Chapter 3

GEOGRAPHICAL AND SEASONAL VARIATION IN FOOD HABITS AND PREY SIZE OF EUROPEAN PINE MARTENS

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Abstract: Although the diet of pine martens (*Martes martes*) has been described in detail from many locations in Europe, the geographical variation in their food habits is unknown. I reviewed the food habits of the pine marten over most of its geographical range, using 43 winter and 23 summer diet studies. Throughout Europe, the most important prey of martens was small mammals, which represented 47% of all prey in winter (range 14–81%), and 42% in summer (range 12–68%). Small mammals were followed in decreasing order of importance by plant (primarily berries) material (16% in winter, 21% in summer), birds (15 and 13%), medium-sized mammals (10 and 4%), and invertebrates (5 and 15%). Plant material and insects were more frequently consumed in southern regions than in northern Europe during winter. Medium-size mammals and large birds were consumed more often at higher latitudes. The proportion of small mammals (mainly rodents) in marten diets increased from the Mediterranean to northern regions, and reached a peak in the temperate deciduous and mixed woodlands; it declined further north in boreal forests. Across all studies, pine martens showed a functional response to fluctuating rodent numbers, but this was much more significant for bank voles (*Clethrionomys glareolus*) than for other rodent species. During winter, there was a trend towards a wider food niche and larger prey in the north compared to the south. Prey size in marten diets was negatively correlated with marten body size, but positively related to the number of days with snow cover. The diet of pine martens varied significantly with latitude and longitude during winter, suggesting that winter is a period of limited food availability.

1. INTRODUCTION

European pine martens (*Martes martes*) are widespread in Europe, inhabiting areas from northern Portugal and Spain to northern Finland and Russia (Grakov 1981). They occupy a wide range of habitats from boreal and temperate forests to Mediterranean forests. The broad habitat niche of martens is reflected in their diverse food habits, which include a variety of mammals, birds, amphibians, insects, fruits, as well as ungulate carcasses and mushrooms (e.g., Grakov 1981, Jędrzejewski et al. 1993, Pulliainen and Ollinmäki 1996). The size of prey utilized by martens varies from 3 g to 4 kg and the ability of pine martens to use such a wide range of habitats and prey causes them to be generalist forest carnivores. Many studies, however, suggest that martens are rodent specialists, which respond functionally to fluctuations in rodent abundance (Jędrzejewski et al. 1993, Pulliainen and Ollinmäki 1996, Helldin 1999). To better understand the interactions among predator and prey populations, we must better understand the variation in food habits of marten across their geopraphic range (Marcström et al. 1988).

The pine marten is a medium-size predator, and its body size varies regionally, but does not follow Bergmann's rule (Reig 1992). An alternative hypothesis for latitudinal size changes in carnivores is based on the assumption of a positive correlation between the size of the predator and available prey (Rosenzweig 1966, Erlinge 1987). According to this hypothesis, martens in southern Europe are larger (Reig 1992) and should feed on larger prey, whereas in northern Europe, martens are smaller and should consume smaller prey. Knowledge of the ratio of prey size to predator body size is critical for understanding adaptations of martens to climatic, latitudinal and altitudinal variation.

Although diets of martens have been described in detail from many localities in Europe, large-scale geographical variation in marten food habits is poorly understood. Reviews of numerous studies from western and central Europe (Clevenger 1994) and the former Soviet Union (Grakov 1981) have failed to reveal geographical trends in the food composition of pine martens. Clevenger's (1994) review was based on only 7 studies from western and central Europe, thus leaving a gap in the data set from north-eastern parts of the species' range. Grakov's (1981) comparisons included data only from the former Soviet Union. The purpose of this chapter is to review the food habits of pine martens over most of their geographical range, to describe geographical patterns in dietary composition to evaluate relationships between prey size in the marten diet and body size of martens, and to describe the extent of variation in food habits of martens when rodent abundance fluctuates.

2. METHODS

Data on the diet of European pine martens were taken from the literature (Table 3.1). Studies were selected based on the following criteria: (1) diet composition was estimated by the analysis of stomachs and/or scats; (2) the study

Table 3.1. Description and results of studies on pine marten (*Martes martes*) diet composition, reviewed in this paper. No.: consecutive number of study locations in both seasons. Latitude: °N, Longitude: positive values °E, negative values °W. Diet composition expressed as percentage of relative frequency of prey items (all prey items identified from scats and/or stomach taken as 100%). Prey groups: 1–small mammals, 2–medium-sized mammals, 3–birds, 4–invertebrates, 5–plant material. The unlisted 6th group ("others") sums to 100% in each locality.

No.	Country, locality	Latitude	Longitude	Mean percentage frequency in marten diet					Source
				1	2	3	4	5	
				Winter					
1	Spain, Mallorca	39	2	19.1	3.4	7.6	3.6	56.2	Clevenger 1995
2	Spain, Menorca	40	3	13.7	0	11.9	0.6	70.6	Ruiz-Olmo and Nadal 1991
3	Spain, Menorca	40	3	22.2	2.8	16.3	14.0	39.6	Clevenger 1993
5	Russia, Caucasus Mts.	41	42	25.2	0	6.5	2.3	65.9	Donaurov et al. 1938
8	Swiss, Jura Mts.	47	7	27.4	2.8	10.0	12.0	44.5	Marchesi 1989
9	Ukraine, western part	50	32	48.5	4.5	6.8	17.4	15.2	Polushina 1957
10	Germany, Oberlausitz district	51	15	35.9	5.6	15.1	17.0	20.7	Ansorge 1989
11	Poland, central part	52	20	38.8	10.0	27.9	2.2	6.6	Rzebik- Kowalska 1972
12	Poland, Białowieża Forest	52	55	60.3	0.6	2.9	10.6	9.0	Jędrzejewski et al. 1993
13	Belarus, Białowieża Forest	52	55	80.7	4.7	5.6	3.9	2.6	Datskevich 1979
14	Russia, Zhiguli Mts.	53	30	55.1	22.6	6.4	12.8	0	Yurgenson 1951
15	Belarus, central part	54	28	78.2	4.7	2.5	0	2.6	Serzhanin 1973
16	Belarus, Berezinski Reserve	54	28	68.4	0.5	8.3	5.7	12.4	Serzhanin 1961
17	Russia, Bashirskii Reserve	54	57	81.2	1.2	8.0	6.6	1.2	Mozgovoi 1971
18	Russia, Ural Mts. (Bashkiria)	54	58	63.7	5.6	12.1	10.5	8.1	Aspisov 1973
19	Lithuania	55	24	51.2	2.9	20.4	1.2	18.3	Maldzhiunaite 1959
20	Russia, Tatarskoi region	55	51	51.7	7.6	20.6	9.3	8.7	Aspisov 1973
21	Belarus, north-eastern part	56	30	31.7	3.0	7.6	13.2	34.3	Sidorovich 1997
22	Russia, Gorkovskoi region	57	44	46.4	14.0	29.1	6.2	0.8	Yurgenson 1951
23	Russia, Mariiskoi region	57	48	72.3	10.9	4.0	4.0	6.9	Aspisov 1973
24	Russia, Pskov region	58	29	55.7	21.3	23.0	0	0	Morozov 1976
25	Russia, Kirov region	58	50	51.1	20.9	12.0	4.0	12.0	Pleshak 1976

Table 3.1. Continued.

No.	Country, locality	Latitude	Longitude	Mean percentage frequency in marten diet 1	2	3	4	5	Source
26	Russia, Perm region	58	56	57.0	16.2	9.5	3.3	10.6	Chashchin 1956
27	Russia, Perm region	58	56	53.0	4.1	17.6	4.0	15.8	Grakov 1981
28	Russia, Central Ural Mts.	58	58	55.8	4.4	17.9	19.0	2.9	Bakeev 1966
29	Russia, Novgorod region	59	32	50.5	14.2	17.7	0	7.0	Morozov 1976
30	Sweden, south-central part	60	15	37.1	7.7	10.9	10.6	15.0	Helldin 1999, 2000
31	Sweden, south-central part	60	15	36.5	26.5	9.2	0	0	Storch et al. 1990
32	Russia, Petersburg region	60	32	53.0	12.1	22.9	0	5.7	Morozov 1976
33	Russia, Leningrad region	60	32	64.1	11.4	14.1	0.9	5.7	Novikov et al. 1970
34	Russia, NW Vologodtskoi region	60	37	50.6	7.5	20.6	2.8	11.0	Grakov 1981
35	Russia, Vologodtskoi region	60	40	53.5	13.1	17.7	0.9	12.0	Gribova 1958
36	Norway, southern part	61	10	18.7	10.7	28.0	6.7	26.7	Selas 1992
37	Russia, Pechora river	62	59	32.1	40.7	25.6	1.5	0	Yurgenson 1951
38	Russia, Pechora river	62	59	36.5	14.3	28.8	0	15.9	Yazan 1962
39	Russia, N Dvina river	63	41	34.5	40.4	11.1	0.8	8.9	Grakov 1981
40	Russia, N Dvina river	64	42	38.9	8.6	17.6	5.4	21.4	Parovshchikov 1961
41	Russia, Karelia	65	32	35.2	17.8	23.4	1.4	9.7	Danilov and Ivanov 1967
42	Russia, Karelia	65	32	52.5	12.2	14.2	0	11.8	Morozov 1976
43	Russia, Arkhangelsk region	66	46	44.4	11.4	21.0	1.9	10.9	Grakov 1962
44	Russia, N Ural Mts.	66	60	40.2	5.4	17.7	2.7	33.7	Gashev 1965
45	Finland, Lapland Forest	68	29	54.4	8.2	17.3	1.1	9.3	Pulliainen and Olinmäki 1996
46	Russia, Laplandskii Reserve	68	32	33.9	7.5	30.7	5.6	11.9	Nasimovich 1948
				Summer					
1	Spain, Mallorca	39	2	23.9	0.8	6.9	13.3	48.3	Clevenger 1995
3	Spain, Menorca	40	3	22.0	3.8	20.1	20.5	28.6	Clevenger 1993
4	Spain, Menorca	40	3	11.9	11.0	15.3	34.7	21.2	Moreno et al. 1988

Table 3.1. Continued.

No.	Country, locality	Latitude	Longitude	Mean percentage frequency in marten diet					Source
				1	2	3	4	5	
5	Russia, Caucasus Mts.	41	42	46.1	0.8	13.7	33.5	5.7	Donaurov et al. 1938
6	Spain, Cantabrian Mts.	43	-5	63.7	0.1	1.9	13.7	12.6	Clevenger 1993
7	France, Côte d'Or	47	5	16.0	0.3	4.9	10.2	68.3	Baudvin et al. 1985
12	Poland, Białowieża Forest	52	55	53.1	0.2	13.7	14.8	8.4	Jędrzejewski et al. 1993
13	Belarus, Białowieża Forest	52	55	67.9	5.6	0.8	11.1	9.5	Datskevich 1979
14	Russia, Zhiguli Mts.	53	30	56.0	8.7	1.8	21.7	10.5	Yurgenson 1951
15	Belarus, central part	54	28	67.3	0.6	3.7	9.6	6.0	Serzhanin 1973
17	Russia, Bashirskii Reserve	54	57	67.7	1.2	16.0	7.8	5.9	Mozgovoi 1971
21	Belarus, north-eastern part	56	30	25.1	5.3	23.6	25.6	16.4	Sidorovich 1997
25	Russia, Kirov region	58	50	46.2	10.4	12.6	4.6	23.2	Grakov 1981
30	Sweden, south-central part	60	15	22.0	5.4	11.8	36.7	15.5	Helldin 1999, 2000
36	Norway, southern part	61	10	22.8	11.8	30.6	5.1	28.9	Selas 1992
37	Russia, Pechora river	62	59	35.4	1.5	24.1	20.9	15.1	Yurgenson 1951
38	Russia, Pechora river	62	59	56.0	4.6	11.6	0	27.9	Yazan 1962
39	Russia, N Dvina river	63	41	45.3	0.6	13.8	14.4	17.3	Grakov 1981
40	Russia, N Dvina river	64	42	25.4	4.1	15.5	16.1	35.8	Parovshchikov 1961
41	Russia, Karelia	65	32	43.4	6.3	17.3	4.7	16.5	Danilov and Ivanov 1967
42	Russia, Karelia	65	32	60.1	0.8	8.0	9.6	9.6	Grakov 1981
44	Russia, N Ural Mts	66	60	29.4	2.3	7.4	16.7	42.6	Gashev 1965
46	Russia, Laplandskii Reserve	68	32	56.0	2.9	11.5	8.2	18.4	Nasimovich 1948

covered part of either winter or summer, and the seasons were analyzed separately; (3) the place and time span of the study were described; (4) sample sizes were ≥40 stomachs or scats. These criteria yielded 43 winter and 23 summer diet studies (Table 3.1). For the analysis of diet composition, I standardized occurrences as a percentage of relative frequency, i.e., the total number of occurrences of each food item recovered from scats or stomachs was divided by the total number of items identified across all samples. Food items were classified into 6 food categories: small mammals (<150 g), medium-sized mammals (150–2,500 g), birds, invertebrates, plant material (including fungi), and others (including amphibians and reptiles, ungulate carcasses). The standardized food niche breadth (Krebs 1989) was calculated for these major food groups. A Principal Component Analysis (PCA) with Varimax rotation was performed for relative frequencies of occurrence of each food type to describe the trophic relationships of martens across their geographic range. The PCA factors from relative frequency of occurrence data were regressed against latitude and longitude using simple linear regression. Prior to analyses, all variables were arcsine transformed.

An index of prey size was calculated for 37 winter and 21 summer studies according to Erlinge (1987). Prey size indices were calculated for all locations, where prey had been divided into 9 categories. The following body weight categories were used for assessing prey size: insectivorous mammals: 10 g, small rodents: 25 g, squirrels (*Sciurus vulgaris*): 230 g, hares (*Lepus* spp.) and rabbits (*Oryctolagus cuniculus*): 1,500 g, small birds: 30 g, large birds: 500 g, amphibians and reptiles: 15 g, insects: 3 g, and carrion (ungulate carcasses): 200 g. I assumed that the weight of carrion consumed by martens corresponded to the maximal capacity of their stomach (Grakov 1981). Multiple linear regression analysis was used to evaluate the influence of a series of climatic factors on prey size: monthly temperature (December, January, and February), average winter temperature, number of days with snow cover, average snow depth, and average winter precipitation. Climatic data were taken from Kostin and Pokrovskaya (1961) and Lebedeva et al. (1979). I compared prey size in the marten's diet with body size of martens using average (for males and females) condylobasal length of pine marten skulls (Maldzhiunaite 1957, Anderson 1970, Reig 1989).

For more detailed analysis of the role of rodents in marten diets, percent frequency of occurrence in scats/stomach was used, i.e., the number of scats or stomachs with rodent remains compared with the total number of scats or stomachs sampled. Spearman rank correlation was used to analyze the association between percent frequency of occurrence of rodents in the marten diet and rodent abundance across years. Only studies with ≥4 years of information were included in this analysis. The association between percent occurrence of rodents and occurrence of other food groups was evaluated using Spearman rank correlation.

3. RESULTS

3.1 Geographical Variation in Diet Composition

Small mammals (<150 g) were the most important food for martens throughout their range during both summer ($\bar{x}$ = 42%) and winter ($\bar{x}$ = 47%) (Table 3.2). Small mammals were followed in frequency by birds (13% summer, 15% winter) and plant material (21% summer, 16% winter). Medium-sized (150–2,500 g) mammals were more frequent in diets during winter than during summer, whereas insects and plant material were more frequent in summer (Table 3.2). The PCA generated 3 factors that explained 78% of the total variance in the winter diet, and 76% of the variance in the summer diet (Table 3.3). Factor 1 for the winter season shows a gradient from diets with a high frequency of invertebrates and plant material towards diets dominated by medium-sized mammals and birds. The second factor describes winter diets with a high frequency of plant material towards those with an important contribution of small mammals. Factor 3 describes winter diets with an increasing frequency of others foods (e.g. from footnote a of Table 3.3). In the summer, factor 1 shows a gradient of increasing small mammals and decreasing plant material in the diet (Table 3.3). Factor 2 during summer indicates an increasing frequency of medium-sized mammals and birds. Factor 3 describes summer diets with an in-

Table 3.2. Comparison of diet composition (relative frequency of occurrence) of European pine martens during winter (n = 43 studies) and summer (n = 23) based on data listed in Table 3.1. Seasonal differences were evaluated using a Mann-Whitney U-test (** $P < 0.01$, *** $P < 0.005$, NS = not significant).

Prey group	Winter		Summer		Mann-Whitney *U*-test
	Average	(min-max)	Average	(min-max)	
Small mammals (<150 g)	46.8	(13.7–81.2)	41.8	(11.9–67.9)	NS
Medium-sized mammals (150–2,500 g)	10.3	(0–40.7)	3.9	(0–11.8)	***
Birds	15.3	(2.5–30.7)	12.5	(0.7–30.6)	NS
Invertebrate	5.2	(0.9–19.0)	15.4	(0–36.7)	***
Plant material[a]	15.8	(0.2–70.6)	21.4	(5.7–68.3)	**
Others[b]	6.5	(0–27.8)	5.0	(0–12.8)	NS

[a]Includes fungi.
[b]Includes amphibians, carrion, fish, and reptiles.

Table 3.3. Correlation between prey groups in pine marten diets and factors from a Principal Component Analysis in two seasons. Numbers in bold had loadings >|0.50|.

Prey groups	Winter			Summer		
	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
Small mammals (<150 g)	-0.15	**-0.93**	-0.09	**0.80**	-0.41	-0.41
Medium-sized mammals (150–2,500 g)	**0.84**	-0.25	0.03	-0.02	**0.81**	-0.14
Birds	**0.75**	0.40	-0.17	-0.13	**0.78**	0.13
Insects	**-0.55**	0.11	-0.43	-0.09	0.09	**0.89**
Plant material	-0.49	**0.81**	-0.01	**-0.95**	-0.06	-0.18
Others[a]	-0.04	0.10	**0.93**	0.42	-0.28	0.57
Eigenvalue	2.03	1.59	1.06	2.17	1.36	1.09
Percent of variation explained	33.8	26.5	17.6	35.1	22.7	18.2

[a]Includes amphibians, carrion, fish, and reptiles.

creasing contribution of insects. The first two principal components for the winter season clearly separated study sites from 3 different forest zones (Fig. 3.1). The first factor separated Mediterranean, temperate deciduous forests from temperate mixed forests and from boreal forests. The second factor distinguished temperate mixed forests from boreal forests (Fig. 3.1).

The first PCA factor for the winter season was positively correlated with latitude (r = 0.63, n = 43, P < 0.001), and the second factor was negatively correlated with longitude (r = -0.43, n = 43, P < 0.005). Plant material and insects were more frequently consumed in southern regions; their proportions in marten diets decreased in northern Europe. In contrast, birds and medium-sized mammals were consumed more often at high latitudes. Martens preyed on small mammals more often in the eastern portion of their geographic range, but they consumed more plant material in the western portion of their range. During summer, there were weaker correlations between PCA factors and latitude or longitude (r = -0.41–0.32, n = 23, P > 0.05).

Based on latitudinal trends in the proportions of the major prey groups in diets of martens during winter, I constructed a graphical model of geographical variation in the food habits of pine martens (Fig. 3.2). Small mammals, medium-sized mammals, birds, and plant material formed 90% of the frequency of prey. Small mammals were most important in marten diets in the temperate zone (on average, 50% of frequency at 50–60°N) and their role became smaller at both lower and higher latitudes. The frequency of medium-sized mammals increased from zero at 35–40°N to 15–17% at 65–68°N and, similarly, the proportion of birds increased from 7% at 40°N to 20% at 65–68°N (Fig. 3.2). In 37

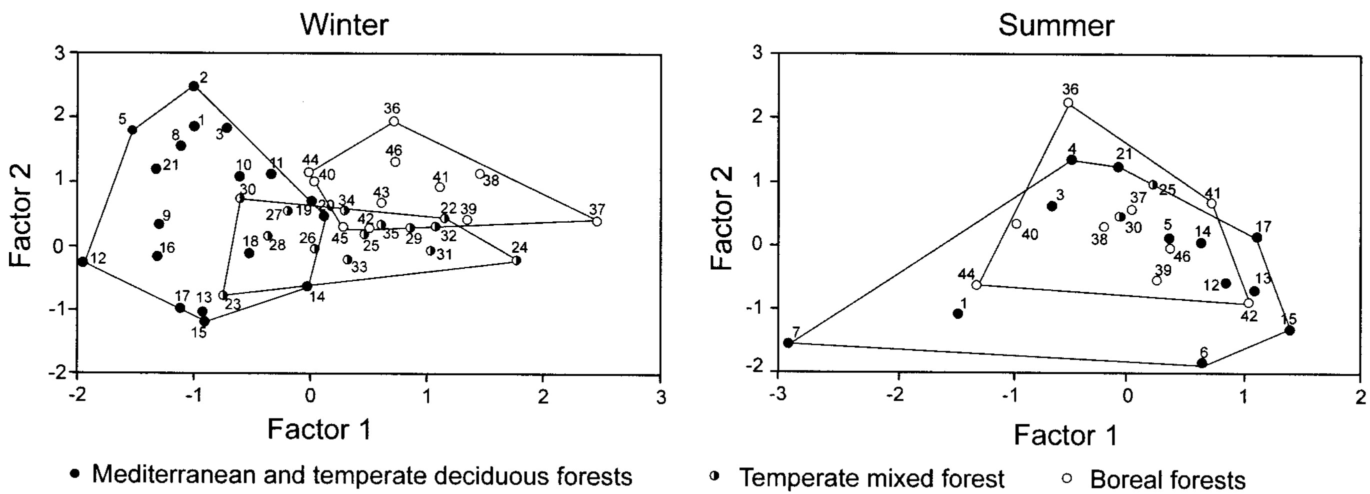
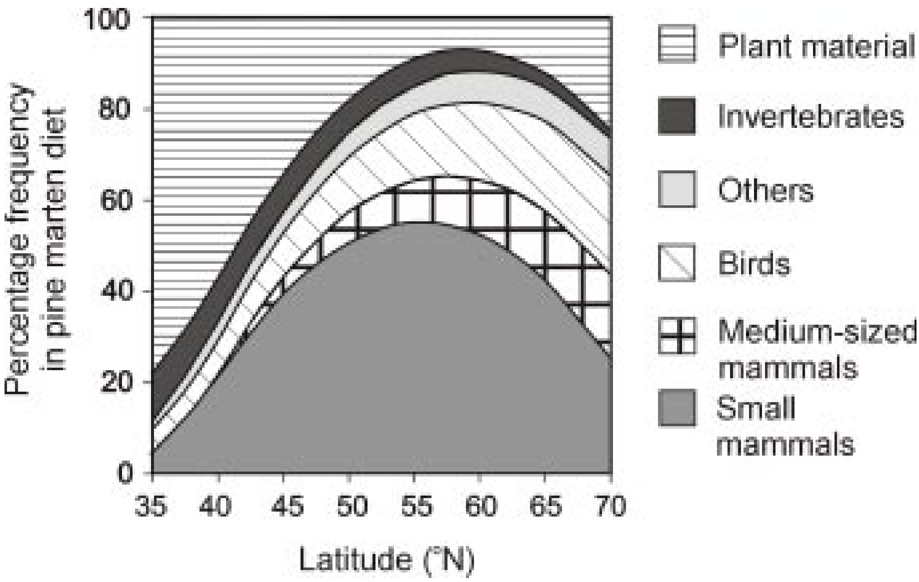


Figure 3.1. Locations of pine marten diet studies, in relation to the first 2 principle components that described 60% of variation in winter diets of martens and 58% of variation in summer diets of martens across 43 winter and 23 summer diet studies conducted in Europe. Numbers correspond with the studies listed in Table 3.1.

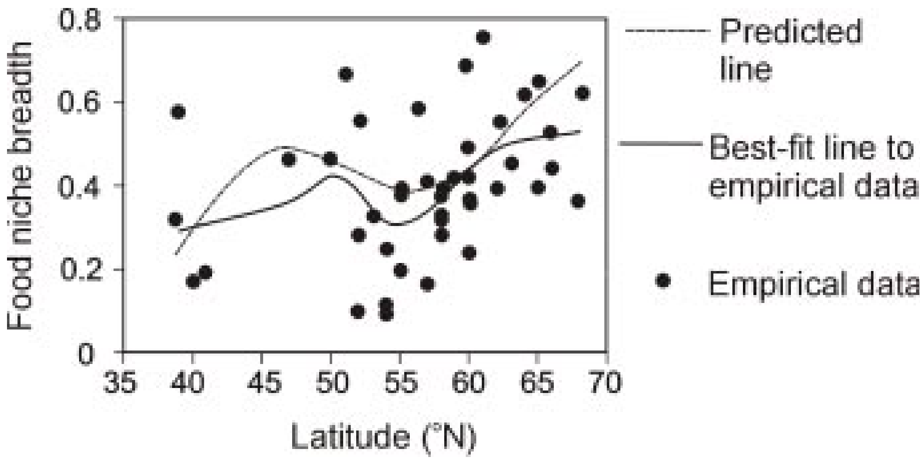
Figure 3.2. Generalized model of latitudinal variation in relative frequency (%) of food categories in winter diets of pine martens (*Martes martes)* in Europe, based on regressions calculated from empirical data (n = 45 localities listed in Table 3.1). The regression equations were as follows: small (<150 g) mammals $Y = -0.14 X^2 + 15.66 X - 379.91$, $r^2 = 0.93$, $P < 0.001$; medium-sized (150–2,500 g) mammals $Y = -22.17 + 0.57 X$, $r^2 = 0.20$, $P = 0.003$; birds $Y = -12.52 + 0.49 X$, $r^2 = 0.21$, $P = 0.002$; invertebrate $Y = 19.36 - 0.25 X$, $r^2 = 0.11$, $P = 0.027$; plant materials (fungi included) $Y = 0.14 X^2 – 16.43 X + 491.03$, $r^2 = 0.83$, $P < 0.001$; others $Y = 0.437 + 0.07 X$, $r^2 = 0.01$, $P = 0.54$.



locations, birds were divided into 2 groups: small and large. The latitudinal increase of birds in the marten diet was due to percent occurrence of large birds ($r^2 = 0.44$, $n = 37$, $P < 0.0005$); the share of small birds was not significant ($r^2 = 0.01$, $n = 37$, $P = 0.25$). In northern Europe, large birds consumed by martens were often capercaillie (*Tetrao urogallus*), hazel hen (*Tetrastes bonasia*), black grouse (*Lyrurus tetrix*), and willow grouse (*Lagopus lagopus*).

The frequency of plant material in the marten's diet decreased from southern to temperate regions (on average, 9% at 57–60°N) and increased again in boreal localities (Fig. 3.2). In southern Europe, martens fed on many plant species such as rowanberries (*Sorbus aucuparia*), carob fruit (*Ceratonia siliqua*), myrtle berries (*Myrtus communis)*, juniper (*Juniperus communis)*, cherries (*Prunus* sp.), rose hips (*Rosa* spp.), figs (*Ficus carica*), and citrus (*Citrus* sp.) (Marchesi 1989, Clevenger 1995, Ruiz-Olmo and Lopez-Martin 1996). In Central Europe, *Rubus* spp. and rowanberries were most often reported as vegetable food of pine martens (Ansorge 1989, Jędrzejewski et al. 1993). In north-

Figure 3.3. Latitudinal variation in standardized food niche breadth calculated for 6 major groups of food. Predicted line is calculated based on the generalized data from Figure 3.2. Best-ft line to empirical data according to Lowess methods (Cleveland 1979).



ern Europe, martens consumed mostly blueberries (*Vaccinium myrtillus*), lingonberries (*V. vitis-idaea*) rowanberries, but also mushrooms (Pulliainen and Ollinmäki 1996, Helldin 2000).

The average standardized food niche breadth was 0.34 (SD = 0.15) in winter, and 0.37 (SD = 0.15) in summer. Food niche breadth did not correlate with sample size (winter: r = -0.15, n = 43, P > 0.05; summer: r = 0.02, n = 23, P > 0.05). In winter, food niche breadth was significantly related to latitude (r^2 = 0.12, n = 43, P = 0.029) but not longitude (r^2 = 0.05, P = 0.136). This indicates a trend towards a wider food niche in northern areas than in southern areas. However, the latitudinal trends in diet were not linear (Fig. 3.3). The food niche was narrow in the south and increased to 50°N. Between 50–60°N food niche breadth decreased, but still further north marten's food niche widened again. Summer values of standardized food niche breadth were not significantly related to latitude or longitude (r^2 = 0.01 and r^2 = 0.07, respectively, n = 23, P > 0.05).

3.2 Variation in Prey Size and Marten Size

Within their geographical range, martens consumed prey weighing as much as 4 kg (hares), and consumed very small prey such as shrews or insects. During both winter and summer, the size of marten prey increased with latitude from 2 g (winter) and 4 g (summer) at 40°N to 20 g (winter) and 7 g (summer) at 68°N (Fig. 3.4). Similarly, the frequency of large prey (squirrels, hares, rabbits, and large birds) in marten diets increased with latitude in both seasons (winter: $r^2 = 0.41$, $n = 37$, $P < 0.001$; summer: $r^2 = 0.31$, $n = 21$, $P = 0.004$).

Relative frequency of medium to large sized (>150 g) prey and prey size index were both negatively correlated with marten body size based on condylobasal length of marten skulls (Fig. 3.5). In the south, larger martens consumed smaller prey, but in the north, smaller martens consumed larger prey. Stepwise regression analysis was used to evaluate the influence of 7 climatic factors on prey size; prey size was significantly related to only the number of days with snow cover ($r^2 = 0.35$, $n = 37$, $P < 0.001$).

3.3 Rodents and Alternative Prey in Diets

The composition of rodent species in the diet of martens varied among regions (Fig. 3.6). In the Mediterranean region, mice in genus *Apodemus* comprised the largest proportion of all rodents consumed ($\bar{x} = 53\%$). Frequency of *Apodemus*, however, declined towards the north. Voles in the genus *Clethrionomys* were most prevalent in the temperate and boreal forests ($\bar{x}$ = 46–52%). *Microtus* represented 27–39% of all rodents in diets in the temperate and boreal regions. In the north, martens also consumed lemmings (*Myopus schisticolor* and *Lemmus lemmus*).

Long-term studies demonstrated that pine martens showed a functional response to fluctuations in rodent numbers; the percent occurrence of rodents in the martens diet was positively related to rodent abundance (7 long-term studies; $r_s \geq 0.54$, duration = 4–11 years, $P < 0.05$; calculated from Gribova 1958, Semenov-Tyan-Shanskii 1959, Grakov 1962, Mozgovoi 1971, Helldin and Lindström 1993, Jędrzejewski et al. 1993, A. Zalewski unpubl. data, Pulliainen and Ollinmäki 1996). Three long-term studies conducted within the temperate deciduous to boreal forests analyzed the dietary response of martens in relation to abundance of various species of coexisting rodents. They all demonstrated significant relationships between martens and abundance of bank voles (*Clethrionomys glareolus*), but not with abundances of *Microtus* or *Apodemus* (Jędrzejewski et al. 1993, A. Zalewski unpubl. data, Pulliainen and Ollinmäki 1996, Helldin 1999). Data collected in Białowieża National Park, Poland over an 11-year period clearly elucidate the relationship between occurrence of rodents in the diet and densities of *Clethrionomys*, but not *Apodemus* (Fig. 3.7).

In years of low abundance of rodents, martens utilized different alternative prey types among regions (Table 3.4). The long-term studies showed that in the lowland deciduous forests, martens ate more birds, amphibians and ungu-

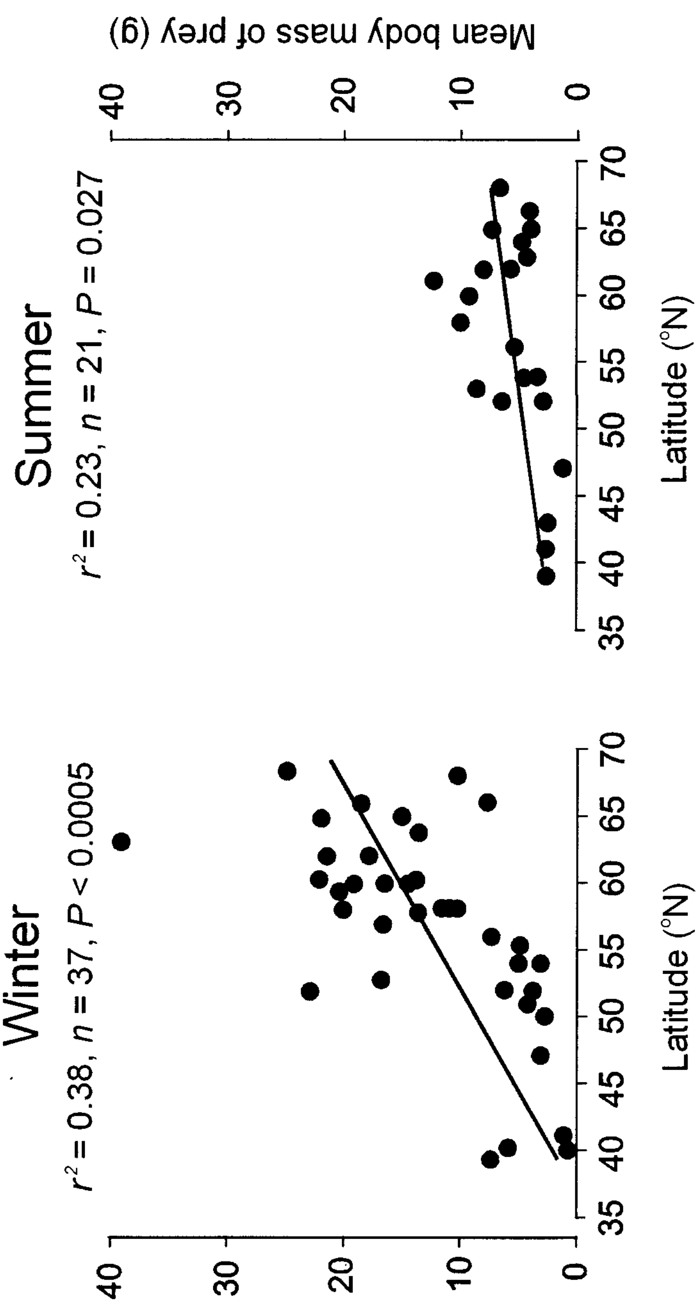


Figure 3.4. Relationship between mean weight of prey in diet of pine martens across Europe in the winter (n = 37 localities) and summer (n = 21) seasons.

Figure 3.5. Relationship between relative frequency of medium to larger-sized (>150 g) prey (squirrels, hares, rabbits, tetraonid birds) in diets of pine martens and mean body mass of all prey and the condylobasal length of male marten skulls. Data on skull size were from Maldzhiunaite (1957), Anderson (1970), and Reig (1989).

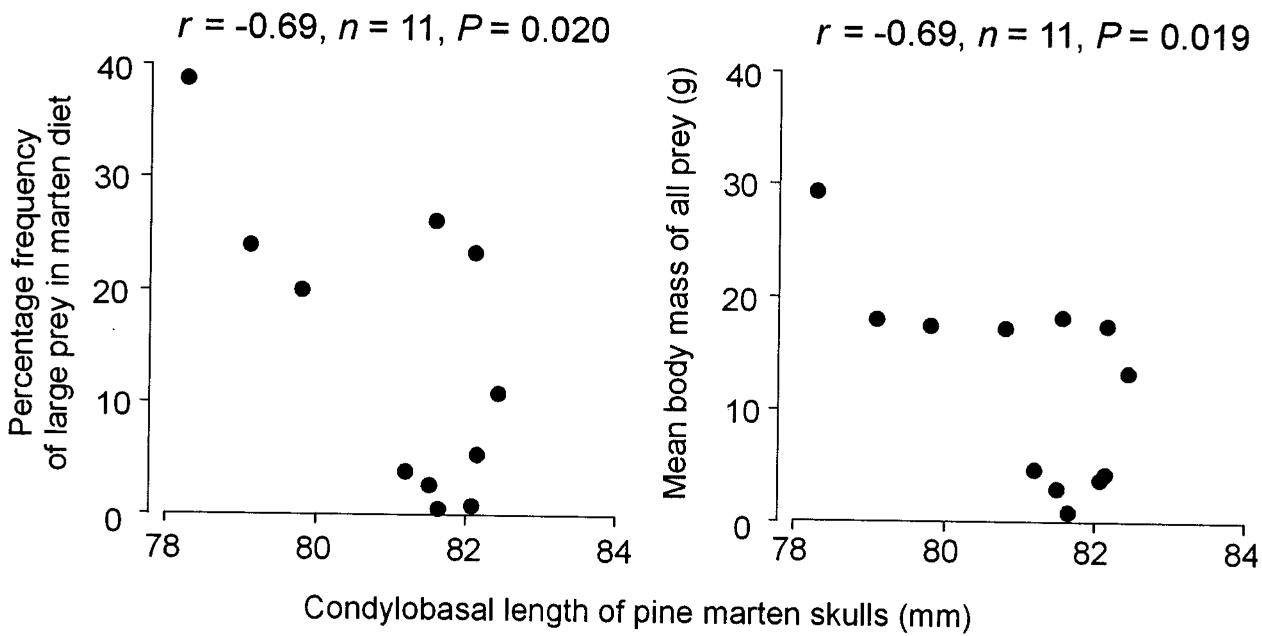
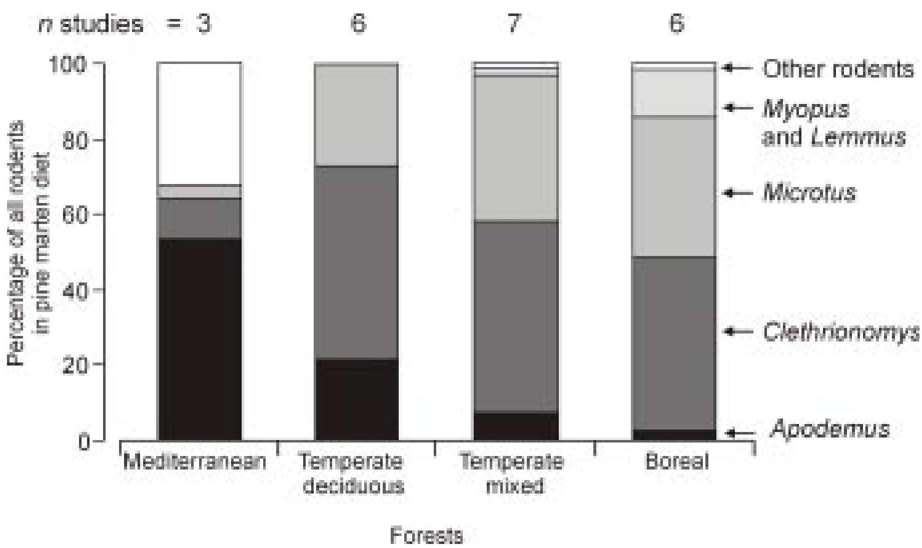


Figure 3.6. Relative frequency of occurrence of 5 groups of rodents in diets of pine martens across 4 biogeographic regions. Sources: Mediterranean forests (Ruiz-Olmo and Nadal 1991, Clevenger 1993, 1995); temperate deciduous forests (Polushina 1957, Maldzhiunaite 1959, Rzebik-Kowalska 1972, Serzhanin 1973, Ansorge 1989, Jędrzejewski et al. 1993); temperate mixed forests (Yurgenson 1951, Gribova 1958, Bakeev 1966, Pleshak 1976, Grakov 1981, Helldin 1999); boreal forests (Nasimovich 1948, Gashev 1965, Parovshchikov 1961, Novikov et al. 1970, Morozov 1976, Pulliainen and Ollinmäki 1996).

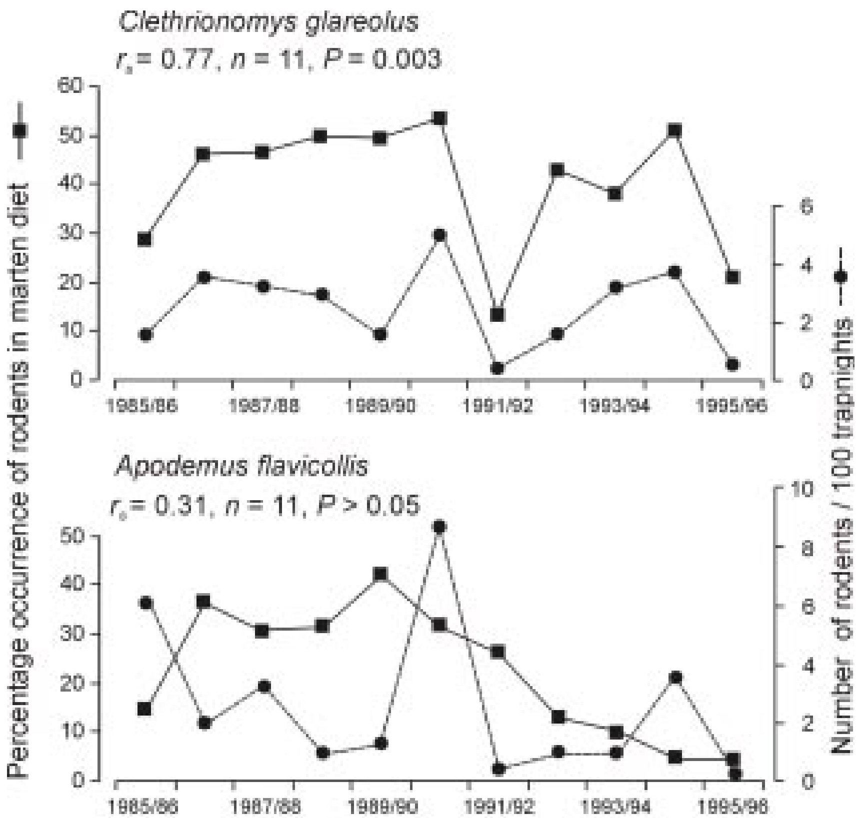


late carcasses, the consumption of which was negatively correlated with consumption of rodents. In the boreal forest, martens consumed more large birds, squirrels, bird eggs, and fruits in years of low rodent abundance. In general, large prey was the alternative prey in Northern Europe.

4. DISCUSSION

I documented a latitudinal variation in diets, food niche breadth, and prey size for pine martens in Europe. The diet of martens varied among years in response to rodent availability and winter conditions (snow cover and temperature) (Jędrzejewski et al. 1993, Pulliainen and Ollinmäki 1996). For example, Helldin's (1999) data were collected during relatively mild winters with a general lack of snow cover; martens ate more berries than in most other studies in this region (Novikov et al. 1970, Morozov 1976, Storch et al. 1990). The percent occurrence of rodents in marten diets varied up to four-fold between years in one study area (Jędrzejewski et al. 1993, Pulliainen and Ollinmäki

Figure 3.7. Eleven-year variations in abundances of bank voles (*Clethrionomys glareolus*) and yellow-neck mice (*Apodemus flavicollis*) during autumn and their percent occurrence in autumn-winter diet of pine martens in Białowieża National Park, Poland. Data on rodent abundance: Pucek et al. (1993), Stenseth et al. (2002); marten diet: Jędrzejewski et al. (1993) and A. Zalewski (unpublished data).



1996). Also, it must be recognized that percent occurrence of food items, although commonly used (Reynolds and Aebischer 1991), overestimates smaller food items (e.g., percent occurrence vs. percent of biomass in insects and fruits) (Jędrzejewski et al. 1993, Helldin 1999). Biomass data would be more informative, but are scarce or have been calculated using different methods among studies.

The latitudinal differences in diet demonstrated the marten's adaptations to varying abundance and availability of food resources. I hypothesize that the most important determinant of dietary composition of martens is the abun-

Table 3.4. Percentage occurrence of alternative prey in winter diet of pine martens and Spearman rank correlations (r_s) between percentage occurrence of rodents and alternative prey in the temperate and boreal regions of Europe.

Country (Source)[a]	*n* years	Alternative prey	Percentage occurrences in marten diet: Average	(min-max)	Correlation with percentage of rodents: r_s	P[b]
Poland (12)	11	Amphibians	21.9	(5.6–47.3)	-0.88	**
		Carcasses	17.8	(5.2–48.2)	-0.73	**
		Birds	9.4	(1.1–29.3)	-0.84	**
Sweden (30)	9	Fruits	23.6	(1.8–52.6)	-0.73	*
Russia (38)	7	Squirrels	19.7	(5.1–41.7)	-0.74	*
		Birds eggs	6.6	(1.4–11.2)	-0.96	***
Russia (43)	8	Large birds	11.2	(2.8–22.5)	-0.76	*
Finland (45)	14	Birds	21.5	(4.0–40.7)	-0.61	*
		Birds eggs	10.9	(0–45)	-0.53	*
		Squirrels	8.1	(0–53.3)	-0.47	*
		Carcasses	6.5	(0–28.6)	-0.52	*

[a]Refers to number of localities in Table 3.1.
[b]* $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

dance and availability of rodents (mainly the bank vole). The proportion of rodents in martens diets was largest in the temperate deciduous forests, where densities of forest rodents are high (Jędrzejewski and Jędrzejewska 1996). Availability of rodents probably decreases in northern latitudes with deeper snow cover (Jędrzejewski et al. 1993). Pulliainen and Ollinmäki (1996), however, did not find a significant reduction of consumption of *Clethrionomys* voles by martens during periods of deep snow cover. In southern latitudes, forest rodent communities were dominated by *Apodemus* mice, which are not a preferred prey of martens (Jędrzejewski et al. 1993).

The latitudinal variation of plant material and insects in the diet of martens might be also related to the regional availability of these food resources. Fruits become more available in the southern region of Europe during winter; they are more frequent in the diet of martens during that period. This was also reported for other predators (stone marten, *Martes foina*, Pandolfi et al. 1996; badger, *Meles meles*, Goszczyński et al. 2000). The lower fruit consumption in northern latitudes may be due to lower abundance, but also because snow cover reduces access to fruit. Pulliainen and Ollinmäki (1996) noted a decreased consumption of berries with increasing snow cover. However, in northernmost regions, martens also consumed mushrooms in winter (Pulliainen and Ollinmäki 1996) and the proportion of plant material in their diets increased. As with fruits, insects are more available to martens in southern Europe because insects are not active in cold winters. Also, the number of insect species consumed was much higher in southern than in northern Europe. In southern Europe, Goszczyński et al. (2000) reported a similar observation for badgers.

The greater frequency of birds in the winter diet of martens from northern latitudes was unexpected. In winter, the availability of birds in northern Europe is much lower due to migration of many species to the south. Thus, increased consumption of large birds such as hazel hen, capercaillie, black and willow grouse which are year round residents, was the likely source of this diet change. Similar to birds, squirrels are probably more available during severe winter conditions. Although very agile and difficult to capture, squirrels are less active in winter and are often captured in their dens (Pulliainen and Ollinmäki 1996). In Poland, the proportion of squirrels in the marten's diet increased only in the harshest winters (Jędrzejewski et al. 1993, A. Zalewski unpubl. data).

Pine martens clearly preferred *Clethrionomys* to *Microtus* voles. Thompson and Colgan (1990) reported a similar finding for the American marten (*Martes americana*) in Ontario. A potential reason for preference for *Clethrionomys* may be similar habitat selection by predator and prey. *Clethrionomys* and martens both favor forests, while *Microtus* voles inhabit grasslands, fields, and other open areas (Pucek 1983, Goszczyński 1985, Brainerd et al. 1994, Jędrzejewska and Jędrzejewski 1998).

The marten's diet was flexible across time and space. Predators should have a broader diet in unproductive environments, where prey items are relatively rare and searching time is longer (Begon et al. 1990). Indeed, food niche breadth of martens increased with latitude. In contrast, Martin (1994) recorded the lowest diet diversity for American marten in the subarctic. This may be explained by the fact that a larger prey item provides food for a longer period, hence reducing kills per unit time, and ultimately resulting in a less diverse diet (Martin 1994). In this study, however, broader niches were documented for populations of martens in northern regions, which tended to consume larger prey.

Body size of European pine martens increases from north to south (Reig 1992). For Mustelids, several hypotheses have been proposed to explain this variation: adaptation to winter condition (especially snow cover) (Petrov 1962), and character displacement between competing Muselids (McNab 1971). An alternative hypothesis for latitudinal size trends in carnivores suggests a correlation between the size of predator and prey available (Rosenzweig 1966, Erlinge 1987). However, an inverse relationship was apparent based on the information reported here; size of European pine martens was inversely related to prey size. Perhaps, martens could increase foraging efficiency by hunting larger prey in the north, thus reducing the duration of activity and energy loss at lower temperatures. Compared to larger martens, smaller individuals have lower food requirements, so they could reduce activity by hunting larger prey. Such behavior may enable smaller martens to stay longer in insulated resting sites and to minimize energy expenditure. Thus, the Mustelids' adaptation to cold climates probably involves a reduction in the duration of exposure to low temperature and a behavioral adaptation to prey selection, rather than an increase in body size (morphological adaptation).

In conclusion, this review documented that the European pine marten is a rodent specialist (particularly on *Clethrionomys*) but is opportunistic as well, feeding on various alternative prey in different biogeographic regions. Its diet varies significantly with latitude and longitude, and the variation in winter diet is more pronounced than during the summer. This suggests that winter is the most food limited season for pine martens.

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