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A long-term study of the winter food niche of the pine marten *Martes martes* in northern boreal Finland

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The diet of the pine marten *Martes martes* (Linnaeus, 1758) was studied during 16 successive winters in an uninhabited area in northern boreal Finland. The results are based on 5677 scats analyzed. The present data support earlier findings that the pine marten is an opportunistic generalist, its most favoured food apparently being small rodents, especially *Clethrionomys* spp. The significant year-to-year variation in the frequency of occurrence of this favoured prey in the diet of the marten correlated positively with summer trapping numbers for these species. Snow cover decreased the martens' consumption of *Microtus* spp. but not *Clethrionomys* spp. or the wood lemming *Myopus schisticolor*. The first real alternative in the absence of small rodents appeared to be the red squirrel *Sciurus vulgaris*, and in its absence carcasses of reindeer *Rangifer tarandus tarandus* and eggs. Other food items included birds, the mountain hare *Lepus timidus*, the common frog *Rana temporaria*, berries and mushrooms. There was some evidence that the occurrence of red squirrels in the diet was dependent on the abundance of both squirrels and small rodents. We suggest that in northern boreal Finland martens primarily forage for small rodents, and larger prey, which is less available and more difficult to catch, is captured incidentally.

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Key words: *Martes martes*, winter diet, between-year variation, northern boreal Finland

Introduction

Research carried out so far (eg Nasimovič 1948, Höglund 1960, Weckwerth and Hawley 1962, Danilov and Tumanov 1976, Goszczyński 1976, Morozov 1976, Pulliainen 1981a, Zielinski *et al.* 1983, Buskirk and MacDonald 1984, Reig and Jędrzejewski 1988, Marchesi and Mermod 1989, Nagorsen *et al.* 1989, 1991, Slough *et al.* 1989, Storch *et al.* 1990, Thompson and Colgan 1990, Jędrzejewski *et al.* 1993) has shown that the Eurasian pine marten *Martes martes* (Linnaeus, 1758) and North American pine marten *M. americana* possess very similar food intake patterns, although the latter is smaller in size. These species are generally regarded as generalists and opportunists in their feeding behaviour, although Rosenzweig (1966) concluded that the North American pine marten is a microtine specialist. Thompson and Colgan (1990) state that North American pine martens

are "catholic in selection of prey and make use of most available mammalian prey, ruffed grouse, passerine birds, berries and insects".

It is generally known that the abundances of small rodents, other mammals and sedentary tetraonid birds and the yields of berries vary considerably from year to year under subarctic conditions (eg Siivonen 1957, Hansson and Henttonen 1985, Laine 1988). Although numerous studies have been made of the diet of the Eurasian pine marten, only a few analyze food selection in terms of availability, or else they are of short duration and can easily lead to wrong interpretations. The purpose of this paper is to record how year-to-year changes in the availability of the main potential food items of the Eurasian pine marten are reflected in the composition of its food in northern boreal Finland.

Material and methods

The 300 km^2 study area is situated in Finnish Forest Lapland and includes the 110 km^2 Värriö Nature Reserve, surrounding Värriö Subarctic Research Station (67°45'N, 29°37'E). The eastern part of the Värriö Nature Reserve includes 2 fell ridges (Pulkkatunturi-Sauoiva and Värriötunturi) running in a north-south direction about 5 km apart. Ravines are typical in the fell terrain. The area is in a virgin state and uninhabited. Spruce *Picea abies* forests and mixed forests are dominant, and together with scots pine *Pinus sylvestris* forests they make up over 65% of the area. Birch *Betula* spp. forests cover 3.0% of the total area, open bogs 13.5%, mountain birch *Betula pubescens* sub.sp. *czerevanovii* forests 7.0% and treeless fell summits 9.5%. The forests are mature, including a large number of standing and fallen dead trunks. The density of trees generally is very low and in some areas there are young spruce and pine saplings among the very old trees. Some of the forest area outside the Nature Reserve has been felled. There is snow on the ground from October to May (average 17.10.–20.5.), with an average maximum snow depth of 80 cm (range 54–99 cm) in the forests.

Table 1. Numbers and sex of pine martens tracked and numbers of scats collected.

Winter	Female	Male	Unknown sex	Scat number
1976/77	1	1	2–5	158
1977/78			4–8	639
1978/79			4–9	1123
1979/80			4–7	780
1980/81	2	3	0–2	465
1981/82	3	2	0–1	230
1982/83	2	3	1	409
1983/84	4	5		103
1984/85	2	4	1	92
1985/86	2	3	1	36
1986/87	2	2	1	271
1987/88	3		2	312
1988/89	3		2	481
1989/90	3	1	5	243
1990/91	1	1	4	190
1991/92	2	2	2	145
Total				5677

The study was carried out over 16 successive winters, 1976/77–1991/92. The numbers of individuals tracked and their sex ratio are shown in Table 1. The figures for 1976/77–1983/84, when radio telemetry was not used, are estimates. The individuals of unknown sex were tracked without catching them. Martens were tracked for over 13 000 km by skiing and a total of 5677 scats were collected and analyzed. After washing the samples on a sieve, the clean material was sorted out and dried at room temperature. Food items were identified by comparing them to reference collections of vertebrate hairs, feathers and bones, berry skins and seeds from the Zoological Museum, University of Oulu. The guides of Siivonen (1977), Debrot *et al.* (1982) and Teerink (1991) were used for identifying the mammals to species/genus or family. Regrettably, voles and shrews were not identified to family until 1986/87 and therefore most of the statistical analysis concern only the data for 1986/87–1991/92. In the absence of diagnostic features, it was often impossible to identify the bird remains to species. Similarly the eggshells had lost their colour and could therefore be classified only by size. Mushroom remains, notably *Rhizopogon* spp., were mainly identified on their smell.

The data are presented in percentages of the total scat volume and as frequencies of occurrence. The data for October, November and April were excluded when comparing the winters. Although there were some significant differences also between the midwinter months, December–March (Table 2), the data for these are combined.

Shannon-Weaver diversity indices (H') were calculated for the winters of 1986/87–1991/92 and the differences between them were tested according to Zar (1984):

$$H' = \frac{n \log n - \sum_{i=1}^{k} f_i \log f_i}{n}$$

where, k is the number of categories, f_i the number of observations in category i and n the sample size. H' increases as the distribution of the total diet among the categories becomes more even. The magnitude of H' is also affected by the number of categories, the maximum diversity being $H'_{max} = \log k$. Eleven categories were used to calculate the diversity of the diet: voles, shrews, red squirrel *Sciurus vulgaris*,

Table 2. Chi-square analysis of monthly differences (October–April) in the food choice of the marten. Cases also significant in December–March underlined. * – $p < 0.05$, ** – $p < 0.01$, *** – $p < 0.001$.

Winter	df	Voles and shrews χ^2	Squirrel χ^2	Hare χ^2	Reindeer carcasses χ^2	Birds χ^2	Eggs χ^2	Berries χ^2
1976/77	6	14.59 *			27.13 ***	22.08 **		75.60 ***
1977/78	6	10.41 ns				13.88 *	3.90 ns	29.85 ***
1978/79	6	18.02 **		46.06 ***		20.76 **		
1979/80	6	34.94 ***	142.46 ***	55.97 ***	59.47 ***	37.23 ***	95.72 ***	292.77 ***
1980/81	6	26.05 ***		46.25 ***	38.78 ***	19.79 **	24.29 ***	93.06 ***
1981/82	5	8.52 ns				10.66 ns		
1982/83	5	5.00 ns				5.11 ns		
1983/84	6	11.44 ns				6.75 ns	18.45 **	60.02 ***
1984/85	3	7.92 *						
1985/86	2	9.49 **						
1986/87	5	4.69 ns		30.76 ***		8.95 ns	8.23 ns	31.48 ***
1987/88	5	15.62 **				8.98 ns	8.67 ns	
1988/89	5	18.91 *			34.45 ***	26.31 ***	33.71 ***	
1989/90	5	23.45 ***				34.54 ***	17.81 **	158.74 ***
1990/91	4	14.16 **	49.27 ***			2.71 ns	20.00 ***	61.76 ***
1991/92	4	6.09 ns	12.82 *			4.72 ns		

mountain hare *Lepus timidus*, other mammals, reindeer *Rangifer tarandus tarandus*, tetraonids, other birds, eggs, common frog *Rana temporaria*, and berries.

Data on small rodent abundances in Lapland in 1976–1983, based on game questionnaires sent out by the Finnish Game and Fisheries Research Institute (Lindén 1988), were used to compare the occurrence of small mammals (voles and shrews) in the winter diet of the marten in 1976/77–1983/84 with their abundances in those years. From 1983 onwards the abundances of small rodents and shrews were estimated by pitfall trapping. Ten traps of diameter 20 cm and depth 19 cm were placed in two rows about 10 m apart in each of the three most favoured habitats of the pine marten ($\Sigma = 30$ traps), ie spruce-dominated mixed forest, spruce forest and pine forest (for habitat selection of the pine marten, see Pulliainen 1981b). The traps, filled with water, were checked daily by noon from the end of May to the beginning of October (usually the snowless season). The results are given as captures/100 trap nights (Fig. 1).

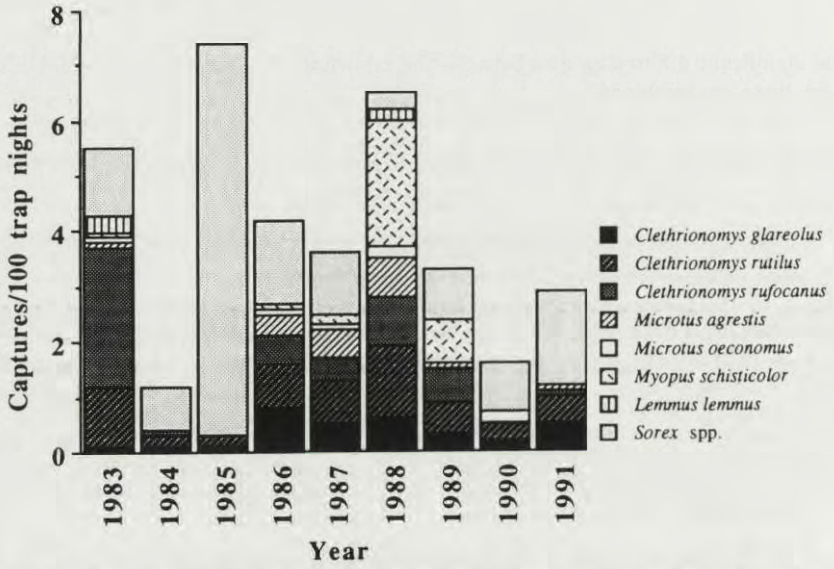

Fig. 1. Abundance (captures/100 trap nights) of small rodents and shrews in three pitfall trap fields, ie 30 traps (spruce-dominated mixed, spruce and pine forests).

The numbers of tracks of squirrel and hare crossing an observation line of length 5970 m were used to indicate the abundance of the species in the area. The results are expressed as crossings/10 km (Fig. 2; for further details see Pulliainen 1981c).

Semi-domestic reindeer *Rangifer tarandus tarandus* were grazing in the area during the period in question, and some wolves *Canis lupus* and wolverines *Gulo gulo* were also present occasionally every winter. These together with accidents and starvation caused the deaths of some reindeer, thus producing carcasses which were available for the martens. The yearly variations in the availability of carcasses are not known.

The willow grouse *Lagopus lagopus* is the most abundant tetraonid species in the area, its populations fluctuating widely from year to year. The statistics of the Finnish Game and Fisheries Research Institute (unpublished) show that the populations of willow grouse and of the black grouse *Tetrao tetrix* were increasing from 1976 to 1978 and from 1985 to 1987. The capercaillie *Tetrao urogallus* was abundant in 1978 and 1986, but the population of the hazel grouse *Bonasia bonasia* was very low throughout and the rock ptarmigan *Lagopus mutus* occurs only occasionally in this area.

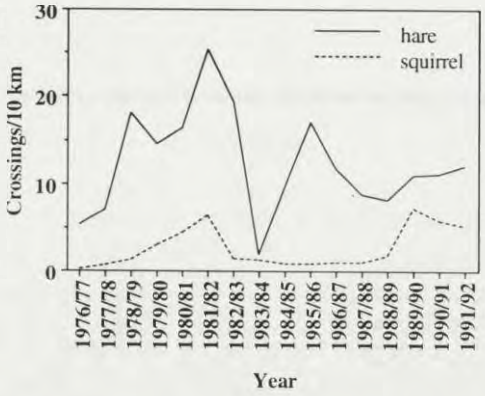

Fig. 2. Numbers of tracks of squirrel and hare crossing an observation line of length 5970 m.

The abundance of berries was determined in six 10 × 10 m sample plots situated in different habitats. The results are given as fresh weight per sample plot. The snow depth data were provided by the Research Station's Meteorological Centre.

Results

General

The composition of the food of the pine marten (by volume) in the study area during the winters of 1976/77–1991/92 is shown in Fig. 3, containing combined

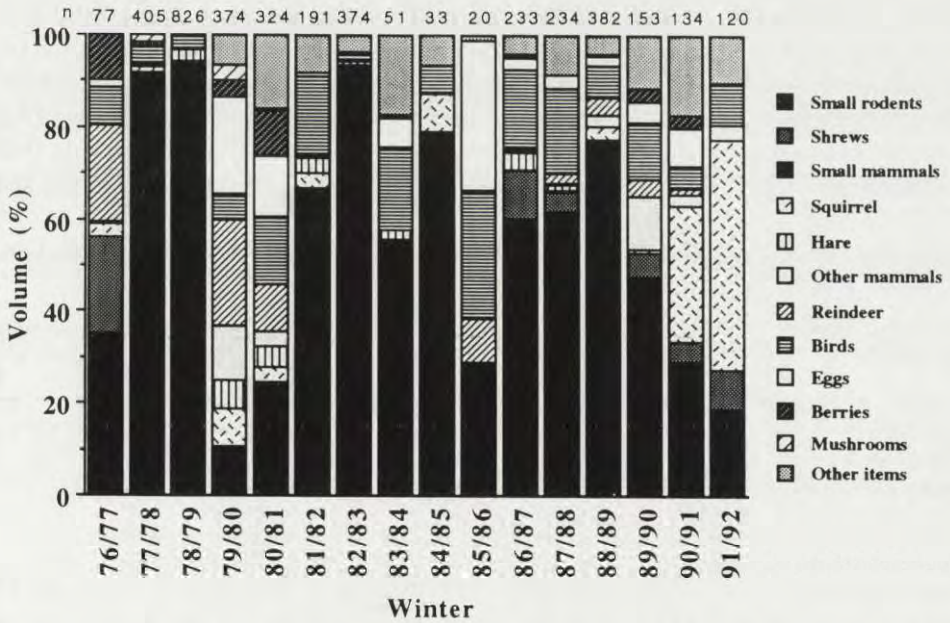

Fig. 3. Proportions (in % of volume) of food items in the scats of the martens, December–March 1976/77–1991/92. *n* – number of scats.

Table 3. Abundance of small rodents (captures/100 trap nights), dietary breadths of the marten (Shannon-Weaver diversity indices H') and yearly differences between the indices 1986/87–1991/92, derived from the proportions of 11 prey categories: voles, shrews, squirrels, hares, other mammals, reindeer, tetraonids, other birds, eggs, frog and berries.

	Abundance	H'	1987/88	1988/89	1989/90	1990/91	1991/92
1986/87	2.6	0.54	ns	***	**	**	**
1987/88	2.5	0.48		**	***	***	ns
1988/89	5.9	0.46			***	***	ns
1989/90	2.5	0.68				ns	***
1990/91	0.7	0.68					***
1991/92	1.2	0.46					

data for December–March each winter. The yearly (December–March) diversities of the diet (Shannon-Weaver index) in 1986/87–1991/92 are shown in Table 3.

Small rodents and shrews

The following small rodent and shrew species (small mammals) were identified in the diet of the pine marten: bank vole *Clethrionomys glareolus*, northern red-backed vole *C. rutilus*, grey-sided vole *C. rufocanus*, field vole *Microtus agrestis*, root vole *M. oeconomus*, wood lemming *Myopus schisticolor*, Norwegian lemming *Lemmus lemmus*, water vole *Arvicola terrestris*, muskrat *Ondatra zibethica*, common shrew *Sorex araneus*, masked shrew *S. caecutiens* and lesser shrew *S. minutus*. Pygmy shrew *S. minutissimus* and water shrew *Neomys fodiens* were recorded only in the pitfall traps. The rodents belonging to the genus *Clethrionomys* were the most frequent, their remnants being recorded in 64.1% of all occurrencies of small mammals (Table 4). The corresponding proportion of *Microtus* rodents was 8.1%, that of wood lemming 10.0% and that of shrews 10.2%. Low frequencies were recorded for Norwegian lemming (0.5%), water vole (0.2%) and muskrat (0.2%). There were 6.8% of unidentified rodent remnants in the scats.

Table 4. Occurrence of voles and shrews in the scats of the marten, December–March 1986/87–1991/92. *n* – number of scats, No – number of occurrencies, % – percent of occurrence.

Winter:	1986/87		1987/88		1988/89		1989/90		1990/91		1991/92	
Food item	*n* = 233		*n* = 234		*n* = 382		*n* = 153		*n* = 134		*n* = 120	
	No	%	No	%	No	%	No	%	No	%	No	%
Clethrionomys spp.	142	60.9	137	58.6	229	59.9	78	51.0	48	35.8	14	11.7
Microtus spp.	21	9.0	11	4.7	35	9.2	12	7.8	1	0.7	2	1.7
Myopus schisticolor	4	1.7	10	4.3	68	17.8	16	10.5	2	1.5	–	–
Lemmus lemmus	–	–	2	0.9	3	0.8	–	–	–	–	–	–
Arvicola terrestris	–	–	–	–	2	0.5	–	–	–	–	–	–
Ondatra zibethica	–	–	–	–	2	0.5	–	–	–	–	–	–
Undet. microtids	–	–	13	5.6	44	11.5	–	–	–	–	12	10.0
Total microtids	164	70.4	173	73.9	321	84.0	90	58.8	51	38.1	28	23.3
Sorex spp.	31	13.3	19	8.1	4	1.1	22	14.4	9	6.7	18	15.0

The differences between the winters (December–March) in the occurrence of small mammals in the diet of the pine marten were statistically highly significant (χ^2 = 1606.4, df = 15, p < 0.001). Three peaks at intervals of 4–6 years (1977/78–1978/79, 1982/82 and 1988/89) were recorded in the diet, the lows taking place in the winters of 1979/80 and 1985/86. In addition, a few small mammals were found in the scats of pine martens in winter 1991/1992. However, only limited data were obtained in the winters of 1983/84–1985/86. Vole abundances in Lapland in 1976–1983, as given by Lindén (1988), correlated positively with the occurrence of small mammals (small rodents and shrews) in the diet of marten (Spearman rank: r_S = 0.88, n = 8, p < 0.01). The amounts of small rodents (frequency of occurrence) consumed by the pine martens in 1986/87–1991/92 are related to their availability during the previous summer (Fig. 4). The occurrence of *Clethrionomys* spp. and wood lemming in the scats of martens correlated positively with the summer numbers of the species, but there was no significant relationship in the case of *Microtus* spp. The occurrence of shrews also reflected the abundance of these species (r = 0.81, df = 5, p = 0.054), but did not show a negative correlation with that of small rodents (r = 0.62, df = 5, p = 0.19). There was no significant correlation between the abundance of small rodents and the diversity of the diet (r = 0.64, df = 5, p = 0.17). Although the occurrence of small rodents and shrews in the diet of the pine marten was not stable through all the winters, between-month differences during the mid-winter months (December–March) were recorded only in two winters, 1989/90 and 1991/92 (Table 2).

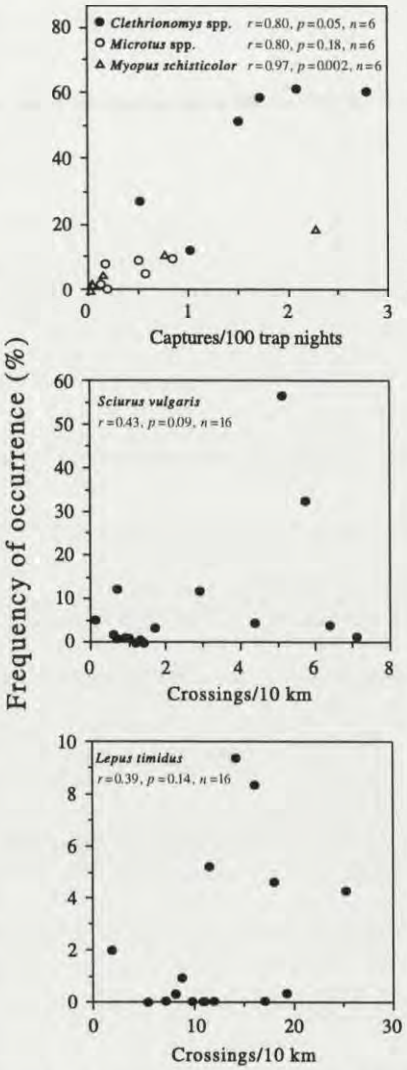

Fig. 4. Frequency of occurrence of small rodents, squirrels and hares in the scats of martens in relation to the abundance of these prey species in the area (pitfall data on small rodents 1983/84–1991/92, squirrel and hare crossings of a 5970 m observation line 1976/77–1991/92).

The occurrence of *Microtus* spp. in the scats of the marten decreased as snow depth increased (Fig. 5; R^2 = 0.14, df = 32, p = 0.03), but there was no such relationship for *Clethrionomys* spp. (Fig. 5; R^2 = 0.003, df = 32, p = 0.76), the wood lemming (R^2 = 0.04, df = 32, p = 0.27) or shrews (R^2 = 0.009, df = 32, p = 0.59). Squirrels

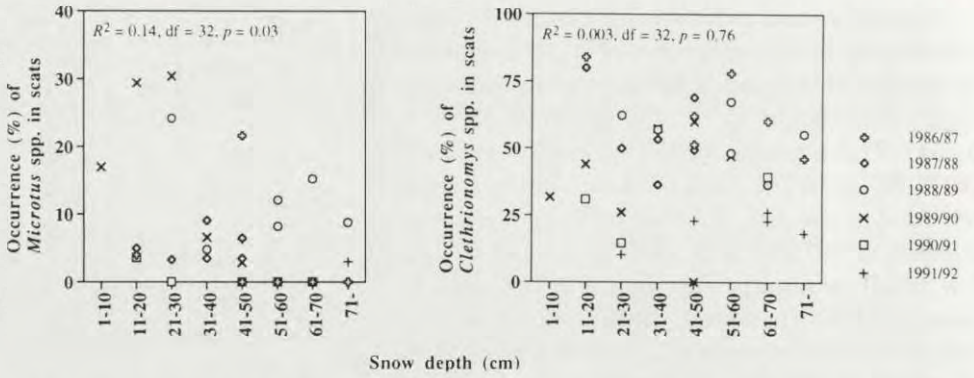

Fig. 5. Relationship between the occurrence of *Clethrionomys* spp. and *Microtus* spp. in the scats of the marten and snow depth, each point representing a mean for scats collected at a given snow depth in each year.

(r = 0.94, df = 5, $p < 0.01$) and eggs (r = 0.95, df = 5, $p < 0.05$) were items replacing small rodents in the diet of the marten in 1986/87–1991/92. For the whole period 1976/77–1991/92 reindeer carcasses (r = 0.52, df = 13, $p < 0.05$) were also found to be an alternative food replacing small mammals (small rodents and shrews) in addition to the above-mentioned squirrels (r = 0.55, df = 12, $p < 0.05$) and eggs (r = 0.68, df = 13, $p < 0.05$).

Table 5. Occurrence of mammals, birds and eggs in the scats of the marten, December–March

Winter:	1976/77		1977/78		1978/79		1979/80		1980/81		1981/82		1982/83	
Food item	n = 77		n = 405		n = 826		n = 375		n = 324		n = 191		n = 374	
	No	%	No	%	No	%	No	%	No	%	No	%	No	%
Microtids and *Sorex* spp.	56	72.7	388	95.8	805	97.5	55	14.7	110	34.0	144	75.4	368	98.4
Sciurus vulgaris	4	5.2	7	1.7	4	0.5	43	11.5	13	4.0	7	3.7	–	–
Lepus timidus	–	–	–	–	38	4.6	35	9.3	27	8.3	8	4.2	1	0.3
Mustela nivalis	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mustela erminea	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Martes martes	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eptesicus nilssoni	1	1.3	–	–	–	–	–	–	–	–	–	–	–	–
Rangifer tarandus	22	28.6	3	0.7	2	0.2	102	27.2	52	16.0	–	–	4	1.1
Undet. mammals	–	–	1	0.2	3	0.4	36	9.6	6	1.9	7	3.7	–	–
Total mammals	76	98.7	393	97.0	817	98.9	258	68.8	194	59.9	160	83.8	370	98.9
Tetraonids	2	2.6	5	1.2	29	3.5	6	1.6	–	–	22	11.5	–	–
Passerines, woodpeckers	6	7.8	2	0.5	8	1.0	3	0.8	–	–	6	3.1	–	–
Undet. birds	3	3.9	27	6.7	42	5.1	96	25.6	132	40.7	23	12.0	15	4.0
Total birds	11	14.3	34	8.4	79	9.6	105	28.0	132	40.7	51	26.7	15	4.0
Eggs	–	–	7	1.7	–	–	72	19.2	38	11.7	1	0.5	6	1.6

Other mammals

The other mammal species identified in the scats of the pine marten were as follows: red squirrel, mountain hare, least weasel *Mustela nivalis*, stoat *Mustela erminea*, pine marten, northern bat *Eptesicus nilssoni*, and reindeer (Fig. 3, Table 5). The least weasels, stoats, pine martens and northern bats are classified as "other mammals" in Figs 4 and 5. Reindeer carcasses, squirrels and hares constituted the most important food items in this category, their occurrences in the diet varying significantly from winter to winter ($\chi^2 = 588.9$, df = 15, $p < 0.001$; $\chi^2 = 1459.2$, df = 15, $p < 0.001$; $\chi^2 = 139.3$, df = 15, $p < 0.001$, respectively) and unlike the small mammals, their occurrences also varied markedly in the course of the winter months (Table 2). No correlations were recorded between the occurrences of remnants of the squirrels ($r = 0.43$, df = 15, $p = 0.09$) or the hares ($r = 0.39$, df = 15, $p = 0.14$) in the scats and figures indicating the abundances of these species (Fig 4). The increase in the frequency of occurrence of squirrels in the diet of the martens in 1990/91 and 1991/92 coincided with an increase in the local squirrel population and a simultaneous decrease in the small rodent population, although no significant relationship could be found between the occurrence of squirrel remains in the scats (So) and the abundance of small rodents (Ra) and squirrels (Sa) 1983/84–1991/92 (So = 4.74 + 3.65Sa–1.61Ra, $R^2 = 0.31$ df = 9, $p = 0.27$). There was no correlation between the diversity of the diet and the abundance of squirrels ($r = 0.62$, df = 5, $p = 0.19$) or hares ($r = 0.93$, df = 5, $p = 0.28$).

1976/77–1991/92. Explanations as in Table 4.

1983/84 $n = 51$		1984/85 $n = 33$		1985/86 $n = 20$		1986/87 $n = 233$		1987/88 $n = 234$		1988/89 $n = 382$		1989/90 $n = 153$		1990/91 $n = 134$		1991/92 $n = 120$	
No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%
36	70.6	30	90.9	6	30.0	190	81.5	174	74.4	322	84.3	100	65.4	58	43.3	43	35.8
–	–	4	12.1	–	–	2	0.9	2	0.9	13	3.4	1	0.7	43	32.1	64	53.3
1	2.0	–	–	–	–	12	5.2	2	0.9	1	0.3	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	1	0.7	–	–	4	3.3
–	–	–	–	–	–	3	1.3	2	0.9	10	2.6	6	3.9	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	15	9.8	–	–	–	–
–	–	–	–	–	–	–	–	–	—	–	–	–	–	–	–	–	–
–	–	–	–	2	10.0	4	1.7	6	2.6	15	3.9	8	5.2	2	1.5	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	4.5	1	0.9
37	72.5	31	93.9	8	40.0	199	85.4	184	78.6	353	92.4	123	80.4	106	79.1	105	87.5
4	7.8	1	3.0	2	10.0	32	13.7	36	15.4	42	11.0	22	14.4	–	–	12	10.0
–	–	2	6.0	2	10.0	37	15.9	26	11.1	10	2.6	21	13.7	10	1.5	4	3.3
11	21.6	–	–	3	15.0	18	7.7	8	3.4	7	1.8	3	2.0	3	2.2	4	3.3
15	29.4	3	9.1	7	35.0	87	37.3	70	29.9	59	15.4	46	30.1	13	9.7	20	16.7
11	21.6	–	–	9	45.0	32	13.7	24	10.3	40	10.5	22	14.4	33	24.6	–	–

Birds and eggs

The following bird species were identified in the scats of the pine martens: capercaillie (both males and females), black grouse (both males and females), willow grouse, dipper *Cinclus cinclus*, Siberian jay *Perisoreus infaustus*, great spotted woodpecker *Dendrocopos major*, three-toed woodpecker *Picoides tridactylus*, crossbill *Loxia* sp., pine grosbeak *Pinicola enucleator*, Siberian tit *Parus cinctus*, willow tit *P. montanus*, brambling *Fringilla montifringilla* (juv.), bluethroat *Luscinia svecica* (juv.) and fieldfare *Turdus pilaris*. The three lastmentioned species undoubtedly represented carcasses remaining from the previous summer. No eggshells other than "tetraonid-size" were found. Thirty six out of 39 scats examined in January 1992 and 12 out of 41 in February were left by two pine martens that had been released and therefore could not contain any cache items (eggs).

The occurrence of birds (χ^2 = 359.2, df = 15, $p < 0.001$) and remnants of eggs (χ^2 = 362.1, df = 15, $p < 0.001$) in the diet (Table 5) showed significant annual variation. The occurrence of birds was fairly stable throughout the winters, but that of eggs varied more (Table 2).

Berries and mushrooms

Berries of the following species appeared to belong to the diet of the pine martens: blueberry *Vaccinium myrtillus*, cowberry *V. vitis-idaea*, bog whortleberry *V. uliginosum*, crowberry *Empetrum hermaphroditum*, common Juniper *Juniperus communis* and rowan *Sorbus aucuparia*. Significant year-to-year differences (χ^2= 1135.6, df = 15, $p < 0.001$) in the occurrence of these berries in the diet were found, but there were no correlations with berry yields, even for the most common species, the crowberry (r = 0.07, df = 15, p = 0.8) and blueberry (r = 0.47, df = 15, p = 0.06). Crowberry yields varied from 0.5 kg to 3.7 kg fresh weight per are (100 m^2), the corresponding figures for blueberry yields being 0 and 0.3 kg. Berries are mainly consumed in early winter, ie October–November, their consumption decreasing with increasing snow depth ($y = 35.402 - 0.559x$, R^2 = 0.35, df = 82, p = 0.0001).

Mushrooms (especially *Rhizopogon rubescens*) also occurred in the diet in the early winter. The differences between winters being significant (χ^2 = 1115.8, df = 15, $p < 0.001$).

Other food items

The category "other food items" includes needles, decayed wood, cardboard and plastic. Remnants of common frog were also included in this category in Fig. 3, because frog bones were not identified separately at the beginning of the period. This item was recorded every winter during the period 1987/88–1990/921. The mean frequency of occurrence of frogs in the scats (December–March) was 9.1% (range 0.0–20.9%), the highest frequencies being in March. The occurrence of insects (ants and beetles) was sporadic, but remnants of wasps occurred 19 times in November 1990 (representing approx. 140 individuals of red wasp *Vespula rufa* and cuckoo wasp *V. austriaca*).

Discussion

As in many other parts of their range (Nasimovič 1948, Laanetu and Veenpere 1971, Goszczyński 1976, Morozov 1976, Reig and Jędrzejewski 1988, Marchesi and Mermod 1989, Jędrzejewski *et al.* 1993) the pine martens of the subarctic region of northern Finland appeared to favour small rodents in their winter diet, *Clethrionomys* species being the most numerous prey. It is very unfortunate that there are no trapping data on small mammals for the early part of the period studied here, but if we compare the abundance figures for voles in Lapland in 1976–1983 (Lindén 1988), which are consistent with the field observations and data on tree saplings damaged by small rodents reported by Pulliainen (1981a), with the occurrence of small mammals in the winter diet of the marten, a significant positive correlation can be found. There were peaks in the abundance of voles in the years 1977, 1978 and 1982, and similarly the occurrence of small mammals in the diet of the marten was very high in 1977/78, 1978/79 and 1982/83. Small rodents may even be overrepresented in the diet in such a situation as more small rodents are killed than can be immediately eaten (Pulliainen 1981a). The lows in the abundance of voles were also consistent with their occurrence in the diet of the marten. In the winters 1986/87–1991/92 the occurrence of *Clethrionomys* spp., wood lemming and shrews in the diet of the martens correlated with their numbers in the previous summer, but not the occurrence of *Microtus* spp. Hence our results regarding cyclic microtine populations did not contradict the finding of Jędrzejewski *et al.* (1993) in their 7-year study in Poland that the year-to-year variation in marten diet was shaped by variations in rodent numbers, especially those of the bank vole. The population dynamics of forest rodents in Poland was shown to be a combination of moderate years and regular outbreak-crash years. Similarly, the proportions of red-backed vole *Clethrionomys gapperi* and deer mouse *Peromyscus maniculatus* in the diet of the American marten in Ontario, Canada, correlated with the absolute abundances of the species, but the proportions of the meadow vole *Microtus pennsylvanicus* did not (Thompson and Colgan 1990).

Another factor affecting the martens' probability to catch small rodents in winter besides the prey density is the differences in habitat selection between *Clethrionomys* and *Microtus* in winter. *Microtus* voles favour grasslands (Henttonen *et al.* 1977, Kemppainen 1990), open areas from which martens are known to keep away in the winter in order to avoid predation by the red fox *Vulpes vulpes* or raptors (Pulliainen 1981b). Bank voles, on the other hand, favour forests (Henttonen *et al.* 1977, Kemppainen 1990), habitats similar to those of martens (Pulliainen 1981b). Energetic aspects may also be involved. Hargis and McCullough (1984) stated that martens may avoid openings as foraging grounds because of the increased energy expenditure caused by digging. Furthermore, Koehler and Hornocker (1977) reported that American pine martens use clearcut areas more

when the snow cover is thin than when there is a lot of snow. *Clethrionomys* species spend more time on the snow than do *Microtus* voles, and also climb into trees (Siivonen 1977, Pulliainen and Keränen 1979) which makes them vulnerable to predation by the marten. *Microtus* voles, however, spend most of their time under the snow, so that the marten has to invest energy in digging. Jędrzejewski *et al.* (1993) state that snow depth is an important factor that reduces the marten's consumption of bank voles but does not affect preying on mice (*Apodemus* sp.) or *Microtus* voles. This was the opposite to our findings under more snowy conditions, where only the proportion of *Microtus* voles in the diet of the marten was affected by the snow depth. Although martens are agile and dig directly through the snow cover, they frequently take advantage of sites with less snow, eg the sides of fallen logs, to gain access to subnivean spaces which are also hiding places of *Clethrionomys* voles (Pulliainen 1981a, Jędrzejewski *et al.* 1993).

The avoidance of clearcut areas and/or the consumption of *Microtus* by martens in Sweden did not change after the decline in the number of red foxes (Storch *et al.* 1990). Storch *et al.* (1990) assumed it was the snow conditions rather than competi- tion with foxes that limited their consumption of *Microtus* voles in winter and that martens are too small and not morphologically adapted to use the effective field vole catching technique of foxes: location by acoustic means and pin-pointing through the snow after a high leap in the air. The assumption is supported by data from Poland, where a rapid crash in *Microtus* populations was followed by a decline in this element of the martens' diet, whereas foxes continued to prey intensively on the declining *Microtus* stocks (Jędrzejewski and Jędrzejewska 1993). This may also be considered an indication of greater flexibility and ability of the pine marten to exploit alternative food items. The martens' ability to move about in the tree canopy also broadens its selection of prey relative to that of the red fox (Lindström 1989).

Squirrels were an important item replacing small rodents in the winter diet of marten. Höglund (1960) and de Jounge (1981) found that the proportion of squirrel in the diet of the marten was dependent on the relative abundance of voles and squirrels. This was not confirmed in the present long-term data, but there are some details that support it. In the two winters of 1990/91 and 1991/92 the red squirrel appeared to be the first real living mammal alternative in the study area in the absence of small rodents (Figs 4 and 5). These were years of simultaneously increased squirrel populations and decreased small rodent populations, whereas when squirrels and small rodents were both abundant, in 1981/82, the martens preyed mainly on the latter. Marchesi and Mermod (1989) regarded red squirrels as secondary prey, due to the fact that they are agile and can escape, thus entailing a high capturing expenditure. This is probably true despite the fact that in Finnish Lapland squirrels are often captured in their dreys or nearby after a short chase. In California, where the most frequent prey of the American marten consisted of voles, the consumption of chickarees *Tamiasciurus douglasii* began to exceed that of voles as the snow cover made voles less available and the chickarees became

more accessible as they began using terrestrial cone caches and subnivean dens, so that without the necessity for arboreal pursuit, predation on chickarees was probably more energetically rewarding during the winter (Zielinski *et al.* 1983).

When red squirrels were also scarce, the small rodents were replaced as food items by reindeer carcasses and previously stored eggs. The abundance of reindeer carcasses undoubtedly changes from winter to winter due to the different numbers of predators present and the snow conditions. Carcasses were alternative winter prey sources for martens in Poland as well, where they preferred to feed on remains of wolf and lynx kills rather than on ungulates that had died from undernutrition and/or disease (Jędrzejewski *et al.* 1993). Storch *et al.* (1990) assumed that the increased exploitation of cervid carcasses by martens could be explained as an effect of relieved competition from foxes rather than by a change in the availability of carcasses.

A notable difference between the American pine martens studied by Thompson and Colgan (1990) in Ontario and ours is that the former tended to maximize the inclusion of large prey items in their diet, particularly the snowshoe hare *Lepus americanus*. Although our pine martens are larger in size, the local mountain hare *Lepus timidus* do not play any significant role in their diet, and can be considered an occasional prey item. In fact, pine martens in this study area do not display any special tendency to exploit this resource, as became obvious during the trackings, as the pine martens mostly passed fresh tracks of hares without showing any response (Pulliainen and Heikkinen 1980). The hare population in the present area fluctuates, as do those of most other mammals (Pulliainen 1981c, Pulliainen and Tunkkari 1987), but the average population density of the species may be so low that the local pine martens tend to hunt them only occasionally. The snowshoe hare, on the other hand, is periodically superabundant in North America, with a cycle of 8 to 11 years (Keith 1963). It may also be important that the mountain hare weighs 2.0–5.8 kg (Siivonen 1977) whereas the snowshoe hare usually weighs less than 1.4 kg (Whitaker 1989).

Together with squirrel, tetraonids seemed to replace small rodents in the diet of the marten during the snowy season in Russian Karelia (Danilov and Tumanov 1976). Nasimovich (1948) regarded microtids and tetraonids as the basic food of the marten in Russian Lapland. The remains of birds, mainly tetraonids, were frequently found in the scats of the marten in the adjacent Finnish Forest Lapland, but their occurrence had no correlation with that of small rodents. Therefore, birds can be considered an occasional yet important prey item in the present study area. The great amount of unidentified bird remains in the scats at the beginning of the period studied here and the change in the method used to estimate the local tetraonid abundance in 1989 (Lindén *et al.* 1989) made further statistical analyses inappropriate.

According to MacArthur and Pianka (1966), diet width is related to the responses of predators once they encounter prey. As an opportunistic generalist, the marten pursues a large proportion of the prey it encounters, whereas a

specialist would continue searching. In years with dense small rodent populations the marten acts more like a specialist, as its diet consisting mainly of these rodents. The great diversity of food items that the marten exploits in the subarctic region of northern Finland allows considerable variation in diet breadth, and there were significant differences in the diversity between the winters (Table 3). Although we could not find a significant correlation between the diversity of the marten's diet and the abundance of its most favoured food, ie small rodents (or any other major food item) in 1986/87–1991/92, the diversity index was lowest in 1988/89, when the abundance of small rodents was greatest, and correspondingly highest in 1989/90 and 1990/91, both years of low small rodent density. Thompson and Colgan (1990) found the diet niche to be negatively correlated with the absolute abundance of most major prey species. Diet width in Switzerland and Poland was also observed to differ between the seasons, being narrowest in winter and spring (Marchesi and Mermod 1989, Jędrzejewski *et al.* 1993). The same result was reported by Thompson and Colgan (1990) for the years when food was abundant, while during the years with scarce food the diet width was highest in winter.

According to Begon *et al.* (1990) a predator should have a broader diet in an unproductive environment, where prey items are relatively rare and searching time is longer, than in a productive environment. Since species richness increases with decreasing latitudes (Begon *et al.* 1990), one would also expect a latitudinal trend to be found in the diet diversity of the marten. Clevenger (1994) compared the diet widths calculated from year-round data in 7 reports and did not find any latitudinal trend in the diet diversity of the Eurasian pine marten, but if we take two long-term studies and compare the winter diet diversity of the marten in northern boreal Finland (68°N) and in pristine deciduous forests in Poland (52°N, Jędrzejewski *et al.* 1993) the result is as expected: the diet width is significantly ($p < 0.001$) greater in Finland ($H' = 0.77$ / $H' = 0.67$, $H'_{max} = 1.04$). The opposite result was reported for the American pine marten, as Martin (1994) found it to have its lowest diet diversity in the subarctic. Also, diets dominated by large prey such as snowshoe hares and red squirrels were of relatively low diversity. The latter is explained by the fact that a bigger prey item provides food for a longer period hence reducing kills per unit time and ultimately equating with a less diverse diet (Martin 1994).

In conclusion, marten appears to be a mixture of a predator to some extent favouring *Clethrionomys* voles and an opportunist that in conditions of low abundance of microtine rodents flexibly responds to high densities of a new prey source (eg squirrel), and is also able to utilize several compensatory prey species showing a flexible feature in its choice of prey.

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