Pine marten home ranges, numbers and predation on vertebrates in a deciduous forest (Białowieża National Park, Poland)

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Pine marten *Martes martes* — prey relationships were studied in 1985/86–1992/93 in Białowieża National Park (E Poland), which protects the last remnants of the pristine deciduous forests of European lowland. Winter densities of martens, surveyed by snowtracking (in 1985/86–1988/89 and 1990/91), were from 4.44 to 6.49 inds/10 km². In 1991–93, six martens were radiotracked. Their winter densities were 7.57 inds/10 km² in 1991/92 and 3.6 inds/10 km² in 1992/93. Mean home range of male martens was 2.23 km² and that of females 1.49 km². Martens' ranges were smaller (by 33% on average) in autumn–winter than in spring-summer. Forest rodents, the bank vole *Clethrionomys glareolus* and the yellow-necked mouse *Apodemus flavicollis*, were the main prey of martens. Autumn densities of these rodents were moderate in 1985–89 and 1992 (26–78 inds/ha), extremely high in 1990 (315 inds/ha, as an effect of heavy crop of tree seeds in 1989), and very low in 1991 (11 inds/ha). Numbers of marten correlated with those of rodents with 1-year time lag. Every year, during 197 days of autumn-winter (1 October–15 April), martens removed from 2 to 8 rodents from an average hectare (mean 5.5), which constituted from 2% to 31% (mean 15%) of autumn densities of rodents. Predation impact was heavy in years of low densities of rodents and rather small during rodent outbreak. Martens' predation on 4 alternative prey in the cold seasons was estimated. During autumn–winter, they removed 0.01–0.18 birds, 0.1–2.0 shrews, and 0.2–3.7 frogs, and consumed 1.4–68.7 g of ungulate carcasses from 1 ha. Martens took the largest quantities of alternative prey during the rodent crash year.

1. Introduction

Pine marten *Martes martes*, a generalist resident predator (according to Andersson & Erlinge, 1977), inhabits both boreal and nemoral forests of Europe and coexists with cyclic rodents in the north and non-cyclic ones in central and western Europe. Marten's reproduction cycle with delayed implantation does not allow its fast numerical response to varying prey numbers. Potentially, however, pine marten as a generalist predator (Goszczyński 1976, 1986a, Pulliainen 1980) can show a clear dietary (functional) response to variation in rodent abundance.

This paper presents the 8-year (1985–1993) investigations on the pine marten-prey relationships in Białowieża National Park (East Poland). This primeval forest is characterised by a biome-specific rhythm of synchronous masting of oak *Quercus robur*, hornbeam *Carpinus betulus*, and maple *Acer platanoides*, at 6–9-year intervals (Pucek et al. 1993). Forest rodents, the bank vole *Clethrionomys glareolus* and the yellow-necked mouse *Apodemus flavicollis*, respond to heavy seed crop by winter breeding, then the outbreak in the following year, and a crash after the outbreak (Pucek et al. 1993). In other years, rodents have moderate densities.

Our study covered 6 years of moderate densities of rodents and 2 outbreak-crash years. The aims were: (1) censusing the numbers of pine martens and estimating the size of their home ranges; (2) investigating the functional responses of martens to the changes in rodent numbers; (3) estimating martens' predation on rodents, shrews, birds, and amphibians, and their consumption of ungulate carcasses in the cold season. The study was part of a long-term research on predator-prey relationships in Białowieża Primeval Forest (e.g. Jędrzejewski et al. 1989, Jędrzejewski & Jędrzejewska 1993). Data on diet composition and foraging ecology of the pine marten were presented in detail by Jędrzejewski et al. (1993).

2. Material and methods

2.1. Study area

Białowieża National Park (BNP, 52°43′N, 23°54′E) covering 47.5 km², forms part of the extensive woodlands (1450

km²) located on the Polish-Belarusian border. BNP (UNESCO's Man & Biosphere Reserve and World Heritage Site) protects the last remnants of the pristine forests of European lowland, still unaltered by human activity. The forest is dominated by mature stands of oak, hornbeam, lime *Tilia cordata*, and maple, with admixtures of spruce *Picea abies*. Alderwoods (with black alder *Alnus glutinosa*) cover wet localities. Flood-plain forest with ash *Fraxinus excelsior*, black alder, and elm *Ulmus scabra* is found in the vicinity of small rivers. Mixed coniferous forests of spruce and pine *Pinus sylvestris* grow on poorer sandy soils. The average age of tree stands is 130 years. Detailed information on the vegetation of BNP is given by Faliński (1986). Western and northern borders of BNP are small rivers (Narewka and Hwoźna) with narrow belts of treeless marsh. In the south, BNP adjoins the meadows and fields of the Białowieża Glade. The climate of BNP is transitional but continental features prevail. During the study, the mean temperature of January varied from –14.5°C in 1987 to 2.2°C in 1989. The maximum snow cover (recorded in winter 1986) was 570 mm.

2.2. Estimating the densities of pine martens

In the winters of 1985/86–1990/91 (except for the snowless winter 1989/90), snowtracking was conducted on the grid of transects (total length 59.2 km) covering 11.2 km² in the central-western part of BNP. During the 2nd and 3rd days after a new snow fall, the transects were walked and the tracks of martens crossing each section were counted. Most sections were 533 m long, and each section was walked between 2 and 10 times during each winter. In this paper, data collected on the entire 11.2-km² area are used to evaluate the effect of snow on marten mobility. For estimation of marten density, only the data from the southern part (6.5 km²) of the study area are used to make the results comparable with the radiotracking data collected there in 1991–93. The total lengths of snowtracking done on transects (on 6.5 km²) were: 109.9 km in 1985/86, 179.5 km in 1986/87, 192.0 km in 1987/88, 52.7 km in 1988/89, and 49.4 km in 1990/91. The number of recorded tracks was converted into the number of tracks km^{-1} day^{-1}. The mean index (N tracks km^{-1} d^{-1}) for the entire study area for each winter was used for estimating the densities of martens according to the method by Priklonsky (1965). Mean percent error of Priklonsky's method is 8%. The mean N tracks km^{-1} d^{-1} were: 2.343 in 1985/86, 2.977 in 1986/87, 2.954 in 1987/88, 2.789 in 1988/89, and 2.035 in 1990/91. For detailed description of rationale of Priklonsky's method, see Jędrzejewski & Jędrzejewska (1993).

Information on daily movement distance (DMD) of martens was derived from radiotracking and snowtracking of individual martens. In two radiotracked martens (female 6 and male 4, see Appendix), data on their daily activity in winter were available as the mean number of 15-min periods, when martens were found active. On average, they were active on 378 min/day (i.e. 25.2 quarters).

In 162 cases (from 10 days), the straight line distance between consecutive localisations (at 15-min) was accurately determined; it ranged from 0.01 to 0.53 km, on average 0.13 km ($SD = 0.096$). Thus, the daily distance travelled by martens and measured as a zigzag of straight line sections was 3.276 km. During snowtracking of martens (see Jędrzejewski et al. 1993), marten trail was followed. The observers measured the length of trail by pacing and noted all points where the trail crossed the marked grid of transects. From a total of 64,107 m of snowtracking, we chose 40 sections of marten trail that crossed the marked transects twice. We calculated the 'index of trail winding' as the ratio of the average length of a real trail of marten (mean 548.5 m, SD =367.8, n = 40) to the average straight line distance between the two points where a trail section crossed the marked transects (mean 249.7 m, SD = 152.8, n = 40). This index (equal 2.2) was then multiplied by an estimate from radiotelemetry (3.276 km), which resulted in DMD equal to 7.2 km. Goszczyński (1986b) gave the same figure (mean DMD = 7.2 km) from several studies on pine marten movements done by snowtracking in winter.

In 1991/92 and 1992/93, densities of martens were estimated by mapping of home ranges of all martens that were livetrapped and radiotracked in the cold seasons. Two adult martens that were trapped and radiotracked in the spring–summer of 1992 were also included into density estimates for winter 1991/92, because they were old individuals and, as judged from the tracks on snow recorded in winter, they had resided in the area earlier. For calculation of densities, martens were prescribed to the 6.5 km^2 study area proportionally to the percentage area of their ranges located within the delimits of the study area.

2.3. Home range estimates

Since 1991, live trapping and radiotelemetry of martens were conducted on 6.5 km^2 (southern part of the whole 11.2 km^2 study area). Twenty-five box traps (baited with eggs and honey) were placed in a regular grid on 6.5 km^2 and locked open permanently. When marten tracks or signs of eating the bait were noticed, the trap was set. A total of 7 martens were caught and radiocollared from April 1991 to February 1993. Six of them (2 males and 4 females) yielded enough data for calculating home ranges (Appendix). A captured marten was anaesthetised with Ketalar®, its sex, age (as juv. or adult), and body mass were determined. A radiocollar (12 g on average) was fitted around marten neck.

Martens were followed by foot from a maximum of 300-m distance and their movements and localisations were mapped. Radiotracking consisted of continuous 4 to 24h/day sessions during which localisations were taken at 15-min intervals. On days, when no continuous sessions were done, a marten was localised once per day (at various times of a day or night). For each marten, the localisations used for estimating the home range were all localisations done once daily and localisations from continuous tracking sessions taken at 15-min intervals when a marten was

active and once during each inactivity period. Home range size was estimated with the program McPaal (Stuwe 1988). Two estimators were used (White & Garrott 1990): (1) Minimum Convex Polygon (MCP) with 100% of data points; (2) Dixon-Chapman harmonic mean (HM) with 95%, 90% and 75% of data points. The HM estimator was done only when a total number of localisations was >50.

2.4. Marten functional response and predation impact

Estimation of pine marten impact on rodents and other prey was based on analysis of 1131 scats from the autumn-winter seasons (1 October–15 April) of 1985/86–1991/92 (Jędrzejewski et al. 1993). Marten predation on rodents, birds, shrews, amphibians and its consumption of ungulate carcasses was calculated based on densities of martens, their diet composition and food requirements. Number of a given prey specimens (Np) was calculated as:

$$Np = D \times (DFC \times Bp)/BMp \times 197 \text{ days}$$

where: D = densities of pine martens/ha; DFC = daily food consumption, 189.6 g (Ryszkowski et al. 1973); Bp = fraction of a given prey biomass in marten diet; BMp = mean body mass of this prey. Body masses used were: bank vole 17 g, yellow-necked mouse 31 g, frog 10.1 g, bird 108 g, shrew 7.5 g. In the case of ungulate carcasses only the total biomass (g) taken by martens from 1 ha was calculated.

Body masses of rodents and shrews were taken from autumn trapping of small mammals in 7 plots located in various forest types of BNP (see Jędrzejewski et al. 1993). In the case of shrews, the mean mass of various species was calculated (weighted by the proportions of *Sorex araneus, S. minutus* and *Neomys fodiens* in marten diet). To determine the mean body mass of frogs *Rana temporaria* taken by martens, the maximum diameter of *acetabulum* in the *junctura* plane was measured in 78 *ilia* recovered from marten scats. The correlation of *acetabulum* diameter and body mass of 57 brown frogs captured in Białowieża was calculated ($Y = X^{3.029}$, $R^2 = 0.945$, $n = 57$) and used to obtain the body mass of frogs eaten by martens. The mean body mass of birds recovered from marten scats and identified to species (details in Jędrzejewski et al. 1993) were calculated according to the data in Sokołowski (1979).

Data on marten predation on rodents during the winters of 1986/87 through 1988/89 (for the entire 11.2-km^2 study area) were briefly presented by Jędrzejewski & Jędrzejewska (1993) as a part of the impact of the predator community on forest rodents.

2.5. Estimating the numbers of rodents, shrews, and ungulate carcasses

Data on population dynamics of rodents and shrews came from a long-term trapping of small mammals in BNP

Clethrionomys glareolus

$Y = 0.676 + 0.281 X$

$R^2 = 0.956$, $P < 0.0005$

Apodemus flavicollis

$Y = 0.774 + 0.152 X$

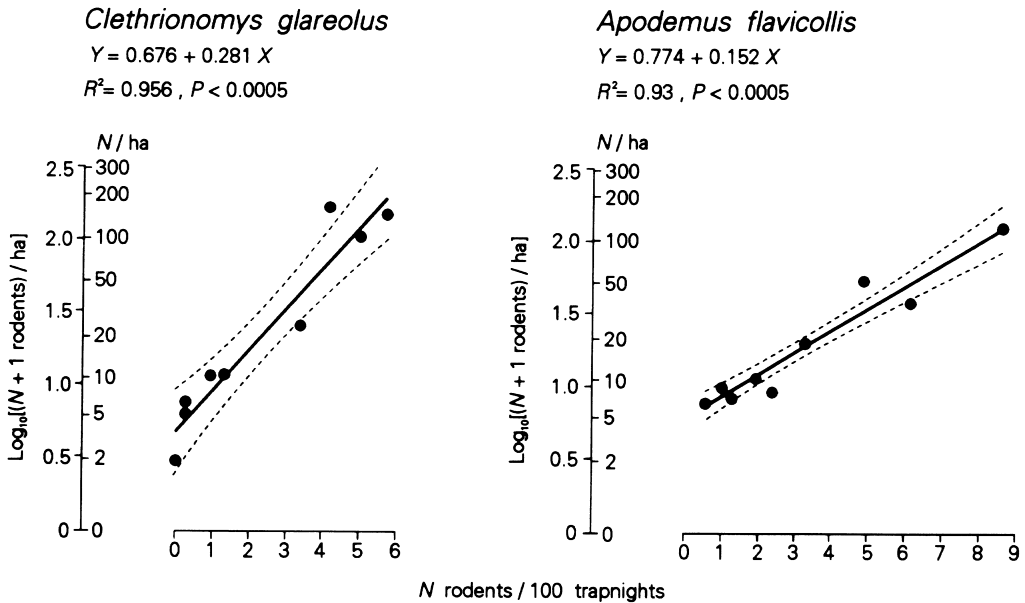$R^2 = 0.93$, $P < 0.0005$

N rodents / 100 trapnights

Fig. 1. Conversion of indices of rodent abundance (N rodents/100 trapnights; data from the long-term trapping in oak-lime-hornbeam forests of Białowieża National Park) into densities (N rodents/ha) by relating the indices to the density estimates obtained in the same years and seasons, on study plots located in the same forest type of BNP. Density estimates (spring, summer and autumn in bank voles; summer and autumn in mice) from Sikorski (1989, and unpubl. data), Wołk & Kozłowski (1989), Wójcik (1993), and Jędrzejewski et al. (1995). Dashed lines indicate 95% confidence intervals.

(Pucek et al. 1993, and Z. Pucek unpubl.), and included the numbers of bank voles, yellow-necked mice and *Soricidae* per 100 trapnights in spring (April–May), summer (July), and autumn (September–October) of 1983–1993. For estimating rodent densities in summer and autumn during 1985/86–1993, we correlated the results of studies done by various researchers within our 11.2 km^2 study area on densities of mice (9 seasons) and bank voles (9 seasons) with our indices of rodent numbers obtained concurrently by the long-term trapping (Fig. 1).

In the winters of 1986/87–1992/93, the western part of BNP (ca. 15 km^2 including the 6.5-km^2 study area) was searched for carcasses of ungulates either killed by wolves and lynx, or those that had died from other causes.

3. Results

3.1. Numbers of forest rodents and pine martens

Population dynamics of bank voles and yellow-necked mice in BNP (analysed in detail by Pucek et al. 1993) shows seasonal fluctuations; numbers increase from spring till early autumn due to reproduction. Over winter, rodents decline to low numbers. Heavy seed crops in 1982 and 1989,

typically, caused winter breeding of rodents and outbreak of their numbers in 1983 and 1990, respectively (Fig. 2). Extremely high numbers of rodents decreased rapidly, and they crashed in the following springs (in 1984 and 1991).

Numbers of martens in the 7 autumn-winter seasons were rather stable ($CV = 24\%$) and varied only 2 times between min and max recorded numbers (Fig. 2, Table 1). In 1991/92 and 1992/93, the density of marten was estimated by mapping the home ranges of the radiotracked martens known to live in the 6.5-km^2 study area (Fig. 3). In the cold season of 1991/92, one year after rodent outbreak, 6 martens resided there (2 males and 4 females). Moreover, marten tracks were often observed on the eastern border transect beyond the territories of females 6 and 33, possibly indicating part of an untrapped marten's range. Based on the assumption of an additional 0.5 marten in the study area, we marked this possible underestimate in Fig. 2. In 1991/92, female ranges did not overlap each other, whereas those of males did. Extensive overlap was also recorded between male and female ranges (Fig. 3).
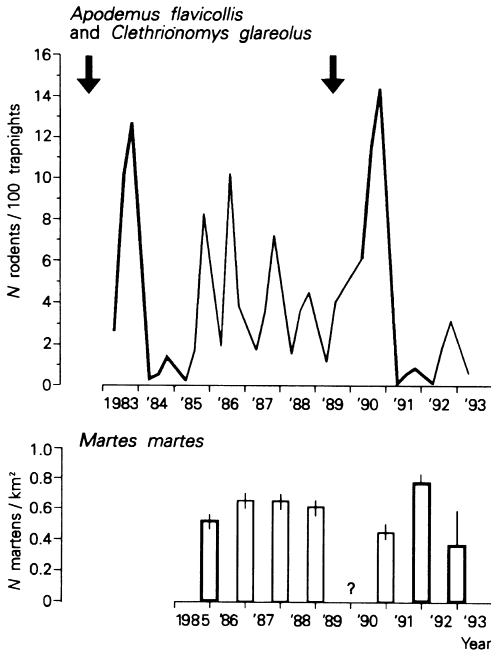
Fig. 2. Autumn–winter density indices of pine martens (lower panel) in relation to forest rodent abundance (upper panel) in BNP. Arrows denote heavy seed crops of oak, hornbeam, and maple. Thick lines denote outbreaks and crashes of rodents after the heavy seed crop and marten numerical response to the extreme numbers of rodents. Vertical lines on marten density bars are estimates of sampling error in 1985/86–1990/91 (martens censused by snowtracking) and possible underestimate of densities in 1991/92–1992/93 (martens censused by radiotracking).
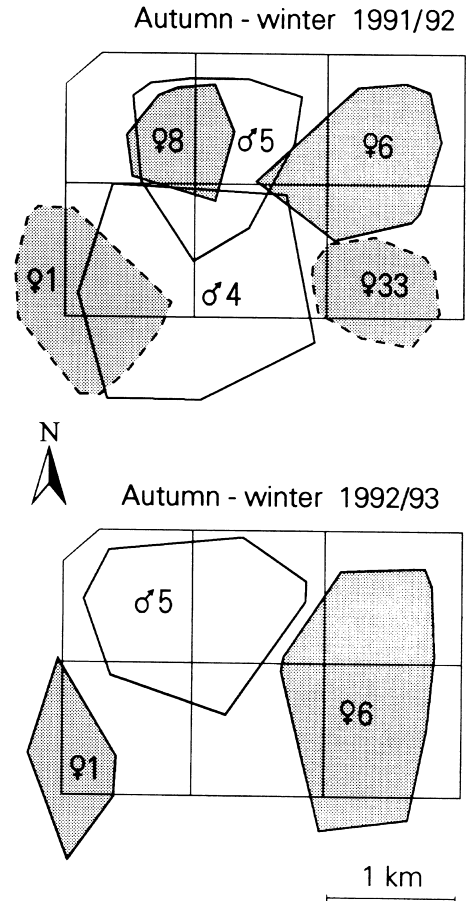

Fig. 3. Map of home range distribution of martens on a 6.5-km² area in BNP in two winters. Continuous lines denote ranges of martens radiotracked during a given winter. Dashed lines mark ranges of adult martens that were radiotracked in spring and summer 1992 and apparently were present in the area during the preceding winter. Home ranges are Minimum Convex Polygon estimates. Marten symbols as in Appendix.

In 1992/93, only 3 martens were trapped and radiotracked in the area and their home ranges did not overlap (Fig. 3). Additionally, a non-collared marten was observed once on the southern border transect (between the ranges of females 1 and 6), and tracks of an untrapped marten (a female as determined by urine marks on trail) were seen within the male 5's territory. These additional 1.5 martens in the area are shown as maximum underestimate in Fig. 2.

Numbers of marten were not related to the current year numbers of rodents. Numerical response of resident martens to rodent numbers only occurred with 1-year lag and it was log shaped (Fig. 4). Had the numbers of martens varied within the ranges of error shown in Fig. 2

for each winter, the numerical response would remain the same, with a clear 1-year lag in relation to rodent dynamics.

In winters of 1985/86–1990/91, the effect of snow cover on marten mobility was evaluated. On average, the index of track abundance (N tracks km^{-1} × day^{-1}) decreased by 43% between the snow depth of 1–10 cm and >40 cm ($Y = 3.746-0.04X$, $n = 36$, $R^2 = 0.163$, $P < 0.05$) (Fig. 5).

3.2. Marten home ranges

Martens were radiotracked during the rodent crash year 1991 and in 1992–93 during moderate numbers of rodents. The average home range (100% MCP) was 183 ha, female ranges (149 ha) being 2/3 of those of males (223 ha) (Table 2). In 7 cases, we compared the spring–summer range of an individual with its autumn-winter range. The cold season ranges were smaller by 8–54% (on average 33%, SD=17.6) than the warm season ranges. The most intensely utilised part of mar-

ten home ranges (including 75% of innermost localities) covered only 25–52% (on average 40%, SD=8.6) (Table 2).

3.3. Functional response and predation impact on forest rodents

Mean numbers of voles and mice taken by a marten per day in autumn–winter was compared to the autumn densities of these two main prey. The observed 40-fold changes in autumn vole

Table 1. Numerical and functional responses and predation by pine marten on 6 prey groups in the autumn-winter seasons (1 October–15 April) in Białowieża National Park. Funcional response: N prey specimens or prey biomass eaten by a marten per day; predation impact: N prey specimens or prey biomass eaten by all martens per 1 ha. Estimates of rodent abundance: trapping indices (N/100 trapnights; see Fig. 2) converted to densities using the regression equations in Fig. 1. *rodents bred throughout winter. ? = no data.

| Parameter	1985/86	86/87	87/88	88/89	89/90	90/91	91/92	92/93
N martens/km^2	0.511	0.649	0.644	0.608	?	0.444	0.757	0.362
Clethrionomys glareolus								
Bank voles in autumn (*N*/ha)	17.8	15.0	60.0	42.4	31.1*	194.3	4.7	19.0
N voles eaten by a marten/day	1.2	5.1	5.2	4.3	4.5	5.0	1.1	?
N voles eaten by martens/ha	1.2	5.5	5.6	5.1	?	4.4	1.7	?
Biomass of voles eaten/ha (g)	21.2	94.3	95.0	87.2	?	75.1	28.6	?
Apodemus flavicollis								
Mice in autumn (*N*/ha)	50.3	10.9	17.8	7.5	9.5*	121.0	6.3	7.3
N mice eaten /day	0.6	1.9	1.3	1.4	1.6	1.5	1.2	?
N mice eaten /ha	0.6	2.4	1.6	1.6	?	1.3	1.8	?
Biomass of mice eaten/ha (g)	19.5	75.4	51.0	51.1	?	42.0	54.6	?
Soricidae								
Shrews in autumn (*N*/100 TN)	0.73	0.13	0.30	0.32	0.36	0.29	0.09	0.57
N shrews eaten/day	0.1	0.4	0.8	1.6	0.3	0.2	0.7	?
N shrews eaten/ha	0.1	0.5	1.1	2.0	?	0.2	1.0	?
Biomass of shrews eaten/ ha (g)	0.9	4.1	7.9	14.8	?	1.3	7.6	?
Birds								
N birds eaten/day	0.02	0.01	0.03	0.09	0.004	0.01	0.12	?
N birds eaten/ha	0.02	0.01	0.04	0.11	?	0.01	0.18	?
Biomass of birds eaten/ha (g)	1.7	1.0	4.1	11.6	?	1.0	19.2	?
Amphibians								
N frogs eaten/day	0.7	0.1	0.2	0.6	0.1	0.1	2.5	?
N frogs eaten/ha	0.7	0.2	0.2	0.7	?	0.1	3.7	?
Biomass of frogs eaten/ha (g)	7.1	1.7	2.4	7.0	?	1.0	37.9	?
Ungulate carcasses								
N carcasses found	?	53	41	24	9	136	43	23
Carcass eaten/day (g)	1.7	1.9	7.0	14.2	8.5	3.0	46.1	?
Carcass eaten/ha (g)	1.7	1.4	8.9	17.0	?	2.6	68.7	?
Total biomass eaten/ha (g)	191	242	241	227	?	166	283	?
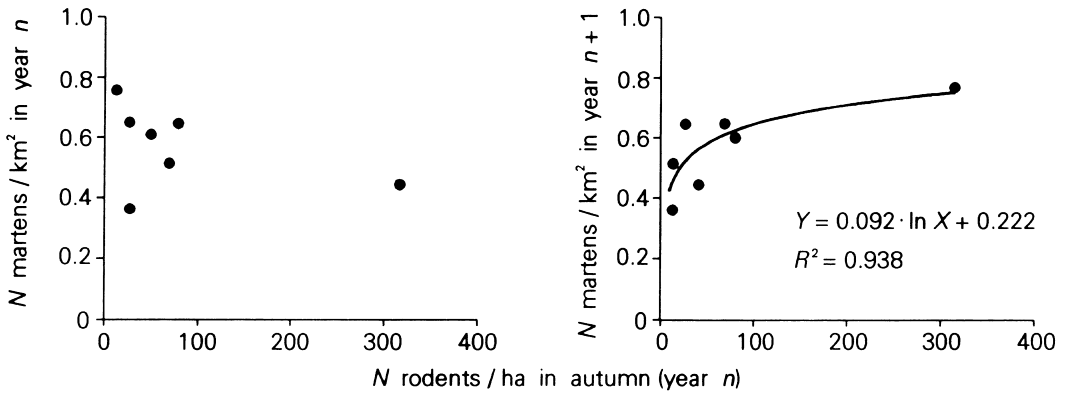
Fig. 4. Numerical response of marten (autumn–winter densities) to the variation in autumn numbers of forest rodents in BNP in the same year (left panel) and with 1-year lag (right panel).

density were followed by only 5-fold increase in marten hunting rate for voles (Table 1) and the functional response best fitted the logarithmic curve (Fig. 6). The 19-fold changes of mouse

numbers were not reflected in the marten's hunting rate for mice (Fig. 6).

In the autumn-winter seasons, martens removed from 1.2 to 5.6 voles and from 0.6 to 2.4

Table 2. Home range sizes (ha) of martens radiotracked in BNP in 1991–1993. N = total number of localisations used for home range estimation and accepted as 100% in both methods. Mean HR = mean home range size (home ranges from the 4 listed periods and not individuals were units for calculating mean values). D mean HR = diameter of the mean home range (m) calculated on the assumption of a circular range. *not included into mean values.

|	Marten No.	N	Min Convex Polygon 100%	Harmonic Mean		
				95%	90%	75%
Spring–summer 1991	M 4	935	349.3	233.5	188.4	133.0
Autumn–winter 1991/92	M 4	216	265.2	160.2	112.2	65.7
	M 5	117	139.9	135.3	104.1	61.3
	F 6	51	121.6	84.1	65.9	39.4
	F 8	42	58.91*	–	–	–
Spring–summer 1992	M 5	202	187.7	173.1	146.5	97.7
	F 1	140	119.4	116.0	86.2	43.0
	F 6	453	258.3	204.1	170.1	111.9
	F 8	154	127.7	101.6	82.7	49.9
	F 33	175	67.5	70.1	57.0	34.7
Autumn–winter 1992/93	M 5	179	173.3	136.0	115.7	83.2
	F 1	15	65.9*	–	–	–
	F 6	84	198.3	145.1	131.2	72.0
Mean HR (males)			223.0	167.6	133.4	88.2
(*SD*)			(84.2)	(40.2)	(34.7)	(28.9)
D mean HR (m)			1685	1461	1303	1060
Mean HR (females)			148.8	120.2	98.8	58.5
(*SD*)			(68.0)	(48.7)	(43.3)	(29.2)
D mean HR (m)			1376	1237	1122	863
Mean HR (all)			182.6	141.7	114.5	72.0
(*SD*)			(81.5)	(49.4)	(41.8)	(31.7)
D mean HR (m)			1525	1343	1207	957
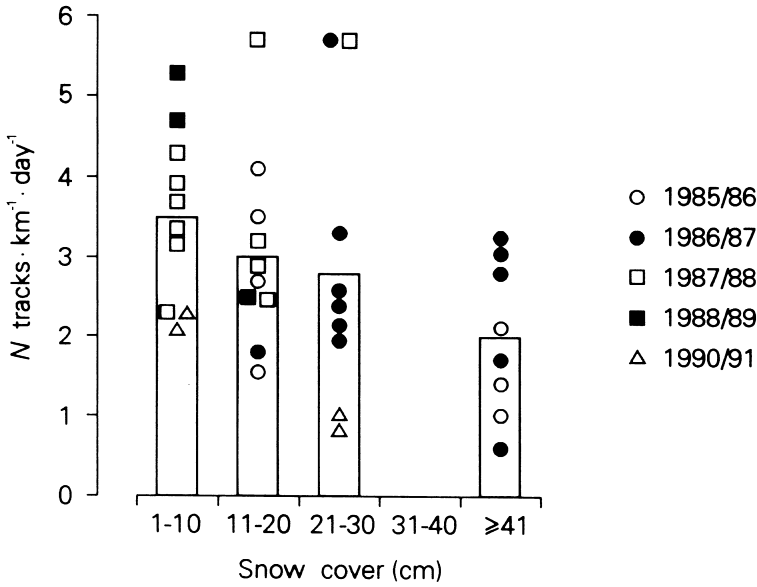
Fig. 5. Number of marten tracks in relation to the depth of snow (data from snowtracking on the grid of transects covering 11.2 km^2 in BNP). Points are the mean values for daily tracking on >10 km of transects (Y = 3.746– 0.04X, n = 36, R^2 = 0.163, P < 0.05). Bars are aver-aged values for a given range of snow depths.
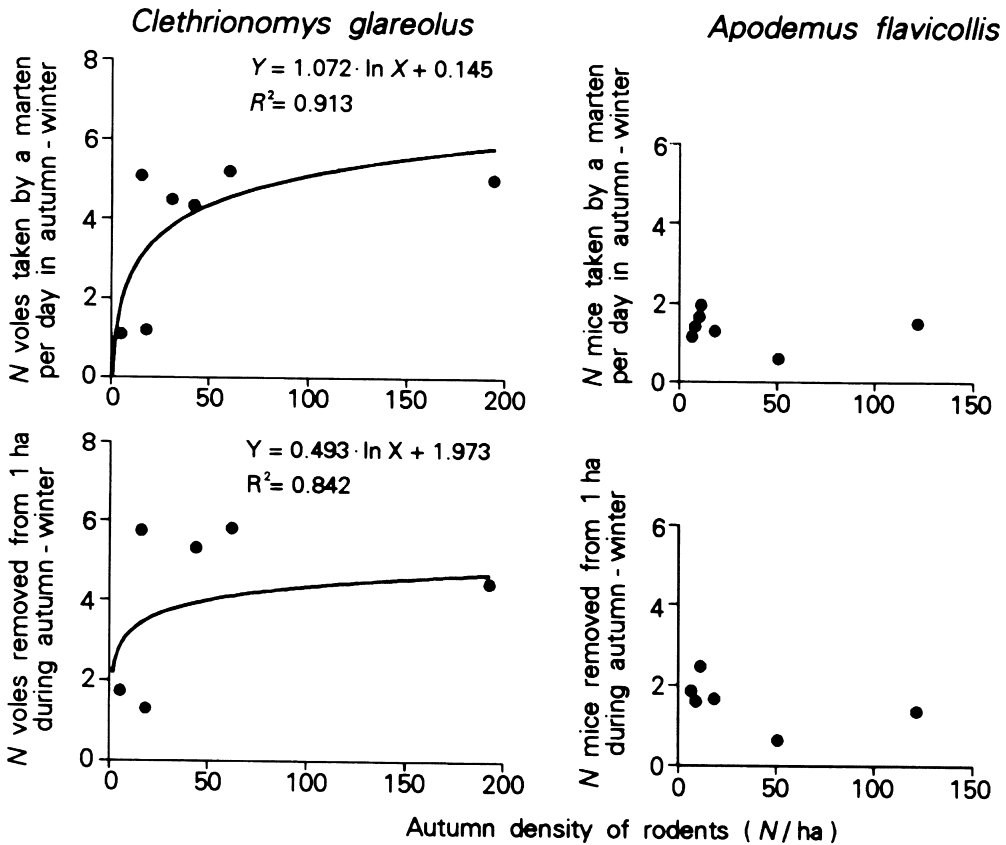

Fig. 6. Upper panel: functional (dietary) response of martens in autumn–winter (1 October–15 April) to autumn (September/October) densities of voles and mice. Lower panel: autumn–winter predation by martens on voles and mice (number of rodents removed/ha) in relation to autumn density of rodents. Each point = one year.
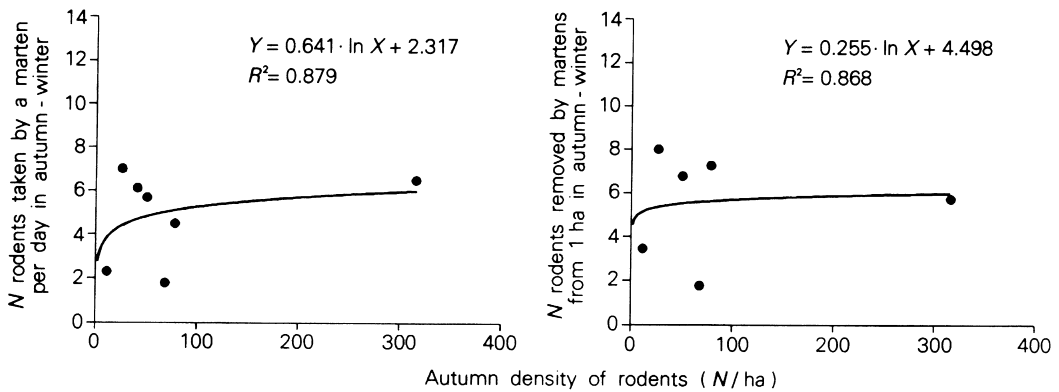
Fig. 7. Left panel: functional (dietary) response of martens to the combined numbers of forest rodents (voles and mice) in autumn–winter. Right panel: autumn–winter predation by martens on forest rodents in relation to rodent density in autumn. Each point = one year.
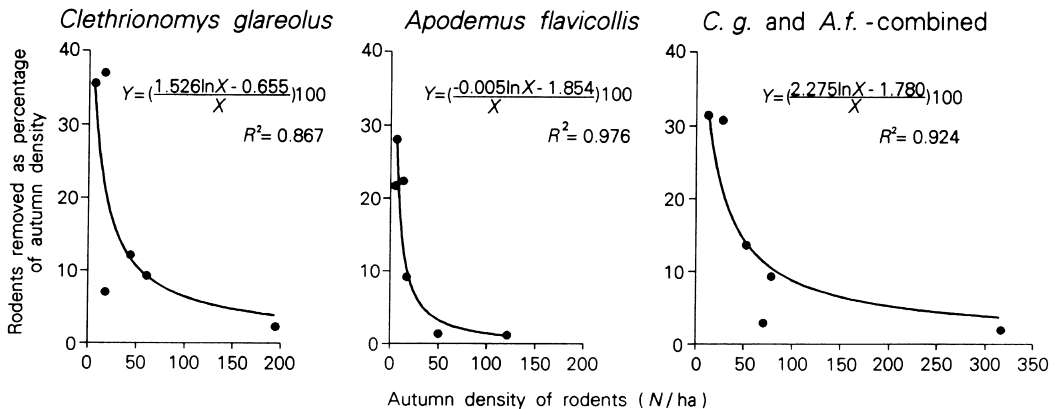

Fig. 8. Percent predation by marten in relation to rodent densities in BNP (voles and mice separately, and combined numbers of both species) in autumn–winter. Each point = one year.

mice from 1 ha (Table 1). Predation on voles showed a tendency to grow logarithmically with increasing density of voles but marten predation on mice was very stable and not related to mouse density (Fig. 6). Both the functional response of martens to the combined numbers of rodents and their predation on both species were only weakly logarithmically related to the combined density of forest rodents (Fig. 7). For both species of rodents, predation by marten was expressed as percentage of autumn densities of rodents (Fig. 8). On average, martens removed 17% of autumn numbers of voles and 14% of those of mice. Both voles and mice suffered the heaviest

predation (up to 36–37% of voles and 28% of mice) at low densities, and negligible impact (1–2%) during their outbreak. The same pattern of percent predation was found when pooled numbers of voles and mice were analysed (Fig. 8).

3.4. Pine marten predation on alternative prey

During 197 days of the cold season, martens ate from 0.1 to 2.0 (mean = 0.82) shrews, mainly *Sorex araneus*, from 1 ha (Table 1). During snowtracking of individual martens, we found on average 0.3 shrews per 10 km of trail killed
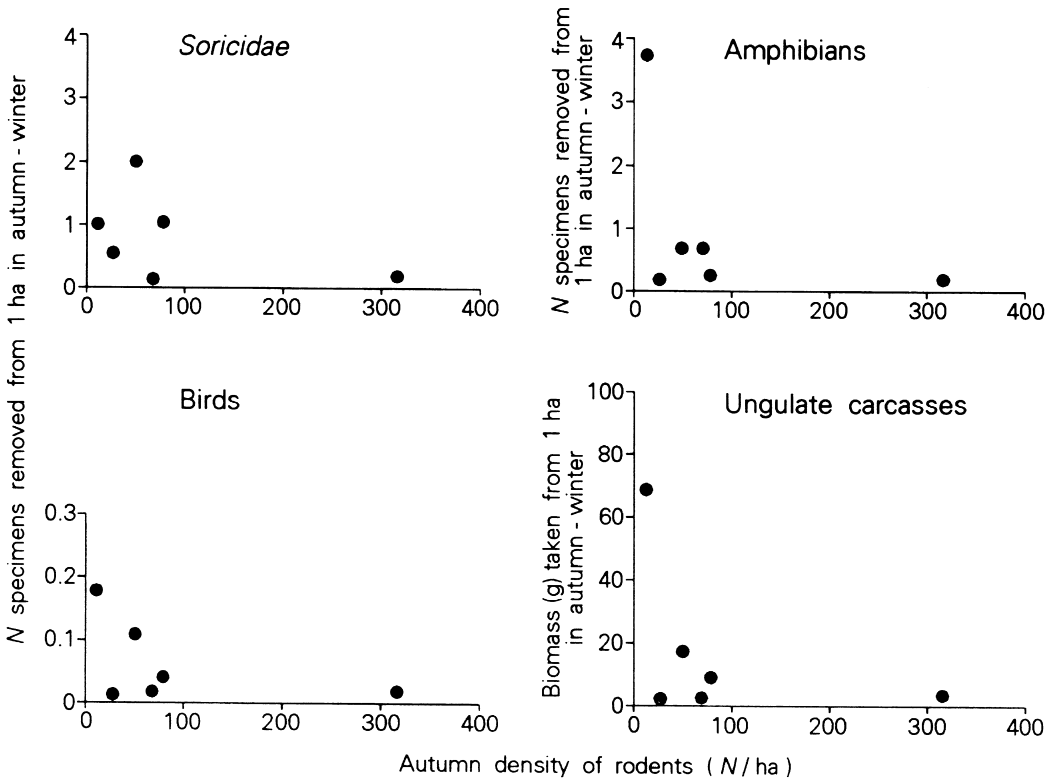
Fig. 9. Martens' predation on shrews, birds, frogs and their consumption of ungulate carcasses in autumn–winter in relation to rodent densities in autumn. Each point = one year.

but not eaten (data pooled for all winters). Based on the daily movement distance (7.2 km), and the average density of martens in BNP (0.568 ind/km^2), we estimated that martens killed and left uneaten 0.24 shrews/ha during the cold season. Thus, the total predation was on average by 25% higher than that calculated for consumed shrews only. Martens' intensity of preying on shrews in autumn-winter (functional response) was not related to shrew abundance in autumn ($R^2 = 0.09$, $n = 7$, *NS*), neither was their total predation on shrews ($R^2 = 0.11$, $n = 6$, *NS*) (Table 1).

Birds, an important prey to martens in spring and summer, were only rarely captured in the cold season. Each marten caught from 1 to 24 birds during the entire autumn-winter season. From 0.1 to 3.7 frogs (predominantly *Rana temporaria*) from 1 ha were captured by martens during the cold season. Their consumption of frogs per day was not related to the mean temperature of winter ($R^2 = 0.02$, $n = 7$, *NS*), neither

was their total predation on frogs ($R^2 = 0.12$, $n = 6$, *NS*). The intensity of martens' scavenging on ungulate carcasses (functional response) and their total consumption of carcasses were not related to the abundance of carcasses ($R^2 = 0.06$, $n = 7$, *NS*, and $R^2 = 0.12$, $n = 6$, *NS*, respectively) (Table 1).

Martens' predation on alternative prey was shaped by rodent abundance (Fig. 9). Since the relationships between marten's predation on alternative prey and the density of forest rodents were non-linear, we logarithmically transformed the measures of rodent abundance and marten predation of alternative prey, and conducted the multiple regression analysis including also weather parameters as independent variables. Autumn-winter consumption of birds by martens was shaped by two factors: rodent abundance and the mean temperature of winter (predation on birds grew with warmer temperature) ($R^2 = 0.954$, $n = 6$ years, $P = 0.01$). Martens' consumption of ungulate carcasses was determined

by the abundance of rodents and the mean snow cover (consumption of carcasses decreased with growing snow cover) ($R^2 = 0.946$, $n = 6$ years, $P = 0.013$). Martens' predation on frogs and shrews also showed a tendency to be higher in the years of low numbers of rodents, but the regressions were not significant.

4. Discussion

4.1. Population fluctuations of pine marten — numerical response of a carnivore with delayed implantation

The estimated numbers of martens during the cold seasons showed remarkably little variation, despite nearly 30-fold changes in rodent density. Obviously, before dispersal of young in late summer, numbers of marten were higher than those in the cold season. During our study we observed 5 litters of young martens that had just left their nests. They included 1, 2, 2, 4 and 4 kittens (mean 2.6, $SD = 1.34$). Given a sex ratio close to 1:1, and the above mean litter size at weaning, we can estimate that, in late summer, the number of martens in BNP could be from 0.83 to 1.74 ind/km². Therefore, the minimum winter and maximum summer numbers of marten varied nearly 5-fold during the study.

Pine marten reproduction cycle is characterised by mating in July–August, pregnancy with delayed implantation, and birth of young in March–April of the following year (Pucek 1984, Velander 1991). Such a long breeding cycle makes it impossible for martens to quickly respond numerically to the varying abundance of prey. Moreover, the significant increase of marten numbers one year after rodent outbreak is also prevented by poor food supply (crash of rodents) during rearing of young. In effect, the density of resident martens in 1991/92 was only by 22% higher in comparison to the average densities in 4 years shaped by moderate numbers of rodents (1985/86–1990/91). The decline of resident martens (one year after the crash) was not very dramatic either. The number of martens in the post-crash years (1985/86 and 1992/93) were, on average, 23% lower than those in moderate years. Dramatic fluctuations of marten

numbers are also prevented by adaptation of this species to use alternative resources: mainly birds and fruit in summer, and insectivores and ungulate carcasses in winter (Jędrzejewski et al. 1993).

There are little data on pine marten population fluctuations in Europe. Indices of abundance from hunting statistics (even as long-term as 53 years in Grakov 1981) reflect the trapping effort, conditions and policy rather than marten population trends. Pulliainen (1981) showed a 13-year data on snowtracking of martens in Finland (where min and max indices of abundance varied about 15-fold), but the data on cyclic rodent abundance were not available. Moreover, in boreal and subarctic conditions, marten fluctuations may also be linked with those of the red squirrel *Sciurus vulgaris* (Yurgenson 1954, Pulliainen 1984).

Two long-term studies show the fluctuations of stoat *Mustela erminea* (another mustelid with delayed implantation) in relation to the varying abundance of their prey. Kaikusalo (1982) censused stoat, weasel and vole numbers at Kilpisjärvi (Finland) in 1968–1978. They all showed 4–5-year cycles. Stoat numbers did not depend on vole numbers of the same year ($R^2 = 0.17$, $n = 11$ years, $P = 0.212$), but they did with 1-year lag ($R^2 = 0.41$, $n = 10$ years, $P = 0.046$, both calculated by us from data of Kaikusalo). Debrot (1983) presented data on linked fluctuations of stoat and the water vole *Arvicola terrestris* in Switzerland. Stoat numbers were not determined by water vole abundance of the current year ($R^2 = 0.01$, $n = 27$ years, $P = 0.663$), but they were by the preceding year's abundance of voles ($R^2 = 0.59$, $n = 27$ years, $P < 0.0005$, both calculated by us from Debrot's data). In contrast, a weasel *Mustela nivalis* which has a short reproductive cycle responded numerically to rodent abundance with no time lag, both in Białowieża (Jędrzejewski et al. 1995) and Kilpisjärvi (Kaikusalo 1982).

4.2. Predation on rodents by a resident generalist predator with delayed numerical response

Andersson and Erlinge (1977) have classified predators into 4 groups according to their feed-

ing habits and residency: specialists, generalists, residents and nomadic species. Generalist predators with open access to alternative prey were predicted to stabilize rodent numbers due to S-shaped functional response to increase of rodent numbers and a shift to alternative resources when prey declines. However, in the case of pine marten, the assumption of S-shaped functional response was unrealistic. Functional response of marten to changes in rodent numbers was clear only in the case of the bank vole, its preferred prey, and it was log shaped (type II response, Holling 1959). Our detailed long-term study on marten diet (Jędrzejewski et al. 1993) evidenced that martens (1) are specialised on one prey type (forest rodents, mainly the bank vole), and (2) are adapted to exploit alternative resources when rodents are scarce. In result, marten is able to stay in the area and continue to hunt rodents even at the autumn densities of the latter as low as 11 ind/ha, when rodent specialist, the weasel, has gone extinct from the study area (Jędrzejewski et al. 1995).

Predation impact by martens (as number of rodents removed from unit area) did not vary much between years. It was a product of martens' functional and numerical responses which, in the sequence of outbreak and crash of rodents, had opposite vectors. During rodent outbreak, a slight increase of the consumption of rodents by martens, but not yet increase in marten numbers, was recorded. During a crash year, decline in the consumption rate coincided with higher numbers of marten. As a result, absolute measures of predation were little variable, and the percent predation was inversely dependent on rodent density. Very high predation impact in the crash year (over 30% of autumn numbers of rodents) indicates that martens deepen and prolong the low phase of rodents. High predation by resident predators during rodent low phase was found in earlier studies by Pearson (1966), Fitzgerald (1977), and Goszczyński (1977). Also, predation by tawny owls and weasels in BNP had similar effects on rodents: their pressure was heavy at low densities of prey (Jędrzejewski et al. 1995, W. Jędrzejewski et al. unpubl.). However, pine marten, due to its delayed numerical response, was the only species of predator the predation rate of which was inversely density dependent over the entire range of rodent densities.
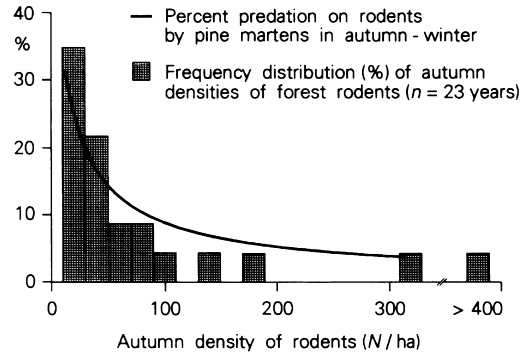

Fig. 10. Percent predation curve of marten in autumn–winter in relation to rodent densities in BNP (as in Fig. 8) compared to the frequency distribution of the autumn densities of rodents in 1971–1993 (from Pucek et al. 1993, and this paper; indices of rodent numbers converted to densities by equations in Fig. 1).

We compared the curve of marten predation rate (derived from empirical data points) in autumn-winter with the frequency distribution of autumn densities of rodents over 23 years in BNP (Fig. 10). The heaviest percent predation by martens falls to the prey densities that occur most frequently. Thus, in the pristine forests of BNP, martens are well adapted to the most common densities of their primary prey.

Marten predation on alternative prey depended mainly on the abundance of rodents. This conformed to the alternative prey hypothesis (Angelstam et al. 1984, Korpimäki et al. 1990), which states that predation can be a factor synchronising the cycles of rodents and small game in the northern Scandinavia. However, in the rich deciduous forests, each of the alternative resources played less important role for marten than forest rodents. Thus, it is unlikely to observe clear declines of shrews, birds and frogs during the crash of rodents.

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Appendices

Appendix. Pine martens Martes martes radiotracked in BNP in 1991–93. Home range size: – not estimated; + estimated.

Marten	Body mass (g)	Dates of radiotracking	Number of locations	Home range estimate
Female 2[a]	900	12–16 April '91	4	–
Male 4	1300	8 May–14 Sept., 25 Sept. '91–19 March '92	1151	+
Female 6	1000	18 Nov. '91–1 Apr. '92, 13 June–14 Dec. '92, 13 Feb.–6 July '93	688	+
Male 5	1300	30 Jan.–9 March, 2 Apr.–26 June, 2 Oct. '92–6 May '93	498	+
Female 8	1000	26 March–10 June '92	196	+
Female 1	900	7 May–30 July , 10 Dec. '92–19 Jan. '93	254	+
Female 33[b]	950	8 May–2 June '92	175	+

[a] killed by a red fox or by another marten; [b] disappeared.