81−91.

19. Montalvo, C.I. and Fernández, F.J., Review of the actualistic taphonomy of small mammals ingested by South American predators: its importance in the interpretation of the fossil record, *Asociación Paleontológica Argentina,* 2019, vol. 19, pp. 18−46.

20. Dodson, P. and Wexlar, D., Taphonomic investigations of owl pellets, *Paleobiology,* 1979, vol. 5, no. 3, pp. 275−284.

21. Stewart, K.M., Lebranc L., Matthiesen D.P., and West, J., Microfaunal remains from a modern east African raptor roost: patterning and implications for fossil bone scatters, *Paleobiology,* 1999, vol. 25, pp. 483−503.

22. Fernández-Jalvo, Y., Small mammal taphonomy at La Trinchera de Atapuerca (Burgos, Spain). A remarkable example of taphonomic criteria used for stratigraphic correlations and palaeoenvironmental interpretations, *Palaeogeogr., Palaeoclimatol., Palaeoecol.,* 1995, vol. 114, pp. 167−195.

23. Hadly, E.A., Fidelity of terrestrial vertebrate fossils to a modern ecosystem, *Palaeogeogr., Palaeoclimatol., Palaeoecol.,* 1999, vol. 149, pp. 389−409.

24. Izvarin, E.P., Ulitko, A.I., and Nekrasov, A.E., Palaeontological description of Nizhneirginsky Grotto Upper Holocene sediments (Ufa Plateau, Fore-Urals) with taphonomic and palaeoenvironmental remarks based on bird and small-mammal assemblages, *Quat. Int.,* 2020, vol. 546, pp. 160−169.

25. Rey-Rodríguez, I., López-García, J.M., Stoetzel, E., et al., Palaeoecological reconstructions of the Middle to Late Pleistocene occupations in the Southern Caucasus using rodent assemblages, *Archaeol. Anthropol. Sci.,* 2022, vol. 14, no. 5, p. 96.

26. Montalvo, C.I., Arriaga, L.C., Tallade, P.O., and Sosa, R.A., Owl pellet dispersal by wind: Observations and experimentations, *Quat. Int.,* 2012, vol. 278, pp. 63−70.

27. Lyman, R.L., *Vertebrate Taphonomy,* Cambridge: Cambridge Univ. Press, 1994.

28. Andrews, P., and Fernández-Jalvo, Y., Seasonal variation in prey composition and digestion in small mammal predator assemblages, *Int. J. Osteoarchaeol.,* 2018, vol. 28, pp. 318−331.

29. Heisler, L.M., Somers, C.M., and Poulin, R.G., Owl pellets: A more effective alternative to conventional trapping for broad-scale studies of small mammal communities, *Methods Ecol. Evol.,* 2016, vol. 7, pp. 96−103.

30. Biedma, L., Román, J., Godoy, J.A., and Calzada, J., Using owl pellets to infer habitat associations and clarify the regional distribution of a cryptic shrew, *J. Zool.,* 2019, vol. 308, pp. 139−148.

31. Kiamos, N., Lymberakis, P., Rallis, G., and Poulakakis, N., Barn Owl (*Tyto alba*) prey in Evros (Greece) and the discovery of a new mammal for the Greek fauna, *J. Nat. Hist.,* 2019, vol. 53, pp. 1691−1705.

32. Viteri, M.C., Stegner, M.A., and Hadly, E.A., Assessing the reliability of raptor pellets in recording local small mammal diversity, *Quat. Res.,* 2022, vol. 106, pp. 1−10.

33. Yom-Tov, Y. and Wool, D., Do the contents of barn owl pellets accurately represent the proportion of prey species in the field? *Condor,* 1997, vol. 99, pp. 972−976.

34. Trejo, A., and Guthmann, N., Owl selection on size and sex classes of rodents: Activity and microhabitat use of prey, *J. Mammal.,* 2003, vol. 84, pp. 652−658.

35. Comay, O. and Dayan, T., What determines prey selection in owls? Roles of prey traits, prey class, environmental variables, and taxonomic specialization, *Ecol. Evol.,* 2018, vol. 8, pp. 3382−3392.

36. Avenant, N.L., Barn owl pellets: A useful tool for monitoring small mammal communities, *Belg. J. Zool.,* 2005, vol. 135, pp. 39−43.

37. Van Riper, C., and Van Wagtendonk, J., Home range characteristics of great gray owls in Yosemite National Park, California, *J. Raptor Res.,* 2006, vol. 40, pp. 130−141.

38. Bull, E.L., Henjum, M.G., and Rohweder, R.S., Nesting and foraging habitat of great gray owls, *J. Raptor Res.,* 1988, vol. 22, pp. 107−115.

39. Mirski, P., Ivanov, A., Kitel, D., and Tumiel, T., The ranging behaviour of the Great Grey Owl *Strix nebulosa*: a pilot study using GPS tracking on a nocturnal species, *Bird Study,* 2021, vol. 68, pp. 129−134.

40. Korpimäki, E. and Norrdahl, K., Predation of Tengmalm's owls: numerical responses, functional responses and dampening impact on population fluctuations of microtines, *Oikos,* 1989, vol. 54, pp. 154−164.

41. Korpimäki, E., Huhtala, K., and Sulkava, S., Does the year-to-year variation in the diet of eagle and Ural owls support the alternative prey hypothesis? *Oikos,* 1990, vol. 58, pp. 47−54.

42. Hipkiss, T., Stefansson, O., and Hörnfeld, B., Effect of cyclic and declining food supply on great grey owls in boreal Sweden, *Can. J. Zool.,* 2008, vol. 86, pp. 1426−1431.

43. Terraube, J., Arroyo, B., Madders, M., and Mougeot, F., Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators, *Oikos,* 2011, vol. 120, pp. 234−244.

44. Zárybnická, M., Sedláček, O., and Korpimäki, E., Do Tengmalm's owls alter parental feeding effort under varying conditions of main prey availability? *J. Ornithol.,* 2009, vol. 150, pp. 231–237.

45. Korpimäki, E., Hongisto, K., Masoero, G., and Laaksonen, T., The difference between generalist and specialist: The effects of wide fluctuations in main food abundance on numbers and reproduction of two co-existing predators, *J. Avian Biol.,* 2020, vol. 51, e02508.

46. Korpimäki, E., Seasonal changes in the food of the Tengmalm's Owl *Aegolius funereus* in western Finland, *Ann. Zool. Fenn.*, 1986, vol. 23, pp. 339–344.

47. Nybo, J.O. and Sonerud, G.A., Seasonal changes in diet of hawk owls *Surnia ulula*: Importance of snow cover, *Ornis Fenn.,* 1990, vol. 67, pp. 45–51.

48. Romanowski, J. and Zmihorski, M., 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 Zool.,* 2008, vol. 57, pp. 411–419.

49. Love, R.A., Webon, C., Glue, D.E., et al., Changes in the food of British Barn Owls (*Tyto alba*) between 1974 and 1997, *Mamm. Rev.*, 2000, vol. 30, pp. 107–129.

50. Lyman, R.L. and Lyman, R.J., Lessons from temporal variation in the mammalian faunas from two collections of owl pellets in Columbia County, Washington, *Int. J. Osteoarchaeol.*, 2003, vol. 13, pp. 150–156.

51. Terry, R.C., Li, C., and Hadly, E.A., Predicting small-mammal responses to climatic warming: autecology, geographic range, and the Holocene fossil record, *Global Change Biol.,* 2011, vol. 17, pp. 3019–3034.

52. Comay, O., Weissbrod, L., and Dayan, T., Predictive modelling in paleoenvironmental reconstruction: The micromammals of Manot Cave, Israel, *J. Hum. Evol.*, 2021, vol. 160, p. 102652.

53. Kulikov, P.V., Zolotareva, N.V., and Podgaevskaya, E.N., *Endemichnye rasteniya Urala vo flore Sverdlovskoj oblasti* (Endemic Plants of the Urals in the Flora of the Sverdlovsk Region), Ekaterinburg: Goschitsky, 2013.

54. Bull, E. L. and Henjum, M.G., *Ecology of the Great Gray Owl. General Technical Report PNW-GTR-265*, Portland: USDA Forest Service, Pacific Northwest Research Station, 1990.

55. Winter, J., Status, distribution and ecology of the Great Gray Owl (*Strix nebulosa*) in California, *MSc Thesis*, San Francisco: San Francisco State Univ., 1986.

56. Borodin, A.V., *Opredelitel' zubov polevok Urala i Zapadnoi Sibiri (pozdnii pleistocen – sovremennost')* (Identification Guide for Vole's Teeth of the Urals and western Siberia (Late Pleistocene–Recent)), Yekaterinburg: Ural. Otd. Ross. Akad. Nauk, 2009.

57. Zykov, S.V., Strukova, T.V., and Rupysheva, T.A., Diagnostics of representatives of Muridae family from Holocene faunas of the Middle Urals, in *Dinamika ekosistem v Golotsene* (Dynamics of Ecosystems in the Holocene), Smirnov, N.G., Ed., Chelyabinsk: Rifey, 2010, pp. 77–81.

58. Zaitsev, M.V., Late anthropogene insectivora from the South Urals with a special reference to diagnostics of red-toothed shrews of the genus *Sorex*, in *Quaternary Paleozoology in the Northern Hemisphere, Illinois State Museum Scientific Papers 27,* Saunders, J.J., Styles, B.W., and Baryshnikov, G.F., Eds., Springfield: Illinois State Mus., 1998, pp. 145–158.

59. Zaitsev, M.V., Voita, L.L., and Sheftel, B.I., *Mlekopitayushchie fauny Rossii i sopredel'nykh territorii. Nasekomoyadnye* (Mammals of the Fauna of Russia and Adjacent Territories. Insectivores), St. Petersburg: Nauka, 2014.

60. Fadeeva, T.V., Insectivorous mammals (Lipotyphla, Soricidae) of the Perm Pre-Ural in the Late Pleistocene and Holocene time, *Quat. Int.,* 2016, vol. 420, pp. 156–170.

61. Bolshakov, V.N., Berdyugin, K.I., and Kuznetsova, I.A., *Mlekopitayushchie Srednego Urala* (Mammals of the Middle Urals), Yekaterinburg: Sokrat, 2006.

62. Kropacheva, Y.E. and Zykov, S.V., An evaluation of individual seasonal changes in dental macro-and mesowear of wild-caught common vole (*Microtus arvalis* sensu lato) by the intravital impressions method, *Mamm. Biol.,* 2022, vol. 102, no. 2, pp. 501–516.

63. Olenev, G.V., Intravital determination of the species of murine rodents by imprints of teeth (in Russian), *Zool. J.*, 1980, vol. 59, pp. 294–295.

64. Zárybnická, M., Riegert, J., and Št'astný, K., The role of Apodemus mice and Microtus voles in the diet of the Tengmalm's owl in Central Europe, *Popul. Ecol.,* 2013, vol. 55, pp. 353–361.

65. Smirnov, N.G. and Kropacheva, Y.E., Main and concomitant prey of the eagle owl (*Bubo bubo*) in problems of historical ecology, *Russ. J. Ecol.*, 2019, vol. 50, pp. 491–495.

66. Salamolard, M., Butet, A., Leroux, A., and Bretagnolle, V., Responses of an avian predator to variations in prey density at a temperate latitude, *Ecology,* 2000, vol. 81, pp. 2428–2441.

67. Tobajas, J., Fernandez-de-Simon, J., Díaz-Ruiz, F., et al., Functional responses to changes in rabbit abundance: is the eagle owl a generalist or a specialist predator?, *Eur. J. Wildl. Res.*, 2016, vol. 62, pp. 85–92.

68. Kropacheva, Y.E., Smirnov, N.G., Zykov, S.V., et al., The diet of the great gray owl, *Strix nebulosa*, at different levels of prey abundance during the nesting season, *Russ. J. Ecol.,* 2019, vol. 50, pp. 43–49.

69. Legendre, P. and Legendre, L, *Numerical Ecology*, Amsterdam: Elsevier, 1998.

70. McCullough, P. and Nelder, J., *Generalized Linear Models*, New York: Chapman Hall, 1989.

71. Statsoft, I. N. C. Statistica version 7.1., 2006.

72. Lukyanova, L.E., The root vole (*Microtus oeconomus* Pall.) and the field vole (*Microtus agrestis* L.) in windfall-pyrogenic habitats of the protected area of the Middle Urals, *Byull. Syktyvkarsk. Univ., Ser. 2: Biol., Geol., Khim., Ekol.*, 2020, vol. 4, pp. 5–19.

73. Lukyanova, L.E., Environmental preferences of the bank vole (*Clethrionomys glareolus* Schreber, 1780) under different biotopical conditions in the protected territory of the Middle Urals, *Russ. J. Ecol.*, 2023, vol. 54, no. 1, pp. 42–53.

74. Kshnyasev, I.A. and Davydova, Y.A., Population cycles and the Chitty syndrome, *Russ. J. Ecol.*, 2021, vol. 52, pp. 70–75.

75. Smirnov, N.G., Kropacheva, Yu.E., and Bachurin, G.N., Dynamics of the modern rodent fauna of the preforest-steppe forests of the Trans-Urals, *Fauna Ural. Sib.*, 2015, vol. 1, pp. 167−175.

76. Bolshakov, V.N., Vasilev, A.G., and Sharova, L.P., *Fauna i populyatsionnaya ekologiya zemleroek Urala (Mammalia, Soricidae)* (The Fauna and Population Ecology of Shrews (Mammalia, Soricidae) in the Urals), Yekaterinburg: Ekaterinburg, 1996.

77. Karyakin, I.V., *Pernatye khishchniki Ural'skogo regiona. Sokoloobraznye (Falconiformes), Sovoobraznye (Strigiformes)* (Raptors of the Ural region. Falconiformes (Falconiformes), Owls (Strigiformes)), Perm: Tsentr Polevykh Issled. Soyuza Okhrany Zhivotn. Urala, 1998.

78. Mikkola, H., *Der Bartkauz Strix Nebulosa*, Wittenberg-Lutherstadt: Neue Brehm-Bucherei, 1981.

79. Bull, E.L. and Duncan, J.R., Great Gray Owl (*Strix nebulosa*), *Birds North Am.*, 1993, vol. 41, pp. 1−15.

80. Duncan, J.R. and Hayward, P.H., Review of technical knowledge: great gray owls, in *Flammulated, Boreal, and Great Gray Owls in the United States: a Technical Conservation Assessment 253*, Hayward, G.D., Ed., 1994, pp. 159−175.

81. Bull, E.L., Henjum, M.G., and Rohweder, R.S., Diet and optimal foraging of great gray owls, *J. Wildl. Manage.*, 1989, vol. 53, pp. 47−50.

82. Szép, D., Klein, Á., and Purger, J.J., The prey composition of the Barn Owl with respect to landscape structure of its hunting area (Zala County, Hungary), *Ornis Hungarica*, 2017, vol. 25, no. 2, pp. 51−64.

83. Kovinka, T., Sharikov, A., Massalskaya, T., and Volkov, S., Structure and heterogeneity of habitat determine diet of predators despite prey abundance: Similar response in Long-eared, Short-eared Owls and Common Kestrels, *Avian Res.*, 2023, vol. 14, p. 100072.

84. Schoener, T.W., Theory of feeding strategies, *Annu. Rev. Ecol. Syst.*, 1971, vol. 2, pp. 369−404.

85. Pulliam, H.R., On the theory of optimal diets, *Am. Nat.*, 1974, vol. 108, pp. 59−74.

86. Cramp, S., *The Birds of Western Palearctic IV*, Oxford: Oxford Univ. Press, 1985.

87. Sadykova, N.O., Some methodical aspects of studying taphocoenoses of small mammals from zoogenic deposits, *Russ. J. Zool.*, 2013, vol. 92, pp. 1142−151.

88. Martínez, J.A. and Zuberogoitia, I., The response of the eagle owl (*Bubo bubo*) to an outbreak of the rabbit haemorrhagic disease, *J. Ornithol*, 2001, vol. 142, pp. 204−211.

89. Nilsson, I.N., Seasonal changes in food of the long-eared owl in southern Sweden, *Ornis Scand.*, 1981, vol. 12, pp. 216−223.

90. Wellicome, T.I., Danielle, T.L., Poulin, R.G., et al., Comparing food limitation among three stages of nesting: supplementation experiments with the burrowing owl, *Ecol. Evol.*, 2013, vol. 3, pp. 2684−2695.

91. Ekimov, E.V., Differences in the proportion and the prey size of male and female of Eagle Owl during the nestling period: the possible and real reasons, in *Sovy Severnoi Evrazii: ekologiya, prostranstvennoe i biotopicheskoe raspredelenie* (Owls of the Northern Eurasia: Ecology, Spatial and Habitat Distribution), Volkov, S.V., Sharikov, A.V., and Morozov, V.V., Eds., 2009, pp. 152−157.

92. Norrdahl, K. and Korpimaki, E., Changes in individual quality during a 3 year population cycle of voles, *Oecologia,* 2002, vol. 130, p. 239−249.

93. Zejda, J., Zukal, J., and Steiner, H.M., Variation in the shape pattern of molars in populations of the bank vole (*Clethrionomys glareolus* Schreb.), *Folia Zool.*, 1994, vol. 43, pp. 121−133.

94. Cheprakov, M.I., Variability of the chewing surface pattern of M 3 and M 1 molars in a cyclic population of the bank vole, *Russ. J. Ecol.*, 2020, vol. 51, pp. 394−398.

95. Faleev, V.I. and Epifantseva, L.Yu., The morphological variability coordinated with the population cycle of the widely distributed (the water vole *Arvicola terrestris* L.) and mountain (the big-eared vole *Alticola macrotis* Radde) vole species, *Izv. Akad. Nauk, Ser. Biol.*, 2000, no. 2, pp. 213−220.

96. Zakharov, M., Pankakooski, E., and Sheftel, B., Phenotypic diversity and population dynamics: Another look (with particular reference to the common shrew *Sorex araneus*), *Acta Theriol.*, 1997, Suppl. 4, pp. 57−66.