



ORIGINAL INVESTIGATION

Effect of felling on red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) diets in transitional mixed forest in Belarus

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Abstract

In transitional mixed forests in northern and central Belarus the influence of intensified felling on the diets of red foxes *Vulpes vulpes* L. and pine martens *Martes martes* L. was investigated in two model forested terrains with sandy and clay top-grounds. A total of 1904 scats of red foxes and 1624 scats of pine martens were analysed over two periods differed by logging rate. When logging rate was conservative, red fox and pine marten diets were found to be similar, but under heavy logging feeding of the predator species shifted. In both model woodlands we found the same pronounced dietary trend of higher consumption of rodents, first of all, *Microtus* voles. The dietary changes were well related to the registered increase in *Microtus* vole numbers and total number of rodents in felling areas. The increased preying on rodents caused lower consumption of other food items, particularly medium-sized mammals (year-round) or/and birds or/and fruits (in the warm season) or/and mammalian carrion (in the cold season). In the conditions of intensified felling the food niches of the red fox and pine marten diverged mostly because of the great difference in the species structure of rodents consumed. Red foxes turned to preying on *Microtus* voles more frequently, but less on bank voles *Myodes glareolus*; while pine martens increased their taking of *Microtus* voles, continued foraging for bank voles and began taking slightly more of *Apodemus* mice. Before heavy logging dietary similarity between the red fox and pine marten was high and did not vary considerably through seasons and study areas, whereas after felling was intensified their diet overlap became lower.

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Introduction

In the European forest zone, woodlands are known to be considerably altered by felling. In Belarus, particularly

heavy impact of logging on forest ecosystems took place in the second half of the twentieth century. Nevertheless, in Belarus, as far back as 10–20 years ago many of woodlands looked lowly disturbed by forestry practice. Since the second half of the 1990s forest exploitation has been markedly intensified. Recent clearcuts appeared in numbers and occupied a substantial part of woodlands. In Belarus, intensified forest exploitation has turned to be patchy because of irregular distribution and different quality of forest roads.

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The red fox *Vulpes vulpes* and pine marten *Martes martes*, being common in woodlands and characterized by high feeding plasticity, respond quickly to ecological changes in forested terrain (e.g. Jędrzejewski et al., 1993a; Jędrzejewska and Jędrzejewski, 1998; Sidorovich et al., 2005, 2006a) and, therefore, appear to be suitable subject for investigating the felling impact on animal ecology. In Belarus and surrounding regions, both predators are found to consume small rodents more when the prey group grows in numbers (e.g. Jędrzejewski and Jędrzejewska, 1992; Jędrzejewski et al., 1993a; Sidorovich et al., 2005, 2006a). Intensified forest exploitation influences population density of the majority of rodent species (Hansson, 1978; Wołk and Wołk, 1982; Kirkland et al., 1985; Aksenova and Bulyuk, 1986; Carey and Johnson, 1995; Bryja et al., 2002; Sidorovich et al., 2008a). It shifts prey supply and diets of red foxes and pine martens and, consequently, may underlay the revealed changes in the predator numbers in recently logged woodlands (Sidorovich et al., 2008a).

The influence of forest exploitation on spatial population structure of the pine marten and red fox has been already investigated in several countries (Hargis, 1982; Steventon and Major, 1982; Thompson, 1986; Snyder and Bissonette, 1987; Bissonette et al., 1988; Hansson, 1994; Henttonen, 1989; Oehler, 1995; Kurki, et al., 1998; Virgos et al., 2002) including Belarus (Sidorovich et al., 2008a). In our mentioned study, red fox numbers was found to grow clearly with the increase in portion of recent clearcuts. Moreover, red fox trails were more frequently registered in clearcuts and their ecotones compared to low-disturbed forests. As to the pine marten, mild logging appeared to be beneficial for the species, but martens decreased in density in response to very intensive felling rates.

The recorded changes in prey supply and distribution of predator species in woodlands strongly altered by forest exploitation suggest that changes in the diet of predators should occur. Still there is a lack of studies on change in red fox and pine marten diets connected with logging. Nevertheless, such a question is worthwhile being investigated, as changed feeding of common predators could shift their predation impact on prey populations and interactions with other predators (Andren et al., 1985; Angelstam, 1986; Andren and Angelstam, 1988; Henttonen, 1989; Fahrig and Grez, 1996; Jędrzejewska and Jędrzejewski, 1998; Kurki et al., 2000; Krebs et al., 2001; Panzacchi et al., 2007a; Wegge and Kastdalen, 2007).

Material and methods

When describing the study areas, besides general geographic description, we paid attention to the revealed patterns of rodent distribution, as the study is addressed to the red fox and pine marten that are both rodent

eat. Woodlands in northern and central Belarus mostly consist of deciduous small-leaved and coniferous trees. Such a mixed woodland is transitional between boreal coniferous forest and more southern broadleaf or coniferous-broadleaf forest. Seed crop in transitional forest is steady, but markedly lower than that in more southern broadleaf woodland of Europe (Jędrzejewski and Jędrzejewska, 1996). Therefore, in transitional woodlands, food supply for rodents is markedly more sustained on multiannual scale and populations of forest rodent species have only seasonal fluctuations with no recurrent cycles of outbreaks and crashes (Jędrzejewski and Jędrzejewska, 1996; Sidorovich et al., 2003, 2005). Conversely, in more southern woodlands of Europe, prevalence of masting broad-leaved trees, which produce intermittently a big amount of nourishing seeds important for rodents, leads to a pronounced cyclicity in forest rodent populations (Jędrzejewska and Jędrzejewski, 1998). Only *Microtus* voles favouring open grasslands and occurring rarely in forest habitats have intermittent between-year population dynamic with a periodicity of 4–5 years (Sidorovich et al., 2003, 2006a).

The data were collected in two areas substantially differing in top grounds that resulted in considerably different habitat carrying capacity for rodents and other prey (Solovej et al., 2001, 2003). The first study area (Minsk and Smolevichi district, Minsk region, central Belarus; 53°N, 27°E) was a densely forested terrain of 48 km² surrounded by a rural area. Surface ground deposits are rich in clay, which ensures good water supply and abundant trace elements, and, consequently, rich soil (hereafter “clay” area). Plant communities in the “clay” area have a high species diversity and productivity, and habitats with high carrying capacity for herbivores dominate. Therefore, species richness and population biomass of rodents in the “clay” area are high (Sidorovich et al., 2003). Before 1998 mature forests dominated by spruce made up about 60% of the woodland structure, and recent clearcuts, which are largely overgrown with grass or additionally covered with early reforestation, constituted less than 10%. In this woodland harboring on rich clay soil, rather high species diversity and biomass of herbal vegetation usually appeared in a year after felling. That immediately favours rodents, and their species richness and density markedly increased (Sidorovich et al., 2008a). To separate recent clearcut with some reforestation and already young forest, we used the feature of evident suppression of grass cover by thickening of young trees as a formal border. Besides mature spruce stands and recent clearcuts, remainder of the woodland (approximately 27%) was represented by mixed coniferous-deciduous forests. Among such mixed forest habitats, young thicket, mid-successional overgrowth and mature stands were present. Small glades with meadows were interspersed throughout the woodland. Intensive felling operations ran from autumn 1998 till the end of our study

in 2006. The reason was wholesale withering of spruce caused by the epizooty of engraver beetles *Ips typographus* appeared after the summer drought of 1992 (Fedorov and Sarnackij, 2001). As a result, since 1999 portions of recent clearcuts and young forests made up 15–50% in different parts of the woodland. Clear cutting was the most common practice of the local forestry, and entirely logged areas ranged from 1 to 100 ha (usually 10–20 ha). Clearcut shape was mostly rectangle.

The second study area (Polotsk district, Vitebsk region, central north of Belarus; 55°N, 29°E) was a forest tract of approximately 250 km². There, surface ground deposits consist of sand mainly (hereafter “sandy” area), with clay only in valleys of glacial lakes and rivers. Soils of the area are barren because of poor water supply. Therefore, the woodland is dominated by pine stands with very poor ground vegetation. Consequently, a species-poor rodent community with very low biomass is characteristic of “sandy” area (Sidorovich et al., 2003). Before 1999 mature and premature pine stands constituted about 60% of the forest on dry land and 19% in raised bogs. On the pine forest floor, mixtures of moss, lichens and berry dwarf shrubs were mostly found, whereas grasses were of negligible importance. Before 2000 in the woodland on sandy deposits, recent clearcuts constituted less than 10%, and very poor habitats on open sands were observed during the first year after forest harvesting. However, with time (3–5 years after logging) thick herbal vegetation appeared in such clearcuts in contrast with mature pine stands. This happens because while logging, heavy forestry machines mix sand with remains of the terrestrial vegetation and tree branches. Such organic matter mixed with sand layers keeps water and gradually produces chemical substances containing nutrient elements available for herbal vegetation. In effect, rodents densely populate such places with high species diversity (Sidorovich et al., 2008a). Timber harvesting being intensified since 2000 changed markedly the woodland structure, and the portion of recent clearcuts and young forests reached gradually about 20–30% of the woodland, and in some localities up to 60% of mature pine stands were logged.

In northern Belarus, severity of winters varies from year to year. Some of winters are rather mild with a fairly short snowy period (1.5–2 months), but the majority of them are quite severe, with a snow cover ranging from 20 to 50 cm (in some habitat up to 90 cm by late winter) and air temperature may be about –20 °C and lower for several weeks. Such hard frost periods usually alternate with thaws lasting for several weeks. However, last three winters (2006–2009) were markedly milder than it used to be. In central Belarus, severity of winter is slightly lower than in northern Belarus, e.g. winter duration is usually two weeks shorter.

Dietary results are based on analysis of 1904 red fox and 1624 pine marten scats collected in the study areas. Respectively, 5952 and 3084 prey individuals and other

food items (presence of fruits, seeds and herbs) were recovered from the scats analysed. The majority of scats were taken on tracks and nearby dens. The scats were collected during 1995–2005 that covered both situations, i.e. conservative forest exploitation and heavy logging. Taking into account cyclicity in *Microtus* voles, the periods chosen included peaks and lows of the prey. Mainly we sampled scats in the situations before and after heavy felling in the years of outbreak and crash in *Microtus* voles. Data on the dynamic of *Microtus* vole populations were known from other studies (Sidorovich et al., 2006a, 2008b). The data obtained were presented for the cold (November–March) and warm season (April–October) separately.

To identify mammalian prey consumed, among hair in a washed scat we checked microscopically all hair pile that looked differently; besides, 10 piles were taken randomly from small hair that presumably belonged to rodents and insectivores (Debrot et al., 1982; Teerink, 1991; Jędrzejewska and Jędrzejewski, 1998). To identify young ungulates (individuals up to about two months old, hereafter young) that can be hunted by red foxes, we combined microscopical analysis with known visual features of their hair. For instance, hair piles of roe deer fawns in scats are markedly shorter, more wiry and carrot-coloured, whereas hair of elder roe deer are longer, fragile and almost discoloured. Sometimes, hooves of young ungulates occurred in the scats, and this helped in ungulate identification, too. Similar approach in identification of young ungulate hair in carnivore scats was applied by Panzacchi et al., (2007a, 2007b). Other scat contents were analysed using the published keys of feathers and bones of birds, amphibian bones, reptilian bones and skin scales (Böhme, 1977; März, 1987). Insects were distinguished by the remains of exoskeleton. Plant material was recorded as food consumed, if much of it (at least, 10% of dry volume) was found in a scat analysed.

The procedure to calculate red fox and pine marten diets was as follows. The number of different prey individuals and other food items, which remains were found in all the scats analysed, was taken as 100% in calculations of relative percentages of various prey occurrence in the diet (hereafter %OC). At that, an incalculable remain of plant matter (fruits or seeds or herbs) in a given scat was taken as one occurrence. To obtain the percentage of food biomass consumed (hereafter %BC), we followed the approach recommended by Jędrzejewska and Jędrzejewski (1998) based on the coefficients of digestibility. Also, we took into account the suggestions by Reynolds and Aebischer (1991) about how to apply the dietary method correctly, and the coefficients of digestibility used were taken from the above-mentioned publication. For lack of our own data on pine marten diet in the “clay” area after heavy logging we used the relevant data by Shamovich (2004) in the analysis.

To compare the overall dietary diversity (trophic niche breadth) we used the Levin's index B (Levins, 1968). The calculation was done for 28 food categories. So, B index varies from one (the narrowest niche) to 28, i.e. the maximum number of food categories used for calculations (the broadest niche possible). The simplified Morisita's index C_H (Krebs, 1998) was used to compare diets. The index varies between zero (exclusive niches) and one (complete overlap). According to value of this index, we formally fixed three levels of dietary overlap: 0–0.33 – rather small overlap; 0.34–0.66 – middling overlap; 0.67–1.0 – 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. Replicated goodness-of-fit test (G -statistic) was used to examine heterogeneity of

percentages and reveal statistical differences between two diet compositions (Sokal and Rolf, 1995).

Results

Red fox diet

Tables 1 and 2 summarise the data obtained on red fox diets in “clay” and “sandy” areas. The gained data were separated seasonally and for the habitat conditions of moderate and heavy logging.

“Clay” area, moderate felling: In the warm season, red foxes mostly relied on mammalian prey (57.3%OC, 73.4%BC). Birds, mammalian carrion and plant food made up a marked supplement to the diet (Table 1).

Table 1. Diets of red foxes in the warm and cold seasons in the ecologically rich woodland on clay top-grounds in relation to felling rate, Minsk and Smolevichi districts, Minsk region, central Belarus, 1995–2005.

Prey item	Before heavy logging (1995–1998)				After heavy logging (1999–2005)			
	Warm season		Cold season		Warm season		Cold season	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
Beetles	22.7	0.7	19.9	0.4	31.2	4.2	2.0	0.1
Other insects	–	–	–	–	0.8	0.1	–	–
Fish	–	–	–	–	–	–	–	–
Amphibians	–	–	–	–	–	–	–	–
Reptiles	–	–	–	–	0.5	0.4	–	–
Shrews	1.2	0.6	0.8	0.5	3.2	2.1	3.6	1.2
Mole	4.4	4.3	0.4	0.1	1.0	0.7	1.6	1.3
Hedgehogs	5.1	14.5	3.1	7.0	0.3	0.7	0.4	0.2
Bank vole	25.5	20.9	24.5	13.7	7.6	7.4	12.0	5.6
<i>Apodemus</i> mice	5.1	2.8	5.1	2.5	5.8	4.7	1.6	0.5
<i>Microtus</i> voles	5.1	3.4	7.0	4.0	20.6	29.4	37.2	45.8
Other rodent species	0.7	0.4	–	–	2.1	1.6	2.8	1.8
Beaver	–	–	–	–	–	–	–	–
Muskrat	0.1	0.2	–	–	–	–	–	–
Hares	4.4	12.8	8.2	22.7	1.8	5.1	4.0	10.0
Red squirrel	1.1	2.6	1.2	2.0	1.8	1.4	1.6	2.7
Mustelids	1.4	2.9	2.8	3.8	1.3	1.2	2.4	3.8
Wild and domestic canids	2.3	7.3	2.8	4.9	3.9	21.6	8.0	17.3
Young wild ungulates (carrion and hunted prey)	0.9	0.7	–	–	1.0	9.8	–	–
Carcasses of non-young wild ungulates	0.7	3.9	5.8	23.0	1.1	0.6	2.4	3.9
Livestock carrion	1.2	1.7	10.9	7.1	0.5	0.9	1.2	0.6
Small birds	5.1	7.1	2.3	2.4	3.2	2.6	1.6	0.5
Big and medium-sized birds	3.5	8.4	3.9	5.3	1.5	1.9	3.4	1.8
Bird eggs	1.4	0.1	–	–	–	–	–	–
Fruits	2.1	1.1	–	–	5.5	1.5	2.6	0.2
Seeds	2.8	2.2	0.8	0.4	1.8	0.8	3.2	0.7
Herbs	3.2	1.4	0.8	0.3	4.0	1.3	7.6	1.6
Honey	–	–	–	–	–	–	–	–
Number of scats analysed	204		126		248		144	
Number of food specimens recovered from the scats analysed	432		257		620		305	
Food niche breadth	7.42	9.79	7.57	7.14	6.45	7.77	5.81	3.14

%OC – percentage of frequency of various prey occurrence in the diet; %BC – percentage of food biomass consumed.

Table 2. Diets of red foxes in the warm and cold seasons in the ecologically poor woodland on sandy deposits in relation to felling rate, Polotsk district, Vitebsk region, northern Belarus, 1995–2005.

Prey item	Before heavy logging (1995–1999)				After heavy logging (2000–2005)			
	Warm season		Cold season		Warm season		Cold season	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
Beetles	15.4	0.2	2.1	0.1	23.0	3.3	12.4	0.1
Other insects	2.6	0.2	–	–	0.6	0.1	–	–
Fish	0.7	0.9	0.4	0.1	0.5	1.2	0.1	0.1
Amphibians	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Reptiles	6.8	1.1	7.2	1.1	0.2	0.3	0.6	0.7
Shrews	1.3	0.3	0.7	0.1	2.4	2.4	1.8	0.9
Mole	0.2	0.5	0.5	0.3	0.4	1.2	1.0	0.9
Hedgehogs	0.9	4.0	1.2	0.9	0.5	2.2	0.6	1.2
Bank vole	28.9	19.3	25.3	17.1	8.3	9.1	19.5	6.2
<i>Apodemus</i> mice	1.2	1.8	1.3	0.6	3.8	4.8	3.7	1.1
<i>Microtus</i> voles	2.1	4.6	4.9	3.7	37.6	25.0	24.4	23.0
Other small rodent species	0.4	1.2	0.3	0.4	1.3	1.4	1.4	1.2
Beaver	0.7	2.0	1.7	2.2	0.7	6.3	3.2	9.6
Muskrat	–	–	–	–	–	–	–	–
Hares	4.3	15.0	5.1	13.4	1.5	6.8	5.4	17.6
Red squirrel	0.2	0.6	0.8	0.5	0.6	0.9	0.8	1.7
Mustelids	0.4	1.9	1.0	0.8	0.9	0.8	2.3	4.2
Wild and domestic canids	0.2	0.5	2.9	4.0	1.6	15.0	4.0	12.1
Young wild ungulates (carrion and hunted prey)	1.7	4.8	–	–	0.7	1.4	–	–
Non-young wild ungulate carcasses	3.0	8.7	31.0	40.8	0.4	4.7	5.2	10.6
Livestock carrion	0.3	0.5	2.9	3.7	0.3	2.1	0.7	2.6
Small birds	2.7	1.7	1.0	0.2	2.1	2.4	2.2	1.9
Big and medium-sized birds	3.9	8.8	1.7	2.2	2.9	1.8	1.7	2.2
Bird eggs	0.6	0.2	–	–	0.1	0.1	0.5	0.1
Fruits	16.8	18.9	3.8	1.4	5.8	5.0	2.1	0.5
Seeds	–	–	0.3	0.1	0.9	0.6	1.6	0.5
Herbs	3.9	0.9	1.0	0.1	2.3	1.2	4.7	1.3
Honey	–	–	–	–	–	–	–	–
Number of scats analysed	234		359		348		241	
Number of food specimens recovered from the scats analysed	732		1436		1446		722	
Food niche breadth	6.69	8.40	6.11	4.07	8.73	10.13	7.89	8.41

%OC – percentage of frequency of various prey occurrence in the diet; %BC – percentage of food biomass consumed.

Among mammals taken by red foxes rodents prevailed, and their portion constituted 36.4%OC and 27.5%BC. The portion of bank voles *Myodes glareolus* was significantly higher than pooled portion of all other rodent species (%OC – 25.5 vs 10.9, $G=6.0$, $P=0.02$; %BC – 20.9 vs 6.6, $G=7.8$, $P<0.01$). Also, red foxes consumed medium-sized mammals a lot with major importance of hares (the snow hare *Lepus timidus* and brown hare *L. europaeus*) and the eastern hedgehog *Erinaceus concolor*.

Seasonally there were no any valuable differences (%OC – $C_H=0.93$; %BC – $C_H=0.71$) with the exception of higher portion of mammalian carrion taken in the cold season (%OC – 8.8 fold, $G=13.7$, $P<0.01$; %BC – 5.4 fold, $G=17.1$, $P<0.01$).

“Clay” area, heavy felling: Since felling was markedly intensified, red fox diet was found being changed (Table 1). The warm-season red fox diet differed significantly from

that, when forest exploitation was moderate (%OC – $C_H=0.46$, $G=61.5$, $P<0.001$; %BC – $C_H=0.37$, $G=84.6$, $P<0.001$). The main difference was in markedly pronounced changes in species structure of rodents consumed. Red foxes relied much more on *Microtus* voles (%OC – 4.0 fold, $G=10.0$, $P<0.01$; %BC – 8.6 fold, $G=23.6$, $P<0.01$), but less on bank voles (%OC – 3.4 fold, $G=10.2$, $P<0.01$; %BC – 2.8 fold, $G=6.7$, $P<0.01$). The consumption of *Microtus* voles prevailed over all other rodent species (%OC – 20.6 vs 15.5, insignificant; %BC – 29.4 vs 13.7, $G=5.9$, $P=0.02$).

In the cold season, many significant changes in the red fox diet were found too (%OC – $C_H=0.46$, $G=77.7$, $P<0.001$; %BC – $C_H=0.31$, $G=99.9$, $P<0.001$), and the felling-related dietary trend was nearly the same as in the warm season. Again, the marked increase was found in foraging for *Microtus* voles (%OC – 5.3 fold, $G=22.7$, $P<0.01$; %BC – 11.5 fold, $G=41.2$, $P<0.01$) and the

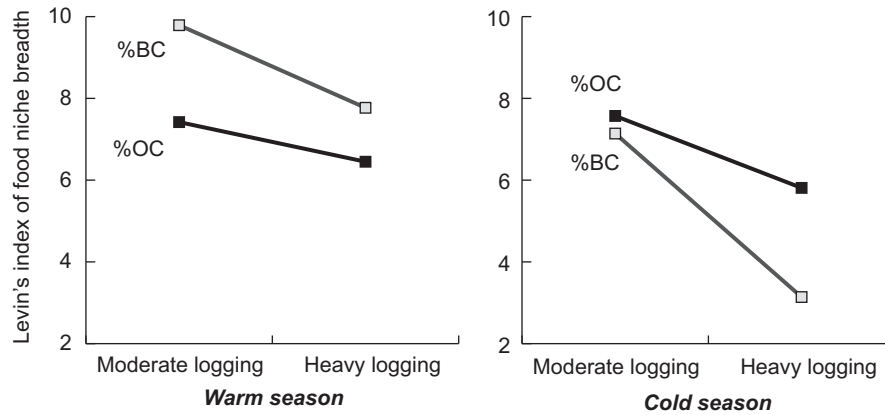


Fig. 1. Changes in food niche breadth of the red fox in relation to felling rate in the ecologically rich woodland on clay top-ground, Minsk and Smolevichi districts, Minsk region, central Belarus, 1995–2005. %OC – percentage of frequency of various prey occurrence in the diet; %BC – percentage of food biomass consumed.

consumption of this rodent group predominated over all other rodent species (%OC – 37.2 vs 16.4, $G=8.3$, $P<0.01$; %BC – 45.8 vs 7.9, $G=29.6$, $P<0.01$). Prevalent feeding of red foxes on rodents, first of all, *Microtus* voles, led to marked decrease in consumption of mammalian carrion, hares and eastern hedgehogs (Table 1). Since the logging rate was intensified, we did not find any significant seasonal differences neither in the dietary structure (%OC – $C_H=0.82$; %BC – $C_H=0.86$) nor in consumption of a particular food item.

A marked trend of food niche breadth decreasing was recorded (Fig. 1). The change was attributable to both seasons and to both dietary calculations, i.e. %OC and %BC.

“Sandy” area, moderate felling: In the warm season, mammals constituted a marked part of red fox diet (42.8%OC, 57.3%BC). In addition, diverse warm-season diet was substantially supplemented with fruits, mammalian carrion and birds. Other food categories were of a negligible importance – altogether only 3.6%BC. Among mammals rodents were the most important prey and constituted 32.6%OC and 26.9%BC. Bank voles were preyed by red foxes more frequently than all other small rodent species (%OC – 28.9 vs 3.7, $G=22.1$, $P<0.01$; %BC – 19.3 vs 7.6, $G=5.3$, $P=0.02$). Among medium-sized prey hares comprised a substantial part of the diet.

In the cold season, red fox diet markedly differed from that in the warm season (%OC – $C_H=0.63$, $G=57.2$, $P<0.01$; %BC – $C_H=0.58$, $G=54.4$, $P<0.01$). Evident absence of fruits in winter conditioned manifold decline in their consumption (Table 2). Conversely, the portion of mammalian carrion in the cold-season diet increased a lot: %OC – 10.2 fold ($G=29.0$, $P<0.01$) and %BC – 4.8 fold ($G=25.0$, $P<0.01$).

“Sandy” area, heavy felling: The warm-season differences in diets were statistically significant (%OC – $C_H=0.46$, $G=71.7$, $P<0.001$, %BC – $C_H=0.55$, $G=58.6$, $P<0.001$). Red foxes caught *Microtus* voles markedly more frequently

(%OC – 17.9 fold, $G=38.6$, $P<0.01$; %BC – 5.4 fold, $G=15.5$, $P<0.01$). This led to decline in consumption of other food items: bank voles, fruits, medium-sized and big birds and reptiles (Table 2).

Concerning the cold season, intensive felling caused marked changes in the red fox diet, too (%OC – $C_H=0.58$, $G=57.9$, $P<0.01$; %BC – $C_H=0.54$, $G=55.0$, $P<0.01$). Principally, the changes revealed were almost the same as in the warm season: increasing portion of *Microtus* voles (%OC – 7.0 fold, $G=24.9$, $P<0.01$; %BC – 6.2 fold, $G=15.5$, $P<0.01$), but decrease in taking other food items, such as mammalian carrion, bank voles, reptiles and others (Table 2).

With intensified felling seasonal differences in the red fox diet became negligible (%OC – $C_H=0.86$; %BC – $C_H=0.88$). Also, red fox diet was registered to be markedly more diversified (Fig. 2). The increase in food niche breadth was revealed for both seasons and both dietary calculations, i.e. %OC and %BC.

Pine marten diet

Tables 3 and 4 summarise the data on pine marten diets in “clay” and “sandy” areas. The data given were separated seasonally and for the habitat conditions of moderate and heavy logging.

“Clay” area, moderate felling: In the warm season, pine martens had quite diverse, but mammal-dominated diet (Table 3). Altogether mammalian prey constituted 50.1%OC and 54.8%BC. Birds also made a significant contribution to the diet (20.9%OC; 37.1%BC). Insects were frequently taken by pine martens, but their biomass consumed was relatively low (19.7%OC; 3.0%BC). Among mammals small rodents prevailed, and their portion constituted 30.4%OC and 26.2%BC. Medium-sized mammals (hedgehogs, red squirrels, hares and muskrats) altogether made up 16.3%OC and 25.1%BC. Portion of bank voles prevailed over all other

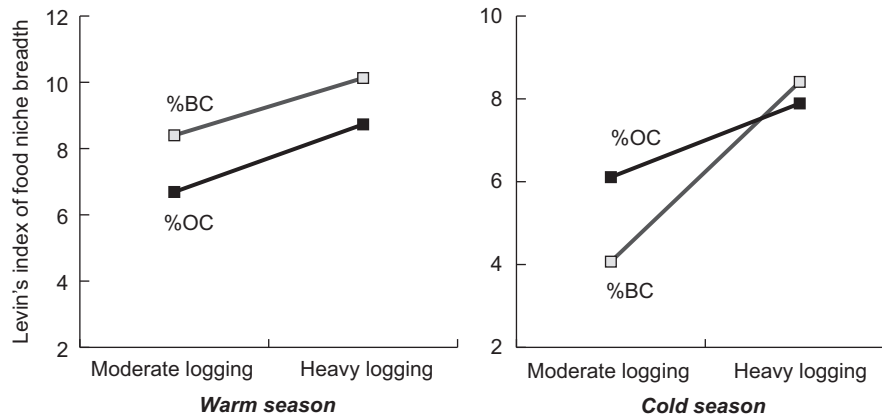


Fig. 2. Changes in food niche breadth of the red fox in relation to felling rate in the ecologically poor woodland on sandy deposits, Polotsk district, Vitebsk region, northern Belarus, 1995–2005. %OC – percentage of frequency of various prey occurrence in the diet; %BC – percentage of food biomass consumed.

small rodent species (%OC – 24.8 vs 5.6, $G=13.1$, $P<0.01$; %BC – 21.7 vs 4.5, $G=12.3$, $P<0.01$).

In the cold season, pine marten diet was similar to that in the warm season (%OC – $C_H=0.89$; %BC – $C_H=0.79$). Only the difference in consumption of birds was statistically significant (%OC – 3.0 fold, $G=7.2$, $P<0.01$; %BC – 2.6 fold, $G=10.6$, $P<0.01$).

“Clay” area, heavy felling: The pine marten diets before and after heavy felling differed significantly (%OC – $C_H=0.72$, $G=59.8$, $P<0.001$; %BC – $C_H=0.44$, $G=99.9$, $P<0.001$). The highest difference was registered in consumption of small rodents that was higher under the conditions of heavy logging (%OC – 1.7 fold, $G=5.3$, $P=0.02$; %BC – 2.7 fold, $G=21.0$, $P<0.01$). *Microtus* voles were taken much more frequently (%OC – 17.7 fold, $G=20.0$, $P<0.01$; %BC – 19.1 fold, $G=31.0$, $P<0.01$), *Apodemus* mice – slightly more (%OC – 2.2 fold, insignificant; %BC – 4.2 fold, $G=4.1$, $P=0.03$), whereas bank voles were consumed at the same level. Portions of birds (%OC – 34.8 fold, $G=20.9$, $P<0.01$; %BC – 61.8 fold, $G=41.6$, $P<0.01$) and medium-sized mammals (%OC – 18.1 fold, $G=14.2$, $P<0.01$; %BC – 31.4 fold, $G=25.3$, $P<0.01$) became much lower (Table 3).

In the cold season, felling-conditioned changes in the pine marten diet were not so pronounced, as in the warm season (%OC – $C_H=0.86$, $G=36.4$, $P=0.10$; %BC – $C_H=0.84$, $G=48.9$, $P=0.09$). Slightly higher consumption of small rodents (%OC – 1.6 fold, $G=4.5$, $P=0.03$; %BC – 1.6 fold, $G=5.0$, $P=0.03$) resulted from more frequent predation on *Microtus* voles (%OC – 22.9 fold, $G=17.0$, $P<0.01$; %BC – 12.8 fold, $G=17.9$, $P<0.01$) and *Apodemus* mice (%OC – 8.1 fold, insignificant; %BC – 13.6 fold, $G=4.7$, $P=0.03$). Medium-sized mammals were preyed less frequently (%OC – 4.6 fold, $G=8.1$, $P<0.01$; %BC – 5.2 fold, $G=17.4$, $P<0.01$).

Again, there were found no seasonal differences in the pine marten diet since heavy logging was undertaken (%OC – $C_H=0.94$, $G=26.8$, $P=0.53$; %BC – $C_H=0.90$, $G=13.6$, $P=0.98$).

Since logging rate was intensified Levin's index declined in the warm season, although in the cold season it did not changed significantly (Fig. 3).

“Sandy” area, moderate felling: In the warm season, pine martens had a diversified diet mostly relied on small rodents (18.3%OC; 23.5%BC), fruits (33.6%OC; 38.9%BC), birds (8.2%OC; 13.5%BC) and beetles (20.5%OC; 7.3%BC). Other food items played a supplementary role (Table 4). Bank voles predominated over all small rodents taken (17.3%OC; 21.5%BC).

In the cold season, pine marten diet differed significantly from that in the warm season (%OC – $C_H=0.32$, $G=88.4$, $P<0.001$; %BC – $C_H=0.27$, $G=99.9$, $P<0.001$) for the reason that it was dominating by mammalian carrion (51.8%OC; 61.2%BC). The consumption of carrion was markedly higher than that in the warm season (%OC – 37.0 fold; $G=60.8$, $P<0.01$; %BC – 21.1 fold; $G=65.2$, $P<0.01$). Rodents, birds and fruits were also fairly important food items (Table 4), but their consumption was lower than that in the warm season.

“Sandy” area, heavy felling: In the conditions of heavy logging we revealed significant changes in warm-season diet of pine martens (%OC – $C_H=0.75$, $G=45.7$, $P=0.02$; %BC – $C_H=0.55$, $G=64.9$, $P<0.001$). Portion of rodents increased (Table 4) due to higher consumption of *Microtus* voles (%OC – 54.5 fold, $G=10.1$, $P<0.01$; %BC – 16.6 fold, $G=6.3$, $P=0.02$) and *Apodemus* mice (%OC – 12.0 fold, $G=5.9$, $P=0.02$; %BC – 4.4 fold, $G=3.5$, $P=0.05$). Conversely, feeding on fruits declined (%OC – 2.2 fold, $G=7.1$, $P<0.01$; %BC – 5.1 fold, $G=23.5$, $P<0.01$).

As it was found before, seasonal differences in diet of pine martens under the conditions of heavy logging were quite pronounced (%OC – $C_H=0.63$, $G=43.6$, $P=0.03$; %BC – $C_H=0.58$, $G=45.6$, $P=0.02$). The main difference was much higher consumption of mammalian carrion in the cold season (%OC – 4.9 fold, $G=15.3$, $P<0.01$; %BC – 3.5 fold,

Table 3. Diets of pine martens in the warm and cold seasons in the ecologically rich woodland on clay top-grounds in relation to felling rate, Minsk and Smolevichi districts, Minsk region, central Belarus, 1995–2005.

Prey item	Before heavy logging (1995–1998)				After heavy logging (1999–2005) ^a			
	Warm season		Cold season		Warm season		Cold season	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
Beetles	19.7	3.0	29.5	6.0	31.0	6.5	21.0	3.6
Other insects	–	–	–	–	–	–	–	–
Fish	–	–	–	–	–	–	–	–
Amphibians	0.6	0.5	3.9	3.0	–	–	–	–
Reptiles	1.4	0.4	–	–	–	–	–	–
Shrews	1.4	0.5	0.8	1.5	1.5	1.9	1.9	1.6
Mole	2.0	3.0	–	–	1.6	1.7	0.4	0.5
Hedgehogs	4.5	5.9	1.6	5.9	–	–	–	–
Bank vole	24.8	21.7	31.0	35.7	23.9	37.3	27.1	33.6
<i>Apodemus</i> mice	3.4	2.0	0.8	0.5	7.6	8.3	6.5	6.8
<i>Microtus</i> voles	1.1	1.3	0.8	1.5	19.5	24.8	18.3	19.2
Other small rodent species	1.1	1.2	–	–	–	–	–	–
Beaver	–	–	–	–	–	–	–	–
Muskrat	1.1	2.5	0.8	3.3	–	–	–	–
Hares	6.5	12.7	3.1	7.6	–	–	1.8	4.3
Red squirrel	4.2	4.0	9.3	12.3	0.9	0.8	1.4	1.3
Mustelids	–	–	–	–	–	–	–	–
Wild and domestic canids	–	–	0.8	1.4	–	–	–	–
Young wild ungulates (carrion and hunted prey)	–	–	–	–	–	–	–	–
Carcasses of non-young wild ungulates	0.9	2.4	–	–	–	–	1.4	4.1
Livestock carrion	–	–	–	–	–	–	–	–
Small birds	20.3	35.1	7.0	14.2	0.6	0.6	11.0	17.9
Big and medium-sized birds	0.6	2.0	–	–	–	–	0.8	1.8
Bird eggs	–	–	3.1	0.6	–	–	0.2	0.1
Fruits	2.5	1.0	7.8	6.7	7.1	6.3	8.4	5.1
Seeds	–	–	–	–	–	–	–	–
Herbs	2.3	0.9	–	–	–	–	–	–
Honey	1.2	0.2	–	–	–	–	–	–
Number scats analysed	255		88		233		166	
Number of food specimens recovered from the scats analysed	355		129		472		327	
Food niche breadth	6.47	5.14	4.87	5.49	4.33	3.59	5.72	5.13

%OC – percentage of frequency of various prey occurrence in the diet; %BC – percentage of food biomass consumed.

^aData were taken according to Shamovich (2004).

$G=21.8$, $P<0.01$). In turn, portion of small mammals and birds decreased (Table 4).

In cold season, we did not find any significant dietary changes that might be connected with logging rate (%OC – $C_H=0.86$, $G=32.5$, $P=0.25$; %BC – $C_H=0.84$, $G=36.6$, $P=0.31$).

Since logging rate was intensified, diet of pine martens became more diversified, but it was evident in terms of %OC only (Fig. 4).

Food niche overlap between the red fox and pine marten

Before heavy logging dietary similarity between the red fox and pine marten did not varied considerably through

seasons and study areas (Table 5) and it was 0.83–0.89 for %OC and 0.67–0.88 for %BC. Since felling was intensified, diet overlap between the predator species became lower (%OC – 0.53–0.76; %BC – 0.40–0.51).

Discussion

In Belarus in transitional mixed woodlands, the red fox and pine marten, being both generalist predators and inhabiting the same habitat plots, are characterized by nearly the same opportunistic seasonal changes in feeding habits and consume the main food items in quite similar proportions (Sidorovich et al., 2005, 2006a). These features become especially intriguing if considering the fact that

Table 4. Diets of pine martens in the warm and cold seasons in the ecologically poor woodland on sandy deposits in relation to felling rate, Polotsk district, Vitebsk region, northern Belarus, 1995–2005.

Prey item	Before heavy logging (1995–1999)				After heavy logging (2000–2005)			
	Warm season		Cold season		Warm season		Cold season	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
Beetles	20.5	7.3	10.6	2.0	10.9	1.4	5.6	0.3
Other insects	–	–	–	–	–	–	–	–
Fish	–	–	–	–	–	–	–	–
Amphibians	0.2	0.01	–	–	0.3	0.02	–	–
Reptiles	9.6	2.7	10.0	3.5	1.0	0.7	1.4	0.1
Shrews	1.4	1.1	0.8	0.3	0.7	0.3	4.2	1.2
Mole	0.4	1.0	0.2	0.7	0.5	0.3	1.4	0.7
Hedgehogs	0.7	2.3	0.8	1.7	1.2	2.4	2.8	3.9
Bank vole	17.3	21.5	11.6	10.7	22.8	20.8	14.1	8.8
<i>Apodemus</i> mice	0.7	1.3	0.6	0.8	8.4	5.7	8.5	4.0
<i>Microtus</i> voles	0.2	0.5	0.1	0.2	10.9	8.3	5.6	3.2
Other small rodent species	0.1	0.2	0.2	0.5	–	–	–	–
Beaver	–	–	–	–	–	–	–	–
Muskrat	–	–	–	–	–	–	–	–
Hares	0.9	2.9	0.6	1.1	2.2	7.0	4.2	7.7
Red squirrel	0.4	1.0	0.8	1.3	1.2	1.4	2.8	2.3
Mustelids	–	–	–	–	–	–	–	–
Wild and domestic canids	–	–	–	–	–	–	–	–
Young wild ungulates (carrion and hunted prey)	–	–	–	–	–	–	–	–
Carcasses of non-young wild ungulates	1.4	2.9	51.8	61.2	5.5	14.2	26.8	50.2
Livestock carrion	–	–	–	–	–	–	–	–
Small birds	3.9	6.5	1.8	2.2	12.9	23.3	4.2	4.9
Big and medium-sized birds	4.3	7.0	1.8	3.0	0.7	2.0	–	–
Bird eggs	1.4	1.9	0.2	0.2	1.5	0.2	–	–
Fruits	33.6	38.9	6.3	9.2	15.2	10.6	18.3	12.7
Seeds	–	–	–	–	–	–	–	–
Herbs	1.3	0.8	1.2	0.2	2.5	1.3	–	–
Honey	1.7	1.2	0.6	1.2	1.5	0.3	–	–
Number scats analysed	344		204		283		51	
Number of food specimens recovered from the scats analysed	837		490		403		71	
Food niche breadth	6.80	7.86	3.27	2.54	7.82	7.74	6.84	3.46

%OC – percentage of frequency of various prey occurrence in the diet; %BC – percentage of food biomass consumed.

population biomass of both predator species is at relatively high level among carnivores and birds of prey (Jędrzejewska and Jędrzejewski, 1998; Sidorovich et al., 2008c). According to Sidorovich et al. (2006b), fairly high dietary overlap between the red fox and pine marten was recorded across the variety of habitats with different carrying capacity and seasons – from 0.54 to 0.95, on average 0.74, estimated by Pianka's index. Therefore, the revealed divergence of food niches of the red fox and pine marten initiated by intensified felling and its ecological consequences is worthwhile considering in detail. According to the dietary data obtained (Tables 1–4), the increased feeding dissimilarity resulted from many changes in consumption of various food items. Among the main felling-related differences between the species diets the following features can be mentioned. First, the increase in consumption of *Microtus* voles by red foxes was higher than that by pine martens. Second, despite felling-related changes in rodent community in woodlands

(Sidorovich et al., 2008a) pine martens continued feeding on bank voles a lot, while the prey portion in red fox diet declined. Third, with the intensified felling rate pine martens began exploiting *Apodemus* mice more, whereas this was not observed in the red fox.

We hypothesize that the dietary dissimilarity found between the red fox and pine marten in forest ecosystems influenced by heavy logging (Table 5) was associated with the increased environmental heterogeneity. Intensified clear cutting creates a higher portion of openings in woodlands. Increased species diversity and biomass of rodent species in recent clearcuts was shown for many European countries (Hansson, 1978; Wołk and Wołk, 1982; Kirkland et al., 1985; Carey and Johnson, 1995; Aksenova and Bulyuk, 1986; Bryja et al., 2002; Fuller et al., 2004), as well as for transitional mixed woodlands in northern Belarus (Sidorovich et al., 2008a). Red foxes adopt the increased food base

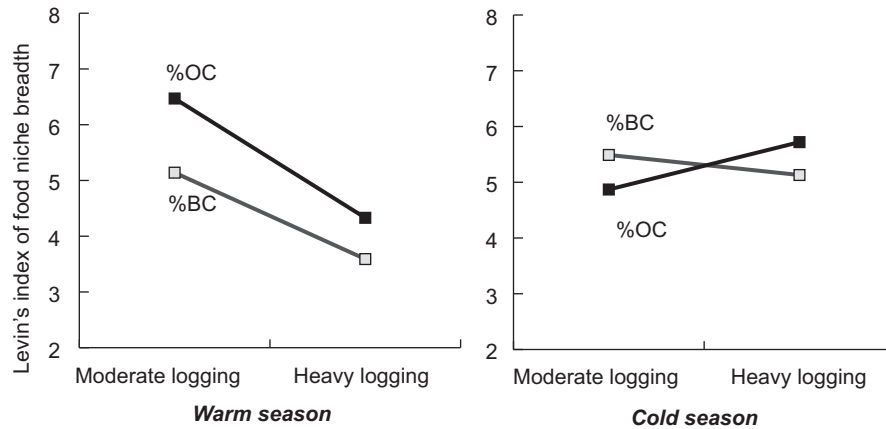


Fig. 3. Changes in food niche breadth of the pine marten in relation to felling rate in the ecologically rich woodland on clay top-ground, Minsk and Smolevichi districts, Minsk region, central Belarus, 1995–2005. %OC – percentage of frequency of various prey occurrence in the diet; %BC – percentage of food biomass consumed.

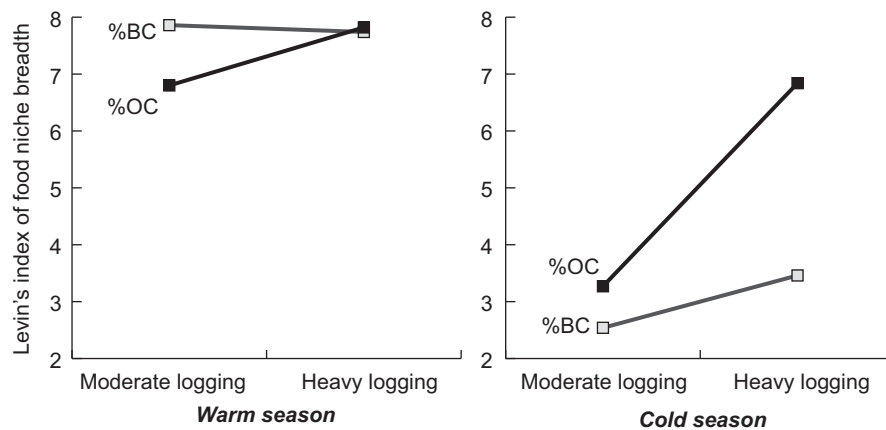


Fig. 4. Changes in food niche breadth of the pine marten in relation to felling rate in the ecologically poor woodland on sandy deposits, Polotsk district, Vitebsk region, northern Belarus. %OC – percentage of frequency of various prey occurrence in the diet; %BC – percentage of food biomass consumed.

Table 5. Dietary overlap (estimated by Morisita's index, C_H) between the pine marten and red fox in the warm and cold seasons in “clay” area (central Belarus) and “sandy” area (northern Belarus) in relation to felling rate.

Morisita's index (C_H)	Before heavy logging (1995–1999)				After heavy logging (2000–2005)			
	Warm season		Cold season		Warm season		Cold season	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
“Clay” area	0.89	0.67	0.83	0.50	0.76	0.42	0.64	0.48
“Sandy” area	0.86	0.78	0.84	0.88	0.60	0.51	0.53	0.40

%OC – percentage of frequency of various prey occurrence in the diet; %BC – percentage of food biomass consumed.

promptly by foraging widely in clearcuts (Virgos et al., 2002; Sidorovich et al., 2008a). Perhaps, red foxes are attracted to clearcuts not only by higher numbers of rodents, but also by appearance of *Microtus* voles that are easier to catch. *Microtus* voles are characterized by less advanced escape-tactics compared to *Apodemus* mice and the bank vole (Jędrzejewski and Jędrzejewska,

1993b; Jędrzejewska and Jędrzejewski, 1998). No doubts, higher numbers of rodents in clearcuts favor pine martens too, as the predator species tends to consume rodents in high proportions throughout the range (e.g. Jędrzejewski et al., 1993a; Zalewski et al., 1995; Pulliainen and Ollinmäki, 1996; Lanszki et al., 1999; Baltrūnaitė, 2001). Nevertheless, there are several

factors that seemingly limit pine martens to forage frequently in clearcuts. First, there is an increased risk of predation from bigger predators, for instance, numerous red foxes (Pulliainen, 1981; Lindström et al., 1995) and several species of avian predators (Korpimäki and Norrdahl, 1989), as it was also described for northern Belarus (Sidorovich et al., 2008a). In a forest pine martens can climb on trees in search for shelters escaping from larger carnivores, while in a clearcut the only place to hide is under suitable tree remnants, from where they could be driven out larger carnivores. Then, pine martens are often limited to forage in clearcuts in winter. Usually snow cover in clearcuts has a harder surface than in forests. This originates mainly from faster melting of snow cover surface during short-term thaw, which then freezes with frost returning. Also, it may be caused by a stronger wind in openings that compacts snow cover surface. Moreover, snow cover in clearcuts is deeper than that under forest canopy. In turn, deeper snow cover with commonly hard surface makes foraging of subniveal rodents by pine martens too difficult (Hargis, 1982; Steventon and Major, 1982; Bissonette et al., 1988; Jędrzejewska and Jędrzejewski, 1998).

Our study on the influence of felling on red fox and pine marten diets was designed to include woodlands on both clay soil and sandy deposits (Solovej et al., 2003). We did not pay much attention to analyzing differences in diets of each predator species in woodlands on clay and sandy top-grounds, as it was already described (Sidorovich et al., 2005, 2006a). Concerning the woodlands differed in habitat carrying capacity, we only aimed to answer the question are differences in dietary response to felling between the localities. The results suggest that there is no such a difference. In both woodlands on clay and sandy soils we found the same more or less pronounced dietary shift directed towards the higher consumption of rodents, especially *Microtus* voles. The changes in feeding of red foxes and pine martens were well-related with the registered increase in *Microtus* vole numbers and total number of rodents in felling areas (Sidorovich et al., 2008a). The revealed changes in food niche breadths of red foxes and pine martens that were different in the woodlands on clay and sandy top-grounds may be explained as follows. In the ecologically rich woodland on clay soil, since logging became heavy, initially diverse diets of both species appeared to be narrower due to tighter specialization in feeding on rodents. In the ecologically poor woodland on sandy deposits, intensified felling led to increase in woodland heterogeneity and seemingly caused more diversified prey supply, although it was initially species-poor (Solovej et al., 2001, 2003).

There are still two pressing questions that were not investigated within the study. First, after intensive logging the revealed dietary shifts in the red fox and

pine marten do not seem to be long-term and, perhaps, would last for 10–15 years. Then, the red fox and pine marten would plausibly face a decline of their food base in the extending young forests that appear in huge logging areas, and the predator species diets would shift again. The preliminary data on rodent numbers in young forests suggest a sharp decline in the prey. So, the positive trend in rodent community initiated by felling and respective changes in predator ecology (Sidorovich et al., 2008a) seem to be short-term. Then, in the conditions of medium-aged successional small-leaved forests rodents, first of all, bank vole grow in number again up to the level that is attributable to mature coniferous forest (Sidorovich et al., 2005).

The second pressing question concern the potential absence of the mentioned positive trends in rodent community and respective changes in predator ecology in the conditions of broad-leaved forests. Indeed, in coniferous forest initially having a poor floor food supply for rodents is getting richer after logging due to appearance of a diverse grass layer. Broad-leaved forests and their clearcuts are usually both inlaid with a lush grass cover. Seed crop in coniferous forest is poorer than in broad-leaved forest. Logging of broad-leaved forests usually impairs seed crop production for a long time. So, perhaps in broad-leaved forest logging immediately leads to decline in food supply for rodents, and therefore, potentially their numbers would decrease. Therefore, the dietary response of pine martens and red foxes to felling may be very different in broad-leaved forests as compared to results of this study.

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