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THE PINE MARTEN'S *MARTES MARTES* ECOLOGICAL NICHE AND ITS RELATIONSHIPS WITH OTHER VERTEBRATE PREDATORS IN THE TRANSITIONAL MIXED FOREST ECOSYSTEMS OF NORTHERN BELARUS

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Abstract: The pine marten's (*Martes martes*) ecological niche and its relationships with other vertebrate predators in transitional coniferous forests – small-leaved woodlands – of northern Belarus were studied. Data on the diet and distribution of pine martens were gathered under different food supply conditions, and across a range of landscape types and seasons. Also, similar data were gathered on the following predators: weasel (*Mustela nivalis*), polecat (*Mustela putorius*), red fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*), Ural owl (*Strix uralensis*), tawny owl (*Strix aluco*), Tengmalm's owl (*Aegolius funereus*), and pygmy owl (*Glaucidium passerinum*). Data were used to calculate ecological niche overlaps between the pine marten and these other species. Variations in the abundance of the main prey were monitored. Data showed that the pine marten acted both as an active predator taking many species of rodents and birds, and as a gatherer, feeding on fruits and scavenging for carrion. The winter density of bank voles (*Clethrionomys glareolus*) drove pine marten numbers. Also, the biomass of carrion was a crucial factor determining pine marten density in late winter. Analysis of the 2

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predatory guilds (generalist predators and rodent eaters) suggested that the species coexisted stably. We observed significant partitioning in the habitats and/or food resources that supported the species' coexistence. However, the naturalised raccoon dog had a negative impact on pine marten populations, due to competition for carrion in late winter.

Introduction

Ecological studies on the pine marten's (*Martes martes*) food habits, habitat use, and population densities have been reported for many regions of Europe, including boreal coniferous woodlands and more southern broad-leaved forests (Nasimovich 1948, Lockie 1961, Geptner et al. 1967, Danilov and Tumanov 1976, Morozov 1976, Pulliainen 1981, Goszczyński 1986, Marchesi and Mermod 1989, Storch et al. 1990, Jędrzejewski et al. 1993, Zalewski et al. 1995, Pulliainen and Ollinmäki 1996, Jędrzejewska and Jędrzejewski 1998, Lanszki et al. 1999 and references therein). Only 2 studies investigated pine martens in the extended transitional mixed forest (Sidorovich et al. 2000, Baltrūnaitė 2003), and the first one was mostly concerned with the influence of the raccoon dog (*Nyctereutes procyonoides*) on the forest generalist guild. Food composition of pine martens in relation to prey diversity and supply was investigated by Jędrzejewski et al. (1993), Zalewski et al. (1995), Pulliainen and Ollinmäki (1996), and Jędrzejewska and Jędrzejewski (1998). Habitat selection and population densities were shown to be connected with diet composition and food abundance (Storch et al. 1990, Jędrzejewski et al. 1993, Zalewski et al. 1995, Jędrzejewska and Jędrzejewski 1998, Baltrūnaitė 2003). This study aimed to analyse the feeding habits and distribution of the pine marten within a vertebrate community of transitional coniferous forests – small-leaved woodlands – of northern Belarus. When investigating the pine marten's ecological niche and its relationships with other vertebrate predators, we also assessed the influence of food supply variations in relation to seasonal and landscape differences.

Study Area

The study was conducted in the fairly natural landscapes of northern Belarus, where man-made habitats (agricultural fields, villages and others) constituted only 8-14% of the area. The region belongs to the extended transitional woodland of the European forest zone, located between the southern deciduous and the northern boreal coniferous forest zones. Of the coniferous tree species, only the spruce *Picea abies* and the pine *Pinus sylvestris* are present. The black alder (*Alnus glutinosa*), the grey alder (*A. incana*), birches (*Betula pendula*, *B. pubescens*), and the aspen (*Populus tremula*) were the most common deciduous trees, with only a few masting deciduous trees such as the oak (*Quercus robur*), the lime (*Tilia cordata*), the maple (*Acer platanoides*), and the ash (*Fraxinus excelsior*) producing quantities of nourishing seeds important to rodents.

Data were collected in 2 areas with broad differences in surface geology and carrying capacities (Sidorovich et al. 2003a, Solovej et al. 2003). The first study area, Gorodok, was approximately 300 km², and situated on the upper reaches of the Lovat river

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(Gorodok district, Vitebsk region, NE Belarus, 55°N, 31°E). High levels of clay in the surface ground deposits result in a good water supply and abundant trace elements, producing rich soils (hereafter referred to as the “clay” area). Plant communities in the “clay” area were diverse and supported an abundant herbivore community. They made up about 51% of the landscape (Table 1). The second study area, Polotsk (Polotsk district, Vitebsk region, central north of Belarus, 55°N, 29°E), was approximately 250 km². The surface ground deposits consisted of sand only (hereafter the “sandy” area), with clay restricted to the valleys of glacial lakes and rivers. The soils of this area were barren and dry. Woodlands dominated by pine stands with limited ground vegetation represented about 60% of the forests on dry land, and 19% on raised bogs (Table 1).

Methods

A total of 1,222 pine marten scats was analysed, from which 3,095 prey items and other food resources (fruits, seeds and herbs) were recovered. Also, to assess food niche overlap between the pine marten and other predatory species, similar dietary data were gathered from previous publications of the same research group (Sidorovich et al., 2000, 2003b, c, in press a, b). These include the analysis of scats of weasels (*Mustela nivalis*) (n = 426), polecats (*Mustela putorius*) (n = 672), red foxes (*Vulpes vulpes*) (n = 1526) and raccoon dogs (n = 653), and the pellets of Ural owls (*Strix uralensis*) (n = 181), tawny owls (*Strix aluco*) (n = 126), Tengmalm’s owl (*Aegolius junereus*) (n = 161), and pygmy owls (*Glaucidium passerinum*) (n = 73). The criteria applied in collecting the above scat and pellet samples were described in the publications mentioned above. Pine marten scats were collected from tracks or known latrines. Predator scats and pellets were collected over a period of 7 years (1995-2001) in the “clay” area and over 5 years (1995-1999) in the “sandy” area. Dietary data were divided into the cold season (November-March) and the warm season (April-October). Identification of mammalian prey was based on skulls, teeth and jaw remnants of small mammals according to Pucek (1981), and 10 hairs randomly taken from each scat or pellet and microscopically determined according to Debrot et al. (1982). Insects were identified by examining the remains of exoskeletons, birds by feathers and bones, amphibians by bones, and reptiles by bones and skin scales (Böhme 1977, März 1987, Jędrzejewska and Jędrzejewski 1998). Plant material was only recorded as food consumed if it comprised more than 20% by volume in a scat.

Dietary composition was calculated as follows: the number of prey items and other food resources identified in scats or pellets was taken as 100% for the calculation of percentages of frequency of prey occurrences in the diet (%OC). Plant remains (fruits, seeds or herbs) in a given scat were taken as one occurrence. Percentage of biomass consumed (%BC) was calculated by using Jędrzejewska and Jędrzejewski’s (1998) coefficients of digestibility, i.e. the ratio of fresh weight of a given food item to the dry weight of its remains in scats. Owl diets, expressed initially in %OC were transformed into prey biomass consumed by using the average weight of each prey species; if the weight of a given prey of an owl was higher than the average daily food intake of a studied owl species (Mikkola 1983), then we used the latter value in the calculations.

Levins's index (Levins 1968) was used to compare dietary diversity (food niche breadth). Pianka's index (Pianka 1973) was applied to evaluate dietary overlap.

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

Habitat type	Gorodok study area		Polotsk study area*	
	Whole study area	Woodland areas only	Whole study area	Woodland areas only
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
Agricultural land, human settlements and miscellaneous	13	<1	5	<1
Recent clearcut	1	3	3*	6*

* Since these figures were compiled, intensive logging in 2001-2003 in the Polotsk study area has led to a marked increase in the proportion of recent clear cuts to about one third of the woodland area

Small mammal abundance was estimated in the main woodland habitats by snap trapping. Fried bread was used as bait. Twenty to 50 snap-traps were set at approximately 5 m intervals for 3 days and checked daily. Captures were identified according to Pucek (1981). Data from about 21,000 snap-trap-nights were used to calculate an abundance index for each census plot based on the number of individuals captured during 100 snap-trap-nights. We visually censused overwintering perching birds on a 50 m-wide transect along established standard routes.

Habitat use by pine martens and other carnivores was studied by radio-tracking (only in the "clay" area) year-round and by snow-tracking in winter (in both study areas). Between May 1996 and February 2004 we radio-tracked 7 pine martens (a total of 7,549 fixes), 7 weasels (5,922 fixes), 1 red fox (687 fixes), 7 raccoon dogs (5,855 fixes), 6 polecats (2,295 fixes), 6 Ural owls (4,751 fixes), and 3 tawny owls (983 fixes). During radio-tracking sessions (typically 1 to 7 sessions were completed per working day), fixes were recorded at intervals of 15 min, or less if the location or activity type changed during the standard interval. Independent data were obtained by choosing at random 1 active fix and 1 inactive fix per radio-tracking session for each individual. Receivers

were provided by Telonics Inc. (Mesa, Arizona), and radio-collars were made by Biotrack Ltd. (Wareham, UK) and Telonics Inc. Pine martens and polecats were caught in wooden box-traps baited with carrion, and immobilised with a sedant injection. Weasels were captured in smaller box-traps baited with laboratory mice, and then radio-tagged mainly without immobilization. Raccoon dogs and red foxes were mainly captured at burrows, with nets, and then immobilized with a sedant injection. Owls were captured by landing net or other catching equipment at nests or artificial nest-boxes. All radio-tagged individuals were released at their place of capture.

Data from snow tracking and radio-tracking were used to relate the activity of individuals to variations in habitat composition. In the case of radio-tracking, the total number of independent fixes was taken as 100% for calculations of percentages of frequency of usage of various habitat types. Similarly for snow-tracking data, we computed the percentage of the pooled length of trails recorded in each biotope type from the total trail length snow-tracked.

Numbers of pine martens, polecats and red foxes were estimated in winter, using the occurrence of each species' trails, on standard routes covering the whole range of habitats, as a proxy for abundance. We did such a track survey twice each winter, at the beginning (usually late November or early December) and end of the snowy period (usually March) over 20 winters (1984-2004) in the "clay" area and 7 winters (1997-2004) in the "sandy" area. An abundance index for each species was calculated as the number of trails crossing the standard route divided by the number of kilometres searched and the number of days since the last snowfall. Thus, we obtained the average number of trails/km of transect/day. The abundances of hares (*Lepus* spp.) and wild ungulates were derived from snow tracking using the same methods.

Population densities were estimated from trail counts using Prikłonsky's formula (Prikłonsky 1965), which was adapted to the habitat conditions of northern Belarus by using estimates of the species' daily movement distance under conditions of different snow cover. Daily movement distance was assessed by a combination of snow tracking and radio-tracking as recommended by Zalewski et al. (1995).

Raccoon dog population density was estimated by searching selected areas in late winter, when pairs are usually slightly active around their hibernation shelters (unpublished data). To census weasels, we counted their track concentrations in early winter under conditions of limited snow cover, when there had been no snowfall for 1 or 2 days (Sidorovich et al., in press b); the number of track concentrations was assumed to equate to the number of individuals. Owls were counted by recording responses to owl calls played on a tape-recorder, while following a specially established route in early spring (Johnson et al. 1981, Sidorovich et al. 2003b).

Population densities of pine martens and other vertebrate predators were estimated using data from the post-reproductive period in the same biological year (early winter, for the weasel, the pine marten, the red fox and the polecat; late winter for the raccoon dog; and early spring for the owls).

The occurrence and cover of different habitat types (hereafter referred to as landscape structure) were recorded on 20 10-km transects located in randomly chosen directions and covering much of the 2 study areas. Statistical analyses involved

Spearman correlation - r_s , t-test of the difference between 2 means, and G-test for homogeneity of percentages (Sokal and Rohlf 1995). The Ivlev's selectivity index (D, modified by Jacobs [1974]) was calculated for the habitats used and rodents consumed.

Results

Landscape-related differences in pine marten diet

In the "clay" area, during the warm season pine martens had a diverse, mammal-dominated (34.3%OC, 47.7%BC) diet and the food niche was relatively broad (Table 2). Birds (17.3%OC, 25.1%BC), berries and other plant food (25.3% OC, 13.6% BC) made a significant contribution to the diet. Other food items (insects, amphibians, reptiles, carrion and honey, the consumption of the last being revealed by the observation of honeycomb remains) were less important – amounting to 7.9%BC (Table 2). Among the mammals, small rodents were the preferred prey and constituted 27.9%OC and 37.3%BC; shrews, though numerous, were rarely taken (2.7%OC). Moles, hedgehogs (*Erinaceus* spp.), red squirrels (*Sciurus* spp.), hares, and muskrats (*Ondatra zibethicus*) together made up only 8.9% BC. The bank vole constituted 77.8% of the rodents preyed upon by pine martens, comprising over a quarter 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's diet - amounting to 6.2%OC. However, when compared with the rodent community structure in woodlands, we found no selection for any rodent species by pine martens in a given situation, e.g. the "clay" area during the warm season (D index from -0.13 to 0.11) or any other combinations of seasons and landscapes (D=-0.35 – 0.36).

Compared with the warm season, the cold season diet of pine martens in the "clay" area was slightly different (Table 2; Pianka's index =0.78 for %OC and 0.85 for %BC). The increase in consumption of 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, pine martens mostly fed on rodents (18.3%OC, 23.5%BC) and berries (31.4%OC, 37.8%BC). Compared with the "clay" area significantly more berries were consumed (3.4-fold, G=13.4, P<0.01); birds (8.2%OC, 13.5%BC versus 12.9% OC, 19.0% BC), rodents and other mammalian prey (amounting to 22.1%OC, 30.8%BC versus 34.3%OC, 47.7%BC) were taken less often. Also, the occurrence of insects and reptiles in the diet was markedly higher in the "sandy" area (Table 2). Among small rodents, bank voles dominated the pine marten's diet (94.5% of all rodents consumed), and this species constituted about one fifth of the food biomass consumed (21.5%BC). Other rodents contributed very little to the predator's diet (2.0%BC). The pine marten's food niche-breadth in the "sandy" area was lower than in the "clay" area (6.8 versus 9.1), but the diet composition was similar (Pianka's index=0.90 for %OC and 0.80 for %BC).

During the cold season in the "sandy" area, the pine marten's 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 (Levins's index= 3.27 for %OC and 2.54 for %BC),

Table 2. Diet of pine martens in the warm and cold seasons in the “clay” and “sandy” areas, northern Belarus (1995-2001). %OC - frequency of prey occurrence in the diet expressed as %; %BC - ratio of prey biomass consumed expressed as %.

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
Moles	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 voles	21.7	27.5	20.1	30.2	17.3	21.5	11.6	10.7
<i>Apodemus</i> mice	3.0	4.4	5.3	7.0	0.7	1.3	0.6	0.8
<i>Microtus</i> voles	1.9	2.5	2.7	3.4	0.2	0.5	0.1	0.2
Other rodents	1.3	2.9	3.1	4.0	0.1	0.2	0.2	0.5
Red squirrels	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
Muskrats	0.1	0.4	-	-	-	-	-	-
Carrion of mammals (wild ungulates, <i>Castor fiber</i> etc.)	2.0	5.7	14.1	21.6	1.4	2.9	51.8	61.2
Small birds	9.9	12.2	3.3	3.9	3.9	6.5	1.8	2.2
Large and medium-sized birds	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
Crane berries	-	-	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 items 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

because the diet was dominated by mammalian carrion (Table 2). The consumption of carrion was significantly higher than in the “clay” area ($G=12.4$, $P<0.01$). About 84% of carrion was carcasses of wild ungulates. Rodents (12.2%BC), birds (5.2%), and berries (8.3%) were also fairly important food items for pine martens. Insects (mainly beetles) and reptiles (lizards) were quite frequently taken by martens (Table 2), but together they constituted only 5.5%BC. In the cold season the pine marten’s diet was

fairly different in the “sandy” and “clay” areas (Pianka's index =0.67 for %OC and 0.69 for %BC). The main differences were that rodents made up a smaller share of the diet in the “sandy” area (2.5 fold for %OC, $G=8.7$, $P<0.01$ and 3.7 fold for %BC, $G=20.4$, $P<0.01$) being substituted by a 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 and habitat-related differences in food supply: small mammals, hares, perching birds and wild ungulate carrion

The bank vole was the most common small mammal in both study areas. In the post-reproductive period (autumn), this species 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 small mammal prey of pine martens might be *Apodemus* mice that were common too, while *Microtus* voles inhabited forest biotopes only rarely. In all habitat types, small mammals attained higher densities in the “clay” area compared with the “sandy” area (Table 3): the weighted-mean abundance of small mammals was about 10 times higher (27.1 versus 2.8 captures/100 snap-trap-nights) and the bank vole's weighted-mean abundance was about 8 times higher (19.0 versus 2.3 captures/100 snap-trap-nights).

The other prey categories that might be important when comparing food availability for pine martens in the study 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 abundant by streams and glacial lakes typically surrounded by ecologically rich woodlands dominated by spruce and/or black alder and having grassy marsh strips in the floodplains. Here, the weighted mean of abundance indices of small rodents was 13-fold higher than in other segments of the woodland with a prevalence of pine stands; the same applied to small perching birds (42-fold), hares (289-fold) and wild ungulates (346-fold).

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

Figure 1 shows landscape-related differences in the multi-annual dynamics of pine marten abundance in the “clay” and “sandy” areas. In early winters, pine martens were more abundant in the “clay” area (3.6 to 12.9 trails/km/day; mean \pm SD was 7.6 \pm 3.0) than in the “sandy” area (0.1–1.2 trails/km/day; 0.5 \pm 0.5) ($t=9.9$, $P=0.001$). This difference was also apparent in late winters (“clay” 1.5–5.9 trails/km/day; 3.1 \pm 1.1 versus “sandy” 0.1–0.8; 0.3 \pm 0.3) ($t=10.4$, $P=0.001$). The variation in between-year dynamics of pine marten abundance (trails/km/day) was greater in poor quality habitats in the “sandy” area ($v=84$ –94%) than in the “clay” area ($v=36$ –40%). There was no correlation in the multi-annual dynamics of the pine marten abundance index between the 2 study areas either in early or late winters.

Table 3. Landscape and habitat-related differences in the small mammal community in mid-autumn (post-reproductive period) in the transitional woodlands of northern Belarus (1996-2001). The number of individuals captured/100 snap-trap-nights is used as an abundance index (min – max/n = number of plots investigated, mean \pm SD (SE)).

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

Pine marten density estimates in early winter (obtained by converting abundance indices) revealed that in the woodlands of the “clay” area population densities varied from year to year between 5 and 11 individuals/10 km² (multi-annual mean 7.1 individuals/10 km²). In the woodlands of the “sandy” area, pine marten densities were estimated from 0 to 6 (mean 1.2) pine martens/10 km² ($t=9.5$, $P=0.001$).

A positive correlation was found in both study areas between pine marten abundance in late winter of one year and bank vole abundance in the previous autumn (“clay” area - $r_s=0.86$, $P=0.01$; “sandy” area - $r_s=0.90$, $P=0.02$). Also, in the “sandy” area we noted a similar correlation with the abundance of wild ungulates ($r_s=0.90$, $P=0.02$).

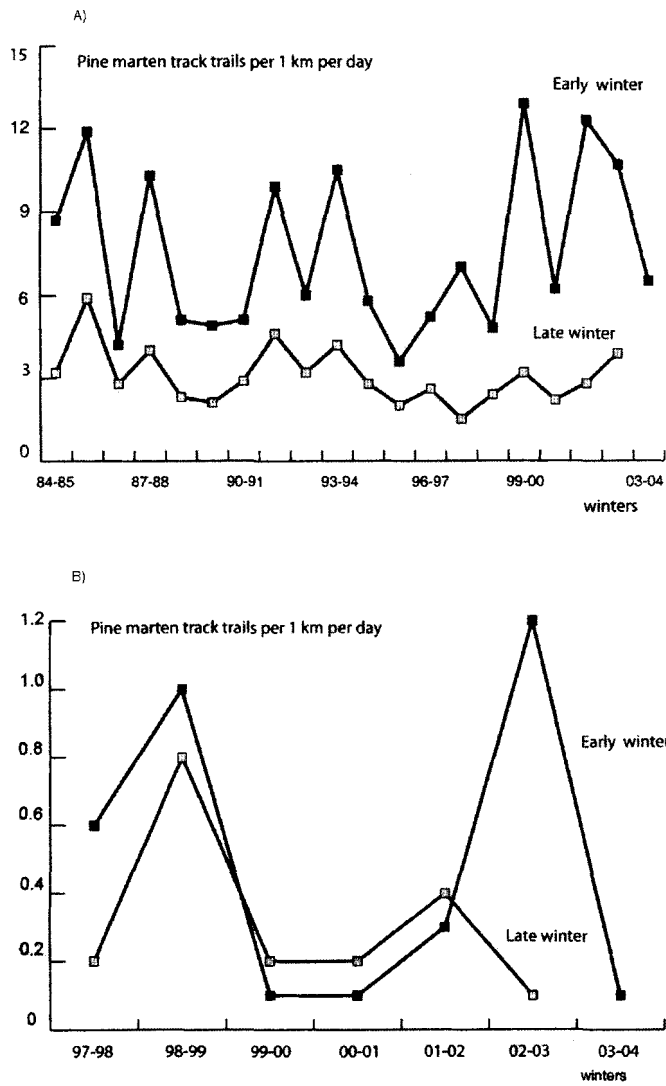


Figure 1. Dynamics of pine marten populations in northern Belarus: A - The woodlands of the "clay" area, Gorodok district, Vitebsk region, north-eastern Belarus, winters 1984-2004; B - The woodlands of the "sandy" area, Polotsk district, Vitebsk region, central-north Belarus, winters 1997-2004.

Landscape-related and seasonal differences in habitat use by pine martens were revealed by telemetry and snow-tracking (Table 4). Pine martens mostly used woodlands (64.9-80.0% of radio fixes and 75.5-84.6% of the total length snow-tracked as shown in Table 4). They positively selected spruce and mixed woodlands dominated by spruce older than 60 years ($D=0.20-0.89$). From 25.4 to 39.4% of pine marten activity detected by both methods was recorded in such habitats. Pine martens showed a great preference for ecotones, notably between woodland and open habitats (glades with dry meadows, grassy marsh patches, clearcuts, etc), which represented 8.7–17.8% of the study area ($D=0.72-0.90$). Stream margins and lake shores within woodland were also positively selected by pine martens ($D=0.79-0.93$). In contrast, black alder swamps, pinewoods on dry land, dry meadows in glades, and grassy marshes were avoided (Table 4). Recent clearcuts ($D=-0.44-0.94$) and pine bogs ($D=-0.53-0.86$) were also avoided. In the “clay” area, a positive correlation was found between pine marten habitat selection and woodland structure (snow-tracking – $r_s=0.73$, $P=0.02$; radio-tracking, cold season – $r_s=0.68$, $P=0.03$; radio-tracking, 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 used pine woods more frequently, both on dry land (4.7-fold, $G=6.2$, $P=0.03$) and in bogs (16.8-fold, $G=6.8$, $P=0.01$), stream margins and lake shores (3.0-fold, $G=4.3$, $P=0.04$), and clearcuts with reforestation (2.9-fold, $G=3.6$, $P=0.07$). In the “clay” area, they spent more time in 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 these differences, there was considerable overlap in habitat selection by pine martens between the study areas in winter (Pianka’s index=0.89). In the “clay” area there was a marked similarity in habitat use between seasons (Pianka’s index=0.88). Nevertheless, some seasonal differences in the use of certain habitats were recorded. In the warm season, pine martens visited clearcuts with reforestation more frequently (4.0-fold, $G=11.0$, $P<0.01$) and used swamp areas, such as black alder woods, grassy marshes and pine bogs, less often (2.5-fold, $G=3.4$, $P=0.07$).

Relationships between the pine marten and ecologically closely related vertebrate predators

Table 5 summarises the analysis of relationships between the pine marten and ecologically closely related vertebrate predators. Comparisons are based upon overlaps in habitat use and dietary composition (expressed as a percentage of biomass consumed), which may be sufficient to indicate ecological similarity between predatory species. The analysis of overlaps in habitat selection (Table 5A) revealed many differences between the pine marten and the other predators, in particular regarding use of patches of open grasslands between wooded habitats. We found a fairly high similarity in the habitat use of the pine marten, the weasel, the red fox, the Ural owl and the naturalized raccoon dog. Marked overlaps in diet were noted between the pine marten and the red fox, polecat, tawny owl and raccoon dog (Table 5B). Despite the similarity found in many pairwise comparisons, inter-specific

Table 4. Landscape-related differences in 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 is percent of habitat use, and the second one in brackets is the value of Ivlev's selectivity index D.

A. Snowtracking

Woodland habitats	"Clay" area, Gorodok district	"Sandy" area, Polotsk district
Woodland types dominated by spruce >60 years old	38.5 (0.36)	25.4 (0.89)
Dry land pine stands >60 years old	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) clear cuts	0.2 (-0.88)	0.2 (-0.94)
Clear cuts with some reforestation older than 2 years	3.5 (-0.35)	10.3 (0.77)
Dry meadows in 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 snow tracking done in km (number of individuals tracked)	109(22)	88(17)

B. Radiotracking in the "clay" area, Gorodok district

Woodland habitats	The warm season	The cold season
Woodland types dominated by spruce > 60 years old	31.0 (0.20)	39.4 (0.36)
Dry land pine stands >60 years old	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)
Margins 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 > 2 years old	23.0 (0.60)	5.8 (-0.10)
Dry meadows in 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 radio-tracked)	1653(5)	1227(4)

Table 5. Parameters of relationships between the pine marten and ecologically closely related vertebrate predators in the transitional woodlands of northern Belarus, 1996-2004.

A. Overlap in habitat use estimated by Pianka index (α) and statistically checked by G-test.

Species compared with pine marten	"Clay" area		"Sandy" area	
	Warm season	Cold season	Warm season	Cold season
Weasel	$\alpha=0.86$ G=21.6, P=0.03	$\alpha=0.70-0.74$ G>26.6, P<0.005	Presumably high	$\alpha=0.89$ G=21.8, P=0.04
Polecat	$\alpha=0.42$ G=110, P<0.001	$\alpha=0.33$ G=134, P<0.001	No data	No data
Red fox	$\alpha=0.82$ G=24.6, P=0.01	$\alpha=0.38-0.76$ G>36, P<0.001	Presumably moderate	$\alpha=0.53$ G=36.1, P<0.001
Raccoon dog	$\alpha=0.79$ G=40.5, P<0.001	$\alpha=0.74$ G=47.3, P<0.001	Presumably high	$\alpha=0.92$ G=19.4, P=0.05
Ural owl	$\alpha=0.28$ G=55.8, P=0.001	$\alpha=0.90$ G=90, P<0.001	No data	Presumably moderate
Tawny owl	$\alpha=0.39$ G=55.0, P=0.001	Presumably moderate	No data	No data
Tengmalm's owl	Presumably high	Presumably high	No data	No data
Pygmy owl	Presumably high	Presumably high	No data	No data

B. Dietary similarity for the percentage of biomass consumed estimated by Pianka index α and statistically checked by G-test.

Species compared with pine marten	"Clay" area		"Sandy" area	
	Warm season	Cold season	Warm season	Cold season
Weasel	$\alpha=0.38$ G=132, P<0.001	$\alpha=0.42$ G=142, P<0.001	$\alpha=0.30$ G=242, P<0.001	$\alpha=0.38$ G=206, P<0.001
Polecat	$\alpha=0.51$ G=76, P<0.001	$\alpha=0.74$ G=90, P<0.001	No data	No data
Red fox	$\alpha=0.54$ G=82, P<0.001	$\alpha=0.71$ G=82, P<0.001	$\alpha=0.77$ G=54.5, P<0.001	$\alpha=0.95$ G=32.4, P=0.06
Raccoon dog	$\alpha=0.72$ G=49, P=0.02	$\alpha=0.53$ G=72, P<0.001	$\alpha=0.62$ G=70, P<0.001	$\alpha=0.88$ G=24.6, P=0.10
Ural owl	$\alpha=0.33$ G=141,	$\alpha=0.36$ G=140, P<0.001	$\alpha=0.48$ G=117,	$\alpha=0.18$ G=171,

Tawny owl	P<0.001 $\alpha=0.56$ G=70, P<0.001	$\alpha=0.65$ G=56, P<0.001	P<0.001 No data	P<0.001 No data
Tengmalm's owl	$\alpha=0.25$ G=198, P<0.001	$\alpha=0.21$ G=209, P<0.001	No data	No data
Pygmy owl	$\alpha=0.39$ G=145, P<0.001	$\alpha=0.40$ G=165, P<0.001	No data	No data

C. Spearman correlations r_s between the densities of the pine marten and other vertebrate predators.

Species compared with pine marten	"Clay" area	"Sandy" area
Weasel	$r_s=0.80$, P=0.01	No correlation
Polecat	$r_s=0.86$, P<0.01	No correlation
Red fox	$r_s=0.40$, P=0.08	$r_s=0.85$, P=0.01
Raccoon dog	$r_s=-0.64$, P=0.01	$r_s=-0.68$, P=0.04
Ural owl	$r_s=0.70$, P=0.04	$r_s=0.74$, P=0.03
Tawny owl	$r_s=0.73$, P=0.03	No correlation
Tengmalm's owl	No correlation	No correlation
Pygmy owl	No correlation	No correlation

differences were often statistically significant (Table 5). Indeed, a pronounced partitioning in resource exploitation was revealed in many cases. Marked sharing of habitat was found in the cold season for the pine marten with the polecat, the red fox and the Ural owl. Different exploitation of food resources was partly detected for the pine marten and the weasel year-round and for the pine marten and the Ural owl in the cold season. Simultaneous partitioning in the usage of both habitats and food was shown by the following pairs: the pine marten – the polecat in the warm season; the pine marten – the Ural owl in the warm season, the pine marten – the tawny owl in the warm season, the pine marten – the pygmy owl year-round, and the pine marten – the Tengmalm's owl year-round.

Spearman's correlation values relating pine marten population densities to those of other vertebrate predators are given in Table 5C. This parameter further characterizes the relationships between species. In both study areas, either no correlation or only a statistically significant positive correlation was found between the population densities of native predatory species; conversely, when comparing the multi-annual population dynamics of the pine marten with those of the raccoon dog, negative correlations are revealed in both study areas.

Discussion

In the coniferous - small-leaved woodlands of northern Belarus the pine marten consumes a wide food spectrum, as has been reported for other regions of the European forest zone (Nasimovich 1948, Lockie 1961, Geptner et al. 1967, Danilov and Tumanov 1976, Morozov 1976, Pulliainen and Ollinmäki 1996, Jędrzejewska and

Jędrzejewski 1998, Lanszki et al. 1999, Baltrūnaitė 2003). The present study revealed a diet comprising different combinations of rodents (mostly bank voles), carrion, berries, and birds. In neighbouring Lithuania to the West, in similar woodlands, the pine marten showed a very similar dietary structure typical of a generalist predator; landscape-related differences in the diet were also revealed (Baltrūnaitė 2003).

In 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 winters, pine martens also consumed a wide spectrum of food (Jędrzejewski et al. 1993, Jędrzejewska and Jędrzejewski 1998). There, rodents made up the bulk of the diet, and *Microtus* voles were quite important. Compared with the present study, the dietary proportion of fruits and other plant material was considerably lower year-round, the role of carrion in the cold season was not so pronounced, there were denser rodent populations, and the abundance of wild ungulate carrion was possibly higher; the biomass of fruits was evidently lower (Jędrzejewska and Jędrzejewski 1998). These differences suggest that, in Białowieża Forest, the apparent dependence of pine martens upon rodents, and the lesser consumption of carrion and berries, results from an opportunistic feeding behaviour. Certainly, pine martens depend on carrion when conditions become difficult for predators (e.g., in late winter, when numbers of prey are reduced, or when deep snow cover increases the energetic costs of active foraging and makes it more difficult to locate and catch the surviving rodents). The rare predation upon *Microtus* voles by pine martens in northern Belarus, and their markedly higher contribution to the diet in Białowieża Forest, may be explained by the very low density of *Microtus* voles in forest habitats in northern Belarus, even in years of population outbreaks, while in 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, probably because they were reluctant to forage in open habitats where *Microtus* voles were concentrated.

The differences found in pine marten food abundance in the transitional woodlands of northern Belarus had a marked effect on the species' population density, which was 6 times lower in the "sandy" area. It also had an effect on habitat selection. In the "sandy" area pine martens were mainly distributed in valleys of glacial lakes, rivers and brooks and their surroundings, while in the "clay" area they were much more evenly spread through the heterogeneous woodlands.

The winter abundance of bank voles drives the pine marten population in the region. Simultaneously, the winter density of wild ungulates and, in turn, the biomass of carrion is also a crucial factor determining pine marten density in late winter just before the reproductive season. In the ecologically poor woodlands of the "sand" area, the pine marten uses several specialisations, such as a diet dominated by carrion in the cold season and by berries in the warm season.

Considering the relationships between the pine marten and the ecologically closely related vertebrate predators, all these species appeared to have similar patterns of resource exploitation in the woodlands of northern Belarus. The observed patterns of population dynamics and significantly overlapping habitat use and diet among the

native predators suggest a stable coexistence. One of the likely mechanisms for their coexistence is the partitioning of habitats and/or food (Begon et al, 1990, Jędrzejewska and Jędrzejewski 1998). The positive correlations between the population densities of these species are seemingly a consequence of their similar responses to changes in food abundance and availability. Indeed, in northern Belarus, such responses have been found for the pine marten in relation to the bank vole and carrion (this study), to the Ural owl and the bank vole (Sidorovich et al. 2003b), and to the red fox, the bank vole, *Microtus* voles and carrion (Sidorovich et al. 2003a, in press a). The negative correlation between the population dynamics of the pine marten and the naturalized raccoon dog suggests a detrimental influence of this introduced species upon the former. This has been confirmed by another detailed study conducted in northern Belarus that revealed strong competition for carrion in late winter (Sidorovich et al., 2000).

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