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Landscape-related differences in diet, food supply and distribution pattern of the pine marten, *Martes martes* in the transitional mixed forest of northern Belarus

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A b s t r a c t . The dietary structure and distribution patterns in pine martens *Martes martes* in situations of different food supply in the coniferous forest of north-eastern Belarus were investigated. A total of 1222 scats were analysed, and snowtracking of pine martens was done each winter. Seven pine martens were radiotracked (n=7549 radiolocations). Abundance of the main prey was monitored. The pine marten acts both as an active predator, mostly taking many species of rodents and birds, and as a gatherer, feeding on fruits and scavenging for carrion. In the ecologically poor woodland on sandy soil the predator specializes in feeding on carrion in the cold season, and on berries in the warm season. The richer food supply in the woodland on clay soil results in a markedly higher population density and fairly even distribution of pine martens than those in the woodland on sandy soil, where pine martens mainly live in valley habitats. The winter density of bank voles drives the pine marten numbers. Also biomass of carrion is a crucial factor determining the predator density by late winter.

Key words: pine marten, *Martes martes*, feeding ecology, population dynamics, Belarus

Introduction

Ecological studies on the pine marten *Martes martes*, investigating feeding habits, dietary composition, habitat use and population density, have been reported for many regions of Europe, including boreal coniferous woodland and more southern broad-leaved deciduous forest (N a s i m o v i c h 1948, L o c k i e 1961, G e p t n e r & N a u m o v 1967, D a n i l o v & T u m a n o v 1976, M o r o z o v 1976, G o s z c z y ń s k i 1986, M a r c h e s i & M e r m o d 1989, S t o r c h et al. 1990, J ę d r z e j e w s k i et al. 1993, Z a l e w s k i et al. 1995, P u l l i a i n e n & O l l i n m ä k i 1996, J ę d r z e j e w s k a & J ę d r z e j e w s k i 1998, L a n s z k i et al. 1999 and references therein). Only two studies have analysed pine marten diets in the extended transitional mixed forest (S i d o r o v i c h et al. 2000, B a l t r ū n a i t ė 2003). Our 2000 recent paper only partly concerns the pine marten, being mostly directed at the influence of the raccoon dog on the forest generalist guild. Food composition of pine martens in relation to prey diversity and supply was investigated by J ę d r z e j e w s k i et al. (1993), Z a l e w s k i et al. (1995), P u l l i a i n e n & O l l i n m ä k i (1996), and J ę d r z e j e w s k a & J ę d r z e j e w s k i (1998). Population density, distribution pattern, and habitat use by pine martens have also been well studied (N a s i m o v i c h 1948, G e p t n e r et al. 1967, D a n i l o v & T u m a n o v 1976, P u l l i a i n e n 1981, S t o r c h et al. 1990, J ę d r z e j e w s k i et al. 1993, Z a l e w s k i et al. 1995, J ę d r z e j e w s k a & J ę d r z e j e w s k i 1998, L a n s z k i et al. 1999, S i d o r o v i c h et al. 2000, B a l t r ū n a i t ė 2003 and references therein), but data from the region of transitional mixed forests are rather scanty. Habitat selection and population density of pine mar-

tens were shown to be connected with diet composition and food abundance (S t o r c h et al. 1990, J ę d r z e j e w s k i et al. 1993, Z a l e w s k i et al. 1995, J ę d r z e j e w s k a & J ę d r z e j e w s k i 1998, B a l t r ū n a i t ė 2003).

The main goal of the present study on the pine marten in northern Belarus was to analyse the species diet, density and spatial distribution in relation to the seasonal and landscape differences in food supply. The secondary aim was to provide detailed data on the pine marten ecological niche in the conditions of European transitional mixed forest.

Study Area

The studies were conducted in fairly natural landscapes of northern Belarus, where manmade habitats (agricultural fields, villages and others) constituted only 8–14% of the total. The region belongs to the extended transitional woodland of the European forest zone. The transitional forest is located between the more southern deciduous and the boreal coniferous forest zones. Only spruce *Picea abies* and pine *Pinus sylvestris* are present among coniferous trees. Black alder *Alnus glutinosa*, grey alder *A. incana*, birches *Betula pendula*, *B. pubescens*, and aspen *Populus tremula* are the most common deciduous trees.

The data were collected in two areas substantially differing in landscape structure. Composition of the surface ground deposits of the last glaciation result in considerably different carrying capacity of the habitats (S i d o r o v i c h et al. 2003, S o l o v e j et al. 2003). The first study area, Gorodok, is situated on the upper reaches of the Lovat river (Gorodok district, Vitebsk region, NE Belarus, 55°°N, 31°°E) and had an area of approximately 300 km^2. There is much clay in the surface ground deposits, resulting in a good water supply and abundant trace elements, producing a rich soil (hereafter "clay" area). Plant communities in the "clay" area have high species diversity and productivity, and habitats with high carrying capacity for herbi-

Table 1. Proportions (%) of the main habitat types in the Gorodok study area ("clay" area) and the Polotsk study area ("sandy" area), northern Belarus, 2000.

Habitat type	Gorodok study area		Polotsk study area*	
	in the whole	in the woodland	in the whole	in the woodland
Dry land pine stand and other wood dominated by pine	4	10	59	60
Wood dominated by spruce	20	23	4	2
Succession deciduous (mostly small-leaved) wood	19	21	3	5
Black alder swamped wood	12	16	<1	<1
Pine bog	4	5	16	19
Water-land ecotone	<1	<1	<1	<1
Aquatic ecosystem	3	3	7	7
Grassy marsh	8	7	<1	<1
Dry meadow	16	11	2	<1
Agriculture field, people settlement and others	13	<1	5	<1
Recent clearcut	1	3	3*	6*

Denotation: * – at present in the Polotsk study area after the intensive felling in 2001–2003 the proportion of recent clearcuts became markedly higher and they compound about a third part of the woodland

vores dominate. Forest types, characterised by abundant and diverse vegetation (such as mature forests dominated by spruce, medium-aged deciduous forests consisting of grey alder, birches and aspen, and black alder swamps) made up about 51% in the landscape structure (Table 1).

The second study area, Polotsk (Polotsk district, Vitebsk region, central north of Belarus, 55°°N, 29°°E), was approximately 250 km^2. The surface ground deposits consist of sand only (hereafter "sandy" area), with clay only in the valleys of glacial lakes and rivers. The soils of the area are very barren and dry. Therefore, the woodland is dominated by pine stands with a very poor ground vegetation, which comprise about 60% of the forest on dry land and 19% in raised bogs (Table 1).

Material and Methods

A total of 1222 pine marten scats were analysed from which 3095 prey individuals and other food objects (presence of fruits, seeds and herbs) were recovered. The scats were collected over a period of seven years (1995–2001) in the "clay" area and during five years (1995–1999) in the "sandy" area. The data obtained were divided into the cold season (November–March) and the warm season (April–October). The majority of scats were found on pine marten tracks or known latrines. Mammal identification was based on: (1) teeth and jaw remnants of small mammals according to P u c e k (1981); (2) ten randomly taken hairs from each scat microscopically determined according to D e b r o t et al. (1982). Insects were distinguished by the remains of exoskeleton, birds by feathers and bones, amphibians by bones, reptiles by bones and skin scales (M ä r z 1987, J e d r z e j e w s k a & J e d r z e j e w s k i 1998). Plant material was merely recorded as food consumed, if much of that was found in a scat analysed. Dietary composition of pine martens was determined as follows. The number of different prey individuals and other food objects found in all the scats analysed was taken as 100% for calculating of frequency percentages of various prey occurrence in the diet (%OC). The remains of plant matter of a particular kind (fruits, seeds or herbs) in a given scat was taken as one occurrence. To obtain the percentage of food biomass consumed (%BC), we followed J ę d r z e j e w s k a & J ę d r z e j e w s k i (1998) based on coefficients of digestibility, i.e. the ratio of fresh weight of a given food item to the dry weight of its remains in scats. To compare the overall dietary diversity (food niche breadth) in different feeding conditions, B index (L e v i n s 1968) was used. The calculation was done for 21 food categories, so B could vary from 1 (the narrowest niche) to 21, i.e. the maximum number of food categories used for calculations (the broadest niche possible). Pianka's index (P i a n k a 1973) was used to evaluate the overlap in diets in different feeding conditions.

Small mammal abundance was estimated in variety of the main habitats in the woodlands by snap trapping. Fried bread was used as bait. From 20 to 50 snap-traps were set at approximately 5 m intervals for three days and checked daily. In total, we obtained data from about 21,000 snap-trap nights.

Habitat use by pine martens was studied by radiotracking. Seven pine martens were radiotracked between May 1996 and February 2001 in the "clay" area. The total number of radiolocations constituted 7549, and for each individual it varied from 901 to 1423 fixes. One fix was chosen to last 15 minutes or less if the location or activity type changes during shorter time. Independent data were obtained by choosing at random one active fix and one inactive fix per session of radiotracking of a given individual. Usually we used from one to seven radiotracking sessions per working day. Receivers were provided by Telonics Inc. (Mesa, Arizona), and radio-collars were made by Biotrack Ltd. (Wareham, UK). Pine martens were

caught in wooden box-traps. The captured pine martens were immobilised by injection of Vetalar, then radiotagged and released in the place of capture. In both the "clay" and "sandy" areas, habitat selection by pine martens was additionally investigated by snowtracking, i.e. by following trails and recording their length in different biotope types. Predator activity was linked with habitat variety. The total number of independent fixes was taken as 100% for calculations of percentages of frequency of various habitat selection by pine martens. As to similar snowtracking data, we computed a percentage of the pooled length of pine marten trail parts in each biotope type from the total trail length snowtracked.

Abundance of pine martens was only studied in winter (as the harshest seasonal period) by means of trail counts on standard routes. We did such a track survey twice each winter, in the beginning of the snowy period (usually by late November or early December) and in the end of snowy period (usually in March) during twenty winters (1984–2004) in the "clay" area and seven winters (1997–2004) in the "sandy" area. The occurrence of pine marten trails, while going by a standard route, was used as a proxy of the species abundance. Abundance index of pine martens was calculated as the number of the species trails crossing our route divided by the number of kilometres inspected and the number of days passed since the last snowfall. As a result of the calculations, we obtained the average number of trails per 1 km transect per day. The survey routes were located across the whole diversity of habitats such as forest types, river valley, glacial lake shore, various marshes, and raised bog. Based on the data obtained by trail counts, the pine marten density was estimated by Priklonsky's formula (Priklonsky 1965), which was adapted to the habitat conditions of northern Belarus by using estimates of the daily movement distance of pine martens in the conditions of different snow cover. Daily movement distance was assessed by combining snowtracking and radio-tracking as recommended by Zalewski et al. (1995).

Similarly, by means of trail counts the abundance indexes of hares and wild ungulates were evaluated. Also, on established standard routes, we visually censused overwintering perching birds in a transect of 50m wide. It was necessary, because hares and perching birds are also prey of pine martens, and carrion from wild ungulate carcases (in particular by late winter) is frequently used by the predator (Sidorovich et al. 2000).

The data on occurrence of different habitat types (hereafter called as landscape structure) was obtained on the established itineraries located in randomly chosen directions and covered much of the study areas. The route length was about 10 km. The total length of such routes made up 217 km for both study areas.

Statistical analysis of the data obtained was done using Spearman correlation, r_s, t-test of the difference between two means, and G-test for homogeneity of percentages (Sokal & Rohlf 1995). Ivlev's selectivity index (D, modified by Jacobs (1974)) was calculated for the habitats used and rodents consumed.

Results

Landscape and habitat – related differences in food supply: small mammals, hares, perching birds and wild ungulate carrion

The bank vole was the most common micromammalian species which occupied all types of forest and other habitats in the woodlands of both study areas. In the post-reproductive period in autumn, bank voles constituted 70 and 82% of the small mammal community in

the woodlands of the "clay" and "sandy" areas, respectively. In terms of abundance, in forest habitats a secondary micromammalian prey of pine martens might be *Apodemus* which were common too, while *Microtus* voles inhabited forest biotopes rarely. Bank voles and *Apodemus*, and small mammals as a whole, were markedly commoner in spruce woods compared with pine stands (S i d o r o v i c h et al. 2003). Moreover, in all habitat types small mammals attained higher densities in the "clay" area compared to that in the "sandy" area (Table 2). The weighted-mean abundance of small mammals was about ten-fold higher in the "clay" than in the "sandy" area (27.1 versus 2.8 inds/100 snap-trap-nights). Concerning the bank vole only, its weighted-mean abundance was respectively about eight-fold higher (19.0 versus 2.3 inds/100 snap-trap-nights). The greater difference in the weighted-mean abundance of small mammals between the woodlands of the "sandy" and "clay" areas compared to such differences for each wood type appeared due to pine stands, with a low density of small mammals predominated (about 79%) in the "sandy" area, while they were not so common (only 8%) in the woodland in the "clay" area (Table 1). Conversely, in the "clay" area patches of open grasslands such as fragments of grassy marshes and dry meadows in glades were rather common (totally about 18% of the woodland area), and were inhabited by *Microtus* voles (Table 2), whose density was high in years of population outbreaks.

Seasonal and between-year variations in small mammal abundance was recorded in the study areas (S i d o r o v i c h et al. 2003). The bank vole population had only seasonal fluctuations with no recurrent cycles of outbreaks and crashes (Fig. 1). *Apodemus* tend to show the same pattern of population dynamics as the bank vole (S i d o r o v i c h et al. 2003). So, the species structure of the forest community of small mammals in northern Belarus is quite stable in the multiannual scale.

Table 2. Landscape and habitat-related differences in small mammal community by mid autumn (post-reproductive period) in the transitional woodlands of northern Belarus, 1996–2001. Number of individuals captured per 100 snap-trap-nights is used as an indicator of small mammal abundance, n – number of plots investigated, min - max (n)
mean ± SD (SE).

Main habitat types in woodlands	"Clay" area	"Sandy" area	Significance of difference, t (P)
Dry land pine stands older than 60 years	2.0 - 41.3(22) 18.43 ± 10.86(2.32)	0 - 6.9(17) 1.98 ± 2.29(0.56)	6.91(0.001)
Forest types dominated by spruce older than 60 years	4.6 - 49.3 (24) 21.8 ± 12.89(2.63)	2.2 - 13.9 (16) 7.70 ± 4.28(1.07)	4.96(0.001)
Medium-aged deciduous (mostly small-leaved) woods	12.2 - 41.3 (13) 26.67 ± 9.42(2.61)	1.2 - 14.1 (8) 8.62 ± 3.97(1.40)	6.09(0.001)
Black alder swamped woods	7.8 - 20.6(7) 15.07 ± 5.81(2.19)	no data	–
Patches of grassland located among forest (dry meadow on glade and grassy marsh)	10.7 - 50.9(28) 39.21 ± 8.15(1.54)	2.7 - 19.8(8) 9.42 ± 4.96(1.75)	12.76(0.001)
Ecotones between forest and open grassland	11.8 - 49.5(19) 38.32 ± 9.7(2.22)	1.7 - 22.5(11) 9.26 ± 9.54(2.87)	7.99(0.001)
Forested river banks	23.4 - 52.8(10) 41.40 ± 7.13(2.26)	9.2 - 39.2(10) 28.75 ± 6.97(2.21)	4.01 (0.001)

The other prey categories which might be important when comparing food supply for pine martens in the "sandy" and "clay" areas, were small perching birds, hares and wild ungulates

which supplied carrion. Weighted means of these prey abundances were markedly higher in the "clay" area than in the "sandy" area: small perching birds – 3 fold, hares – 11 fold, wild ungulates – 14 fold. In the "sandy" area all these prey as well as rodents were more densely distributed at streams and glacial lakes which are normally surrounded by ecologically rich woods dominated by spruces or/and black alders and having grassy marsh strips in the floodplains. There, the weighted mean of abundance index of small rodents was 13 fold higher than in other segments of the woodland with a prevalence of pine stands; small perching birds – 42 fold higher, hares – 289 fold higher, wild ungulates – 346 fold higher. In the "clay" area all these prey were much more evenly spaced due to higher heterogeneity of the woodland and wide spreading of the habitats with fairly high carrying capacity (S o l o v e j et al. 2003).

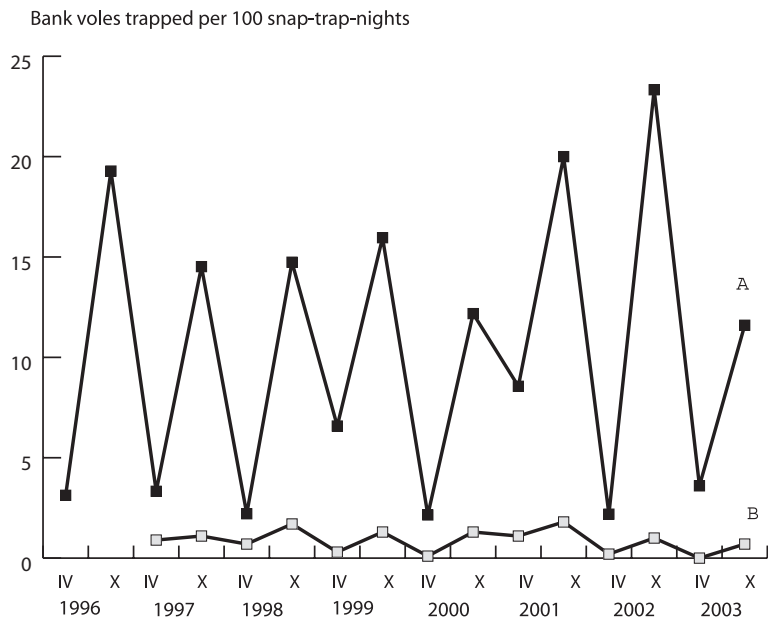

Fig.1. Population dynamics of the bank vole (A) in the spruce forests of the „clay" area and (B) in the pine forests of the „sandy" area, northern Belarus, 1996–2003.

Landscape–related difference in the pine marten diet

In the "clay" area during the warm season, pine martens had a diverse diet and the food niche was relatively broad (Table 3). This predator mostly relied on mammalian prey (34.3%OC, 47.7%BC). Also birds (17.3%OC, 25.1%BC) as well as berries and other plant food (25.3%OC, 13.6%BC) made up a major supplement to the diet. Other food items (insects, amphibians, reptiles, carrion and honey) were less important – totally 7.9%BC (Table 3). Among mammals, small rodents were prefered prey and constituted 27.9%OC and 37.3%BC, whereas shrews, though numerous, were taken rarely (2.7%OC). Moles, hedgehogs, red squirrels, hares, and muskrats totally made up only 8.9%BC. The bank vole constituted 77.8% of the rodents preyed upon by pine martens, comprising almost a third of the total food biomass consumed (27.5%BC). *Microtus* voles, *Apodemus* mice, water voles, and other rodent species were less frequent in the pine marten diet – totally 6.2%OC. However, when compared to the rodent community structure in woodland, we did not find any notable selectivity for rodent species by

pine martens in a given situation i.e. the "clay" area during the warm season (D index from -0.13 to 0.11) as well as in any other combinations of seasons and landscapes (D=-0.35–0.36).

In the "clay" area in the cold season diet of pine martens was slightly different from that in the warm season (Table 3; Pianka's index =0.78 for %OC and 0.85 for %BC). The increase in feeding on carrion was statistically significant (7.0 fold, G=10.2, P<0.01 for %OC; 3.8 fold, G=9.9, P<0.01 for %BC), whereas the consumption of birds decreased (2.8 fold, G=5.5, P=0.02 for %OC; 3.0 fold, G=8.7, P<0.1 for %BC).

In the "sandy" area in the warm season, the pine marten mostly fed on rodents (18.3%OC, 23.5%BC) and berries (31.4%OC, 37.8%BC). Compared to the "clay" area it consumed berries in significantly higher proportions (3.4 fold, G=13.4, P<0.01), while birds (8.2%OC, 13.5%BC versus 12.9%OC, 19.0%BC) as well as rodents and other mammalian prey (totally 22.1%OC,

Table 3. Diets (%OC, %BC) of pine martens in the warm and cold seasons in the "clay" and "sandy" areas, northern Belarus, 1995–2001.

Prey item	"Clay" area				"Sandy" area			
	Warm season		Cold season		Warm season		Cold season	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
Insects	14.6	3.2	16.4	4.8	20.5	7.3	10.6	2.0
Amphibians	1.5	0.7	1.2	0.6	0.2	0.01	–	–
Reptiles	1.7	1.3	2.5	1.1	9.6	2.7	10.0	3.5
Mole	1.9	2.8	1.3	2.0	0.4	1.0	0.2	0.7
Hedgehogs	0.4	1.5	0.7	2.0	0.7	2.3	0.8	1.7
Soricids	2.7	1.5	6.9	4.1	1.4	1.1	0.8	0.3
Bank vole	21.7	27.5	20.1	30.2	17.3	21.5	11.6	10.7
Apodemus mice	3.0	4.4	5.3	7.0	0.7	1.3	0.6	0.8
Microtus voles	1.9	2.5	2.7	3.4	0.2	0.5	0.1	0.2
Other rodent species	1.3	2.9	3.1	4.0	0.1	0.2	0.2	0.5
Red squirrel	0.9	2.6	1.9	4.3	0.4	1.0	0.8	1.3
Hares	0.4	1.6	0.3	1.1	0.9	2.9	0.6	1.1
Muskrat	0.1	0.4	–	–	–	–	–	–
Carrion of mammals (wild ungulates, beaver etc.)	2.0	5.7	14.1	21.6	1.4	2.9	51.8	61.2
Small bird species	9.9	12.2	3.3	3.9	3.9	6.5	1.8	2.2
Big and medium-sized bird species	3.0	6.8	2.5	4.0	4.3	7.0	1.8	3.0
Bird eggs	4.4	6.1	0.4	0.5	1.4	1.9	0.2	0.2
Mountain ash berries	5.7	4.2	11.2	10.3	4.2	7.0	4.1	6.1
Cranberries	–	–	1.2	0.7	0.8	1.3	1.8	2.2
Blue berries	14.1	5.9	–	–	24.1	24.0	–	–
Other berries	3.2	1.1	–	–	2.3	3.5	–	–
Apples	1.9	2.4	0.8	1.4	2.2	3.1	0.4	0.9
Herbs	0.4	0.01	1.8	0.1	1.3	0.8	1.2	0.2
Honey and other bee material	3.3	2.7	1.3	1.0	1.7	1.2	0.6	1.2
Number scats analysed	431		243		344		204	
Number of food specimens recovered from the scats analysed	1164		604		837		490	
Food niche breadth	9.10	8.65	8.70	7.02	6.80	7.86	3.27	2.54

Denotation:
%OC – frequency of prey occurrence in the diet expressed in %;
%BC – ratio of prey biomass consumed expressed in %.

30.8%BC versus 34.3%OC, 47.7%BC) were less often taken by the predator. Also, the frequency of occurrence of insects and reptiles in the diet was markedly higher in the "sandy" area (Table 3). Among small rodents, bank voles dominated pine marten diet (94.5% of the rodents preyed), and the prey species constituted about one fifth of the food biomass consumed (21.5%BC). Other rodent species comprised only a small part of the predator diet (2.0%BC). The food niche breadth was essentially lower than in the "clay" area (6.8 versus 9.1), but the diet composition was rather similar (Pianka's index =0.90 for %OC and 0.80 for %BC).

During the cold season, in the "sandy" area, the pine marten diet differed from that in the warm season (Pianka's index =0.29 for %OC and 0.24 for %BC). The food niche became fairly narrow – 3.27 for %OC and 2.54 for %BC, because the diet was dominated by mammalian carrion (51.8%OC and 61.2%BC). The consumption of carrion was significantly higher than in the "clay" area ($G=12.4$, $P<0.01$). The main source of carrion was carcases of wild ungulates (about 84%). Also, rodents (12.2%BC), birds (5.2%), and berries (8.3%) were fairly important food items of pine martens. Insects and reptiles (mainly beetles and lizards) were quite frequently taken by the predator (respectively 10.6 and 10.0%OC), but they constituted only 5.5%BC. In the cold season the pine marten diets were fairly different in the "sandy" and "clay" areas (Pianka's index =0.67 for %OC and 0.69 for %BC). The main differences were: smaller share of rodents in the "sandy" area (2.5 fold for %OC, $G=8.7$, $P<0.01$ and 3.7 fold for %BC, $G=20.4$, $P<0.01$), and higher consumption of carrion there (3.7 fold for %OC, $G=23.3$, $P<0.01$ and 2.8 fold for %BC, $G=19.1$, $P<0.01$).

Landscape–related distribution and between–year population dynamics of the pine marten in connection with food supply differences

Figure 2 shows the multiannual dynamics of pine marten abundance in the "clay" and "sandy" areas. Landscape-related differences were found. By early winters in the "clay" area from 3.6 to 12.9 (mean±SD was 7.6±3.0) pine marten trails per km per day crossed the route transect, whereas only 0.1–1.2 (0.5±0.5) trails/1 km-day were recorded in the "sandy" area ($t=9.9$, $P=0.001$). By late winters in the "clay" area we revealed 1.5–5.9 (3.1±1.1) trails/1 km-day versus 0.1–0.8 (0.3±0.3) trails/1 km–day in the "sandy" area ($t=10.4$, $P=0.001$). The variation in between-year dynamics of the pine marten abundance (trails/1 km-day) was higher in the poor quality habitats in the "sandy" area – $\upsilon=84–94\%$ versus $\upsilon=36–40\%$ in the "clay" area. No correlation was found between multiannual dynamics of the pine marten abundance index in the "clay" and "sandy" areas both by early and late winters.

By recalculating the assessed values of the pine marten abundance index (trails per 1 km per day) into the species density by means of the Priklonsky's formula the following estimates were obtained. In the woodland of the "clay" area by early winter the predator density varied from year to year between 5 and 11 individuals/10 km^2 and the multiannual mean made up 7.1 individuals/10 km^2, whereas from 0 to 6, on average 1.2 pine martens per 10 km^2 of the woodland was recorded in the "sandy" area ($t=9.5$, $P=0.001$).

A positive correlation between pine marten abundance in late winter of a current year and bank vole abundance of the previous autumn was found in both areas investigated: the "clay" area – $r_s=0.86$, $P=0.01$ and the "sandy" area – $r_s=0.90$, $P=0.02$. Also, in the "sandy" area we revealed the same correlation with abundance of wild ungulates – $r_s=0.90$, $P=0.02$.

By telemetry and snowtracking, the landscape-related and seasonal differences in habitat use by pine martens were studied (Table 4). Pine martens mostly used forest habitats –

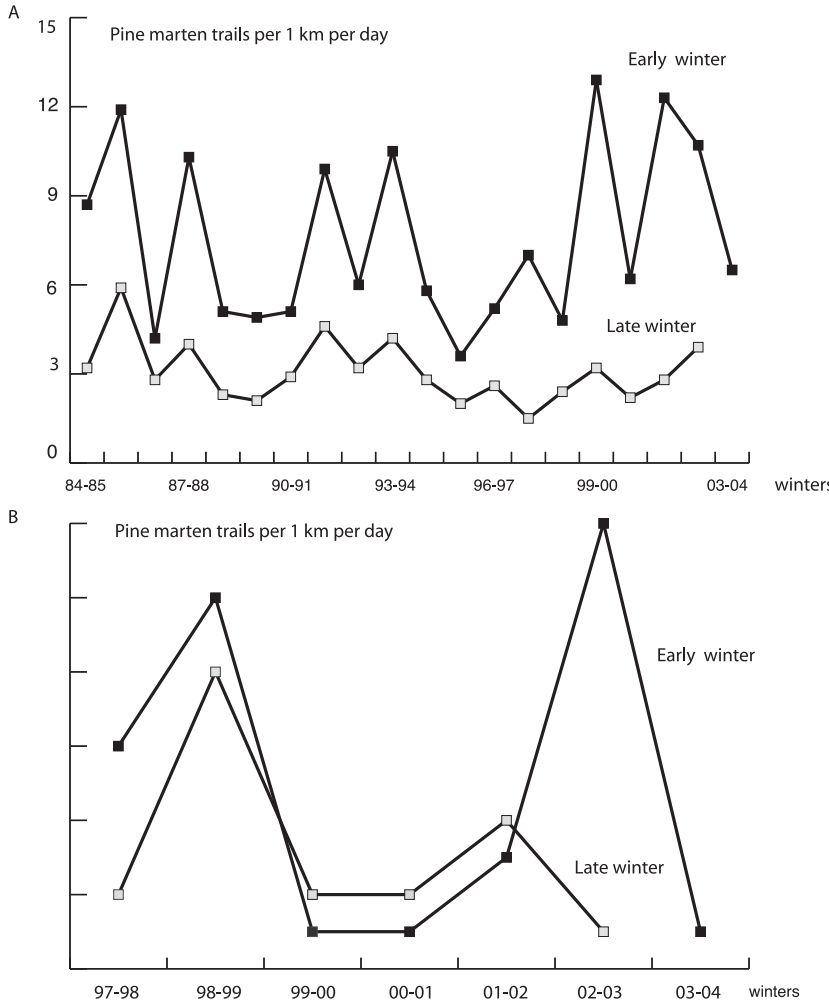

Fig. 2. Dynamics of the pine marten population in northern Belarus Average number of the pine marten trails which crossed 1 km of the inspected route during one day passed after the last snowfall was used as an abundance index. A. The woodland of the „clay" area, Gorodok district, Vitebsk region, north-eastern Belarus, winters 1984–2004. B. The woodland of the „sandy" area, Polotsk district, Vitebsk region, central north of Belarus, winters 1997–2004.

70.0–76.5%. The predator more often selected spruce wood and mixed forest dominated by spruces older than 60 years (D=0.20–0.89). From 25.4 to 39.4% of the pine marten activity registered by both methods were placed in such forest types. Pine martens highly preferred to visit ecotones, first of all, between forest and an open places (glades with dry meadows, grassy marsh patches, clearcuts etc) – 8.7–17.8% (D=0.72–0.90). Stream banksides and lake shores within forest were also favourable habitats selectively used by pine martens (D=0.79–0.93). In contrast, pine martens were mostly reluctant to utilize black alder swamps, pine woods on dry lands, dry meadows in glades, and grassy marshes (Table 4). Also, the predator evidently avoided recent clearcuts (D=-0.44–-0.94) and pine bogs (D=-0.53–-0.86). In the "clay" area a statistically significant positive correlation between the habitat selection by pine martens

and the woodland structure was found: snowtracking – r_s=0.73, P=0.02; radiotracking, cold season – r_s=0.68, P=0.03; radiotracking, warm season – r_s=0.63, P=0.05. Such a correlation was not found in the "sandy" area. In the "sandy" area pine martens more frequently used pine woods both in dry lands (4.7 fold, G=6.2, P=0.03) and in bogs (16.8 fold, G=6.8, P=0.01), stream banksides and lake shore (3.0 fold, G=4.3, P=0.04), and clearcuts with reforestation (2.9 fold, G=3.6, P=0.07), while in the "clay" area it more often visited black alder swamp woods (2.6 fold, G=3.7, P=0.06), dry meadows in glades (5.9 fold, G=2.7, P=0.16), and open grassy marshes (35 fold, G=4.1, P=0.04). Despite the many differences found, the similarity in habitat selection by pine martens between the "clay" and "sandy" areas in winter was high –

Table 4. Landscape-related differences in the habitat selection by pine martens in woodlands during the cold season, Gorodok and Polotsk districts, Vitebsk region, northern Belarus, 1998–2001. The first figure given means a percent of the habitat use, and the second one in brackets is the value of Ivlev's selectivity index D.

A. Snowtracking

Woodland biotopes	«Clay» area, Gorodok district	«Sandy» area, Polotsk district
Forest types dominated by spruce older than 60 years	38.5 (0.36)	25.4 (0.89)
Dry land pine stands older than 60 years	2.4 (-0.64)	11.2 (-0.85)
Pine bogs	0.4 (-0.86)	6.7 (-0.53)
Medium-aged deciduous (mostly small-leaved) woods	18.7 (0.18)	19.2 (0.73)
Black alder swamped woods	13.4 (-0.12)	5.2 (0.83)
Ecotones between forest and open grassland	11.2(0.72)	8.7 (0.84)
Bankside of small streams and shore of fairly small lakes in woodland	4.1 (0.79)	12.3 (0.93)
Recent (up to 2 years old) clearcuts	0.2 (-0.88)	0.2 (-0.94)
Clearcuts with some reforestation older than 2 years	3.5 (-0.35)	10.3 (0.77)
Dry meadows on glades	4.1 (-0.49)	0.7 (0.17)
Patches of open grassy marshes	3.5 (-0.35)	0.1 (-0.67)
Pooled distance of snowtracking done in km (number of individuals tracked)	109(22)	88(17)

B. Radiotracking in the «clay» area, Gorodok district

Woodland biotopes	The warm season	The cold season
Forest types dominated by spruce older than 60 years	31.0 (0.20)	39.4 (0.36)
Dry land pine stands older than 60 years	2.0 (-0.69)	3.3 (-0.53)
Pine bogs	0.1 (-0.82)	0.7 (-0.76)
Medium-aged deciduous (mostly small-leaved) woods	9.1 (-0.24)	13.1 (-0.04)
Black alder swamped woods	4.9 (-0.58)	10.2 (-0.25)
Ecotones between forest and open grassland	17.8 (0.90)	13.3 (0.81)
Bankside of small streams and shore of fairly small lakes in woodland	4.0 (0.79)	6.6 (0.87)
Recent (up to 2 years old) clearcuts	1.2 (-0.44)	0.4 (-0.77)
Clearcuts with some reforestation older than 2 years	23.0 (0.60)	5.8 (-0.10)
Dry meadows on glades	6.6 (-0.27)	5.0 (-0.40)
Patches of open grassy marshes	0.3 (-0.92)	2.2 (-0.54)
Pooled number of independent fixes done (number of individuals radiotracked)	1653(5)	1227(4)

Pianka's index=0.89. In the "clay" area the habitat use by pine martens was investigated in both the warm and cold seasons (Table 4). The data obtained showed a high similarity in the predator habitat selection between the seasons – Pianka's index=0.88. Nevertheless, some seasonal differences were recorded. In the warm season pine martens more frequently visited clearcuts with reforestation (4.0 fold, G=11.0, P<0.01) and less often used swamp areas such as black alder woods, grassy marshes and pine bogs (2.5 fold, G=3.4, P=0.07).

Discussion

In the coniferous – small-leaved deciduous woodlands of northern Belarus the pine marten is characterised by a wide food spectrum as has been reported for other regions of the European forest zone (Nasimovich 1948, Lockie 1961, Geptner & Naumov 1967, Danilov & Tumanov 1976, Morozov 1976, Pulliainen & Ollinmäki 1996, Jędrzejewska & Jędrzejewski 1998, Lanszki et al. 1999, Baltrūnaitė 2003). In northern Belarus the diets of pine martens basically consisted of different combinations of rodents (mostly bank voles), carrion, berries, and birds. Any marked selectivity for rodent species was not revealed. The importance of wild ungulate carrion increased in the cold season compared to the warm season, and the trend was more pronounced in the "sandy" area. Particularly, the consumption of carrion by pine martens increased by late winter (Sidorovich et al. 2000). In the warm season, the proportion of birds in the predator diet was higher. Also in the "sandy" area, berries were more frequently taken by pine martens in the warm season. The main landscape-related dietary differences were as follows. In the "clay" area with rich soil and, in turn, diverse and productive terrestrial vegetation, pine martens much more relied on rodents than in poor quality habitats in the "sandy" area. Conversely, in this ecologically poor woodland, carrion and fruits appeared to be more important food of the predator.

In neighbouring Lithuania, in the same type of woodlands the pine marten showed a very similar dietary structure of a generalist predator, and landscape-related differences in the diets were revealed (Baltrûnaitė 2003). There, the landscape types were also separated in terms of a glaciation deposit composition, with clay plain, hilly moraine highland with a high soil clay fraction, and sand deposits. The main food of pine martens were rodents and wild ungulate carrion, birds and fruits. Feeding on carcasses by pine martens was also much commoner in the cold season. There, a higher consumption of rodents and less frequent consumption of insects year-round, while a lower dietary proportion of fruits in winters was recorded.

In the Białowieża Forest (eastern Poland and western Belarus) also located in the mixed forest zone, but having mostly broad-leaved trees in deciduous stands, richer old soil and milder winter, pine martens also consumed a wide spectrum of food (Jędrzejewski et al. 1993, Jędrzejewska & Jędrzejewski 1998). There, rodents made up the main part of the predator diets, and *Microtus* voles were quite important. In contrast, the dietary proportion of fruits and other plant material was considerably lower year-round, and the role of carrion in the cold season was not so pronounced. According to Jędrzejewska & Jędrzejewski (1998), in the Białowieża Forest there were denser rodent populations, the abundance of wild ungulate carrion was possibly higher, but biomass of fruits was evidently lower. So, the predominant diet of pine martens in the Białowieża Forest reveals opportunistic feeding habits, while carrion is seemingly less relevant as a food resource. Pine martens feed on carrion a lot when it is hard to survive as an active predator, as by late winter

in there are many fewer prey and deep snow provides shelter for the surviving rodents. The rare predation of *Microtus* voles by pine martens in northern Belarus and the markedly higher proportion in the Białowieża Forest may be explained by the very low density of *Microtus* voles in forest habitats in northern Belarus, even in the years of population outbreaks, while in the Białowieża Forest they are commoner in woodlands. It is important to mention that in the transitional woodlands of northern Belarus we found no selective predation on rodent species by pine martens, while the species was reluctant to forage in open habitats, where *Microtus* concentrated.

In the boreal coniferous forest in northern Finland the dietary composition of the pine marten was also diverse and flexible, and the basic winter food being mostly *Clethrionomys* voles (P u l l i a i n e n & O l l i n m ä k i 1996). When rodents were scarce, pine martens fed an red squirrels, birds and scavenged for reindeer carrion.

The food supply of pine martens in the transitional woodlands of northern Belarus was much higher in forested terrain with a clay soil compared to that on sandy soil. These ecological differences resulted in 6 times lower density of pine martens registered in the "sandy" area. Also, a pronounced landscape-related difference in habitat selection by the predator was found. In the "sandy" area pine martens were mainly distributed in valleys of glacial lakes, rivers and brooks and their surroundings, where the food supply was much higher. In the "clay" area the predator activity was much more evenly spaced in the heterogeneous woodland where habitats with fairly high carrying capacity are widely spread and present in each small segment (S o l o v e j et al. 2003).

In the poor quality habitats dwelling on sandy soils pine marten density was about three times more variable than in the ecologically rich woodland on clay soil. There was no correlation between multiannual dynamics of the pine marten abundance index in the "clay" area with that in the "sandy" area both by early and late winters. Substantial differences in the structure, functioning and habitat carrying capacity of the pine marten population in the "clay" and "sandy" areas were found.

In northern Belarus one of the main factors driving the between-year dynamics of pine marten numbers is the autumn density of bank voles. Actually, the autumn density of bank voles (as the commonest rodent species) determines much of the pine marten density through the entire winter or, at least, during the first half of this harsh period. Also, in conditions of prey shortage on the "sandy" area the density of wild ungulate carrion is a very important factor determined pine marten survival through winter. These parameters of food supply markedly influenced pine marten abundance by late winter, i.e. in pre-reproductive period.

Thus, in the transitional coniferous – small-leaved deciduous woodlands of northern Belarus the pine marten is a generalist predator using a wide food spectrum. It acts as an active predator taking many species of rodents, birds and other prey of suitable size. At the same time, the pine marten is a gatherer of fruits (mostly berries) and scavenging of ungulate carrion. In the ecologically poor woodland on sand the predator uses several specialisations, such as a predominant diet of carrion in the cold season, and of berries in the warm season. The richer food supply in the woodland located on clay results in a markedly higher population density and fairly even distribution of the pine marten than those in the woodland on sand, where pine martens mainly live in valley habitats. The winter abundance of bank voles drives the pine marten population in the region. Simultaneously, winter density of wild ungulates and, in turn, biomass of carrion is also crucial factor determining the predator density by late winter just before the reproduction season.

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