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Dietary variations of the Ural Owl *Strix uralensis* in the transitional mixed forest of northern Belarus with implications for the distribution differences

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The dietary structure and distribution patterns of the Ural Owl *Strix uralensis* under conditions of different food supply (seasonal and year-to-year changes and landscape-related differences) in the coniferous small-leaved transitional forest of northern Belarus were studied in 1996–2002. In total, 1474 prey individuals were recovered from the 447 pellets analysed, and a census of Ural Owl active territories was done each year in early spring in the two study plots. In the ecologically rich area in the Gorodok district the Ural Owl population was high and evenly spaced, while in the poor habitats of the Polotsk district, where the abundance of small mammals was ten-fold lower, the Ural Owl was fairly rare (about eight-fold less) with a patchy distribution. In both study areas, Ural Owls took many bank voles, which is the most common forest rodent in each area. During population peak periods of *Microtus* voles, Ural Owls tended to rely much on this prey category. A positive correlation in the abundance indices of the Ural Owl in the current spring and of the bank vole in the preceding spring was observed. The variety of obtained data strongly suggests that the bank vole is the key prey species for the Ural Owl in the transitional forest of northern Belarus, and both the landscape-related differences in the predator distribution and the between-year variations in its abundance are seemingly determined by the distribution patterns and population dynamics of the bank vole.

1. Introduction

The Ural Owl *Strix uralensis* belongs to the Siberian faunal type. Belarus is at the southern border of its present continuous range (Mikkola 1983, Nikiforov *et al.* 1997). In Belarus, Ural Owls inhabit the extended region of a transitional mixed forest zone (Jedrzejewska & Jedrzejewski 1998, Solovey *et al.* 2001, Sidorovich *et al.* 2003) that covers the northern part of the country. Compared with the species in boreal coniferous and southern broad-leaved forests, the small mammal fauna of this region is distinctive (Jedrzejewska & Jedrzejewski 1998). Forest-dwelling small mammal species (mostly the bank vole *Clethrionomys glareolus* and *Apodemus* mice) have no recurrent

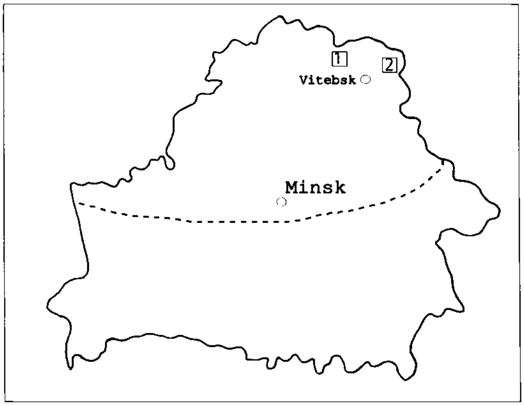

Fig. 1. Location of the two study areas in northern Belarus: (1) the sandy area (Vitebsk region, Polotsk district) and (2) the clay area (Vitebsk region, Gorodok district). A dashed line indicates the southern border of the Ural Owl's present distribution in Belarus according to Nikiforov *et al.* (1997).

cycles of population peaks and crashes; rather the population density is relatively stable over the years.

The characteristics of the small mammal fauna along with the landscape differences were expected to affect the distribution pattern and feeding habits of Ural Owls. Despite many publications on the Ural Owl diet in the boreal coniferous forest zone (Lundberg 1976, 1979, Jäderholm 1987, Korpimäki & Sulkava 1987, Korpimäki *et al.* 1990, Korpimäki 1992), very little is known of the Ural Owl food niche in Belarus.

In the present paper, we study the relationships between Ural Owl distribution pattern and feeding habits and the distribution, abundance and dynamics of its main prey species in northern Belarus during a 7-year period. The main questions addressed are whether the Ural Owl feeding habits and distribution pattern in Belarus have pronounced differences as compared with the boreal forest part of its range and how do the main prey distribution and dynamics affect the spatial structure and trophic niche of the Ural Owl population in the study areas.

2. Study area

The studies were conducted in the fairly natural landscapes of northern Belarus, where man-made habitats (agricultural fields, villages and clearings) make up only 8%–14% of the area. The two areas where the data were collected (Fig. 1) differed substantially in their landscape structure. Additionally, the different soils in the two areas had a considerable affect on the carrying capacity of the habitats (Sidorovich *et al.* 2001, Solovej *et al.* 2001). Both study areas are characterised by river system networks, glacial lakes, large forests and bog ecosystems on rough glacial terrain. The region belongs to the extended transitional zone of the temperate mixed forest area of Europe, which is located between the more southern deciduous and the boreal coniferous forest zones. The spruce *Picea abies* and the pine *Pinus sylvestris* are dominant species among coniferous trees. The black alder *Alnus glutinosa* and the grey alder *A. incana*, birches *Betula pendula*, *B. pubescens*, and the aspen *Populus tremula* are the most common deciduous trees. There are only a few mast-producing deciduous trees, such as the oak *Quercus robur*, the lime *Tilia cordata*, the maple *Acer platanoides* and the ash *Fraxinus excelsior*, which yield a large number of nourishing seeds that are important for rodents. These characteristic features of the plant community seem to be the main reason why the bank vole and other forest rodent species in the transitional forest zone have only seasonal fluctuations with no recurrent cycles of peaks and crashes (Jedrzejewska & Jedrzejewski 1996, our results).

The first study area, the Gorodok area (Gorodok district, Vitebsk region, NE Belarus, lat 55°N, long 31°E), was situated at the upper reaches of the Lovat river and covered approximately 300 km^2. Because the surface ground deposits contain much clay, the water supply is good and the soil is rich (hereafter the "clay" area). Plant communities in the clay area are high in species diversity and productivity, and the habitats have a high carrying capacity for herbivores. Consequently, in the clay area Ural Owls can forage for both main groups of small rodents, i.e. bank voles and mice (large populations inhabiting the rich forest biotopes) and *Microtus* voles, which live mostly in the grasslands and which experience rather frequent (about every four years) population peaks. As a whole, the small mammal community populating the clay area is characterised by high species richness and biomass (Sidorovich *et al.* 2001, our results). A general description of the study area is given in Table 1.

The second study area, the Polotsk area (Polotsk district, Vitebsk region, centrally north of Belarus, lat 55°N, long 29°E), measured approximately 250 km^2. The surface ground deposits in this area consist of sand only (hereafter the "sandy" area). The soils of the area are very barren with poor water supply. Few of the habitats in the Polotsk study area had a high carrying capacity. The forests are dominated by pine stands (Table 1) with a poor-yielding ground layer, thus forming a harsh habitat for small rodents and insectivores. Consequently, the micromammalian community is species-poor with a very low biomass (Sidorovich *et al.* 2001, our results). In the period after September 1999 large-scale felling was begun in the sandy area and large territories were cleared. Such radical transformation of forest habitats substantially affected the native small mammal community structure in the area. Hardly any vegetation could grow on the exposed barren sandy soil of the 1- to 2-year-old clearings, and these areas looked like deserts. But, on the 3- to 5-year-old clearings felling debris had mixed with the surface layer; this had resulted in improved water supply and intensive growth of grass as compared to the native forest biotopes of the sandy area. *Microtus* voles occupied these areas of grassy vegetation, although they had not been observed in the uncut native forest habitats of the area (see Results). Consequently, the species richness and biomass of the small mammal community on the 3- to 5-year-old clearings had increased. Such changes in the small mammal community have undoubtedly affected the Ural Owl feeding behaviour. Thus, when comparing the data obtained in both study areas, we did not use the data collected in the sandy area in 2002, because a substantial part of the area consisted of the 3- to 5-year-old clearings.

The data on Ural Owl ecology were mainly collected in the core parts of the two study areas; these were about 140 km^2 and 190 km^2 for the sandy and the clay areas, respectively. The two study areas were about 80 km apart.

In northern Belarus, the cold season, when there is snow cover and the average air temperature usually drops below 0 °C, normally runs from late October or early November until early April. Winters are fairly severe. Generally, there is also a deep snow cover of 40 cm to 90 cm, and air temperatures of about –20 °C and lower for several weeks are quite common.

3. Material and methods

3.1. Ural Owl surveys

The censuses of Ural Owls were conducted in late March and April in 1996–2002 in the clay area and in 1998–2001 in the sandy area, according to the published methods (Holmberg 1979, Fuller *et al.* 1981, Johnson *et al.* 1981, Voronetsky *et al.* 1990), which are based on the Ural Owl territorial calls. To call Ural Owls, we used a tape-recorder while following a specially established route. We assumed that 600 m would be an appropriate census transect width based on our previous experiences from numerous attempts to listen to such callings at a distance. Thus, we repeated the call every 600 m. The census routes were deliberately chosen in order to investigate all main habitat types in the study areas. The census was done from dusk to about 01:00 and from about 03:00 to dawn mainly by one person on foot. All routes were investigated twice during the spring, with a second control route done in the opposite direction. One stop took about 15–20 minutes since all owl species were recorded. Given

Table 1. Main habitat types (%) in the Gorodok study area (the clay area) and the Polotsk study area (the sandy area), northern Belarus.

Habitat type	Clay area	Sandy area
Dry pine stand and other pine-dominated forest	4	59
Spruce-dominated forest	20	4
Successional deciduous (mostly small-leaved) forest	19	3
Black alder swamp	12	<1
Pine bog	4	16
Aquatic ecosystem	3	7
Grassy marsh	8	<1
Dry meadow	16	2
Fields, villages etc.	13	5
Recent clearings	1	3

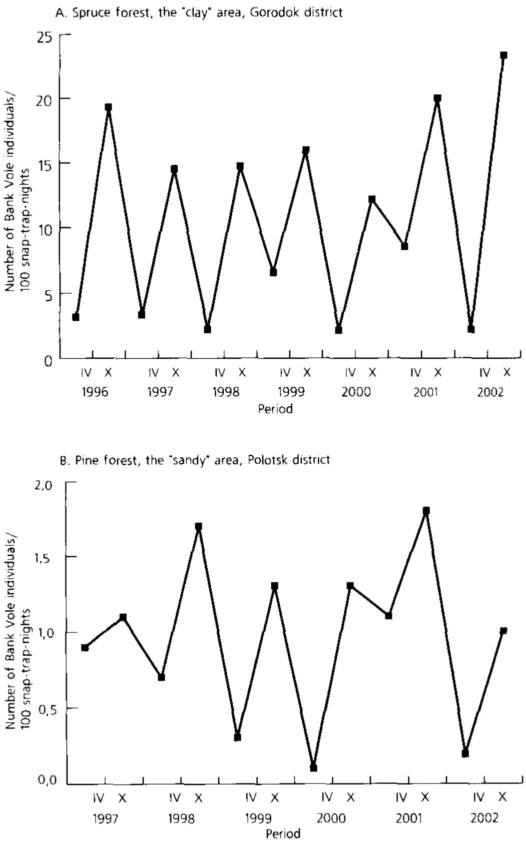

Fig. 2. Population dynamics of the bank vole (A) in the spruce forests of the clay area and (B) in the pine forests of the sandy area.

the selected transect width, the maximum length of a one-night route was about 6 km (10 census points). Censuses were done under suitable weather conditions (with no rain or strong wind).

The following assumption was used. If a territorial call of an individual Ural Owl was observed at least twice along the same route during the initial and the second control census, one active territory was noted. The neighbouring territories were separated from each other on the basis of simultaneous observations of two or more calling birds. Since Ural Owls can be easily sexed by voice (e.g. Lundberg 1980), a duet of male and female on the same territory determined one active territory. However, because the breeding status of the observed birds was not known, the census data were expressed as an abundance index of active territories per 10 km^2 of the area. The number of nest boxes in the study areas was smaller than in Fennoscandian studies (Lundberg 1976, Pietiäinen *et al.* 1986, Korpimäki & Sulkava 1987, Saurola 1987, 1989, Korpimäki 1992, Brommer *et al.* 2002), and it was quite difficult to find all nest sites in the fairly natural landscapes of the study areas.

The calling responses of owls to an artificial provocation reflect to a considerable extent the territorial activity of the birds and do not coincide exactly with the real population density (Lundberg 1980). Thus, some census error is possible and the Ural Owl abundance could be underestimated, because probably not all of the birds responded to our calls. Since we used two or more simultaneously calling owls to determine separate neighbouring territories (unless the two were a mated pair) an overestimation of abundance was unlikely. In this study, "active territory" means that at least one bird is present in the territory and can be used in the abundance comparisons between the landscapes and different years; however, this data probably cannot be used in comparison studies of population densities in other parts of the Ural Owl range.

Each spring in each study area a census of Ural Owls was done on 25–48 km routes on a 600 m transect (about 15–29 km^2) (Figs. 2 and 3). The census routes did not vary during the study period and the length of the routes in the two areas was about equal in a given year. To make the census data more accurate, we used the data available on Ural Owl nesting sites and fledgling broods but detailed searching for nests was not undertaken. In total, 24 fledgling broods and 11 active Ural Owl nests were observed in the study areas. Only two nests and three fledgling broods were seen in the sandy area. The remaining nine nests and twenty-one fledgling broods were found in the clay area.

3.2. Diet analyses

To study the Ural Owl diet, a total of 447 pellets were analysed from which 1474 prey individuals were recovered. The pellets were collected over a period of seven years (1996–2002) in the clay area and during four years (1998–2001) in the sandy area. The data obtained were divided into cold

(November–March) and warm (April–October) seasons, and into periods of *Microtus* population crash (from spring 1997 to spring 1999) and population peak (from mid-summer 1999 to mid-summer 2000). We collected Ural Owl pellets under roosting sites (n = 39) in the known home ranges (n = 20) and under the nests (n = 11).

Small mammal identification was mainly done by two methods. First, we identified skulls and skull remains recovered from pellets by using published keys (Pucek 1981, Görner & Hackethal 1988). Also, ten randomly taken hairs in a pellet were microscopically checked (Teerink 1991) for other mammalian species, which could not be identified by the skulls. This extra control added 7% to the number of individual small mammal species. The other contents of the Ural Owl pellets were identified using the published keys of amphibian bones, reptilian bones and skin scales, feathers and bones of birds (Böhme 1977, März 1987). Insects were distinguished by exoskeleton remains.

The diets, calculated as percentages of prey occurrence, were converted to prey biomass consumed by multiplying with the average weight of each prey species (Pavlovsky 1963, Fedushin & Dolbik 1967, Pikulik 1985, our own measurements). The weight of some prey species (basically hares) was higher than the average daily food intake of the Ural Owl, i.e. 125 g (Mikkola 1970, 1983). In such cases we used the latter value in the dietary calculations.

All prey items were grouped into prey categories according to their importance in the diet. Some of the main prey species formed a separate category.

3.3. Food niche breadth

To compare the overall dietary diversity (food niche breadth) in different feeding conditions, the B index (Levins 1968) was used. The B index varies from 1 (the narrowest niche) to n, i.e. the maximum number of prey categories used for calculations (the broadest niche possible). The frequently applied Pianka's index (Pianka 1973) and the least biased Morisita's index C (Morisita 1959, Krebs 1998) were used to evaluate dietary similarity under the different feeding conditions.

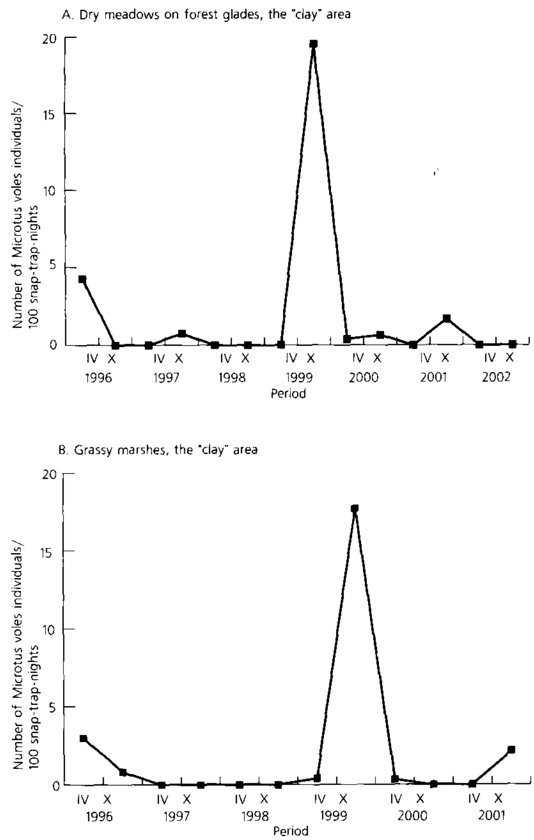

Fig. 3. Population dynamics of *Microtus* voles (A) in the dry meadows and (B) in the grassy marches of the clay area.

The indices vary from 0 (exclusive niches) to 1 (complete overlap). According to the value of these indices, we fixed three levels of dietary overlap: 0–0.49 rather small overlap; 0.50–0.74 medium overlap; 0.75–1.0 large overlap. Food niche breadth and dietary similarity were calculated according to the diets expressed as both percentages of occurrence and ratio of biomass consumed.

3.4. Small mammal abundance

Snap-trapping was used to estimate small mammal abundance in different seasons (April, the pre-reproductive period; October, the post-reproductive period) and in many of the main habitats (Table 1). Fried bread was used as bait in all the habitats investigated. Depending on the habitat size, anywhere from 20 to 50 snap-traps were set at approximately 5 m intervals for three days (checked daily). In each study area, 8–9 locations were investigated annually. Each location included 1–4 trapping plots. We obtained data from about 8000 trapping days in the sandy area and from about 13 000 trapping days in the clay area.

3.5. Habitat surveys

The data on the occurrence of different habitat types (hereafter called landscape structure) were obtained by following specially established routes in random directions. These routes (10 km each) covered much of the study areas. The total length of such routes made up 217 km for both study areas.

3.6. Statistics

Statistical analysis of the data compared was done according to the standard recommendations (Sokal & Rohlf 1995). By testing a correlation between abundance of the Ural Owl and abundance of small mammals (each species and species group separately), the predator abundance index of the current spring was compared with the prey abundance index of either (1) the current spring, (2) the previous spring, or (3) the previous autumn. We used the independent t-test for differences between two means (Sokal & Rohlf 1995).

4. Results

4.1. Landscape-related differences in the Ural Owl diet on a seasonal basis

During the investigation period we identified 30 prey species of the Ural Owl (see Appendix). A total of 28 prey species were detected from the clay area and a total of 16 prey species from the sandy area.

In the warm season, Ural Owls in the clay area had a wide food niche breadth, although they mostly relied on mammals (Table 2). The other prey categories (insects, amphibians and birds) were of minor importance (0.2%–4.8% of numbers). Among mammals, small rodents were preferred (70.1% of numbers, 69.3% of mass). Additionally, the mole *Talpa europaea* and large

Table 2. Diet (% n, % mass) of Ural Owls in the warm season (April–October) in the clay and sandy areas, Vitebsk region, northern Belarus.

Prey item	Clay area		Sandy area	
	% n	% mass	% n	% mass
Insects	9.3	0.2	3.6	0.1
Amphibians	3.3	2.3	–	–
Reptiles	–	–	10.7	2.1
Birds	4.2	4.8	10.7	10.3
Shrews	4.8	0.8	4.8	1.6
Mole	5.8	11.2	–	–
Total small insectivores	10.6	12.0	4.8	1.6
Bank vole	24.1	11.7	61.8	63.1
Mice	3.8	3.8	3.6	2.8
Microtus voles	25.9	25.6	–	–
Water vole	12.3	24.3	1.2	5.0
Other small rodents	4.0	3.9	2.4	4.3
Total small rodents	70.1	69.3	89.1	75.2
Muskrat, hares, red squirrel	2.5	11.4	1.2	10.7
Small mustelids	–	–	–	–
Total mammalian prey	83.2	92.7	95.1	87.5
Number of prey individuals recovered from the pellets	673	94		
Food niche breadth	6.21	5.89	2.06	2.35

mammals (basically hares, *Lepus timidus* and *L. europaeus*) formed an important part of the food biomass, while shrews were of negligible importance. Among small rodents, Ural Owls mainly fed on the bank vole, *Microtus* voles and the water vole *Arvicola terrestris*, whereas mice (mostly species of the genus *Apodemus*) and other small rodents (birch mouse *Sicista betulina* and forest dormouse *Dryomys nitedula*) were rarely consumed (Table 2).

During the cold season in the clay area, the Ural Owl food niche narrowed, so that the owls mostly preyed on *Microtus* voles and bank voles (Table 3). The Ural Owl also preyed on the weasel *Mustela nivalis* in the cold season, while in the warm season the species was not found. Conversely, the proportion of water voles declined considerably from 24.3% to 9.8% of mass in the cold season.

In the sandy area, the food niche was very narrow year-round (Tables 2 and 3), with the Ural Owl mainly feeding on the bank vole (61.8%–68.7% of numbers, 58.8%–63.1% of mass).

The proportion of bank voles in the diet in the sandy area was considerably higher than in the clay area ($G_1 = 15.2$, $P < 0.01$). Among other marked differences, the *Microtus* vole consumption in the sandy area was substantially lower year-round ($G_1 = 29.7$, $P < 0.01$). The dietary similarity between Ural Owls in the clay and sandy areas was not very great (Table 4) and the differences in the proportion of prey consumed were highly significant ($G_1 = 97.5$, $P < 0.001$ calculated for % of number in the warm season; $G_1 = 112.3$, $P < 0.001$, for % of mass in the warm season; $G_1 = 112.6$, $P < 0.001$, for % of number in the cold season; $G_1 = 126.7$, $P < 0.001$, for % of mass in the cold season).

4.2. Changes in the Ural Owl diet in relation to population cycles of *Microtus* voles

The Ural Owl became a more specialised micromammalian predator when the *Microtus* vole populations peaked. At these times, Ural Owls mainly fed on *Microtus* voles (45.0% of number, 29.9% of mass) and bank voles (29.0% of number, 20.4% of mass), but they also fed on water voles (13.3% of mass) and moles (12.9% of mass). The other prey species were then of minor importance (Table 5).

Table 3. Diet (% n, % mass) of Ural Owls in the cold season (November–March) in the clay and sandy areas, Vitebsk region, northern Belarus.

Prey item	Clay area		Sandy area	
	% n	% mass	% n	% mass
Insects	0.2	0.0	–	–
Amphibians	0.8	0.6	–	–
Reptiles	–	–	–	–
Birds	1.3	1.7	14.1	18.3
Shrews	9.3	1.8	10.1	2.8
Mole	3.8	8.2	3.0	10.3
Total small insectivores	13.1	10.0	13.1	13.1
Bank vole	29.8	16.1	68.7	58.8
Mice	7.9	8.7	2.0	1.3
Microtus voles	40.5	44.9	1.0	0.9
Water vole	4.4	9.8	–	–
Other small rodents	0.5	0.5	–	–
Total small rodents	83.1	80.0	71.7	61.0
Muskrat, hares, red squirrel	0.6	3.1	1.0	7.7
Small mustelids	0.9	4.6	–	–
Total mammalian prey	97.7	97.7	85.8	81.8
Number of prey individuals recovered from the pellets	596	111		
Food niche breadth	3.68	3.92	1.98	2.53

After the *Microtus* population crashed, the Ural Owl diet changed considerably ($G_1 = 48.9$, $P < 0.001$ calculated for % of numbers; $G_1 = 31.9$, $P = 0.01$, for % of mass). The proportion of *Microtus* voles in the diet decreased markedly from 29.9% to 4.0% of mass ($G_1 = 22.5$, $P < 0.01$). The shortage of *Microtus* voles in the area led to their gradual replacement in the owls' diet by nearly every other prey type (Table 5). Under these different feeding conditions, the dietary similarity can be expressed as a medium value — Pianka/Morisita's indices were 0.67/0.68 for per cent of numbers, and 0.73/0.74 for per cent of mass. These changes in the Ural Owl diet were observed only in the clay area.

Table 4. Similarity indices (Morisita/Pianka) of the Ural Owl diet in the clay and sandy areas on a seasonal basis, northern Belarus.

Type of dietary calculations	Warm season	Cold season
% n	0.58/0.63	0.58/0.60
% mass	0.37/0.39	0.36/0.36

4.3. Landscape and habitat-related differences in the small mammal community

In the forests of the clay area, twenty micromammalian species were recorded. The dominant species were the bank vole, *Apodemus* mice (mainly the yellow-necked mouse *A. flavicollis*, and the wood mouse *A. sylvaticus*), and *Sorex* shrews (mainly the common shrew *S. araneus*). Nineteen species were caught by snap-traps. Grassland patches (dry meadows on glades and open grassy marshes) interspersed among the forest housed *Microtus* voles (basically the common vole *M. arvalis* and the short-tailed vole *M. agrestis*). Approximately a third of open grassy marsh fragments and black alder swamps were populated by water voles.

The small mammal community in the forests in the sandy area was species-poor. Only seven micromammalian species (again mainly the bank vole) were recorded in forests. Additionally, in forest clearings and glades, six other small mammal species (mainly the common vole and the striped field mouse *A. agrarius*) were found.

In the post-reproductive period in autumn, bank voles constituted about 70% and 82% of the

Table 5. Comparison of the Ural Owl diet (% n, % mass) between *Microtus* voles population crash and peak periods, Vitebsk region, northern Belarus.

Prey item	*Microtus* voles population crash		*Microtus* voles population peak	
	% n	% mass	% n	% mass
Insects	6.9	0.2	3.1	0.1
Amphibians	6.1	4.2	2.1	1.3
Reptiles	1.3	0.2	0.5	0.1
Birds	7.9	11.7	4.0	6.7
Shrews	9.9	2.2	1.8	0.5
Mole	4.4	10.9	4.6	12.9
Total small insectivores	14.3	13.1	6.4	13.3
Bank vole	38.1	23.8	29.0	20.4
Mice	7.4	9.5	2.8	4.0
Microtus voles	6.7	4.0	45.0	29.9
Water vole	5.9	15.1	4.6	13.3
Other small rodents	2.3	2.9	1.0	1.4
Total small rodents	60.4	55.3	82.4	69.0
Muskrat, hares, red squirrel	2.3	10.9	1.0	6.4
Small mustelids	0.8	4.5	0.5	3.2
Total mammalian prey	77.4	83.8	90.3	91.9
Number of prey individuals recovered from the pellets	846	628		
Food niche breadth	5.37	7.55	3.39	5.67

small mammal community in the forests of the clay and sandy areas, respectively. *Apodemus* mice were also common in forests, while *Microtus* voles rarely inhabited forest biotopes. Bank voles and *Apodemus* mice, as well as small mammals on the whole, were markedly more common in spruce woods compared to pine stands. In all forest habitat types, the small mammal population was about five-fold higher in the clay area than in the sandy area ($t \geq 5.0$, $P \leq 0.001$). The weighted-mean abundance was about ten-fold higher (27.1 versus 2.8 inds/100 snap-trap-nights). Concerning the bank vole, its weighted-mean abundance was about eight-fold higher in the forested terrain in the clay area than in the sandy area (19.0 versus 2.3 inds/100 snap-trap-nights).

Conversely, *Microtus* voles mostly inhabited patches of open grassland, such as fragments of grassy marshes and dry meadows, as well as ecotones between forests and open grasslands, especially in their population peak years. In autumn the total small mammal community in these habitats was about two-fold higher than in forests of different types, and 10 out of 14 pairs of comparisons were statistically significant ($t = 2.60$, $P < 0.01$).

The bank vole population showed only seasonal fluctuations with no recurrent cycles of peaks and crashes (Fig. 2). In the main habitat types of both study areas the abundance of the Bank Vole varied more in spring than in autumn (1100% versus 160% for the sandy area and 400% versus 170% for the clay area). *Apodemus* mice inhabiting forests tend to have the same pattern of population dynamics. Thus, the species composition of the forest community of small mammals in northern Belarus is quite stable on a multi-annual scale. Conversely, small mammal abundance was much more variable in patches of open habitats scattered throughout forests. In these habitats, *Microtus* voles often predominated over other micromammalian species, particularly in their population peak years, and the population cycle of *Microtus* voles (Fig. 3) leads to the large fluctuations in both small mammal abundance and species composition. During the study, *Microtus* vole crashes were recorded twice by the late summers (August–September) of 1996 and 2000. Peak numbers were observed in the late summer of 1999.

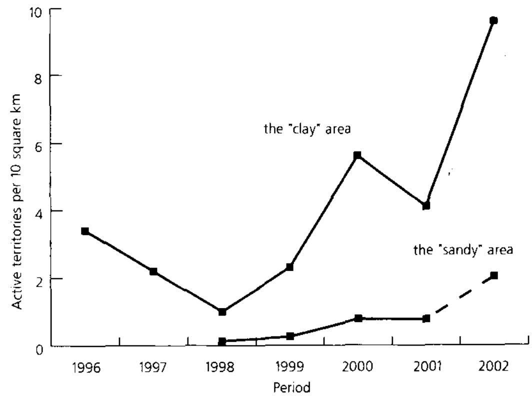

Fig. 4. Year-to-year variation in the Ural Owl abundance index in the clay and sandy areas, Gorodok district, NE Belarus. Data for the sandy area before 1998 are not available. The dashed line indicates the data that were not used in comparisons of the areas (see Material and methods).

4.4. Distribution and abundance of Ural Owls in relation to the landscape structure and small rodent population fluctuations

In the clay area, Ural Owls were spaced fairly evenly in forested habitats. In the fairly natural landscape of the clay area, the abundance index of the Ural Owl varied from year to year between 1.0 and 9.6 (mean 4.0) active territories per 10 km^2 (Fig. 4). The variation in abundance was fairly high (coefficient of variation 72%). There was a high positive correlation between the Ural Owl abundance index of the current spring (active territories per 10 km^2) and the abundance index of Bank Voles of the previous spring (individuals captured per 100 snap-trap-nights) ($r = 0.87$, $P = 0.008$). Also, the Ural Owl abundance of the current spring correlated positively with the abundance index of bank voles of the previous autumn ($r = 0.48$, $P = 0.05$).

In the sandy area, the distribution of Ural Owls was irregular. Here, Ural Owls were found mainly in habitats with glacial lakes surrounded by spruce forests, while the abundance indices were fairly low, on average 0.45 active territories per 10 km^2 (Fig. 4), which is markedly (about eight-fold) lower than the Ural Owl abundance in the clay area ($t = 3.13$, $P = 0.01$). The coefficient of variation was about the same as in the clay area (69%). Ural Owl abundance indices in the two study areas were highly correlated ($r = 0.98$, $P = 0.01$).

5. Discussion

In the ecologically rich Gorodok study area (the clay area) the Ural Owl population was high and evenly spaced, whereas in the poorer quality habitats of the Polotsk study area (the sandy area) the Ural Owl was a fairly rare and irregularly distributed species, mostly inhabiting local plots of spruce-dominated biotopes. The abundance indices of Ural Owls in the two study areas were correlated in a multi-annual scale, but Ural Owl abundance indices were about eight-fold higher in the clay area when compared with the sandy area. The two study areas were less than a hundred kilometres apart, so the main hypothesis used to explain the observed differences was the variation in food supply in the two landscape types as suggested by many earlier studies on owls (Mikkola 1983, Cramp 1985, Jäderholm 1987, Korpimäki & Sulkava 1987, Pietiäinen 1988, Wasilewski 1990, Korpimäki & Hakkarainen 1991, Korpimäki 1992, Jedrzejewska & Jedrzejewski 1998, Mebs & Scherzinger 2000, Brommer *et al.* 2002 and references therein).

The diet of Ural Owls in the European part of its range is fairly diverse with a predominance of micromammalian prey (Lundberg 1976, 1979, Mikkola 1983, Jäderholm 1987, Korpimäki & Sulkava 1987, Korpimäki *et al.* 1990, Korpimäki 1992, Tishechkin 1997). The proportion of small mammals in Ural Owl diets varied from 59% to 97% expressed as frequency of occurrence and from 58% to 94% expressed as percentage of biomass consumed. The bank vole, *Microtus* voles, and the water vole are the main prey species. In northern Europe, it has been shown that the proportion of voles in the Ural Owl diet corresponded to their abundance as estimated by trap census (Korpimäki & Sulkava 1987, Korpimäki *et al.* 1990, Korpimäki 1992).

Under the conditions in the extended region of Europe covered by the coniferous small-leaved transitional forest, the Ural Owl dietary structure has been poorly studied (but see Tishechkin & Ivanovsky 1998, Tishechkin 1997). In order to understand better the feeding habits of such an opportunistic predator as the Ural Owl, its diet should be investigated along each main gradient of dietary variability. In northern Belarus there were substantial differences in the landscape features, which affected the habitat carrying capacity. The sandy area had poor habitats and poor food supply and the rich clay area was characterised by good food supply. In addition, seasonal changes in prey abundance and availability, and the population trend of the preferred prey species, such as *Microtus* voles and the bank vole in the transitional forest zone, were reflected in the diet.

The bank vole was the most common rodent species occupying all biotopes of the study areas. Despite marked yearly population fluctuations in spring, the bank vole population is fairly stable with only seasonal and landscape variations. Conversely, *Microtus* voles have well pronounced four-year population cycles as well as landscape-related differences in abundance. In the sandy area the small mammal community was significantly smaller because the predominant pine stands there provide poor feeding conditions for the rodents. *Microtus* voles were practically absent in the sandy area, so the bank vole was the main available prey species for the Ural Owl during all seasons of the year in this area, while in the clay area *Microtus* voles were quite common in patches of open grassland within forests, especially in population peak years.

In northern Belarus, Ural Owls fed mainly on small mammals, with some generalist feeding on birds and other mammals (squirrels, hares, small mustelids etc.). The owls' winter diet had a higher proportion of bank voles and *Microtus* voles than the summer diet. Water voles were consumed more often in summer than in winter. In the poorer quality habitats in the sandy area, Ural Owls fed on the most available species, i.e. bank voles, whereas in the ecologically rich clay area the diet was more diverse, with a preference for small mammals of many species.

The opportunistic feeding habits of Belarusian Ural Owls become apparent in the pronounced increase in the consumption of *Microtus* voles during their population peak years. This was true however only in the clay area, where *Microtus* population fluctuations were well pronounced. Despite the water vole being the most favourable prey species amongst small mammals by weight, its proportion in the diet declines from summer to winter, most likely because, in winter, water voles stay under the snow cover (Macdonald & Strachan 1999) and are thus less available to raptors.

Ural Owls were significantly more abundant in the ecologically rich clay area than in the poor habitats of the sandy area. The most plausible explanation is the great difference in the food supply between the areas: the small mammal abundance differed ten-fold between the ecologically rich and poor areas. We found that the abundance of Ural Owls showed a similar difference (about eight-fold) as did the small mammals.

Bank voles constituted the main part (70%–82%) of the small mammal community. The positive correlation in the between-year population dynamics of the Ural Owl and the bank vole suggests that the bank vole is the key prey species for Ural Owls in the coniferous small-leaved transitional forests of northern Belarus. The Ural Owl distribution and demography seem to be evolutionarily adapted to the distribution and demography of bank voles. The spring abundance of bank voles is highly dependent on the winter conditions, especially on how much edible green vegetation is available under the snow cover. The autumn abundance of this small mammal species is quite stable between years. Good winter survival of the bank vole provides Ural Owls with an ample food supply at the beginning of the breeding season, which seems to improve the owls' breeding success. Additionally, the young Ural Owls will have a good chance of survival in their first year of life because of the high bank vole population. Thus, two consecutive favourable winters can result in a high spring abundance of Ural Owls due to a productive breeding season after the first winter and good adult and offspring survival during the second winter. Such was the case in 2002, when the Ural Owl spring abundance was very high (Fig. 4). Indeed, good winter conditions for small herbivores such as bank voles were observed during two consecutive winters (2000–2001 and 2001–2002), and the species thrived.

On a population level, *Microtus* voles and the water vole were less important to the Ural Owl. In northern Belarus only a small part of Ural Owls' diet consisted of water voles, and the voles' habitat made up only a small part of the forests. About 20% of the clay area is potential habitat for water voles (open grassy marshes and black alder swamps), but only approximately a third of these areas are regularly populated by water voles (Macdonald *et al.* 2002). In the sandy area, water vole habitats were rare (less than 1%), and these were poorly inhabited by water voles. Although the water vole is only of average importance for a woodland predator like the Ural Owl, it seems to play an important role during the breeding season.

Because *Microtus* voles have a pronounced population cycle, they were important prey only during their population peaks, which lasted a fairly short period of about 10 months and occurred once every four years (see Fig. 3). During the remaining 3 years, *Microtus* voles were a negligible supplement to the Ural Owl diet.

The positive correlation between the Ural Owl abundance in the current spring and the abundance indices of *Microtus* voles in the previous autumn in the clay area indicates that these prey species are important to the predator's winter survival during population peak periods. However, since *Microtus* voles are quite rare after population crashes, it seems unlikely that these prey species could regulate the Ural Owl demography to any considerable extent in northern Belarus. *Microtus* vole population dynamics are mainly reflected in the Ural Owl diet composition.

The data obtained on Ural Owl abundance and population dynamics were quite notable and even surprising. The coefficients of variation of the Ural Owl abundance indices were very high. The Ural Owl in Belarus seems to be a sedentary species (e.g. Tishechkin & Ivanovsky 1998) and the observed fluctuations are quite difficult to explain. The abundance indices of the Ural Owl were very high when compared with the population densities estimated elsewhere in Europe (Lundberg 1976, Pietiäinen *et al.* 1986, Czuchnowski 1997). Earlier observations (Tishechkin & Ivanovsky 1998) showed that the breeding density of the Ural Owl in northern Belarus was 0.45–0.95 pairs per 10 km^2, but the censuses were based on spontaneous observations of owl vocal activity in October–April and following provocation with a tape recording at some selected points, without any distinction between years and landscape types. Such a census technique seems to result in a considerable population underestimation. In the boreal part of the Ural Owl range, we have a much higher population density even if our active territories correspond to only one bird (actually this is true only for unmated owls). In the ecologically rich clay area, we have the highest density of Ural Owls in Europe, although with a large yearly fluctuation. Taking into account that the southern border of the Ural Owl's present continuous range is in Belarus, the observed high density is of double interest.

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Selostus: **Viirupöllön ravinto ja esiintyminen Valko-Venäjällä**

Artikkelin kirjoittajat tutkivat vuosina 1996–2002 viirupöllön ravinnon koostumusta ja lajin esiintymistä Valko-Venäjällä kahdella, elinympäristöltään eroavalla tutkimusalueella. Gorodokin tutkimusalue oli viirupöllön kannalta runsaasti sopivaa ravintoa tarjoava alue, kun taas Plotskin alueella oli viirupöllölle tarjolla vähemmän ravintoa. Tutkimuksessa määritettiin kaikkiaan 1474 saalisnäytettä yhteensä 447 viirupöllön oksennuspalloista. Viirupöllöjen reviirien sijainti selvitettiin vuosittain toistettujen laskentojen avulla. Gorodokissa viirupöllöjä oli runsaasti (keskimäärin 4.0 aktiivista reviiriä/10 km^2) ja pöllöreviirit sijaitsivat tasaisesti koko alueella. Lämpiminä vuodenaikoina Gorodokin viirupöllöjen ravintovalikoima oli laaja. Kylminä vuodenaikoina Gorodokin viirupöllöjen ravintovalikoima yksipuolistui, ravintokohteiden ollessa pääasiassa *Microtus* -suvun myyriä ja metsämyyriä. Plotskin tutkimusalueella viirupöllöjä oli noin kahdeksan kertaa vähemmän (keskimäärin 0,45 aktiivista reviiriä/10 km^2) kuin Gorodokin alueella. Lisäksi Plotskin alueella pöllöreviirit keskittyivät tiettyihin alueen osiin. Plotskissa viirupöllön ravinto koostui vuodenajasta riippumatta pääosin metsämyyristä. *Microtus* myyrien esiintymisen huippuvuosina viirupöllöt saalistivat pääasiassa *Microtus* -suvun myyriä ja metsämyyriä. Myyräkantojen romahtaessa *Microtus* -suvun myyrien paino-osuus viirupöllön ravinnossa laski 4%:iin myyrähuipun aikaisesta 30%:sta. Molemmilla tutkimusalueilla viirupöllön pääsaalislaji oli alueen yleisin myyrälaji, metsämyyrä. *Microtus* -myyrälajien esiintymishuippuina viirupöllöt saalistivat kuitenkin paljon *Microtus*-myyriä. Tutkimuksessa havaittiin positiivinen korrelaatio viirupöllön runsausindeksin ja edellisen kevään metsämyyrien lukumäärän välillä. Tutkimustulokset viittaavat siihen, että metsämyyrä on tärkein viirupöllön esiintymiseen vaikuttava saalislaji Valko-Venäjällä. Metsämyyrän esiintyminen ja populaatiodynamiikka vaikutti sekä viirupöllön esiintymiseen että pöllön runsausvaihteluihin vuosien välillä.

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Appendix. Ural Owl prey species in the clay and sandy areas, northern Belarus. + = detected, – = absent.

Prey species	Clay area (1996–2002)	Sandy area (1998–2001)
Apodemus agrarius	+	–
Apodemus flavicollis	+	–
Apodemus sylvaticus	+	+
Arvicola terrestris	+	+
Bonasa bonasia	+	+
Bufo bufo	+	–
Carabus spp.	+	+
Clethrionomys glareolus	+	+
Dryomys nitedula	+	–
Garrulus glandarius	+	–
Geotrupes stercorarius	+	+
Lacerta agilis	–	+
Lacerta vivipara	–	+
Lepus europaeus	+	–
Lepus timidus	+	+
Micromys minutus	+	–
Microtus agrestis	+	+
Microtus arvalis	+	+
Microtus oeconomus	+	–
Microtus subterraneus	+	+
Mustela erminea	+	–
Mustela nivalis	+	–
Neomys fodiens	+	–
Ondatra zibethica	+	–
Rana temporaria	+	–
Sciurus vulgaris	+	+
Sicista betulina	+	+
Sorex araneus	+	+
Sorex caecutiens	+	+
Sorex minutus	+	–
Talpa europaea	+	+
Turdus spp.	+	+
Undet. Small passerine	+	+