ISSN 1067-4136, Russian Journal of Ecology, 2019, Vol. 50, No. 1, pp. 43–49. © Pleiades Publishing, Ltd., 2019.
Russian Text © Yu.E. Kropacheva, N.G. Smirnov, S.V. Zykov, M.I. Cheprakov, N.O. Sadykova, G.N. Bachurin, 2019, published in Ekologiya, 2019, No. 1, pp. 40–46.

The Diet of the Great Gray Owl, *Strix nebulosa*, at Different Levels of Prey Abundance during the Nesting Season

Yu. E. Kropacheva[a, *], N. G. Smirnov[a, **], S. V. Zykov[a], M. I. Cheprakov[a], N. O. Sadykova[a], and G. N. Bachurin[b]

[a] *Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia*
[b] *Scientific and Practical Center of Biodiversity, Irbit, 623853 Russia*
**e-mail: KropachevaJE@yandex.ru*
***e-mail: nsmirnov@ipae.uran.ru*

Received June 20, 2018; revised June 20, 2018; accepted June 25, 2018

Abstract—Variation in the diet of the Great Gray Owl, a specialist predator, at different levels of prey abundance in different biotopes was studied in the middle Transural region. *Microtus* voles were found to be the main prey, with shrews being alternative prey. In different plots, two types of change in the diet were observed during the nesting season: (1) substitution of *Microtus* voles inhabiting meadow biotopes by *Microtus* voles characteristic of forest habitats, and (2) substitution of the latter by shrews.

Keywords: Great Gray Owl, *Strix nebulosa*, diet, nesting season, prey abundance

DOI: 10.1134/S1067413619010041

Variation in the diet of owls as a mechanism of adaptation to changing conditions has been widely considered by ornithologists from both geographic and temporal aspects [1–6]. The feeding of the Great Gray Owl *Strix nebulosa* has been well studied in Fennoscandia, Belarus, the United States, and Canada [3, 4, 7–9, etc.], but relevant studies performed in Russia are few [10–13]. In terms of foraging behavior, this species is closer to specialist predators than are the Tawny Owl (*S. aluco*) and Ural Owl (*S. uralensis*) [3, 7, 8, 14]. *Microtus* voles are the main prey of *S. nebulosa* in the greater part of its range. However, this species has a wide circumboreal distribution, and differences in its diet have been described [3, 4, 7, 11]. Old-growth taiga forests alternating with open areas such as bogs, burned-out sites, barrens, and meadows are optimal habitats for *S. nebulosa* [3–5, 7], where it hunts prey living in either forest or open biotopes [3, 4, 7, 12, 13]. As a specialist predator, this species depends on the availability of preferred prey, migrating or altering parameters of nesting in response to decrease in its abundance (numerical response) [4, 6]. Changes in the diet because of such a decrease (functional response) are less characteristic of the species and have not been studied sufficiently.

The purpose of this study was to analyze changes in the diet of *S. nebulosa* depending on prey abundance in the central Transural region. To this end, is was necessary to assess diet composition (1) in the owls nesting in plots with different biotopic characteristics, (2) at different levels of prey abundance, and (3) during different periods of the nesting season.

MATERIAL AND METHODS

Study region. Studies were performed in the Irbit district of Sverdlovsk oblast (57°40' N, 63° E) in 2015 to 2017. The results of comparing *S. nebulosa* diet in 1978 and 2015 were published previously [12]. The vegetation of the region consists of uneven-aged forests of mixed species composition alternating with meadows. Artificial nests for *S. nebulosa* were installed in the key ornithological territory KOTR SV-001 "Forest Massif near Zaikovo Village" [12].

Sampling plots around the live nests used in the study (with a radius of 1.5 km) differed in the ratio of different habitat types. In plot 1, meadows with numerous pine–birch forest outliers were prevalent (three nests). Plot 2 was in a continuous forest massif with an overgrowing cutover area and small glades (one nest). The greater part of plot 3 was also covered by forests, but there also were meadow biotopes (two nests). Plot 4 was at the edge of a forest bordering on abandoned farmland (one nest). The distance between the nests within the same plot varied from 0.8 to 1.5 km; between the nests in different plots, from 2.2 to 9 km.

Analysis of pellets. The diet during the nesting season was studied in one pair of owls in 2015, three pairs in 2016, and six pairs in 2017. Fresh pellets were sampled under roosts near the nests one time in 2015 and 2016 (in May) and four to six times in 2017 (in May and June). All pellets from females, males, and chicks were collected. Analysis was based mainly on samples taken in 2017, because the number of live nests in that year reached a peat (six nests), and abundant food supply provided for nesting success. Comparisons of the diet of owls nesting in different plots were made using synchronous samples collected in the same year (in May and in June 2017) to avoid the effect of interannual variation. Only May samples were used to compare the diet of owls nesting in the same plot in different years. Taking into account that in 2017 chicks hatched at the end of May, the samples were divided into two groups: collected before the end of May (during the brooding period) and in June (during the chick-rearing period). Comparisons of the diet in 2017 were performed for plots 1, 2, and 3. All the available material (2015–2017) was used to describe general characteristics of the diet (its composition and the ratio of different prey groups).

Bone remains found in the pellets were cleaned manually. Rodents were identified to the species level; shrews, to the genus level. The number of ingested animals was determined from the maximum number of homonymous bon remains (mandibles). A total of 372 pellets were examined, and 3191 remains of 1323 individuals were identified. Prey species were classified into groups by biotopic and taxonomic criteria: (1) *Microtus* voles inhabiting meadow biotopes (meadows and farmlands): the common vole (*M. arvalis* sensu lato) and narrow-headed vole (*M. gregalis*); (2) *Microtus* voles characteristic of forest habitats (boggy sites, hummocky floodplain areas, glades, overgrowing cutover areas): the root vole (*M. oeconomus*) and field vole (*M. agrestis*); (3) *Clethrionomys* voles: the northern red-backed vole (*C. rutilus*) and bank vole (*C. glareolus*); (4) Ural field mouse (*Sylvaemus uralensis*); (5) shrews (Soricidae); (6) other animals whose remains in the pellets occurred rarely or sporadically: the muskrat (*Ondatra zibethicus)*, wood lemming (*Myopus schisticolor*), European water vole (*Arvicola terrestris*), northern birch mouse (*Sicista betulina*), russet ground squirrel (*Spermophilus major*), least weasel (*Mustela nivalis*), and frogs (*Rana* sp.).

Assessment of the abundance of small mammals. Live trapping with subsequent release was used for this purpose. In 2016, only one round of trapping in plots 1 and 2 was conducted, because the owls aborted nesting by the beginning of June; in 2017, two rounds in plots 1, 2, and 3 were conducted in May and June. Trap lines were set in meadow and forest biotopes (dry and wet sites, forest edges, shrub thickets) within 1-km^2 area around the live nests and exposed for 2–4 days. Trapped animals were marked by finger clipping. For species identification of *Microtus* voles, imprints of the molar occlusal surfaces were taken using Bisico S1 and S4 silicone putties [17]. The numbers of animals trapped per 100 trap–days (ind./100 t-d) were calculated in each plot, for forest and meadow trap line separately. On the whole, 180 trapped animals were identified and classified into the same groups as during pellet analysis: (1) common and narrow-headed voles, (2) root and field voles, (3) northern red-backed and bank voles, (4) Ural field mouse and striped field mouse (*Apodemus agrarius*), and (5) shrews.

Statistical analysis. Student's *t*-test was used to compare the levels of small mammal abundance in different years or months of the same year, and χ^2.test, to compare the diets of owls from different plots in different years and periods of the same nesting season and also to compare the results of trapping in different plots. The above groups of species whose proportions in the pellets or trap catches were no less than 10% were included in analysis, and comparisons were made using mean values for the nests and trap lines (forest and meadow lines separately) located in the same plot. Relations between the proportions of individual prey groups in the diet were evaluated using Spearman's correlation coefficient. The data were presented as mean values with standard deviations.

RESULTS

Abundance of small mammals in 2016 and 2017. According to the results of trapping, differences in the level of small mammal abundance in May between 2016 and 2017 lacked statistical significance ($t = 2.23$, $n1 = 4$, $n2 = 9$, $p = 0.99$), whereas those in the ratio of different species groups were significant ($\chi^2 = 16.9$, $df = 4$, $p = 0.01$). In May 2016, no small mammals were trapped in meadow biotopes, while their abundance in forest biotopes reached 6.25 ± 6 ind./100 t-d, with mice prevailing in catches. The respective levels of abundance recorded in May 2017 were 3.86 ± 1.23 and 2.55 ± 1.97 ind./100 t-d, with common and narrow-headed voles dominating in meadow biotopes and *Clethrionomys* voles in forest biotopes (Fig. 1). Young-of-the-year *Microtus* voles appeared in catches at the end of May 2017. The abundance of small mammals in June became significantly higher than in May ($t = 2.31$, $n1 = 9$, $n2 = 9$, $p = 0.05$). The tendency toward increase in this parameter was more distinct in voles living in meadows, although its changes in individual biotopes lacked statistical significance (meadow: $t = 2.23$, $n1 = 4$, $n2 = 4$, $p = 0.06$; forest: $t = 1.38$, $n1 = 5$, $n2 = 5$, $p = 0.22$). The abundance of small mammals in meadows reached 10.48 ± 5.80 ind./100 t-d, compared to 4.86 ± 3.34 ind./100 t-d in forest biotopes. The ratio of species groups did not change significantly ($\chi^2 = 0.25$, $df = 4$, $p = 0.99$) (Fig. 1).

The results of trapping in the foraging ranges of the owls in 2016 and 2017 are shown in Table 2. Differences in animal abundance between the plots in 2017 lacked statistical significance (plots 1 and 2: $t = 0.37$, $n1 = 8$, $n2 = 2$, $p = 0.72$; plots 1 and 3: $t = 0.46$, $n1 = 8$, $n3 = 8$, $p = 0.05$; plots 2 and 3: $t = 0.44$, $n2 = 2$, $n3 = 8$, $p = 0.05$).

Diet composition. The diet of the owls during the nesting season of 2017 consisted mainly of *Microtus* voles (83%), with approximately equal proportions of those characteristic of meadow (44%) and forest habitats (39%); then followed shrews (10%), *Clethrionomys* voles (4%), and other species (3%).

The diet of owls that nested in different plots in 2017. The composition of the diet in May and June 2017 proved to differ significantly between the plots (plots 1 and 2: $\chi^2 = 25.42$, $df = 4$, $p = 0.01$; plots 1 and 3: $\chi^2 = 31.75$, $df = 4$, $p < 0.001$; plots 1 and 4: $\chi^2 = 63.88$, $df = 4$, $p < 0.001$; plots 2 and 3: $\chi^2 = 72.52$, $df = 4$, $p < 0.001$; plots 2 and 4: $\chi^2 = 27.0$, $df = 4$, $p = 0.01$; plots 3 and 4: $\chi^2 = 37.03$, $df = 3$, $p < 0.001$). In plot 1, root and field voles were its main component (57%), then followed common and narrow-headed voles (32%). In plot 2, root and field voles dominated in the diet (69%), with shrews and the common vole accounting for 13 and 11%, respectively. In plot 3, the common vole was dominant (55%), then followed root and field voles (31%). In plot 4, the diet included approximately equal proportions of shrews (39%) and narrow - headed voles (34%) (Table 2).

Differences in diet composition between years and during the same nesting season. The diet of the owls that nested in plot 1 in May did not differ significantly between years (2015 vs. 2017: $\chi^2 = 6.6$, $df = 4$, $p = 0.9$; 2016 vs. 2017: $\chi^2 = 3.9$, $df = 4$, $p = 0.90$) (Fig. 2a). May samples taken in 2015 included six rodent species; in 2016, eight rodent species and shrews; in 2017, seven rodent species and shrews. The composition of the diet in June significantly differed from that in May ($\chi^2 = 18.66$, $df = 4$, $p = 0.01$) and included eight rodent species, the least weasel, shrews, and frogs (Fig. 2a). The diet of the owls that nested in plot 2 was found to differ significantly between years (2016 vs. 2017: $\chi^2 = 46.91$, $df = 4$, $p < 0.001$) (Fig. 2b), even though six rodent species and shrews were identified in its com-

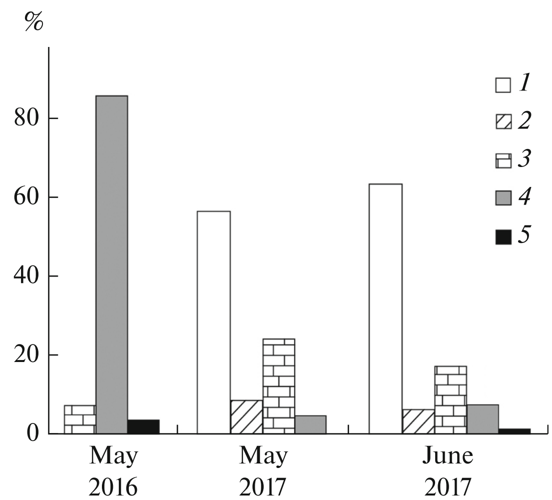

Fig. 1. Proportions (%) of different groups of small mammals in catches: (*1*) *Microtus arvalis, M. gregalis*; (*2*) *M. oeconomus, M. agrestis*; (*3*) *Clethrionomys* sp.; (*4*) *Sylvaemus uralensis*; (*5*) *Sorex* sp. (here and in Fig. 2).

position both in May 2016 and in May 2017 (Table 2). The ratio of species groups significantly changed in June ($\chi^2 = 13.53$, $df = 4$, $p = 0.01$), when six rodent species, shrews, and frogs were recorded (Fig. 2b). The diet of the owls that nested in plot 3 in 2017 included six rodent species, the lest weasel, and shrews in May and seven rodent species and shrews in June. Changes in the proportions of prey species groups lacked statistical significance ($\chi^2 = 0.56$, $df = 4$, $p = 0.1$) (Fig. 2c).

Interrelation of prey groups in the study area. The proportion of common and narrow-headed voles in the diet of the owls was negatively correlated with that of root and field voles (Spearman rank correlations, $r_S = -0.82$, $p < 0.05$) but showed no correlation with the proportion of shrews ($r_S = 0.14$, $p = 0.61$). The proportion

Table 1. Numbers of small mammals per 100 trap–days in live-trap catches from *Strix nebulosa* foraging ranges

Taxon	2016		2017		
	plot 1	plot 2	plot 1	plot 2	plot 3
Microtus arvalis sensu lato	0	0	2.82	0	7.78
M. gregalis	0	0	3.74	0	0
M. oeconomus	0	0	0.1	0	0
M. agrestis	0	0	0.59	1.83	0
Clethrionomys rutilus	0	0.5	3.0	1.67	0.24
Cl. glareolus	0	0.5	0.29	1.5	0.36
Sylvaemus uralensis	2.0	8.5	0.22	1.5	0.72
Apodemus agrarius	0	0.5	0	0	0
Sorex sp.	0	0.5	0.38	0	0
Catch size per 100 trap–days (total catch size)	2 (2)	10.5 (21)	11.14 (71)	6.5 (39)	9.1 (47)

Table 2. Numbers of prey animals identified in pellets from different plots during *Strix nebulosa* nesting seasons (2015–2017)

Taxon	2015	2016		2017			
	plot 1	plot 1	plot 2	plot 1	plot 2	plot 3	plot 4
Microtus arvalis s. l.	11	13	0	68	13	227	0
M. gregalis	25	83	1	82	1	1	14
M. oeconomus	21	40	10	174	42	73	4
M. agrestis	7	10	8	94	45	55	1
Clethrionomys rutilus	2	2	1	8	1	7	2
C. glareolus	1	1	0	6	2	7	3
Arvicola terrestris	0	1	1	1	0	0	0
Sylvaemus uralensis	0	0	1	2	2	0	0
Spermophilus major	0	0	0	0	0	0	1
Sicista betulina	0	1	0	6	1	14	0
Mustela nivalis	0	0	0	2	0	1	0
Sorex sp.	0	6	31	23	17	25	16
Rana sp.	0	0	0	3	2	0	0
Number of pellets	14	38	15	154	45	96	10
Number of identified remains	167	401	130	1148	307	938	100
Number of animals	67	157	53	469	126	410	41

of root and field voles was negatively correlated with the proportion of shrews ($r_S = -0.56$, $p < 0.05$).

DISCUSSION

Comparison of prey species composition with regional small mammal fauna. A total of 14 rodent species were recorded in *S. nebulosa* pellets, all of them mentioned in previous publications on study region. They did not include species considered as rare throughout Sverdlovsk oblast, such as the flying squirrel, Eurasian harvest mouse, and common hamster [16]. However, the pellets proved to contain the remains of wood lemming, a very rare species in the regional fauna.

The diet of owls in different plots. In the diet of the owls that nested in plots with meadow areas (plots 1, 3, and 4), *Microtus* voles characteristic of meadow biotopes (common and narrow-headed voles) dominated over congeneric field and root voles living in forest biotopes (in six out of seven samples). A preference for voles from open biotopes over other prey species was also noted in other parts of *S. nebulosa* range [4, 11, 13]. In the absence of meadows (plot 2), the owls preyed mainly on *Microtus* voles inhabiting forest biotopes. In a large part of S. *nebulosa* range in the European taiga zone, where these owls prefer settling in bogs, grasslands, and burned-out areas, the field vole and, to a lesser extent, the root vole are their main prey [3, 4, 7, 11, 13]. Shrews were the second most abundant prey for the owls in plot 2. These animals are a permanent but not dominant component of *S. nebulosa* diet throughout the species range [3, 5, 7, 8].

The main and alternative prey. In view of the concepts about these kinds of prey [2, 18, 19], it may be concluded that in the study region, as in the greater part of *S. nebulosa* range [3, 4, 7], *Microtus* voles are the main prey for this species. The ratio between two biotopic groups of these voles in the owl diet and factors responsible for changes in this ratio in the study region need special analysis. Relevant factors may include the preferences of the owls for a certain foraging biotope, the relative abundance of species from these groups, and the size and social structure of prey [20]. In the study region, relationships between prey groups are as follows: the proportion of *Microtus* species forming colonies in the meadows (common and narrow-headed voles) is negatively correlated with that of species inhabiting forest biotopes (root and field voles), which, in turn, is negatively correlated with the proportion of shrews.

At the current stage of research, our data on the proportion of species groups and their interrelation suggest that *Microtus* voles forming colonies in the meadows are the most readily available and probably preferred prey for *S. nebulosa* in the study region. Congeneric voles from forest biotopes are the next preferred group, while shrews may be regarded as alterna-

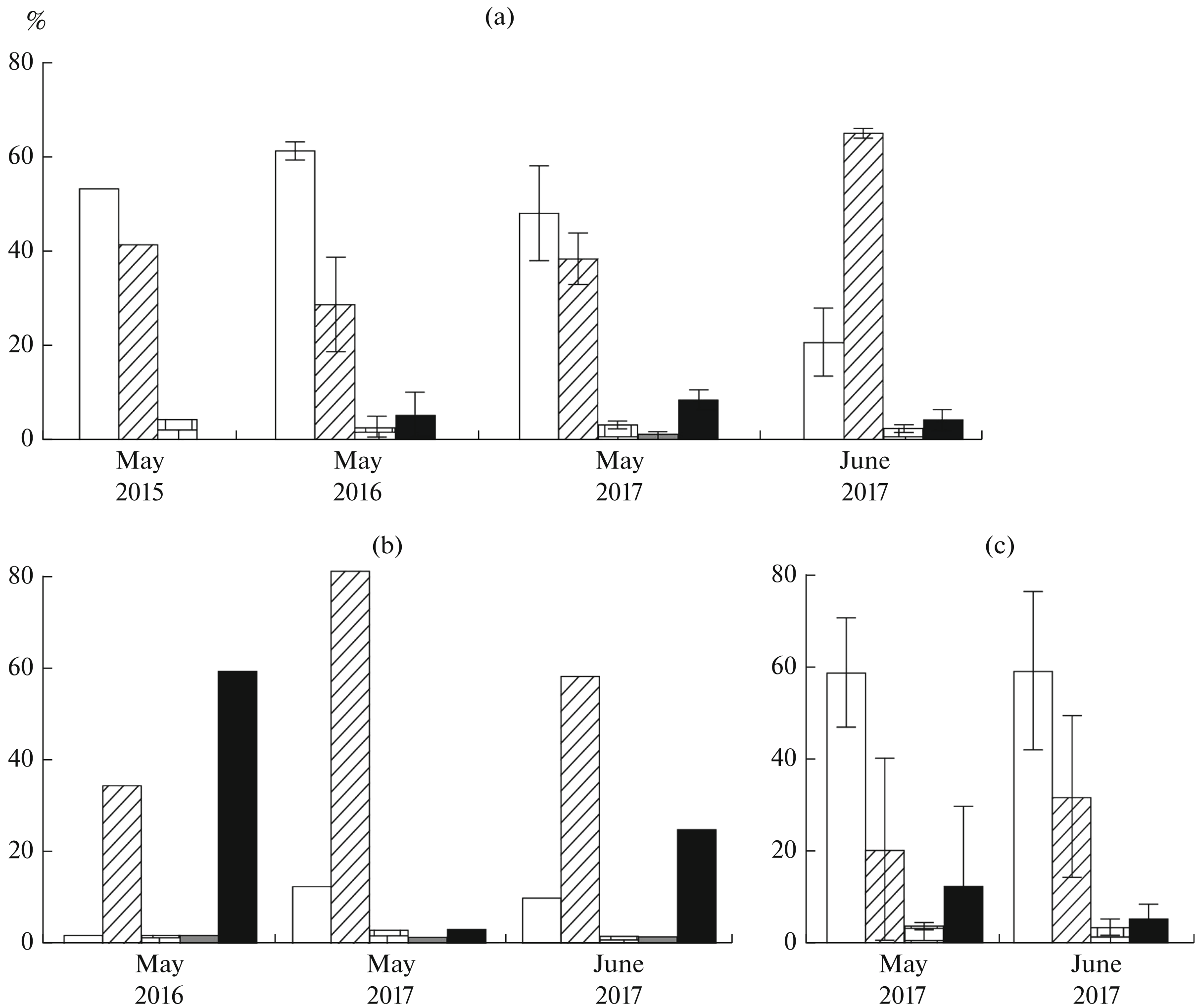

Fig. 2. Proportions (%) of different groups of small mammals in *Strix nebulosa* diet: (a) plot 1, (b) plot 2, (c) plot 3.

tive prey. This is in agreement with data on *S. nebulosa* diet in other parts of its range [3, 4, 7, 11, 15] and with the results of radio-tagging studies, which show that this species prefers foraging in the meadows and forest areas without undergrowth [4, 20].

Interannual dynamics of diet composition. In 2015–2017, compared to 1978, *Microtus* voles from meadow biotopes remained to be dominant in the diet of the owls nesting in the meadow (plot 1), while the proportion of *Microtus* voles characteristic of forest biotopes became higher; the remains of water voles in the pellets occurred sporadically, whereas in 1987 they accounted for about 10% of the diet [12]. These changes appear to be explained by fluctuations in the abundance of prey species in the study area. Compared to 1978 and 2015 [12], *S. nebulosa* diet in 2016 and 2017 included a greater number of rodent species and, in addition, the least weasel, shrews, and frogs. According to the theory of optimal diets, the abundance of basic prey animals is the key factor: when their abundance is insufficient, an alternative prey is consumed, and the species diversity of the diet increases [21]. It is likely that in 1978 and 2015, when the diet included a smaller number of species in the absence of alternative prey (shrews), the abundance of the main prey was sufficiently high.

The food supply to the owls in 2016 was very poor, but no shift to less preferred prey groups was observed in the meadow (plot 1), probably because of their absence. In the forest (plot 2), the owls in May showed a functional response to the deficit of their basic prey by shifting to the alternative prey (shrews). This was followed by a numerical response at the end of ay: the owls abandoned their nests in both plots.

Dynamics of diet composition during the nesting season of 2017. The results of trapping showed that the abundance of small mammals tended to increase between May and June. This tendency was more distinct in voles living in the meadows than in those inhabiting forest biotopes. The ratio of species groups in trap catches remained unchanged, unlike that in the diet of the owls nesting in plots 1 and 2: in plot 1, the proportion of the most preferred prey (*Microtus* voles from open biotopes) decreased, while that of the second preferred prey (*Microtus* voles from forest biotopes) increased; in plot 2, the proportion of *Microtus* voles from forest biotopes decreased, while the proportion of alternative prey (shrews) became higher.

Since chick rearing is the most energy-intensive stage of nesting in altricial birds [22], the food demand of the owls in the corresponding period (June) was higher than during brooding (May) [22, 23]. Apparently, the abundance of preferred prey proved to be insufficient, despite a slight increase in the number of small mammals in trap catches. This evoked a functional response manifested as the expansion of the foraging range to less preferred biotopes, with consequent changes in the dietary proportions of biotopic groups of *Microtus* voles in plot 1 and increase in the proportion of alternative prey in plot 2. The owls nesting in the forest plot with meadow areas (plot 3) showed no significant changes in the diet between May and June 2017.

CONCLUSIONS

Microtus voles were found to be the main prey for the Great Gray Owl in the study region, with shrews being alternative prey. *Microtus* species inhabiting open biotopes (common and narrow-headed voles) dominated in the diet when the owl's home range included meadow areas; in the absence of such areas, species characteristic of forest biotopes (field and root voles) were dominant. Several types of changes in the foraging behavior and two types of change in the diet were observed during the nesting season: (1) substitution of *Microtus* voles inhabiting open areas by *Microtus* voles from forest biotopes, and (2) substitution of the latter by shrews. As an extreme variant of response to insufficient food supply, the owls abandoned the nests during transition from brooding to rearing.

The results presented above contribute to the body of data on the feeding and diet of the Great Gray Owl not only in different habitats but also at different levels of prey abundance in the study region and help to fill the gap in knowledge of this species in the Ural–West Siberian part of its circumboreal range.

ACKNOWLEDGMENTS

The authors are grateful to V.N. Bachurin and I.A. Smorkalov for their help in field research.

This study was performed under State Assignment for the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, and partially supported by the Integrated Research Program of the Presidium of the Ural Branch of the Russian Academy of Sciences (project no. 18-4-4-3) and the Russian Foundation for Basic Research (project no. 16-04-01017).

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. This article does not contain any studies involving animals performed by any of the authors.

REFERENCES

1. Korpimäki, E. and Norrdahl, K., Numerical and functional responses of Kestrels, Short-eared Owls and Long-eared Owls to vole densities, *Ecology,* 1991, vol. 72, no. 3, pp. 814–826.
2. 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, no. 1, pp. 231–237.
3. Mikkola, H., *Der Bartkauz Strix nebulosa,* Wittenberg-Lutherstadt: Ziemsen, 1981.
4. Bull, E.L. and Duncan, J.R., Great Gray Owl (*Strix nebulosa*), in *The Birds of North America,* vol. 41, Poole, A. and Gill, F., Eds., Philadelphia, PA: Academy of Natural Sciences, 1993, pp. 1–15.
5. Sulkava, S. and Huhtala, K., The Great Grey Owl (*Strix nebulosa*) in the changing forest environment of northern Europe, *J. Raptor Res.,* 1997, vol. 31, pp. 151–159.
6. Hipkiss, T., Stefansson, O., and Hörnfeldt, B., Effect of cyclic and declining food supply on Great Grey Owls in boreal Sweden, *Can. J. Zool.,* 2008, vol. 86, no. 12, pp. 1426–1431.
7. Duncan, J. 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,* General Technical Report RM-253, Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 1994.
8. Tishechkin, A.K., Comparative food niche analysis of *Strix* owls in Belarus, in *Ecology and Conservation of Owls of the Northern Hemisphere: Proc. 2nd Int. Symp.,* Winnipeg, Canada, 1997, pp. 456–460.
9. Solheim, R. and Stefansson, O., Life span, dispersal and age of nesting Great Grey Owls *Strix nebulosa lapponica* in Sweden, *Ornis Svecica,* 2016, vol. 26, pp. 125–134.
10. Karyakin, I.V. Borodataya neyasyt', in *Pernatye khishchniki Ural'skogo regiona*: Sokoloobraznye (Falconiformes) i Sovoobraznye (Strigiformes) (Great Gray Owl in Raptors of the Ural Region: Falconiformes (Falconiformes) and Owls (Strigiformes)), Perm': Tsentr polevykh issledovaniy Soyuza okhrany zhivotnykh Urala, 1998. pp. 385–395.
11. Pukinskii, Yu.B., The Great Gray Owl, in *Ptitsy Rossii i sopredel'nykh regionov: Sovoobraznye, Kozodoeobraznye, Strizheobraznye, Raksheobraznye, Udodoobraznye, Dyatloobraznye* (Birds of Russia and Neighboring Regions: Strigiformes, Caprimulgiformes, Apodiformes, Coraciiformes, Upupiformes, Piciformes), Moscow: KMK, 2005, pp. 86–98.
12. Smirnov, N.G., Kropacheva, Yu.E., and Bachurin, G.N., Dynamics of recent rodent fauna in pre-forest-steppe

forests of Transural region, *Fauna Urala Sibiri,* 2015, no. 1, pp. 167–175.

13. Shepel', A.I., The Great Gray Owl *Strix nebulosa* Forster, 1772 in the Volga–Kama region, *Vestn. Udmurt. Gos. Univ., Ser. Biol. Nauki o Zemle,* 2011, vol. 4, pp. 85–89.
14. Korpimäki, E., Niche relationships and life-history tactics of three sympatric *Strix* owl species in Finland, *Ornis Scand.,* 1986, vol. 17, pp. 126–132.
15. Borodin, A.V., *Opredelitel' zubov polevok Urala i Zapadnoi Sibiri (pozdnii pleistotsen-sovremennost')* (Identification Key to the Teeth of Voles from the Urals and Western Siberia: From the Late Pleistocene to the Recent Period), Yekaterinburg: Ural. Otd. Ross. Akad. Nauk, 2009.
16. Bol'shakov, V.N., Berdyugin, K.I., Vasil'eva, I.A., and Kuznetsova, I.A., *Mlekopitayushchie Sverdlovskoi oblasti: Spravochnik-opredelitel'* (Mammals of Sverdlovsk Oblast: Guide and Identification Key), Yekaterinburg: Yekaterinburg, 2000.
17. Olenev, G.V., Species identification of murine rodents based on teeth imprints of living animals, *Zool. Zh.,* 1980, no. 2, pp. 294–295.
18. 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.
19. 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, no. 6, pp. 3382–3392.
20. 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, no. 2, pp. 130–141.
21. Pulliam, H.R., On the theory of optimal diets, *Am. Nat.,* 1974, vol. 108, pp. 59–74.
22. Wellicome, T.I., Danielle, Todd, 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, no. 8, pp. 2684–2695.
23. Franclin, A.B., Breeding biology of the Great Gray Owl in Southeastern Idaho and Northwestern Wyoming, *The Condor,* 1988, vol. 90, no. 3, pp. 689–696.

Translated by N. Gorgolyuk