

The effects of sex, age, season and habitat on diet of the red fox *Vulpes vulpes* in northeastern Poland

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Received: 10 June 2010 / Accepted: 17 December 2010 / Published online: 22 February 2011
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Abstract The diet of the red fox *Vulpes vulpes* was investigated in five regions of northeastern Poland by stomach content analysis of 224 foxes collected from hunters. The red fox is expected to show the opportunistic feeding habits. Our study showed that foxes preyed mainly on wild prey, with strong domination of *Microtus* rodents, regardless of sex, age, month and habitat. Voles *Microtus* spp. were found in 73% of stomachs and constituted 47% of food volume consumed. Other food items were ungulate carrion (27% of volume), other mammals (11%), birds (9%), and plant material (4%). Sex- and age-specific differences in dietary diversity were found. Adult males and juvenile foxes had larger food niche breadths than adult females and their diets highly overlapped. Proportion of *Microtus* voles increased from autumn to late winter. Significant habitat differences between studied regions were found. There was a tendency among foxes to decrease consumption of voles with increasing percentage of forest cover. Based on our findings, red foxes in northeastern Poland can be recognized as a generalist predators, consuming easily accessible and abundant prey. However, high percentage of voles consumed regardless of age, sex, month, or habitats may indicate red fox specialization in preying on *Microtus* rodents.

Keywords Food habits · Food niche breadth · Northeastern Poland · Prey selection

Introduction

The red fox *Vulpes vulpes* Linnaeus, 1758 is one of the most widely distributed and common predators worldwide. Its high plasticity, permitting adaptation to different habitats and food resources, as well as successful oral vaccination campaigns against rabies and decreasing hunting pressure resulted in a significant increase of its populations in Europe since the 1980s (Beresiński and Panek 2000; Chautan et al. 2000; Gołdyn et al. 2003; Goszczyński et al. 2008).

Numerous studies of the red fox diet show it to be a generalist predator, feeding mainly on prey which are abundant and easily accessible. Red fox feeds most frequently on small mammals, but utilize also other food items such as carrion, birds and other mammals when voles are scarce (Goszczyński 1974; Papageorgiou et al. 1988; Jędrzejewski and Jędrzejewska 1992; Dell'Arte et al. 2007). The opportunistic feeding habits and diet variation of the red fox are shaped by various factors. Habitat type, by shaping variable prey availability, may strongly influence the diet of this medium-sized carnivore (Kolb and Hewson 1979; Leckie et al. 1998; Sidorovich et al. 2006). Similarly, red foxes respond to seasonal variation in availability of food, indicating dietary opportunism (Goszczyński 1986; Jędrzejewski and Jędrzejewska 1992; Baltrunaite 2001; Baltrunaite 2002).

Sexual dimorphism is observed in red foxes (Cavallini 1995); however, prey composition in relation to sex or age classes of foxes has rarely been described (Englund 1965; Weber 1997; Panzacchi et al. 2008). Panzacchi et al.

Communicated by: Andrzej Zalewski

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(2008) found that diet of cubs was less diverse and included a higher percentage of mammals and birds, while adult foxes were fed upon smaller food sources. Among *Carnivora* males often hunt larger preys than females. The diet differences may have the benefit of reducing intra-specific competition (McDonald 2002; Sliwa 2006; Zalewski 2007).

Red foxes, in most cases, create monogamous pairs or social groups; however, social relationships are more intimate only in breeding and reproductive period (Cavallini 1996).

The aim of this paper was to investigate the influence of various factors such as habitat type, month, age, and sex on fox diet in well-preserved habitats of northeastern Poland. We predicted that foxes will feed on wild prey species and their diet will be adjusted to the habitat of studied areas. Given the opportunistic character of red fox diet, we hypothesized that an increase in forest cover resulting in a decrease in availability of *Microtus* voles (typical mammals of open areas) will lead to increased consumption of other prey by red foxes.

Study area

The study was carried out in five areas located in northeastern Poland (Fig. 1), which is characterized by extensive largely unmodified habitats. The forest cover in

this region averages 29% and is higher than in central and western Poland. The five regions differed in habitat composition, but not in climatic conditions. The distance between southernmost area and northernmost area was about 200 km, therefore latitudinal variation in diet is not expected. Red foxes were shot in hunting districts (game management areas covering 4,000–10,450 ha, managed by forestry offices or hunting clubs) within the regions.

Characteristics of regions

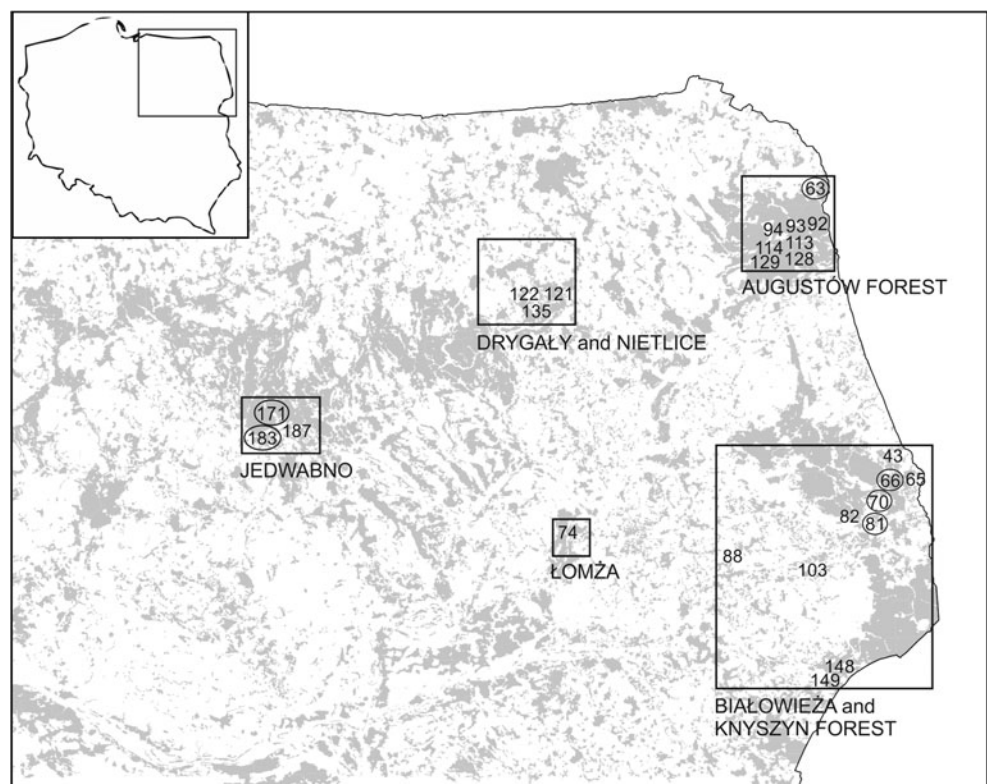
Region 1

Jedwabno is an old military training ground covered by coniferous forests (49% of the area). Open habitats, meadows, and marshes of sedges *Carex* and reeds *Phragmites* comprise a substantial part of the landscape. Foxes were collected mainly in hunting district nos. 171 and 183 (with 64% and 50% of forest cover respectively).

Region 2

Drygały and Nietlice area. Drygały forest district is an old military area covered largely (83%) by coniferous forests. Nietlice marsh is a natural reserve which is a remnant of a drained lake. Wetlands (meadows and sedge and reed marshes) cover 70% of this area.

Fig. 1 Distribution of regions (marked by squares) where red fox stomachs were collected in northeastern Poland. Numbers denote hunting districts located in the main regions. *Circled numbers* are hunting districts with larger number of stomachs collected and used in habitat analysis



Region 3

Augustów Forest is an extensive forest dominated by coniferous (85% of the forest area) and alder bog forests. The main hunting district was no. 63 (with 84% forest cover).

Region 4

Białowieża and Knyszyn Forest is covered by deciduous, mixed, and coniferous forest (42% of the area) and less intensively cultivated agricultural fields (meadows, pastures, wastelands). In many places, abandoned fields are encroached by different stages of forest succession. Most of the foxes came from hunting district nos. 66, 70, and 81 (varying in the percentage of forest cover, i.e., 76%, 23%, and 40%, respectively).

Region 5

Łomża is an old military area, reforested in recent years. The dominant habitat is pine forest (59%), within which many open stands occur.

The percentage of forest cover data in hunting districts were gathered from Regional Offices of Polish Hunting Association.

In all areas, large forest complexes are surrounded by mosaics of woodlands and agriculture (including meadows and arable lands). Locally, areas of abandoned fields and wastelands are being covered by tree succession. Mammal communities are dominated by rodents of open fields (*Microtus* spp.) and forest rodents (*Clethrionomys glareolus*, *Apodemus flavicollis*; Niedziałkowska et al. 2010), which potentially constitute the main food resource for the red fox. The abundance of hare *Lepus europaeus* has decreased in recent decades, but it is still widespread (32,200 individuals in Podlasie and 18,600 in Mazury region; Kamieniarz and Panek 2000). Moreover, large predators, such as wolf and lynx, which occur in this region (Jędrzejewski et al. 2002a) may provide additional resources of food for foxes in the form of prey remains. The studied areas are characterized by the occurrence of numerous bird species including black grouse and other *Galliformes* (Zawadzka and Zawadzki 2006).

Average temperatures in the study area in September–November ranged from 1.7 to 14.3°C, depending on the geographical location, and nearly no snowfall appeared in this period (0.9 cm, on average). December and February were the coldest months, with average temperatures of –8.5 to –6.8°C (December) and –6.3 to –4.9°C (February). The deepest mean snow cover occurred in December (5.8–14.6 cm) and in February (7.1–17.4 cm). In March, 3.5 cm of snow, on average, persisted on the ground and mean temperatures

varied from 0.2 to 0.7°C. Data were taken from weather stations located in or in close vicinity of studied areas.

Materials and methods

Red fox carcasses were collected from September 2002 to March 2003 during fox control operations conducted as part of the black grouse conservation project of the Northern-Podlasiian Society for Protection of Birds (PTOP). Each fox was sexed, weighed, and measured. Age of foxes (juveniles or adult) was determined on the basis of the relative width of the lower canine pulp cavity as measured on X-ray pictures of teeth (Knowlton and Whittemore 2001). Assuming that fox cubs were born in early April (Goszczyński 1995; Jędrzejewska and Jędrzejewski 1998), we categorized foxes from 6 to 12 months old as juveniles and individuals >1.5 years of age as adults.

Stomachs were removed from carcasses and frozen until analysis. Of 282 fox stomachs collected in total, 224 (79%) contained food items and were used for further analysis. Stomach volume was measured and food items were washed through a 1 mm wire sieve. Prey remains were identified to the lowest taxon possible and divided into six major food categories: (1) small mammals (Arvicolinae, Muridae, Soricidae); (2) other mammals (hare, carnivores, etc.); (3) ungulate carrion; (4) birds; (5) plant material; and (6) other food (amphibians, fish, invertebrates, anthropogenic food). Other vertebrates, invertebrates, and anthropogenic food were grouped together due to their minor significance in the analyzed material. Small mammals, largely rodents and insectivores, were identified by dentition according to Pucek (1984). Remains of other mammals were identified by microscopic examination of the cuticle scales, medulla patterns, and cross-sections of guard hairs according to Debrot et al. (1982). Bird remains were identified by examining feathers, claws, and beaks. Amphibians were recognized based on bones according to the key of Böhme (1977). Vegetative materials (seeds, grass) were recognized according to Rutkowski (2004).

Wet weights and volumes of each food item in the stomachs were measured separately or if separation was not possible, food remains were measured jointly, and the percentage of different food items was visually estimated.

The contribution of each food category in the fox diet was expressed as: (1) percentage of occurrence (%Occ.), the proportion of stomachs with a given food item or prey group, (2) percentage of volume (%VC), the proportion of given food volume in the total stomach volume, (3) percentage of biomass consumed (%BC), the percentage of the wet weight of a given food or prey group in the total wet weight of the stomach content (Goszczyński 1972).

The data were analyzed within the following groups: age, sex, month, region, and hunting district. Due to low number of stomach samples, region 5 was excluded from comparisons between regions; however, stomachs collected there were used in other analysis. To verify the influence of habitat type on fox diet, the stomach content was analyzed in six hunting districts, for which we had more detailed information of percentage of forest cover, and a sufficient number of stomachs was collected (Fig. 1).

Food niche breadths of foxes were estimated by Levins' index B (Levins 1968):

$$B = \frac{1}{\sum_n p_i^2}$$

where p_i is the proportional volume of each prey group i . The calculation was done for six food categories, so B index could vary from 1, the narrowest, to 6, the broadest niche possible, when the maximum number of food categories was consumed.

Pianka's index α_{ij} (Pianka 1973) was used to estimate dietary niche overlap:

$$\alpha_{ij} = \frac{(\sum_n p_{ia} p_{ja})}{\sqrt{(\sum_n p_{ia}^2)(\sum_n p_{ja}^2)}}$$

where p_{ia} and p_{ja} are the proportions of prey group a used by species groups i and j , respectively, and n is the total number of prey groups. Pianka's index varies from 0 (when dietary niches are the least similar to each other) to 1 (when food niches are the most similar).

Statistical analyses were carried out using Pearson's Chi-square test for overall diet comparisons within groups of foxes of different age, sex, month, region, and hunting district. Nonparametric Kruskal–Wallis tests for mean weight and volume comparisons were computed only on the samples with food. The relationship between percentage of forest cover and percentage of occurrence of prey groups was tested by r^2 , the correlation coefficient of multiple determination. The analyses were conducted using Statistica 9.0.

Results

Specific food items

In the studied areas, foxes relied mostly on voles, which were found in 72.7% of stomachs, comprising 46.9% of the diet by volume. The common vole *Microtus arvalis* was preyed upon most often, followed by *Microtus oeconomus* and *Microtus agrestis* (Table 1). The secondary food was ungulate carrion (mainly wild boar and cervids), which

constituted 26.8% of total volume consumed (Table 1). Other mammals, mainly brown hare and carnivores, were found in 12.7% of the stomachs examined and comprised 10.7% of the total fox diet by volume. Among birds, which accounted for 8.9% of the diet by volume, *Galliformes* were preyed upon the most frequently. Although plant material occurred in 51.6% of the stomachs examined, it constituted only 3.6% of the total fox diet by volume. The most frequently consumed plant was grass. Other food items, which included amphibians, fish, invertebrates (mainly ground beetles Carabidae), and food of anthropogenic origin (food scraps, garbage), were of minor importance (1.4% of volume; Table 1).

Age and sex differences

Mean (\pm SD) body weight of adult males (6.4 ± 0.7 kg) was significantly higher than that of adult females (5.3 ± 0.7 kg) and juveniles (5.5 ± 1.0 kg; Kruskal–Wallis test, $H_2 = 40.58$, $p < 0.0005$). However, the difference in average volume of stomach contents was not statistically significant between sex–age groups (adult males, 107 ± 86 ml; adult females, 103 ± 63 ml; juveniles, 88 ± 71 ml; Kruskal–Wallis test, $H_2 = 3.97$, $p = 0.137$). Overall, dietary differences between those groups were statistically significant ($\chi^2 = 35.8$, $df = 10$, $p < 0.0005$). Females mostly relied on voles, while adult males and juveniles preyed more on other mammals and birds (Fig. 2). The diets of adult males and juveniles were more diverse ($B = 3.0$ and 3.4 , respectively) than that of adult females ($B = 1.8$). Dietary niche overlap between young foxes, and adult males was high, $\alpha = 0.98$.

Furthermore, sex differences in the diet of adult foxes increased during the breeding season (January–March; $\chi^2 = 37.6$, $df = 5$, $p < 0.0005$) in comparison to the pre-breeding period (September–December; $\chi^2 = 23.2$, $df = 5$, $p < 0.0005$). Males more often hunted birds in the breeding season than before, while females ate more birds in pre-breeding period. The consumption of small mammals increased in the breeding season in both sexes.

Variation between months

There were significant differences between months in the diet of foxes ($\chi^2 = 95.8$, $df = 20$, $p < 0.0005$). There was an increasing consumption of small mammals in continuous months. The September–November period was characterized by the highest percentage of ungulate carrion and plant material consumed by foxes. Birds were hunted mainly during colder months—December, January, and February (Fig. 3). The broadest food niche ($B = 3.54$) occurred in the coldest month—December (Fig. 3). Dietary niche overlap varied from 0.75 to 0.99 and was the highest between

Table 1 Diet composition of red fox in northeastern Poland based on analysis of stomachs collected from September 2002 to March 2003

Food item	Occurrence (%)	Volume (%)	Biomass (%)
Rodents			
Common vole (<i>Microtus arvalis</i>)	23.2	21.8	21.4
Field vole (<i>Microtus agrestis</i>)	2.2	1.7	1.7
Tundra vole (<i>Microtus oeconomus</i>)	7.6	7.3	7.1
Unidentifiable voles (<i>Microtus</i> spp.)	39.7	16.1	16.2
Bank vole (<i>Myodes glareolus</i>)	1.8	0.4	0.4
Yellow-necked mouse (<i>Apodemus flavicollis</i>)	0.5	0.6	0.6
Wood mouse (<i>Apodemus sylvaticus</i>)	0.5	0.3	0.3
Red squirrel (<i>Sciurus vulgaris</i>)	0.5	0.1	0.1
European beaver (<i>Castor fiber</i>)	0.5	+	+
Total	76.5	48.3	47.8
Insectivora			
Common shrew (<i>Sorex araneus</i>)	0.9	0.2	0.2
European hedgehog (<i>Erinaceus europaeus</i>)	0.5	+	+
European mole (<i>Talpa europaea</i>)	0.5	+	+
Total	1.9	0.2	0.2
Other mammals			
Brown hare (<i>Lepus europaeus</i>)	2.2	3.4	3.7
European polecat (<i>Mustela putorius</i>)	0.9	0.6	0.6
European badger (<i>Meles meles</i>)	0.5	0.5	0.5
Pine marten (<i>Martes martes</i>)	0.5	0.5	0.5
Beech marten (<i>Martes foina</i>)	0.5	0.3	0.3
Red fox (<i>Vulpes vulpes</i>)	1.3	0.5	0.6
Raccoon dog (<i>Nyctereutes procyonoides</i>)	1.3	3.2	3.1
Domestic dog (<i>Canis familiaris</i>)	1.3	0.2	0.2
Domestic cat (<i>Felis catus</i>)	2.2	1.4	1.4
Total	10.7	10.6	10.9
Carrion of ungulates			
Wild boar (<i>Sus scrofa</i>)	10.3	11.9	11.7
Deer (Cervidae)	10.7	9.2	9.1
Cattle	0.9	0.4	0.4
Domestic pig	0.9	0.5	0.5
Sheep	0.5	0.6	0.6
Unidentifiable carrion	5.8	4.3	4.5
Total	29.1	26.8	26.8
Mammals total	118.2	85.9	85.7
Birds			
Yellowhammer (<i>Emberiza citrinella</i>)	0.9	0.1	0.1
Eurasian jay (<i>Garrulus glandarius</i>)	0.5	0.1	0.1
Pigeon (<i>Columba</i> sp.)	0.5	+	+
Tetraonidae	3.1	1.3	1.4
Black grouse (<i>Tetrao tetrix</i>)	0.9	0.5	0.5
Phasianidae (unidentifiable)	0.5	+	0.1
Grey partridge (<i>Perdix perdix</i>)	0.9	0.3	0.3
Common pheasant (<i>Phasianus colchicus</i>)	0.5	0.4	0.4
Chicken (<i>Gallus gallus domesticus</i>)	0.5	0.1	0.1
Unidentifiable birds	12.9	6.0	6.1
Total	21.2	8.9	9.1

Table 1 (continued)

Food item	Occurrence (%)	Volume (%)	Biomass (%)
Plant materials			
Cereal	10.7	0.3	0.4
Seed	2.7	0.1	0.1
Sunflower seed	0.5	+	+
Apple	4.5	1.0	0.9
Pear	4.5	1.3	1.4
Raspberry	0.5	+	+
Bilberry	0.5	+	+
Grass	27.7	0.8	0.9
Total	51.6	3.6	3.6
Other food			
Amphibians	0.9	+	+
Fish	1.8	0.6	0.7
Invertebrates (Carabidae)	1.8	0.1	0.1
Anthropogenic food	3.1	0.6	0.7
Total	7.6	1.4	1.5

January and February and between January and March ($\alpha=0.99$ in both cases) and the lowest between September to November and February ($\alpha=0.75$).

Influence of habitat type on fox diet

The percentage of prey groups in fox diets differed significantly between the main regions ($\chi^2=37.0$, $df=15$, $p=0.001$). In all regions, small mammals followed by ungulate carrion were the main food items consumed by foxes. The main differences were found in consumption of other mammals, which was higher (13–19.8% of volume) in forest regions (3 and 4) than in less forested areas (1 and 2; 1.2–3.9% of volume; Fig. 4). Furthermore, the fox diet was more diverse in the forested areas, ($B=3.3$; Fig. 4).

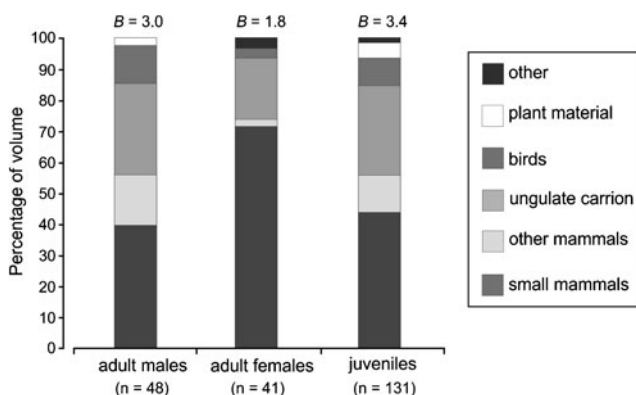


Fig. 2 Stomach content of age–sex groups of foxes in northeastern Poland. Numbers above bars denote food niche breadth values, numbers below bars denote sample sizes

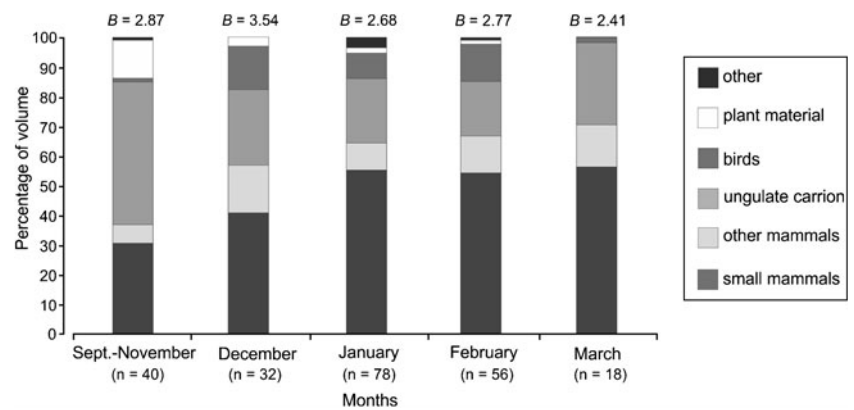
The differences were much higher when comparing smaller hunting districts within these regions, for which detailed data on forest cover were given ($\chi^2=408.1$, $df=25$, $p<0.0005$). The tendency of vole occurrence and of wild ungulate carrion occurrence associated with increasing percentage of forest cover was observed to decline and to increase, respectively; however, the relationship was not significant due to small sample size ($r^2=0.46$, $n=6$, $p=0.14$ and $r^2=0.64$, $n=6$, $p=0.056$, respectively; Figs. 5 and 6).

Discussion

According to the hypothesis, the red fox food composition was expected to vary depending on habitat, age, or sex. However, in all habitats and age–sex groups, *Microtus* voles were the most important prey. *Microtus* rodents seem to be an easily accessible and abundant prey for foxes, since their population densities can reach over 1,000 individuals/ha (Mackin-Rogalska et al. 1986; Briner et al. 2007). Red fox is also well adapted to prey on rodents (Englund 1965; Goszczyński 1974). Although forested habitats may offer diverse food sources, foxes prefer to forage mainly in open fields, where voles are abundant (Goszczyński 1985, 1995).

This study confirmed the importance of ungulate carcasses as a source of food for foxes in northeastern Poland. Red fox is a very effective scavenger (Sidorovich et al. 2000; Selva et al. 2005). In Białowieża Forest, signs of their activity were recorded on 71% of available ungulate carcasses, which is more often than signs of raccoon dogs or raptors (Selva et al. 2005). Remains of large carnivore (wolf and lynx) kills are an

Fig. 3 Monthly variation of red fox diet in northeastern Poland. *Numbers above bars* denote food niche breadth values, *numbers below bars* denote sample sizes



important food resource for different carnivores (Sidorovich et al. 2000; Selva et al. 2005), especially when other resources are scarce (Jędrzejewski and Jędrzejewska 1992). Wolves occur in all of the studied areas and lynxes inhabit three eastern regions, so their predation may support red foxes and other scavengers. In Białowieża Forest, wolves kill, on average, 72 red deer, 16 roe deer, and 31 wild boar over a 100 km² area annually (Jędrzejewski et al. 2002b).

Fox carcasses were collected from hunters in the areas of black grouse conservation. Birds, mostly Tetraonidae, constituted 9% of the red fox diet in the studied areas, which indicates that fox predation may be an important factor in grouse mortality here, especially during winter. Fox predation has been reported as an important factor shaping black grouse populations (Marcström et al. 1988; Lindström 1994b; Selås 1998), particularly during low densities of cycling vole populations (Marcström et al. 1988; Kurki et al. 1997).

Variation in the dietary composition of foxes in relation to age has been examined by several authors. Kolb and Hewson (1980) and Weber (1997) who studied the diet of fox cubs noted that offspring ate essentially the same food as adults. Lindström (1994a) and Panzacchi et al. (2008) showed that fox cubs ate a significantly higher percentage

of large prey items at dens, while the diet of adults consisted of smaller food sources. Furthermore, the authors referred their results to the optimal foraging theory (Panzacchi et al. 2008 after Schoener 1979), in which red foxes reduce the energy expenditure connected with returning to the den by maximizing the size of the prey transported (Panzacchi et al. 2008). Juvenile foxes in this study were relatively mature, developing their hunting skills during the dispersal period, which occurs at the age of 6–12 months (Harris and Trehwella 1988). Age of foxes did not affect the dietary composition markedly. We noted that the diets of adult males and young foxes converged; both had large food niche breadths and hunted bigger and potentially more difficult to obtain prey such as birds and other mammals, whereas females concentrated mainly on small mammals. Although our results revealed sex differences, according to Englund (1965), males and females in 6–18 months old choose similar food during the whole year. Sex-specific diet preferences within adult foxes may be an effect of sexual dimorphism, but since the young foxes utilized similar prey species as adult males, the difference in food taken by females is probably related to the breeding period. From January to February, during the fox breeding period, females may utilize smaller foraging

Fig. 4 Diet of red foxes in four main regions in northeastern Poland. *Numbers above bars* denote food niche breadth values, *numbers below bars* denote sample sizes

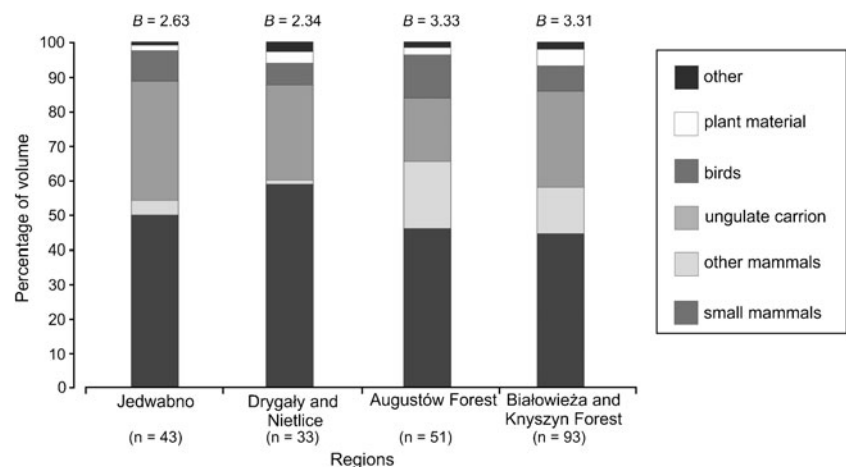
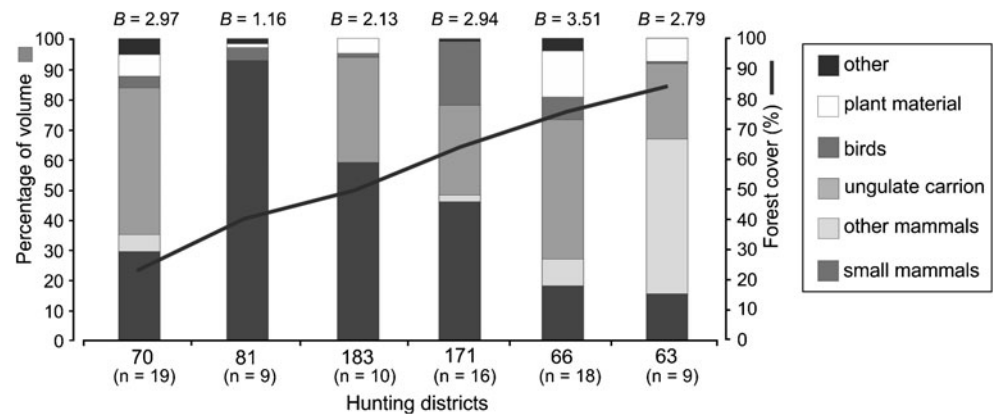


Fig. 5 Diet of red foxes in relation to forest cover in six hunting districts of north-eastern Poland. Numbers above bars denote food niche breadth values, numbers below bars denote sample sizes



territories and prefer eating more easily accessible prey. According to Travaini et al. (1993), the reduction of the female home range size is a result of energetical and behavioral shifts due to breeding activity. These results may be consistent with studies on mustelids, where resource partitioning between sexes according to prey size is considered a secondary effect of sexual size dimorphism which has evolved from differences in the energetic requirements during reproduction (Moors 1980; McDonald 2002; Zalewski 2007). Furthermore, Henry et al. (2005) suggest that reproductive females monopolize the richest food patches at the expense of younger nonreproductive females. This may explain the high percentage of the most preferred prey, i.e., voles consumed by adult females.

Variation in fox diet between months probably results from changes in climatic conditions, which influence the abundance of the food resources. Such correlation was noted by Cavallini and Lovari (1991) and Lucherini and Crema (1994). Goszczyński (1986) found that high densities of voles reduce seasonal differences in food composition. Consumption of carrion by foxes usually increases from late autumn to early spring, as other seasonally available prey or items become scarce or less accessible due to snow cover (Jędrzejewski and Jędrzejewska 1992; Sidorovich et al. 2006). However, voles were the staple

food of foxes during almost the whole period. Only in September–November period, the amount of ungulate carrion outnumbered the amount of voles consumed. Winter 2002–2003, when this study was carried out, was remarkably severe with heavy snowfalls. Indeed foxes' food niche breadth was the broadest in December, which was the coldest month (-8.5 to -6.8°C), with the deepest snow cover, when foxes have to enrich their diet with buffer foods (such as ungulate carrion, other mammals, or birds).

Several authors have observed that variations in fox diet are related to the abundance of potential prey species in various habitats (Kolb and Hewson 1979; Leckie et al. 1998; Sidorovich et al. 2006). In Belarus, foxes preyed mainly on rodents in rich (in terms of food diversity and availability) habitats, while in areas of poor food supply, they foraged mainly on carrion in winter or fruits in warm period (Sidorovich et al. 2006). Moreover, during *Microtus* population outbreaks, red foxes tended to rely greatly on this prey (Sidorovich et al. 2006). According to Kjellander and Nordstrom (2003), the diet and litter sizes of red foxes follow vole cycles without a time lag. In the study of Jędrzejewski and Jędrzejewska (1992), the share of *Microtus* in the diet dropped during the sharp decline of the vole population in Białowieża Forest, but not below 30% of the total biomass consumed by foxes. During the period of this study, the number of *M. oeconomus* was high in the area of Białowieża Forest (Zub et al. in review 2011), resulting in a considerable amount of voles in the fox diet. Indeed, considering the four main regions, small mammals (which constituted mainly voles) were the most important food source. Detailed comparison of the influence of habitat type on fox diet revealed very high variation in diet composition (e.g., voles varied from 15% to 93%) and declining consumption of voles with increasing percentage of forest cover in the area of hunting districts. It shows opportunistic feeding habits of red foxes and compensatory role of food resources other than voles. Considering fox preferences for rodents of open fields, such as *Microtus* spp., the lack of preferred prey species in forest areas forces predators to

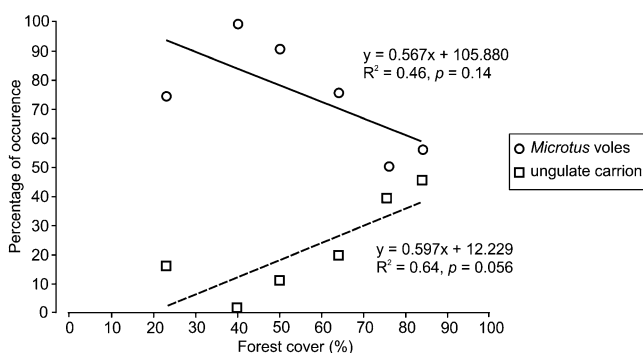


Fig. 6 The relationship between frequency of occurrence of voles and ungulate carrion in fox diet and the percentage of forest cover in hunting districts

utilize other sources of food. In agricultural lands of western Poland, common voles constituted 93% of the total biomass consumed by red foxes (Goszczyński 1974), but in central Poland, where densities of small rodents were lower, a compensatory response was found between similar proportions of small mammals, birds, and hares consumed (Goszczyński 1986). Here, the secondary food was mainly ungulate carrion, as has been also observed in Białowieża National Park (Jędrzejewski and Jędrzejewska 1992), but birds and other mammals were also found especially in more forested areas.

The red fox is recognized as a generalist predator, eating easily accessible and abundant prey. However, due to the opportunistic habits of the species, in particular habitats it easily adapts to specialization. No food resource survey studies were conducted simultaneously; however, the high percentage of voles in the fox diet occurring regardless of age, sex, month, or habitat diversification may indicate a fox specialization in hunting for *Microtus* rodents.

Acknowledgments We are grateful to Michał Kaszuba of the Polish Society for Birds Protection who helped us in collecting fox carcasses from hunters and Dr. Karol Zub who helped in the identification of birds. We also thank Joanna Kocik who determined the age of foxes by teeth analysis. The study was supported by Ekofundusz foundation within the project “Conservation of black grouse and capercaillie in northeastern Poland” and was funded by the Mammal Research Institute, Polish Academy of Sciences. We are also grateful to Dr. A. Eycott for the editorial assistance with the manuscript and to Dr. C. Dickman and two anonymous reviewers for their helpful and critical comments.

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