

Diet of sympatric pine marten (*Martes martes*) and stone marten (*Martes foina*) identified by genotyping of DNA from faeces

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Martes martes and *Martes foina* occur sympatrically in most of Europe. Little is known about differences between trophic niches of these species, because martens are difficult to observe and it is impossible to distinguish between scats of both species based on their morphological features. To resolve this problem, we used DNA extracted from faeces for species identification. This method allowed us to compare the diet of the two species in the area of their sympatric occurrence in central Poland. We analysed the composition of 287 scats of stone martens and 155 of pine martens. Both species fed mainly on small rodents, birds and fruits. Although the trophic niches of both martens highly overlapped, we found significant quantitative differences in their food composition. Pine martens fed more frequently on rodents and birds, and stone martens on fruits and insects. These differences were also visible in the seasonal perspective. Although both martens exploited the same forest habitat, genetic identification of faeces allowed us to indicate significant differences in the diet of these closely related species.

Introduction

The stone marten *Martes foina* and the pine marten *Martes martes* coexist within the majority area of Europe. They are the most similar sympatric carnivores in Europe, taking into account phylogenetic relationships, body size, morphology, coloration, foraging behaviour, and

activity patterns (another similar species, the sable *Martes zibellina* is absent from Europe excluding Ural). This multidimensional similarity makes the pine marten and stone marten very interesting objects for comparative studies.

The main feature that differentiates these two species is habitat selection. Pine martens are strongly associated with forest habitats and

they avoid open areas such as fields and meadows (Grakov 1972, Pulliainen 1980a, Fedyk *et al.* 1984, Brainerd 1990, Zalewski *et al.* 1995), although they can hunt at forest edges (Marchesi 1989, Jędrzejewski *et al.* 1993, Heldin 2000). Pine martens can settle in small forests among fields if they are connected by shelterbelts (Marchesi 1989). Stone martens are associated with human settlements and their close surroundings, they live in villages, towns and cities, but they are also encountered in woods and rocky areas (Waechter 1975, Delibes 1983, Skirnisson 1986, Krüger 1990, Broekhuizen & Müskens 2000). The two species may coexist in fragmented habitat with patches of forests, fields, meadows and farm buildings (Marchesi *et al.* 1989), and may co-occur in the same forest patches (Goszczyński *et al.* 2007, Pilot *et al.* 2007).

Diet composition of the pine marten inhabiting forests (Jędrzejewski *et al.* 1993, Zalewski *et al.* 1995, Birks 2002, Zalewski 2004), and the stone marten living in rural or agricultural environments (Tester 1986, Lanszki *et al.* 1999, Lanszki 2003) and in forested rural areas (Genovesi *et al.* 1996) were analysed in a number of studies, using the method of analysis of food remnants in faeces. These studies indicate that both these predators are food generalists. Small mammals, birds, insects and fruits were the staple diet in a proportion depended on food supply and prey densities (Höglund 1960, Lockie 1961, Pulliainen 1980b, Tester 1986, Lindström 1989, Genovesi & Boitani 1997).

In other studies, the diets of the pine marten and stone marten were compared based on their skeletal remnants or dentition. Based on trace elements in skeletons of both species of marten, Gruppe and Kruger (1990) indicated that the diets of these species differ significantly, and the stone marten uses a wider food spectrum than the pine marten. Wolsan *et al.* (1985) showed that the two species differ in the dentition, which also suggests that these predators use different array of food.

In the review of feeding ecology of pine martens and stone martens in Europe, Clevenger (1994) compared the diet composition of both species. However, this comparison was based on articles where either the pine marten or the stone marten was studied separately, and thus little is

known about differences in the diet of both species in the areas of their sympatric occurrence. The examination of this issue demands a very precise distinguishing of scats of both species and limitation of their collection only to environments used by both species simultaneously. However, it is impossible to distinguish scats of both species based on their morphological features. Thus, the diet composition of the pine marten and stone marten in the areas of their sympatric occurrence was analysed jointly as taht of *Martes* sp. (Goszczyński 1976, 1986a, Goszczyński & Pośluszny 2000). Only one study (Marchesi *et al.* 1989) was devoted to comparative analysis. In this study, authors compared the diet of the two species based on faeces collected in shelters previously located with radio-telemetry. This study revealed that pine martens preyed upon small mammals and birds more frequently than stone martens. This approach solves the problem of distinguishing scats of both martens, but it has some limitations: the diet analysis is necessarily limited to radio-tracked individuals, a number of which is usually much smaller than the total population size, and thus the number of available samples is substantially limited.

Another solution for the problem of distinguishing faeces of pine martens and stone martens is the application of molecular techniques. Molecular genetics provides reliable methods of species identification, and is increasingly used for distinguishing faeces of different species (Reed *et al.* 1997, Farrell *et al.* 2000, Mills *et al.* 2000, Davison *et al.* 2002, Dalén *et al.* 2004). For distinguishing between different mustelid species, the method based on digestion of mitochondrial DNA with species-specific restriction enzymes was used most frequently (Hansen & Jacobsen 1999, Riddle *et al.* 2003, Gómez-Moliner *et al.* 2004). This method was also applied to distinguish between the pine marten and stone marten (Vercillo *et al.* 2004). Domingo-Roura (2002) proposed another method of genetic distinction between the pine marten and stone marten, based on species-specific and substantially different allele lengths of a microsatellite locus. In this study, we identified faeces of the pine marten and stone marten using two microsatellite loci, *Mel10* (Domingo-Roura 2002) and *Ma18* (Davis & Strobeck 1998), both of which significantly

differ in allele lengths between these two species (Domingo-Roura 2002, Pilot *et al.* 2007). Based on the analysis of the content of genetically identified faeces, we examined and compared the feeding habits of stone martens and pine martens co-occurring in the same forest patches.

Materials and methods

Study area

The study was carried out in central Poland, in the vicinity of the town Rogów (51°48'N, 19°53'E), in 2001–2004. The study area covered 105 km². A field-forest mosaic is a characteristic feature of the landscape of this area. Forests are diverse in size (from about 0.6 km² to more than 10 km²). The dominant stand types are fresh pine forest (accounting for 46% of stand area) and mixed deciduous forest (38%). The rest of the area is covered mainly by coniferous forest (10%) and alder forest (2%). Forests are dominated by Scots pine (*Pinus silvestris*) and the remaining species are common oak (*Quercus robur*), sessile oak (*Quercus petraea*), common larch (*Larix deciduas*) and birch sp. (*Betula* sp.). The undergrowth is formed from oaks, hornbeam (*Carpinus betulus*), beech (*Fagus sylvatica*), hazel (*Corylus avellana*), black elder (*Sambucus nigra*) and aspen (*Populus tremula*). Blackberry (*Rubus sylvaticus*) is the predominant species in the undergrowth, bilberry (*Vaccinium myrtillus*) occur more rarely (Zielony 1993). The average age of forest stands is approximately 55 years. In such tree stands there are a few natural shelters to be used by martens, e.g. tree hollows, or rotten and non-removed trunks of cut trees.

The small (about 1 ha) fields within the study area are dominated by arable land and cut across by hedges and roads. Apple orchards neighbouring with forest can be an additional attractive source of food for martens. Moreover, among fields occur shelterbelts and small patches of coppies formed of blackthorn (*Prunus spinosa*), wild pear (*Prunus communis*), wild apple (*Malus silvestris*), elder (*Sambucus nigra*) and hip rose (*Rosa canina*).

The annual amplitude of air temperature is 20.5 °C. January is the coldest month of the

year (average monthly temperature is –3.5 °C) and July is the warmest month (+17.8 °C). The first ground frost can occur on 10 October and the last one around 15 April. In the study area, snow cover is present for around 63 days per year (data from the meteorological station of the Warsaw Agricultural University in Rogów).

Among the rodents inhabiting forests in the study area, the most numerous species is the bank vole (*Clethrionomys glareolus*) and yellow-necked mouse (*Apodemus flavicollis*) (Kłosińska 2000, Babińska-Werka unpubl. data). The common vole (*Microtus arvalis*) is the dominant species in open areas, occupying mainly long-term crops (meadows, clover) and balks. In the environs of Rogów the density of the common vole reaches about 80 individuals per hectare (Goszczyński 1986b). In the study period, small-game density was low as compared with that in 1980s and 1990s. For example, the spring density of hares (*Lepus europaeus*) decreased from 24 individuals per 1 km² in 1980 (Wasilewski 1991) to 8–10 individuals per 1 km² in 1999–2003 (Juszko 2006). The same situation was observed in the case of pheasant (*Phasianus colchicus*) and partridges (*Perdix perdix*) (The LZD Rogów inventory data). Apart from the martens, red foxes (*Vulpes vulpes*), badgers (*Meles meles*), domestic cats (*Felis catus*) and dogs (*Canis familiaris*) are the most numerous predators in the study area.

Sample collection

We collected 1375 samples of faeces which based on their morphology were classified as those of martens. Scats were gathered along forest paths and inside the stands. It was known from previous studies (Goszczyński 1986a, Goszczyński *et al.* 2007, Pilot *et al.* 2007) as well as from local hunting and road kills that in the forests of the study area both species of marten are present. Distribution of faeces of the stone marten and the pine marten in the patches of forest in the study area is presented in Fig. 1 (only a part of the study area is shown). Some places characteristic for martens occurrence were checked: clumps of spruce, pine polewoods and some potential shelters: tree hollows and nests of

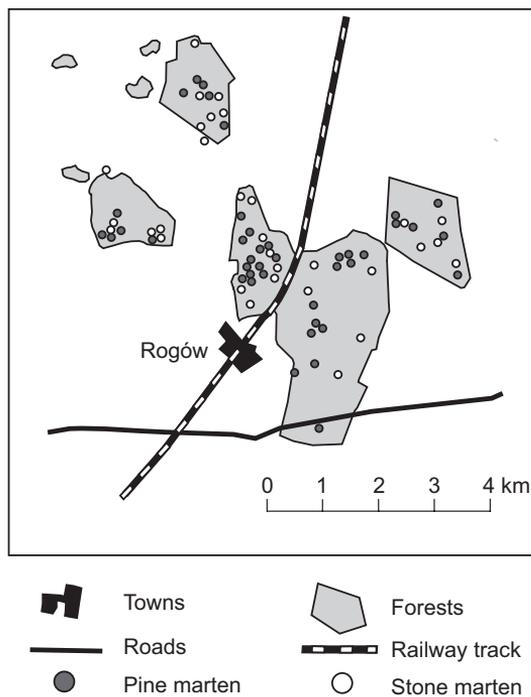


Fig. 1. Distribution of faeces of the stone marten and the pine marten in small patches of forest in the vicinity of the town Rogów (51°48'N, 19°53'E) in central Poland (only a part of the study area is shown). Reprinted with permission of Blackwell Publishing from the article by Pilot *et al.* (2007).

birds of prey. Additionally, faeces were collected during snow-tracking as well as in the lofts and attics of 5 buildings in the vicinity of forests (the buildings situated farthest from and closest to the forest edges were 300 m and 10 m away, respectively). Faeces were picked up with sticks (for each scat a new stick was used to avoid contamination of one sample by another), placed in individual plastic bags with identification numbers written on them and kept frozen at -70°C prior to genetic analysis. For the DNA extraction we used a piece of faeces about 1 cm long that was cut off using a clean scalpel. The remaining part of the faeces was used for the analysis of food composition.

Genetic analyses

We extracted DNA and analysed two microsatellite loci for 365 faecal samples that were chosen

from the total number of 1166 faeces collected in the forests in such a way as to obtain possibly even proportion of samples from different forest patches and in different seasons. Additionally, we analysed 20 faeces randomly chosen from 209 faeces found in buildings neighbouring with forests.

DNA was extracted from faeces using a QIAamp DNA Stool Mini Kit (Qiagen), following the manufacturer's instruction. DNA extractions were performed in a laboratory room that was free of concentrated marten DNA. The analysis of PCR products was performed in another laboratory situated in another building. In order to control for contamination, a negative control was added to each extraction set and to each PCR reaction set. Using the faecal DNA as a template, two microsatellite loci were amplified: *Mel10* and *Ma18*. The microsatellite locus *Mel10* was described as a species-specific marker that allows for distinguishing between *Martes martes* and *Martes foina* due to substantial differences in allele length detected for these two species (Domingo-Roura 2002). We also analysed the microsatellite locus *Ma18*, originally developed in the American marten *Martes americana* (Davis & Strobeck 1998). This locus may also serve as a marker that differentiates the two European species of marten (Pilot *et al.* 2007).

Primers used for amplification of the locus *Mel10* in martens amplify the same region in two other mustelid species: polecat *Mustela putorius* and American mink *Mustela vison* (present in Poland in the wild for about 25 years). Faeces of these species can most easily be confused with faeces of martens. However, the length of alleles in these species differs from their lengths in martens (Pilot *et al.* 2007). That allowed us for distinguishing between faeces of martens and faeces of these species. In the case of the locus *Ma18*, primers used for its amplification in martens amplify the same region in polecat and the length of alleles in that species differs from their lengths in martens. No amplification product has been detected in the American mink, but only one individual of this species was tested (Pilot *et al.* 2007).

Microsatellites *Mel10* and *Ma18* were amplified in reaction conditions described by Pilot *et*

al. (2007), using forward primers labelled with 6-FAM and TET dyes, respectively. DNA fragments were visualized using an ABI Prism 377 DNA sequencer (Applied Biosystems). The program GeneScan 3.1 was used to analyse allele lengths. Each locus was amplified twice for each sample. Only samples for which amplification products were received twice at each of the two loci were assigned to species (for details, see Pilot *et al.* 2007). As the result from one locus was the control for the second one, the simultaneous application of these two markers allowed us to obtain reliable results.

Based on the differences in the length of these two microsatellite loci, among scats found in the forests we identified 78 scats of stone martens and 155 scats of pine martens. Additionally, we identified two scats of other mustelids: the polecat and the American mink. Eleven of 20 analysed scats from human dwellings were identified as those of stone martens, and no result was obtained for the rest of these samples. We failed to assign to species 36% of samples, which was most probably due to DNA degradation, although we cannot exclude that some of these samples originated from non-mustelid carnivores (most likely the red fox). Preliminary analysis based on genotyping of faecal DNA at 10 microsatellite loci indicated that stone marten faeces originated from at least 25 different individuals, and pine marten faeces from at least 34 individuals (M. Pilot unpubl. data).

Analysis of diet composition

The analysis of diet composition was based on 155 faeces of pine martens and 78 scats of stone martens collected in the forests. Additionally, we analysed 209 faeces of stone martens collected from human dwellings neighbouring with forests. We assumed that all of the 209 faeces collected from the attics originated from stone martens, because only stone martens were observed in the vicinity of those buildings. In central and eastern Europe only one case of pine martens inhabiting an attic was registered in Holland (Brokhuizen & Müskens 2000), presumably because of scarcity of forests. The genetic analysis of a random sample of faeces gathered from

human dwellings confirmed that all successfully identified samples originated from stone martens. Moreover, we found during snow-tracking that martens from buildings visited neighbouring forests regularly and foraged there. Because of that we decided to treat jointly faeces of stone martens found in both habitats: 78 from forests and 209 from buildings. Thus, the sample of 287 faeces of stone martens and 155 faeces of pine martens was used to show annual and seasonal variability of diet composition of both species.

Analysis of faeces composition was performed according to commonly used methodology (Lockie 1959, 1961, Goszczyński 1974). Samples were rinsed in the 500 μm sieves under a stream of tap water and indigested remains were segregated into basic categories such as small rodents, insectivorous mammals, hares and other mammals, birds, insects and fruits. Macroscopically visible remains of undigested material were classified as fragments of skeleton, feathers, chitin, stones and peel of fruits, hairs and other. The indigested remains were air-dried to a constant weight and, to evaluate the biomass of the eaten food, the weight of each group was multiplied by an index characterizing their coefficient of digestibility (Lockie 1959, 1961, Goszczyński 1974, 1976).

Small mammals were identified to species or genus based on the morphology of their teeth (Pucek 1984) or hair. We identified guard hairs of small mammals and carrion by using keys of cuticle scale and medulla patterns (Dziurdzik 1973, Teenrink 1991). Birds were grouped into 3 classes: small, medium and large. It was possible to classify only some of them to species or genus through comparison with collection of skeletons and feathers. Insects and fruits were identified through comparisons with gathered collections. Results of diet analyses were displayed as a percentage of biomass and percentage of occurrence of all categories of food in faeces. In the latter case the general number of occurrence of given category was divided by occurrence of all food categories. We applied two methods of presentation of the data on food composition (biomass and frequency of occurrence) to assure that the conclusions concerning differences in the diet of the two species are consistent between these methods. Some prey items (e.g. insects) may

occur in high frequency, but may have little contribution to the total biomass eaten.

Statistics

Frequency of occurrence of various food components was used to evaluate differences in the content of stone marten faeces from forests and buildings, and to evaluate interspecific differences in food of the stone marten and pine marten. For that goal, the χ^2 -test and the test of two percentages (Bailey 1995) were applied. To estimate the trophic niche breadths of the stone marten and pine marten, we used the standardized Levins index (B_{sta}) (Colwell & Futuyama 1971). Dietary overlap was evaluated by using the Pianka index (O) (Pianka 1973). Both indices were applied to the percentage occurrence of food categories in the whole diet. The Levins index formula is:

$$B = \frac{1}{\sum_{i=1}^n p_i^2}$$

where n is the number of food categories and p is the proportion of records in each food category (i) set at 100%. The standardized Levins index formula is:

$$B_{sta} = (B - 1)/(B_{max} - 1)$$

where B is the Levins index (Levins 1968) and B_{max} is the total number of food categories recog-

nized. Results range from 0 to 1.

The Pianka index formula is:

$$O_{jk} = \frac{\sum_{i=1}^n p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^n p_{ij}^2 \sum_{i=1}^n p_{ik}^2}}$$

where p_{ij} (or p_{ik}) is the proportion of foodcategory i recorded in diet of the species j (or k).

Results

Comparison of stone marten's faeces composition found in forests and in buildings

The diet composition determined from analyses of faeces collected in the attics of buildings slightly differs from that from faeces gathered in the forest. When we compared frequency of occurrence of various components of food, insects were more often encountered in scats of martens from human dwellings, while insectivorous mammals were more frequently found in scats collected in the forest (Table 1). Though we found these differences, insects and insectivorous mammals constituted small percentage of biomass taken by stone martens and the difference in the distribution of biomass share of different prey items in the diet was not statistically significant ($\chi^2 = 14.69$, $df = 15$, $P > 0.1$) (Table 1).

Table 1. Mean annual food composition based on 78 stone marten's faeces collected in forests and 209 stone marten's faeces from buildings presented as relative frequency of occurrence (F , %) and percentage of biomass (Bio). Significant P values (Student's t -test) are set in boldface.

Food items	Forests			Buildings			t	P
	N	F	Bio	N	F	Bio		
Rodents	24	18.5	20.2	87	19.2	31.3	0.2	> 0.05
Undetermined <i>Soricidae</i>	3	2.3	4.3	0	0	0	2.1	< 0.05
Hares	2	1.5	4.4	3	0.7	0	0.9	> 0.05
Undetermined mammals	8	6.2	5.6	20	4.4	4	0.8	> 0.05
Ungulate carcasses	1	0.8	0.9	0	0	0	0.8	> 0.05
Birds and eggs	21	16.1	14.1	58	12.8	13	0.9	> 0.05
Insects	14	10.8	1.1	116	25.7	4.8	4	< 0.001
Fruits	57	43.8	49.4	168	37.2	46.9	1.4	> 0.05
Total	130	100	100	452	100	100		

Differences in food composition between the stone marten and pine marten

Comparison of feeding habits of the two species indicates generalistic character of their diet. Both martens ate plant food as well as animals. Small rodents, fruits and birds were three most important food categories of both species (Table 2). Insectivorous mammals, hares, other mammals and insects composed the complementary food. The latter prey was often registered in scats of both species, although in biomass eaten it constituted an insignificant component of food. Analyses of frequency of occurrence of various categories of food indicated that the pine marten fed on small rodents and birds significantly more frequently than the stone marten. On the contrary, fruits and insects were more often encoun-

tered in scats of the stone marten (Table 2). Similar tendency was observed in biomass eaten. Also the whole spectrum of the pine marten diet was significantly different from the stone marten diet ($\chi^2 = 69.99$, $df = 15$, $P < 0.001$). The annual value of the trophic niche breadth (B_{sta}) of both species was similar and the niche overlap (O) was high (Table 2).

Among rodents, bank vole was the species most preyed upon by the pine marten and constituted up to 1/3 of all rodents eaten. In contrast, the stone marten more often caught voles *Microtus* sp. The differences in consumption of these rodents by both martens were statistically significant (Table 3). Apart from previously mentioned rodent's species, both species of marten ate also mice (Muridae and *Apodemus* sp.), but the differences were not statistically sig-

Table 2. Mean annual food composition based on 287 stone marten's and 155 pine marten's faeces collected in forests from the same area presented as relative frequency of occurrence (F , %) and percentage of biomass (Bio). Significant P values (Student's t -test) are set in boldface.

Food items	Stone marten			Pine marten			t	P
	N	F	Bio	N	F	Bio		
Rodents	111	19.1	26.8	101	37.4	55.9	5.6	< 0.001
Undetermined <i>Soricidae</i>	3	0.5	0.9	7	2.6	4.9	2.4	< 0.05
Hares	5	0.9	2.5	1	0.4	0.6	0.9	> 0.05
Undetermined mammals	28	4.8	5.3	9	3.3	0.5	1.0	> 0.05
Ungulate carcasses	1	0.2	0.2	0	0	0		
Birds and eggs	79	13.6	13.2	61	22.6	24.3	3.2	< 0.01
Insects	130	22.3	3.9	39	14.4	0.4	2.8	< 0.01
Fruits	225	38.6	47.2	52	19.3	13.4	5.9	< 0.001
Total	582	100	100	270	100	100		
Trophic niche breadth, B_{sta}		0.41	0.31		0.43	0.22		
Trophic niche overlap, O		0.83	0.70					

Table 3. Rodent prey of pine marten and stone marten presented as percentage of occurrence. Trophic niche breadths (B_{sta}) calculated for small rodents determined to species, genus or families (undetermined rodents were excluded from calculations). Significant P values (Student's t -test) are set in boldface.

Rodent category	Stone marten		Pine marten		t	p
	N	Percentage	N	Percentage		
Bank vole (<i>Clethrionomys glareolus</i>)	9	22.5	37	58.7	4.0	< 0.001
Microtinae	17	42.5	4	6.4	4.5	< 0.001
<i>Apodemus</i> sp.	8	20	13	20.6	0.1	> 0.05
Muridae	6	15	9	14.3	0.1	> 0.05
Total	40	100	63	100		
Trophic niche breadth, B_{sta}		0.80		0.48		
Other undetermined small rodents	71		38			

nificant. When the frequency distribution of all rodent prey categories was compared between the pine marten and stone marten, the difference was statistically significant ($\chi^2 = 22.89$, $df = 7$, $P < 0.001$). As compared with the pine marten, the stone marten utilized a wider species diversity of rodents (Table 3).

Only pigeons (*Columba* sp.), starling (*Sturnus vulgaris*) and goldcrest (*Regulus regulus*) were represented both in the diet of the stone marten and pine marten. Other birds were encountered either in stone marten faeces: domestic hen (*Gallina gallina*) great spotted woodpecker (*Dendrocopos major*), trush (*Turdus* sp.) and blackbird (*Turdus merula*) or in scats of pine martens: pheasant (*Phasianus colchicus*), jay (*Garrulus glandarius*), blue tit (*Parus caeruleus*) and wren (*Troglodytes troglodytes*). All of the mentioned species were eaten by martens sporadically (from 1 to 3 cases of occurrence) and only remains of blue tit were found five times. Eggshells were registered rarely in the faeces of stone martens and pine martens (4 and 2, respectively). Small birds of undetermined species constituted about 1/3 of taken birds (Table 4). No statistically significant differences between the

two marten species in the frequency distribution of bird prey categories were registered ($\chi^2 = 23.29$, $df = 35$, $P > 0.9$; Table 4).

Among fruits eaten by both martens apples, which occur mainly in orchards, prevailed. They constituted about 80% of fruits eaten in case of the pine marten and about 41% in case of the stone marten. Fruits of trees typical for human settlements (gardens) like pears, plums, cherries and grapes occurred more frequently in the stone marten's diet (about 50% of fruits eaten) than in the pine marten's diet (about 8%). Only two other species of fruits were found in the diet of both martens: bird cherry (*Prunus padus*) and rowan (*Sorbus aucuparia*) but only the rowan was more frequently eaten by pine martens. When we compared the frequency distribution of all the fruit species eaten by martens, we found marginally significant differences between the two marten species ($\chi^2 = 53.98$, $df = 25$, $P < 0.06$). The index of diversity of consumed species of fruit was higher in the stone marten than in the pine marten (Table 5).

Among insects found in faeces of both species of martens, forest insects constituted a similar part, about 1/3 of all insects. However, the pine

Table 4. Bird prey of stone marten and pine marten presented as percentage of occurrence.

	Stone marten		Pine marten	
	N	Percentage	N	Percentage
Undetermined birds	28	35.4	18	29.5
Undetermined small birds	27	34.2	20	32.8
Undetermined medium-sized birds	4	5	8	13.1
Domestic hen (<i>Gallina</i> sp.)	1	1.3	0	0
Pigeons (<i>Columba</i> sp.)	3	3.8	1	1.6
Starling (<i>Sturnus vulgaris</i>)	2	2.5	2	3.3
Trushes (<i>Turdus</i> sp.)	1	1.3	0	0
Blackbird (<i>Turdus merula</i>)	2	2.5	0	0
Great spotted woodpecker (<i>Dendrocopos major</i>)	1	1.3	0	0
Woodpecker (<i>Dendrocopos</i> sp.)	1	1.3	0	0
Robin (<i>Erithacus rubecula</i>)	3	3.8	0	0
Goldcrest (<i>Regulus regulus</i>)	1	1.3	1	1.6
Cuckoo (<i>Cuculus canorus</i>)	1	1.3	0	0
Wren (<i>Troglodytes troglodytes</i>)	0	0	1	1.6
Jay (<i>Garrulus glandarius</i>)	0	0	2	3.3
Pheasant (<i>Phasianus colchicus</i>)	0	0	1	1.7
Blue tit (<i>Parus caeruleus</i>)	0	0	5	8.2
Eggs	4	5	2	3.3
Total	79	100	61	100
Trophic niche breadth, B_{sta}		0.17		0.21

marten caught *Carabus auronitens* more often while the stone marten preyed more frequently on *Geotrupes stercorococcus*. Out of remaining forest and ecotone dwelling insects, 5 taxa were found in scats of both species of martens. Only *C. nemoralis* was slightly more frequently used by the pine marten, and cockchafers (*Melolontha melolontha*) constituted 1/4 of all insects eaten by the stone marten. Other insects were represented rarely (from 1 to 2 cases of occurrence) in the food of both the stone marten and pine marten (Table 6). When we compared the frequency distribution of different insects in the diet of the two martens, no statistically significant difference was found ($\chi^2 = 38.8722$, $df = 39$, $P > 0.5$).

Seasonal changes in the diet of the stone marten and pine marten

In the diet composition of both species, seasonal changes in consumption of rodents, birds, fruits and insects were registered. Although seasonal changes in consumption of various components of food by the stone marten and pine marten were not always statistically significant, (Table 7), some regularity, however, was found. In each of the analysed seasons, small rodents and birds were more often encountered in the pine marten's food, whereas the stone marten more

frequently than the pine marten ate fruits and insects (Table 7). With the exception of spring, the value of seasonal trophic niche breadth for both species of martens was nearly equal. The index of similarity of diet composition was the highest in summer (Table 7). Higher seasonal share of small mammals and birds, and lower share of insects and fruits in the pine marten's diet as compared with that of the stone marten was also confirmed by the analysis of biomass of different food items (Fig. 2).

For the stone marten, fruits were the most important category of food during the year. The largest quantities of fruits (nearly half of biomass consumed) were eaten in summer and fall (Fig. 2). However, remains of fruits were most frequently encountered in the stone marten's diet in winter (Table 7). Small rodents constituted another important category of food of the stone marten. In each season they exceeded 1/5 of consumed biomass (Fig. 2). Birds and eggs were components of large importance during the year: over 10% of occurrence in food. Birds were the most frequently registered in scats from winter, fall and spring (Table 7). We also found an exceptionally high consumption of insects in spring (Table 7 and Fig. 2).

Rodents were the most important food category for the pine marten during the year. Their consumption in each season made up almost

Table 5. Share of various fruits in stone marten's and pine marten's food presented as percentage of occurrence. Significant *P* values (Student's *t*-test) are set in boldface.

	Stone marten		Pine marten		<i>t</i>	<i>p</i>
	<i>N</i>	Percentage	<i>N</i>	Percentage		
Apples (<i>Malus</i> sp.)	93	41.4	41	78.8	5.7	< 0.001
Pears (<i>Pyrus</i> sp.)	28	12.5	1	1.9	2.9	< 0.01
Plums (<i>Prunus</i> sp.)	52	23.1	3	5.8	3.4	< 0.01
Cherries (<i>Cerasus</i> sp.)	32	14.2	0	0	3.2	< 0.01
Grapes (<i>Vitis</i> sp.)	8	3.6	0	0		
<i>Prunus padus</i>	2	0.9	2	3.9	1.3	> 0.05
Berries (<i>Rubus</i> sp.)	6	2.7	0	0		
Elders (<i>Sambucus nigra</i>)	1	0.4	0	0		
<i>Cornus</i> sp.	1	0.4	0	0		
Rowan (<i>Sorbus aucuparia</i>)	1	0.4	3	5.8	2.3	< 0.05
Blackthorn (<i>Prunus spinosa</i>)	1	0.4	0	0		
<i>Fragaria</i> sp.	0	0	1	1.9		
Undetermined fruits	0	0	1	1.9		
Total	225	100	52	100		
Trophic niche breadth, B_{sta}		0.24		0.05		

half of food consumed (Fig. 2). Birds were another component of a great importance eaten by pine martens. Bird remains constituted over 40% of the biomass in spring. Fruits constituted an important food category in summer and were of the same importance in the diet of the pine marten as rodents (Fig. 2 and Table 7). Similarly as the stone marten, the pine marten fed on insects most frequently in spring, but in terms of biomass eaten insects did not composed a significant component of pine marten's diet, barely 1% (Fig. 2).

Discussion

Results of our research indicate on a polyphagous character both the stone marten and pine marten.

Both martens utilised a wide array of food types, especially rodents, fruits, birds and insects. The food niche of both species of marten highly overlapped ($O = 0.83$ and $O = 0.70$ for percentage of occurrence and biomass, respectively). However, significant quantitative differences in their food composition were observed. Stone martens ate fruits most frequently followed by rodents, birds and insects. On the other hand, rodents made the staple of the pine marten's diet, while birds and fruits constituted complementary food.

Identification of both species of martens poses a difficulty, and only one study concerning the food composition of two marten species on the same area based on the analysis of faeces was conducted so far (Marchesi *et al.* 1989). These authors reported that the pine marten consumed small mammals and birds significantly more

Table 6. Share of various insects in the stone marten's and pine marten's diet presented as percentage of occurrence. Significant *P* values (Student's *t*-test) are set in boldface.

	Stone marten		Pine marten		<i>t</i>	<i>p</i>
	<i>N</i>	Percentage	<i>N</i>	Percentage		
<i>Carabus auronitens</i>	2	1.5	9	23.1	4.1	< 0.001
<i>Carabus hortensis</i>	1	0.8	2	5.1	1.5	> 0.05
<i>Pterostichus niger</i>	0	0	1	2.6		
<i>Geotrupes stercorosus</i>	33	25.4	2	5.1	3.1	< 0.01
<i>Nebria bravidolis</i>	1	0.8	0	0		
<i>Prionus coriarius</i>	4	3	0	0		
<i>Carabus coriaceus</i>	2	1.5	0	0		
<i>Cerambycidae</i>	1	0.8	0	0		
Typical forest insects total	44	33.8	14	35.9		
<i>Carabus nemoralis</i>	6	4.6	7	17.9	2.4	< 0.05
<i>Geotrupes vernalis</i>	5	3.8	1	2.6	0.4	> 0.05
<i>Melolontha melolontha</i>	35	26.9	1	2.6	4.2	< 0.001
<i>Carambidae</i> sp.	3	2.3	4	10.2	1.9	> 0.05
<i>Catops</i> sp.	0	0	1	2.6		
<i>Phosphuga</i> sp.	0	0	1	2.6		
<i>Carabus</i> sp.	0	0	2	5.1		
<i>Geotrupes</i> sp.	2	1.5	1	2.6	0.4	> 0.05
<i>Vespidae</i> sp.	10	7.7	2	5.1	0.6	> 0.05
<i>Coleoptera</i> sp.	2	1.5	0	0		
<i>Formicidae</i> sp.	1	0.8	0	0		
<i>Selatossomus</i> sp.	1	0.8	0	0		
<i>Pissodes</i> sp.	1	0.8	0	0		
<i>Staphylinus</i> sp.	1	0.8	0	0		
<i>Silpha</i> sp.	1	0.8	0	0		
<i>Aphodius</i> sp.	1	0.8	0	0		
<i>Agelastica</i> sp.	1	0.8	0	0		
Isopoda	1	0.8	0	0		
Undetermined insects	15	11.5	5	12.8	0.2	> 0.05
Total	130	100	39	100		
Trophic niche breadths, B_{sta}		0.2		0.27		

Table 7. Seasonal changes in the diet of stone marten and pine marten in 2001–2004 presented as relative frequency of occurrence. SM = stone marten, PM = pine marten. Significant *P* values (Student's *t*-test) are set in boldface.

	Spring				Summer				Autumn				Winter			
	SM %	PM %	<i>t</i>	<i>P</i>	SM %	PM %	<i>t</i>	<i>P</i>	SM %	PM %	<i>t</i>	<i>P</i>	SM %	PM %	<i>t</i>	<i>P</i>
Rodents	10.4	26.7	2.5	< 0.05	22.1	31.2	0.7	> 0.05	16.4	48.7	4.0	< 0.001	22.5	47.4	3.7	< 0.001
Undetermined <i>Saricidae</i>	0	3.3			1.3	0			0	0			0	3.2		
Hares	0	0			0.9	0			0	0			3.4	1.0	1.1	> 0.05
Undetermined mammals	8.3	4.2	1.0	> 0.05	3.9	6.3	0.4	> 0.05	6.5	0			1.1	3.2	0.9	> 0.05
Ungulate carcass	0	0			0	0			0	0			1.1	0		
Birds and eggs	14.7	24.1	1.4	> 0.05	11.2	12.5	0.1	> 0.05	15.0	18.0	0.5	> 0.05	15.7	24.2	1.4	> 0.05
Insects	45.8	22.5	2.8	< 0.01	26.0	18.8	0.7	> 0.05	18.7	12.8	0.9	> 0.05	9.0	4.2	1.3	> 0.05
Fruits	20.8	19.2	0.2	> 0.05	34.6	31.2	0.3	> 0.05	43.4	20.5	3.1	< 0.01	47.2	16.8	4.5	< 0.001
Total of percentage	100	100			100	100			100	100			100	100		
Total number of occurrences	48	120			231	16			214	39			89	95		
Trophic niche breadth, <i>B</i> _{sia}	0.35	0.51			0.43	0.43			0.37	0.29			0.32	0.31		
Trophic niche overlap, <i>O</i>					0.97				0.73				0.73			

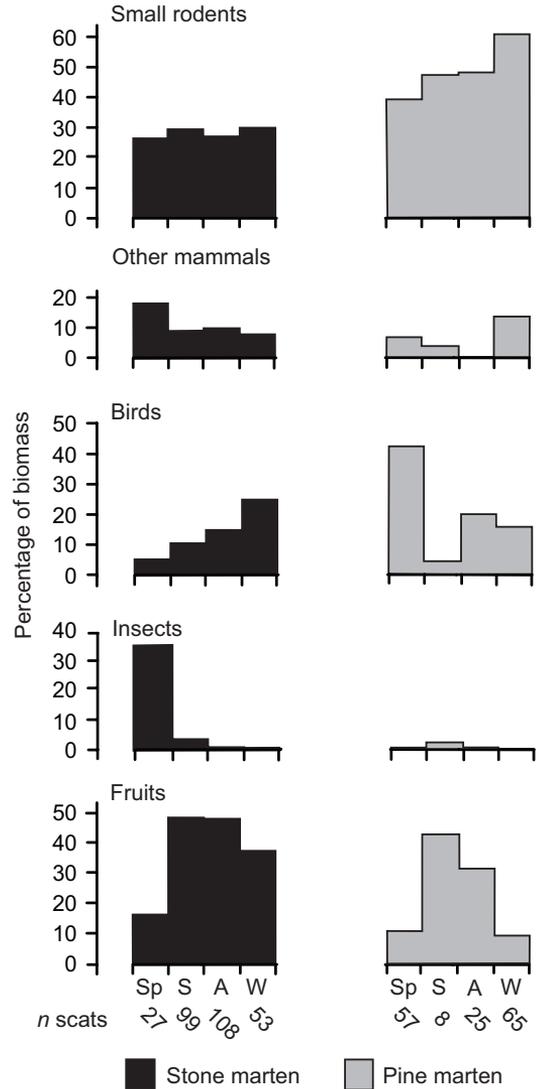


Fig. 2. Changes in proportion (percentage of biomass) of different components in the diet of stone marten and pine marten in 2001–2004. (Sp. = Spring, S = Summer, A = Autumn, W = Winter).

often than the stone marten, which is in agreement with our study. Also Clevenger (1994) in a review of studies concerning diet analysis of both species of martens from allopatric locations of occurrence emphasises the importance of fruits and insects in the stone marten's diet. A high share of fruits that we found in the diet of the stone marten was also registered by other authors (Tester 1986, Lachat Feller 1993, Serafini & Lovari 1993, Genovesi *et al.* 1996, Sidorovich 1997, Lanszki 2003). According to

our results, fruits constitute an important food category of the stone marten not only in summer and autumn but also in winter when martens ate apples and pears lying on the ground under the trees, sometimes digging them up from under the snow (Goszczyński 1976, Goszczyński & Posluszny 2003). Also Tester (1986) found that in winter stone martens fed on fruits remaining on trees.

Common vole was a rodent that was the most frequently eaten by the stone marten, but also bank vole as well as mice was often preyed upon. Common vole is a typical field- and meadow-dwelling rodent, and bank vole is a living-forest species (Pucek 1984). Our results suggest that the stone marten obtain food from both open areas and woods, as mentioned in previous studies (Genovesi *et al.* 1996, Lanszki *et al.* 1999, Lanszki 2003).

Birds were taken by the stone marten throughout the year. Contrary to other studies (Tester 1986, Serafini & Lovari 1993, Lanszki *et al.* 1999, Lanszki 2003), we found the lowest share of birds in spring. It was presumably caused by outbreak of insects (*Melolontha melolontha*) in the spring 2002. In such huge quantities these insects could become an alternative source of easily available food.

The group of forest insects, which we found in the food of the stone marten, further supports the suggestion that the stone marten uses food obtained in forests (Genovesi *et al.* 1996, Lanszki 2003). Unfortunately in previous studies of the pine marten's diet, insects were rarely identified to species (Lachat Feller 1993, Serafini & Lovari 1993) and only Lachat Feller (1993) found a forest-dwelling species *Carabus auronitens*.

Our study showed that the composition of the pine marten's diet varies seasonally. Similarly to other authors (Lockie 1961, Storch *et al.* 1990, Clevenger 1994, Jędrzejewski *et al.* 1993, Zalewski *et al.* 1995, Sidorovich 1997, Birks 2002), we found a constant, high share of rodents in the food of pine martens during the year. In the study area rodents were eaten most frequently by the pine marten in fall and winter, and rarely in spring and summer. Among rodents that were caught, bank vole and *Apodemus* sp. dominated. Many authors (Jędrzejewski *et al.* 1993, Heldin

1999, Zalewski 2004) point out at functional response (*sensu* Solomon 1949) reflected in a positive correlation between population density of the bank vole and its frequency in the pine marten's diet. As we did not conduct rodent trapping in our study, we are not able to confirm this correlation. We found that the pine marten occasionally preyed upon *Microtus* sp. According to Marchesi *et al.* (1989) and Jędrzejewski *et al.* (1993), *Microtus* sp. are probably caught on the edges of forests, because the pine marten avoid open areas (Grakov 1972, Pulliainen 1980a, Fedyk *et al.* 1984). On the other hand, Brainerd (1990) suggested that in fragmented habitat with patches of forest, the pine marten can catch rodents inhabiting shelterbelts. We did not find any remains of squirrels (*Sciurus vulgaris*) in the scats of either species of marten. Squirrels frequently occur in the diet of the pine marten in northern Europe, but are less frequent in the diet of this carnivore in central Europe (Nasimovich 1948, Grakov 1962, Zalewski 2004).

Birds were an important food category and in contrast to Jędrzejewski *et al.* (1993) we registered their high share in food of the pine marten in spring and winter. In the study of Jędrzejewski *et al.* (1993) a share of birds was substantially lower than this showed in our research. This discrepancy could result from different microclimate and weather conditions (e.g. average low temperature in January and period of snow cover persistence) in Rogów and Białowieża regions. In more severe climate, lack of birds in winter can be compensated by increased consumption of small rodents and carcasses. That phenomenon was revealed by Pulliainen (1980b) in his study of the pine marten in Scandinavia. Fruits constituted a complementary food of the pine marten and were taken mainly in summer and fall, but even in winter their quantities were significant. Such a high frequency of fruits in the diet in winter has only been found very rarely (Ansorge 1989) at that latitude. Likewise, data presented by Zalewski (2004) in his review indicate that so high a consumption of fruits is more likely to be noted in southern countries than in Poland. Such a high share of fruits in the pine marten's diet in central Poland could be a reflection of the proximity of both orchards and forests to our study area. Similarly, as in case of other

studies from the same latitude (Jędrzejewski *et al.* 1993), insects did not constitute an important component of the pine marten's diet.

In our study, the breadth of trophic niches of both species was similar: standardized Levins index equalled 0.41 in the pine marten and 0.43 in the stone marten. Clevenger (1994) in his review of feeding ecology of the pine marten and stone marten in Europe also reported similar breadth of trophic niches of these species (0.42 and 0.45, respectively). Marchesi *et al.* (1989) also indicated similar breadth of trophic niches of both martens in Switzerland, (0.69 in the pine marten and 0.74 in the stone marten). The absolute values of trophic niche breadth were incomparable between different studies, because each study distinguished particular prey items at a different level of detail. However, in each study the relative values of the breadth of trophic niche were similar for the pine marten and stone marten, and in each case the niche breadth of the stone marten was slightly larger than that of the pine marten. In our study area, in a field-forest mosaic, stone martens obtained food both in forests and in open areas, while pine martens concentrated their foraging activity mainly in forests. Although the index of the niche breadth calculated for the main food categories was similar for both species, stone martens used a wider array of food: they used more species of fruits and insects and their hunting pressure on different species of small rodents was more equally distributed.

Powell and Zielinski (1983) predicted that food competition among species within the Mustelidae should be most intense within *Martes* and *Mustela*. Indeed, high food niche overlap of the two species of European martens may suggest strong interspecific competition. However, in the mosaic landscape of central Poland this competition may be limited by differences in habitat selection by the pine marten and stone marten. Diet overlap varied seasonally and was highest in summer, when the supply of different types of food: rodents, birds, insects and fruits, was the most steady. It may suggest that the similarity of food niches results from opportunistic foraging strategies of both species. Similar explanation was given by Zielinski and Duncan (2004) for the high degree of overlap in diets of sympatric American martens and fishers *Martes pennanti*

in California. According to these authors, the similarity may be due to the relatively large pool of diverse and available resources that are exploited by both species by using similar modes of foraging. Additionally, Zielinski and Duncan (2004) indicated, after Hespdenheide (1975), that competing organisms typically respond first by expanding habitat preferences or foraging behaviour, rather than by changing dietary breadth. They suggested that fishers and martens in their study area may differ in respect to microhabitat use, activity time, or some other niche axis. In the case of the pine marten and stone marten in our study area, both species exploited the same forest habitat (Pilot *et al.* 2007), but they substantially differed in the ways of area searching and foraging behaviour, as well as in an attitude towards open areas and human settlements (Goszczyński *et al.* 2007). This allowed abundant and diverse kinds of food to be exploited by both species without intense competition.

This paper is the first attempt to compare the diet of the stone marten and pine marten inhabiting the same area by using a method of genetic identification of faeces of the two species. Although in our study area both martens exploited the same microhabitat, we were able to distinguish their faeces, which allowed us to indicate significant differences in the diets of these closely related species. We confirmed previous presumptions about the existence of these differences, which were based on dentition comparisons between the pine marten and stone marten (Wolsan *et al.* 1985), and reviews of feeding ecology of both martens in Europe (Clevenger 1994, Zalewski 2004). Our study proves the suitability of genetic identification of faeces for the studies of diet of sympatric carnivores, which has been earlier demonstrated based on example of felids from the Neotropics (Farrell *et al.* 2000). In case if traditional methods of distinguishing faeces of different species by size, shape or smell fail, genetic analyses may be the best way of species identification.

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