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ORIGINAL PAPER

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Summer food of sympatric red fox and pine marten in the German Alps

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Abstract Based on fecal analyses, we compared summer diet composition and trophic niche breadth for the sympatric red fox *Vulpes vulpes* ($n = 55$ scats) and pine marten *Martes martes* ($n = 64$) in the foothills of the German Alps. Mammals accounted for 41 and 51% of the consumed biomass by pine martens and red foxes, respectively, and no single mammal species exceeded 8% of the diet. The larger red fox consumed a wider range of prey sizes than the smaller pine marten, and both consumed large amounts of plants and also insects. Whereas the Levins index suggested that both predators have specialist feeding niches, the Shannon-Wiener index showed that both predators were relatively generalist. Despite its preliminary nature, our study suggests that a strict distinction between generalist and specialist trophic niches is not justified for medium-sized carnivores in the Alps, particularly as results greatly depend on the indices used.

Keywords Alps · Diet · *Martes martes* · Trophic niche breadth · *Vulpes vulpes*

Introduction

Based on the breadth and variability of their diets, or their trophic niches, carnivorous mammals are often characterized within a spectrum ranging from specialist to generalist feeders (e.g. Jedrzejewski et al. 1989; Jedrzejewska and Jedrzejewski 1998). In Europe, the red fox (*Vulpes vulpes*) (e.g. Englund 1965; Goszcynski 1974) and the pine marten (*Martes martes*) (Moors 1980; De Marinis and Masseti 1991) have both been described as opportunistic feeding generalists. Still, distinct feeding habits are well described: red foxes show a preference for *Microtus* voles (e.g. Macdonald 1977; Storch et al. 1990), while pine martens take *Clethrionomys* voles more frequently (e.g., Pulliainen 1981; Storch et al. 1990). Also, because of the larger size of the red fox and the broader range of habitats used, a wider feeding niche may be expected in the red fox than in the smaller pine marten, a specialist of mature forest habitats (Storch et al. 1990). In general, the mean size of prey in the diet is positively correlated with the size of the predator (Jaksic and Braker 1983; Jedrzejewski et al. 1989), and we expected a similar relationship for the predators studied. In this paper, we describe summer food composition and trophic niche breadth based on fecal analyses for the sympatric red fox and pine marten in the foothills of the Bavarian Alps, Germany. Because our study was restricted to one summer in a single area, results should be considered preliminary.

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Methods

The study was conducted in the foothills of the Bavarian Alps on the Teisenberg mountain (47°48′N, 12°47′E), with elevation ranging from 700 to 1300 m above sea level. Except for a 30-ha pasture at its summit, the mountain was covered by Norway spruce (*Picea abies*) forest. Among the larger herbivores, roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), mountain hare (*Lepus timidus*), and capercaillie (*Tetrao urogallus*) were common. European hares (*L. europaeus*) and chamois (*Rupicapra rupicapra*) were more rare. The larger carnivorous mammal species recorded on Teisenberg were red fox, European badger (*Meles meles*), pine marten, weasel (*Mustela nivalis*), and stoat (*M. erminea*); stone martens (*Martes foina*) were common in the farmland valleys surrounding the study area.

A network of gravel roads was maintained throughout the ca. 29-km^2 study area, amounting to a density of 2.7 km roads/km^2. During June–August 1999, three censuses of the whole network of forest roads (length = 79 km) were carried out to detect red fox and pine marten scats. Because stone martens had not been recorded in the study area since fieldwork began in 1988 (I. Storch, unpublished), we labeled all marten scats found as pine marten.

Table 1 Keys used for identification of undigested remains in the feces of red foxes and pine martens

Taxon	Undigested remains	Identification keys
Insects	Exoskeletons–abdominal, thoracic, testicular	Chinery (1986); Freude et al. (1965); Harz (1975); Müller (1986); Seifert (1996); Steinmann and Zombori (1985); Zahradnik (1985)
Mammals	Hairs–cuticular-scale castings, medullar patterns, cross sections	Brunner (1974); Day (1966); Debrot (1982)
Mammals	Teeth	Brohmer (1984); Corbet (1980); März (1987)
Birds	Feathers	Day (1966)
Plants	Berries, seeds, stalks	Garcke (1972); Rothmaler (1994); Schmeil and Fitschen (1968)

Table 2 Taxonomic groupings used in determining niche breadth

Insects	Plants	Mammals	Birds	Others
Coleoptera	Ericaceae	Murinae	Passeriformes	Arachnida
Hymenoptera	Rosaceae	Gliridae	Falconiformes	Mollusca
Dermoptera	Gramineae	Sciuridae		Isopoda
Diptera	Selaginellaceae	Arvicolinae		
Saltatoria		Soricidae		
Odonata		Talpidae		
Lepidoptera		Leporidae		
Insect larvae		Cervidae		

Within 3 days of collection, samples were autoclaved for 60 min at ~70 °C and 1.5 bar to arrest enzymatic and fungal degradation of the samples. The scats were mapped and 55 red fox and 64 pine marten scats were selected for analysis, equally from all 100-m altitude intervals. For the fecal analysis, the samples were washed through sieves, dried for 12 h at 70 °C, and broken up in petri dishes. Dietary components were identified to the extent permitted with the aid of identification guides and reference collections (Table 1). Samples were identified under a 4–40× magnification binocular microscope and were overlaid on a 5-mm grid to allow the estimation of their volume as a percentage of the scat in 5% increments (< 5, 5, 10, ..., 95, 100%) (Lockie 1959; Kruuk and Parish 1981). For each food item, this percentage was multiplied by the dry mass of the scat to approximate the dry mass of the individual dietary component and then multiplied by a digestibility correction factor in order to estimate the percentage of the biomass this item represented in the diet (Lockie 1959, 1961; Goszczynski 1974). Food items composing < 5% of a scat were recorded as an occurrence, but were not used in the calculation of consumed biomass.

Results were expressed in terms of relative frequency of occurrence, defined as the number of times a specific item occurred as a proportion of the total number of recorded items (Prigioni and Tacchi 1991), and in terms of consumed biomass. Prey items were grouped taxonomically (Table 2) and trophic niche breadth was calculated using the Levins index (Levins 1968) and the Shannon-Wiener index (Pielou 1975) based on both frequency of occurrence and consumed biomass. In both indices, scores range from a minimum niche breadth near 0 to a maximum of 1. To assess the relationship between predator and prey size, we estimated the average weights for all predator and mammal prey species according to a guide book (Corbet and Ovenden 1980).

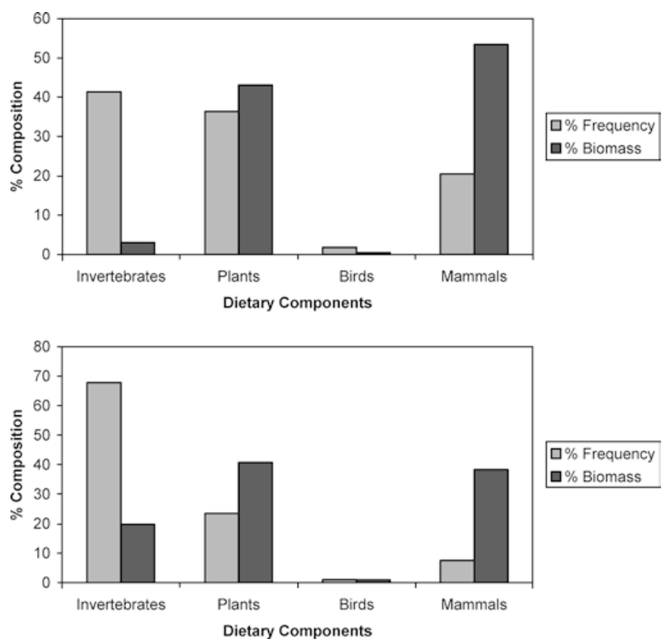

Fig. 1 Food composition of red foxes (*above*) and pine martens (*below*) as frequency of occurrence (%) and consumed biomass

Results

Diet composition

The most frequently occurring food categories in the red fox feces were insects and plants (Fig. 1). In terms of consumed biomass, however, insects made up only 3%, while plants and mammals made up 46 and 51%, respectively. Roe deer, field vole (*Microtus agrestis*), and red squirrel (*Sciurus vulgaris*) made up the largest proportion of the mammalian prey, but no single species accounted for more than 8% of the diet. The largest contributors of plants and insects were the order Graminaceae and family Carabidae. Birds played a negligible role in the diet of red foxes (see Fig. 1, Table 3).

Close to two thirds of food items encountered in the pine marten scats were from insects, most notably from

Table 3 Diet composition[a] of red fox and pine marten as revealed through fecal analysis

	Red fox		Pine marten	
	Frequency of occurrence (%)	Consumed biomass (%)	Frequency of occurrence (%)	Consumed biomass (%)
INSECTA	40.45	3.02	65.34	8.38
Coleoptera	29.55	2.54	36.46	4.42
Carabidae	18.64	1.94	17.33	2.35
Carabus auronitens	7.27	0.72	2.17	0.49
Carabus violaceus	1.36	0.20	1.81	0.27
Carabus granulatus	0.91	0.12	0.72	0.06
Calosoma spp.	0.45	0.01		
Loricera pilicornis			1.08	0.01
Pterostichinae	4.55	0.67	4.33	0.69
Pterostichus cupreus	0.91	0.04	2.89	0.41
Misc. Carabidae	3.18	0.17	4.33	0.41
Curculionidae	3.18	0.27	13.36	1.51
Hylobiinae	0.91	0.11	0.72	0.08
Hylobius abietis			0.72	0.22
Liparus glabirostris			0.36	0.00
Liparus spp.	0.45	0.01	1.81	0.30
Misc. Curculionidae	1.82	0.15	9.75	0.91
Scarabaeidae			0.36	0.01
Scolytidae			0.36	< 0.01
Staphylinidae	0.45	< 0.01		
Philontus spp.	0.45	< 0.01		
Geotrupidae	1.82	0.05	1.81	0.21
Geotrupes spp.	0.45	< 0.01		
Misc. Geotrupidae	1.36	0.05	1.81	0.21
Misc. Coleoptera	5.45	0.28	3.25	0.34
Hymenoptera	4.09	0.06	22.02	3.35
Formicidae	2.73	0.01	17.69	3.00
Camponotus spp.	0.45	< 0.01	3.97	0.54
Formica spp.			5.78	1.37
Misc. Formicidae	1.36	0.01	3.97	0.43
Tetramorium spp.	0.91	< 0.01	3.97	0.66
Misc. Vespidae			0.72	0.11
Misc. Hymenoptera	1.36	0.05	3.61	0.25
Diptera			1.81	0.04
Trichoceridae			0.36	< 0.01
Trichocera anulata			0.36	< 0.01
Misc. Diptera			1.44	0.04
Calliphoridae larvae	0.45	0.01		
Dermaptera	0.45	< 0.01	0.72	0.03
Saltatoria	0.45	0.27	0.36	0.36
Lepidoptera			0.36	< 0.01
Odonata			0.36	0.05
Misc. insects	5.00	0.16	3.25	0.19
Insect larvae	0.91	< 0.01	0.36	< 0.01
ARACHNIDAE			0.36	0.00
ISOPODA	0.45	< 0.01		
MOLLUSCA	0.45	< 0.01	2.17	0.39
PLANTAE	36.36	45.59	23.47	46.02
Ericaceae	5.00	13.83	2.89	10.02
Vaccinium myrtillus	5.00	13.83	2.89	10.02
Rosaceae	6.36	9.78	4.69	23.89
Prunus spinosa	2.27	3.65	1.44	11.43
Prunus cerasus			0.36	2.98
Rubus spp.	2.73	5.23	1.44	7.29
Sorbus spp.			0.36	0.81
Misc. Rosaceae seeds	0.91	0.37	0.72	0.08
Misc. Rosaceae skins	0.45	0.53	0.36	1.30
Graminaceae	10.91	16.05	2.53	1.96
Selaginellaceae	1.82	0.01		
Misc. Plants	12.27	5.91	13.36	10.16
AVES	1.82	0.43	1.08	4.37
Passeriformes	1.36	< 0.01	1.08	4.37
Falconiformes	0.45	0.43		
MAMMALIA	20.45	50.96	7.58	40.83
Murinae	1.36	1.48	0.72	1.14

Table 3 (Contd.)

	Red fox		Pine marten	
	Frequency of occurrence (%)	Consumed biomass (%)	Frequency of occurrence (%)	Consumed biomass (%)
Apodemus flavicollis	0.91	1.33		
Apodemus spp.			0.36	0.92
Misc. Murinae	0.45	0.15	0.36	0.22
Gliridae	1.82	6.19	1.44	8.30
Eliomys quercinus			0.72	1.15
Muscardinus avellanarius	0.91	0.87	0.72	7.15
Glis glis	0.45	0.16		
Misc. Gliridae	0.45	5.15		
Sciuridae	1.36	4.55	1.08	7.29
Sciurus vulgaris	1.36	4.55	1.08	7.29
Arvicolinae	9.55	24.21	2.17	10.77
Ondatra zibethicus	0.91	4.31		
Clethrionomys glareolus	1.82	4.61	0.36	5.61
Arvicola terristris	1.36	3.05	1.08	4.18
Pitymys subterraneus	0.91	3.13		
Microtus agrestis	3.18	6.21		
Microtus arvalis	0.45	1.19		
Misc. Arvicolinae	0.45	1.71	0.36	0.98
Soricidae	2.73	2.62	0.36	3.26
Sorex minutus	0.91	0.31	0.36	3.26
Sorex araneus	0.45	0.00		
Crocidura leucodon	0.91	1.52		
Crocidura russula	0.45	0.79		
Talpidae	1.36	1.25	0.36	0.31
Talpa europea	1.36	1.25	0.36	0.31
Leporidae	0.91	2.63	0.72	8.07
Lepus timidus	0.91	2.63	0.72	8.07
Mustelidae			0.36	1.49
Martes foina			0.36	1.49
Cervidae	0.91	7.92		
Capreolus capreolus	0.91	7.92		
Misc. mammals	0.45	0.09	0.36	0.21
Number of scats	55		64	
Number of food items[b]	220	147	277	223

[a]Data structured taxonomically into CLASS, Order, Family, Subfamily, *Species*

[b]Food items comprising < 5% of a scat were recorded as an occurrence but not used in the calculation of consumed biomass

the Carabidae and Formicidae families (Fig. 1, Table 3). Again, in terms of consumed biomass, plants (mostly Rosaceae) and mammals dominated the diet. While the most frequently targeted mammalian species were water vole (*Arvicola terrestris*) and red squirrel, it was the mountain hare, the red squirrel, the hazel dormouse (*Muscardinus avellanarius*) and the bank vole (*Clethrionomys glareolus*) that represented the largest proportions of the consumed biomass. As in foxes, amphibians and reptiles were not found in the marten diet.

Trophic niche breadth

Based on frequency of occurrence of food items, both the Levins and the Shannon-Wiener indices indicated a greater niche breath for the red fox as compared to the pine marten. Based on consumed biomass, however, very similar values were indicated for the two species (Table 4). While mammals accounted for 51 and 41% of the consumed biomass, respectively, the red fox fed on a broader range of mammal prey sizes ($n = 39$ items, 5–21,000 g, median 35.5 g, mean = 1,346 g, SD = 4,676) than did the pine marten ($n = 16$ items, 5–2,850 g, median 111.3 g, mean = 470 g, SD = 937). Although the fox diet included mammals several times larger than the largest marten prey recorded, there was no significant difference (Mann-Whitney U-Test, $U = 258$, $p = 0.316$) in prey sizes between foxes and pine martens.

Table 4 Niche breadths calculated from taxonomically grouped food items (see Table 2)

Predator species	No. scats analyzed	Levins index		Shannon-Wiener index	
		Frequency	Biomass	Frequency	Biomass
Red fox	55	0.23	0.31	0.69	0.70
Pine marten	64	0.15	0.34	0.57	0.73

Discussion

Diet composition

Red fox diets vary among studies and over time, leading to the description of the red fox as a generalist and opportunistic feeder (Baltrunaite 2003). Our results were in accordance with accounts from other parts of Europe: red foxes on Teisenberg fed on a large variety of items;

voles, and especially *Microtus* (e.g., Macdonald 1977; Storch et al. 1990; Baltrunaite 2003), played a major role in their diet, and plants and insects were also readily taken. As elsewhere in Europe, red foxes consumed primarily grasses and berries when they ate plants, and they ate many beetles (Witt 1976; Cantini 1991; Debernardi et al. 1991; Pandolfi and Bonacoscia 1991; Prigioni 1991; Prigioni and Tacchi 1991; Storch and Kleine 1991). Unlike elsewhere, birds were rare in the red fox diet of our study (Prigioni and Tacchi 1991; Skirnisson 1986). The Falconiformes remains that we found might have originated from carrion. Isopods and mollusks were low in quantity and may have been inadvertently collected with the scat or coincidentally ingested by the red fox. As in other European studies (Clement and Saint Girons 1982; Marchesi and Mermod 1989; Clevenger 1993), we found that the pine martens took more insects than did the red foxes. Overall, however, we found that the greatest biomass in the marten diet was composed of fruits and mammals. The importance of the fruits *Prunus spinosa*, *Vaccinium myrtillus*, and *Rubus* spp. has been repeatedly noted for summer diet in martens (Goszczynski 1976; Skirnsson 1986; Marchesi and Mermod 1989; Cantini 1991; Bertolino and Dore 1995). Mammal remains were low in frequency, but proved important in terms of consumed biomass, with the well-documented emphasis being on *Clethrionomys* voles and dormice (e.g. Lockie 1961; Marchesi and Mermod 1989). Overall, our evidence concurs with the well-documented feeding-generalist interpretation of the pine marten.

Trophic niche breadth

The two different niche-breadth indices provided us with widely differing interpretations regarding the characterizations of the predators' feeding niches. Whereas the Levins index gave the impression that both the predators studied tended toward specialist-feeding niches, the Shannon-Wiener index presented both predators as relatively generalist. This difference is due to the greater relative importance that the Shannon-Wiener index places on rare items, whereas Levins index puts most importance on the evenness of the distribution of items (Pielou 1969). Similarly, the use of frequency of occurrence can produce different conclusions from the use of consumed biomass. Using the former, the importance of food items that pass through the gastrointestinal tract relatively undigested (i.e., insect exoskeletons, plant lignin/cellulose) is increased. The use of biomass data requires the assumption that the digestibility coefficients measured in controlled experiments are relatively consistent in different habitats. Thus, both measures are based on questionable assumptions. Nevertheless, we consider biomass data a better reflection of dietary composition (Lockie 1959; Kruuk and Parish 1981). Therefore, while the calculations of trophic niche breadth using occurrence data tended to show the predators as being more specialist than those using biomass data, the long-standing representations of the red fox and pine marten as generalists lead us to place greater stake in the results of the Shannon-Wiener index. Despite its preliminary nature, our study suggests that a strict distinction between generalist and specialist trophic niches is not justified for medium-sized carnivores in the Alps, particularly as results greatly depend on the indices used.

To better characterize the ecological relationships between these species we would need a greater sample size based on some years of field collection, and we would need to understand the relative abundance and distributions of the food resources and the relative amount of time and energy that are expended by predators in their feeding activities (Baltrunaite 2003).

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