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Dietary overlap among generalist carnivores in relation to the impact of the introduced raccoon dog *Nyctereutes procyonoides* on native predators in northern Belarus

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Abstract

Feeding habits and dietary overlap among forest generalist carnivores (brown bear *Ursus arctos*, red fox *Vulpes vulpes*, badger *Meles meles*, pine marten *Martes martes*, polecat *Mustela putorius*, and raccoon dog *Nyctereutes procyonoides*) in natural forested landscape of northern Belarus (Gorodok and Rossony districts) were studied. In the warm season (April–October), generalist carnivores were characterized by a fairly wide food spectrum. Predominant items of their diets were fruits, small mammals, insects and birds. Although several pairs of species, such as brown bear-badger, raccoon dog-badger, pine marten-red fox, and pine marten-raccoon dog, had considerable dietary overlap, there was little evidence of a competition for resources in the generalist guild in the warm season. In the cold season (November–March), the food niches of active generalist predators became narrower and considerably overlapped, which coincided with a substantial decrease in food abundance and availability. In this period of poor food supply, generalists mostly consumed wild ungulate carrion, small mammals, and fruits. By inhabiting the same habitats, several pairs of species, such as pine marten-red fox, polecat-red fox, polecat-raccoon dog, polecat-pine marten, may compete for food. In the harshest period of late winter and early spring, in conditions of deep and/or soft snow cover in forest, it is energetically expensive to move around and the majority of food search fails. Thus, all generalists were forced to feed on carrion, the abundance of which substantially affected all generalist carnivores with the probable exception of raccoon dog. The obtained data on the predator abundance suggest that after the raccoon dog had reached a high population density, the native generalist predators began to decline.

Key words: carnivores, feeding ecology, Belarus

Introduction

In Europe, carnivores characterized by a wide food spectrum, such as badger *Meles meles*, pine marten *Martes martes*, polecat *Mustela putorius*, brown bear *Ursus arctos*, red fox *Vulpes vulpes*, and the introduced raccoon dog *Nyctereutes procyonoides* compose a generalist guild which is an important part of the vertebrate predator communities (Macdonald 1995; Jedrzejewska and Jedrzejewski 1998). There is a considerable number of studies on feeding habits of generalists inhabiting forest ecosystems (Lockie 1959, 1961; Geptner et al. 1967; Goszczynski 1986; Tumanov and Smelov 1980; Kruuk 1989; Weber 1989; Lode 1990, 1991; Pazhetnov 1990; Vaisfeld and Chestin 1993; Neal and Cheeseman 1996; Sidorovich 1997; Jedrzejewska and Jedrzejewski 1998 and references therein). There are, however, fewer publications in which dietary overlap of forest generalists has been estimated (Weber 1989; Lode 1991; Sidorovich 1997; Jedrzejewska and Jedr-

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zejewski 1998). Also, detailed studies of these predators inhabiting natural forested landscapes have been conducted only in the Bialowieza Primeval Forest, Poland (Jedrzejewska and Jedrzejewski 1998). In the extensive transitional zone of temperate mixed forest located between the more southern deciduous and the boreal coniferous forest zones and characterized by a specific combination of habitat conditions for predators, this question has not been studied, with the exception of a preliminary study on the dietary overlap of pine marten and polecat (Sidorovich 1997). Patterns of interspecific sharing of food resources can be best revealed by studying wildlife in pristine ecosystems. Another aspect of this study was to investigate a competition for resources between native predators and the introduced raccoon dog.

Thus, by conducting this study in natural landscape of northern Belarus, we aimed to investigate species-specific features of feeding ecology of forest generalist carnivores and estimate dietary overlap between native predators and the introduced raccoon dog in a seasonal dynamic of habitats, with their implications on population changes of the native species. Another important goal of the study was to reveal possible negative trends in numbers and structure of the native generalist guild in connection with the invasion of the raccoon dog.

Material and methods

The study was carried out in two areas located in northern Belarus. The first study region was an area of approximately 20×40 km at the head of the Lovat river, Gorodok district, Vitebsk region. The second study region was an area of approximately 40×60 km located between the three medium-sized rivers: Drissa, Nischa, and Svolna in Rossony district, Vitebsk region. The study areas are characterised by fairly natural conditions of river network, glacial lakes, large forests, and bog ecosystems on rough glacial terrain.

Both areas belong to the extended transitional region of temperate mixed forest located between the more southern deciduous and the boreal coniferous forest zones. Spruce *Picea abies* and pine *Pinus sylvestris* are dominant species among coniferous trees. Black alder *Alnus glutinosa* and grey alder *A. incana*, birches *Betula pendula*, *B. pubescens*, and aspen *Populus tremula* are the most common deciduous trees, whereas there are few masting deciduous trees such as oak *Quercus robur*, lime *Tilia cordata*, maple *Acer platanoides*, and ash *Fraxinus excelsior*, which produce a large amount of nourishing seeds for rodents. Therefore, in the transitional forest zone rodents have only seasonal fluctuations with no recurrent cycles of outbreaks and crashes (Sidorovich et al. 2000). Also, rodent abundance in this area is significantly lower than in the more southern deciduous forest, such as the Bialowieza Forest (Jedrzejewska and Jedrzejewski 1998). In the study areas, during the warm season other common prey of vertebrate predators are amphibians (Pikulik 1985) and migratory birds (Nikiforov et al. 1997). Wild ungulates are not as common there as in the more southern deciduous forest (Jedrzejewska and Jedrzejewski 1998). Similar to the Bialowieza Forest (Jedrzejewski et al. 1992), wolf predation together with deep snow cover act as important factors affecting wild ungulate mortality, keeping the density of these animals at a lower level than in the deciduous forest. Overexploitation by humans leads to an additional reduction in their numbers (Sidorovich 1989). Lower density of wild ungulates causes scarcity of carrion, which is an important food resource for many species of vertebrate predators in the cold season (Sidorovich 1997; Jedrzejewska and Jedrzejewski 1998).

In northern Belarus, winters are fairly severe. Normally, there is a deep snow cover of 40 to 90 cm, and air temperatures of about −20 °C and lower for several weeks are quite common. During winter and especially in late winter and early spring (when there is still a deep snow cover in forests), food resources are much scarcer, and their abundance decreases and is not renewed.

We studied the diets of forest generalist predators by analysing their scats. The majority of data was obtained over a period of 7 years (1992–1998), with the most intensive study period falling between 1996 and 1998. Scats were collected on a regular basis from latrines (badger, raccoon dog, polecat, pine marten) and main dens (polecat, red fox, pine marten). Identity of the occupants of dens and latrines was well known from the long-term field experience in the study areas (snowtracking, visual observations, identification of tracks, live capturing, radiotracking or trapping). In the cold season,

the majority of scats was collected at tracks, when it was possible to distinguish tracks of the above-mentioned species. Also, many scats of polecats, pine martens, badgers, red fox, and raccoon dogs were collected during radiotracking studies on these species. A total of 429 excrements of brown bears, 642 of badgers, 789 of red foxes, 653 of raccoon dogs, 831 of pine martens, and 437 of polecats were gathered and analysed.

By analysing the scats, we tried to determine as many different individuals of prey and other food items (bird eggs, fruits, and herbs) as possible by means of both identification of species and size difference. The contents were identified microscopically, using the published keys of mammalian hair (Debrot et al. 1982) or teeth (Pucek 1981), fish scales, teeth, and vertebrates (Galkin 1953; März 1987), amphibian bones (Böhme 1977; März 1987), reptilian bones and skin scales (März 1987), feathers and bones of birds (März 1987). Beetles and crayfish were distinguished by remains of their exoskeletons, molluscs and bird eggs by remnants of their shell. In the cases of badger and raccoon dog scats (with the exception of winter scats of raccoon dogs), microscopic search for earthworm chaetae and estimation of their abundance was fulfilled as described by Kruuk (1989).

More detailed research on feeding ecology of generalist carnivores was carried out in the harshest period of late winter and early spring in the condition of deep and/or soft snow cover, when we carried out additional snowtracking to study the feeding habits of these predators. Totally, each species was tracked for longer than 160 km in this season. Each year in late winter, we inspected an area of 5–7 km^2 to find all wild ungulate carcasses. We regularly surveyed wild ungulate carcasses to reveal the species consuming the carrion. A total of 172 carcasses (98 wild boars *Sus scrofa* and 74 elks *Cervus elaphus*) was found and inspected.

As the two study areas are very similar in habitat conditions and seem to be only two parts of the same large forest, the dietary data obtained in these different parts of the forested area were pooled. In calculations of the percentage of occurrence of various food items in the diet (%OC), the total number of scats analysed was used as 100%. The main measure of the diets was the percentage of food biomass consumed (%BC), because it more accurately expresses the proportion of each food item in the total biomass of food consumed by a predator. To obtain the percentage of food biomass consumed, we followed the approach recommended by Jedrzejewska and Jedrzejewski (1998) based on coefficients of digestibility (collected from the literature), i. e. the ratio of fresh weight of a given food item to the dry weight of its remains in scats. To compare the overall dietary diversity (food niche breadth) of generalist carnivores, B index (Levins 1968) was calculated for 16 food categories. B index varies from 1 (the narrowest niche) to 16 i. e. the maximum number of food categories used for calculations (the broadest niche possible). In order to evaluate the overlap of food niches, Pianka's (1973) index α was calculated, which varies from 0 (exclusive niches) to 1 (complete overlap). Both the food niche breadths and dietary overlaps were calculated according to the diets expressed as a percentage of food biomass consumed.

To estimate a possible change in the density of native generalist species as a response to the raccoon dog invasion, we used an abundance index for each species. The abundance index of the species of generalist carnivores was based on the data obtained by counting their track trails which crossed our route. Each year in 1989–1998, we used the same two routes, one of 36 km located in the Gorodok study area, and the other one of 44 km in the Rossony study area. The routes were specially placed across the whole diversity of habitat types such as a variety of forest types, river valley, glacial lake shore, reed and sedge marshes, and pine bog. To evaluate the abundance of badger and brown bear (which are normally inactive in winter in Belarus), we conducted a track survey in early spring, when the species were already active and snow cover still persisted. The abundance index of each carnivore species was calculated as the number of its track trails crossing our route, divided by both the number of kilometres inspected and the number of days passed from the last snowfall, and multiplied by two. As a result of the calculations, we obtained the average number of the tracks per 1 km transect per 2 days.

Results

Feeding habits and dietary overlap

In the warm season, the majority of generalists (pine marten, badger, raccoon dog, and brown bear) consumed a wide spectrum of food (Tab. 1 a). Their food niche breadths calculated by Levins's formula varied from 4.25 to 6.60. Insects (mainly beetles) and fruits

(berries and apples) were common food of all these generalists. Badgers mainly fed on earthworms, molluscs, amphibians, small mammals, birds, cereal seeds, and herbs. Brown bears consumed numerous cereal seeds and herbs. Raccoon dogs mainly consumed molluscs, amphibians, birds and their eggs, carrion, and herbs. Pine martens frequently fed on small mammals, honey, birds and their eggs. The above-mentioned predators had large dietary overlaps (badger-brown bear, raccoon dog-badger, raccoon dog-pine marten; Pianka's index = 0.72–0.79) or intermediate dietary overlaps (brown bear-raccoon dog, pine marten-badger, pine marten-brown bear; Pianka's index = 0.45–0.69). Red fox and polecat were characterized by narrower food niches (Levins's index = 2.85 and 3.08, respectively). Red fox basically consumed mammals of small (mainly voles) and medium size (hares, muskrat, red squirrel, and hedgehog), birds, and fruits (mainly billberries and apples), whereas polecat mainly fed on amphibians, small mammals and birds. There was no considerable overlap in the diets of red fox and polecat (Pianka's index = 0.58), and between the two species and the other four generalist carnivores (Tab. 1 a), with the ex-

Table 1. Diet composition (expressed in percentage of occurrence of various food items in the scats analysed (%OC), and in percentage of food biomass consumed (%BC)) of the generalist carnivores in northern Belarus, 1992–1998. B-index of food niche breadth (Levins 1968). α-index of food niche overlap after Pianka (1973). Both B and α were calculated for the sixteen listed food items.

a) in the warm period (April–October)

Food category	Badger		Brown bear		Red fox		Raccoon dog		Pine marten		Polecat	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
Insects	82.5	27.3	70.4	18.4	24.3	3.0	67.5	10.9	31.1	14.6	4.7	0.9
Molluscs	10.4	1.0	–	–	–	–	10.6	3.5	0.4	<0.1	1.0	0.1
Earthworms	22.7	11.7	–	–	–	–	1.3	0.4	–	–	–	–
Crayfish	0.6	0.1	–	–	–	–	1.3	0.6	–	–	1.7	0.7
Fish	0.5	0.1	0.5	<0.1	0.5	0.1	5.7	1.5	–	–	2.0	1.2
Amphibians	13.9	4.2	–	–	0.5	<0.1	32.1	13.1	1.8	0.4	67.3	45.8
Reptiles	6.2	0.8	–	–	1.2	0.3	3.2	0.9	2.2	0.3	4.4	1.3
Small mammals	11.8	6.4	0.7	<0.1	70.1	55.7	9.2	6.5	39.8	34.7	32.0	30.6
Medium-sized mammals	1.4	1.1	–	–	13.6	9.1	3.3	2.2	2.2	1.7	–	–
Birds	13.4	7.3	–	–	27.2	16.5	32.7	17.4	24.1	17.5	17.5	13.7
Bird eggs	2.5	0.7	0.5	<0.1	3.6	0.8	8.8	1.7	7.2	2.1	4.7	1.2
Ungulate and other carcasses	5.3	4.8	8.2	7.5	7.3	5.9	11.0	9.3	4.7	4.0	5.1	4.0
Fruits	54.4	21.6	55.9	34.5	19.0	7.7	56.3	27.0	37.5	21.8	1.7	0.5
Cereal seeds	38.8	10.2	35.4	20.1	2.7	0.9	4.4	1.9	–	–	–	–
Herbs	9.7	2.7	40.5	19.3	0.5	<0.1	13.6	3.1	0.6	<0.1	0.7	<0.1
Honey	–	–	0.7	0.1	–	–	–	–	6.9	2.9	–	–
Number of the scats analysed	642		429		441		455		502		446	
Index of food niche breadths B	6.26		4.25		2.85		6.60		4.45		3.08	
	Index of food niche overlap α:											
Badger	–		0.79		0.33		0.76		0.65		0.24	
Brown bear			–		0.14		0.69		0.45		0.02	
Red fox					–		0.42		0.89		0.58	
Raccoon dog							–		0.72		0.52	
Pine marten									–		0.51	
Polecat											–	

Table 1. b) in the cold period (November–March)

Food category	Red fox		Raccoon dog		Pine marten		Polecat	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
Insects	0.8	<0.1	11.2	2.0	26.0	10.8	7.0	1.1
Molluscs	–	–	12.7	3.9	–	–	0.4	<0.1
Crayfish	–	–	0.3	<0.1	–	–	–	–
Fish	–	–	1.0	0.5	–	–	1.2	0.5
Amphibians	–	–	10.2	3.6	2.5	0.7	30.4	22.8
Reptiles	0.2	<0.1	4.8	1.0	1.4	0.4	4.7	1.5
Small mammals	80.1	56.4	10.7	6.0	60.3	42.6	38.9	31.9
Medium-sized mammals	9.4	8.2	3.1	2.4	4.9	3.6	0.4	1.0
Birds	8.9	5.4	5.6	2.8	13.1	7.0	3.5	2.3
Bird eggs	–	–	–	–	1.9	0.5	–	–
Ungulate and other carcasses	34.8	28.3	71.5	53.0	19.1	16.3	41.6	38.2
Fruits	7.3	1.7	41.2	21.8	31.4	17.1	1.2	0.7
Cereal seeds	–	–	3.3	0.9	–	–	–	–
Herbs	1.1	<0.1	14.2	2.1	0.3	<0.1	1.6	<0.1
Honey	–	–	–	–	2.7	1.0	–	–
Number of the scats analysed	437		393		366		257	
Index of food niche breadths B	2.47		2.97		3.92		3.34	
	Index of food niche overlap α:							
Red fox	–		0.52		0.92		0.83	
Raccoon dog			–		0.53		0.73	
Pine marten					–		0.74	
Polecat							–	

c) in the harshest period characterized by scarce food supply (either deep snow cover in late winter and early spring or deep and soft snow cover in any time of winter)

Food category	Badger		Brown bear		Red fox		Raccoon dog		Pine marten		Polecat	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
Insects	9.6	6.5	14.6	3.4	–	–	5.0	0.8	15.7	6.0	2.0	<0.1
Molluscs	–	–	–	–	–	–	3.3	0.9	–	–	–	–
Amphibians	13.5	4.9	–	–	–	–	5.0	2.1	–	–	9.1	3.7
Reptiles	1.9	0.6	–	–	–	–	1.7	0.4	2.0	0.7	–	–
Small mammals	3.8	2.2	–	–	38.9	29.4	2.5	2.2	47.1	30.4	30.1	19.9
Medium-sized mammals	–	–	–	–	3.3	3.0	–	–	3.9	3.1	–	–
Birds	–	–	–	–	3.3	2.1	0.8	1.0	6.7	4.7	2.0	1.1
Ungulate and other carcasses	65.4	61.1	73.1	62.5	72.8	64.9	88.4	70.6	55.9	50.1	80.6	75.3
Fruits	23.1	20.5	36.6	22.7	–	–	17.3	11.8	7.8	4.9	–	–
Herbs	15.4	4.2	48.8	11.4	2.8	0.6	28.1	10.2	2.0	0.1	–	–
Number of the scats analysed	52		41		180		121		102		98	
Index of food niche breadths B	2.36		2.19		1.97		1.91		2.84		1.65	
	Index of food niche overlap α:											
Badger	–		0.99		0.87		0.98		0.84		0.92	
Brown bear			–		0.84		0.98		0.81		0.89	
Red fox					–		0.90		0.98		0.98	
Raccoon dog							–		0.85		0.95	
Pine marten									–		0.95	
Polecat											–	

ception of pine marten and red fox (Pianka's index = 0.89) as consumers of voles, birds and fruits.

In the cold season in the conditions of severe climate in northern Belarus, active generalist carnivores such as polecat, pine marten, red fox, and raccoon dog (this introduced species only partly sleeps in winter) mainly consumed carrion of wild ungulates, small mammals and fruits (cranberries, cowberries, and ashberries). The food niche breadth of each predatory species was narrower (Levins's index = 2.47–3.92) than in the warm season. Also in the cold season, red foxes preyed on hares and resident birds; raccoon dogs frequently consumed insects, molluscs, amphibians, and herbs; pine martens fed on insects and resident birds, and polecats consumed many amphibians (Tab. 1 b). The dietary overlaps were either fairly high (pine marten-red fox, raccoon dog-polecat, polecat-pine marten, polecat-red fox; Pianka's index = 0.73–0.92) or moderate (raccoon dog-red fox, pine marten-raccoon dog; Pianka's index = 0.52–0.53).

Table 2 presents the percentages of occurrence of different species of small mammals preyed upon by generalist carnivores in the warm and cold seasons. Microtine voles, bank vole, and mice of the genus *Apodemus* were most important mammalian prey. Red foxes specialized in feeding on microtine voles and striped field mouse, whereas bank vole and mice of the genus *Apodemus* were the main mammalian prey for pine martens. Bank vole, microtine voles, water vole, mice of the genus *Apodemus* and insectivores were fairly equally important for polecats and raccoon dogs.

During the harshest period of late winter and early spring, which is very often characterized by deep and/or soft snow cover, all studied generalists mainly fed on carrion (55.9–88.4% OC and 50.1–75.3% BC, Tab. 1 c). Therefore, they considerably overlapped in the diets (Pianka's index = 0.81–0.99, Tab. 1 c). Also, in this unfavourable period of poor food supply, red foxes, pine martens, and polecats supplemented their diets with mammalian prey, whereas raccoon dogs as well as brown bears and badgers (already active by early spring) frequently fed on cranberries when these fruits were available at pine bogs (Tab. 1 c).

The snowtracking data (Tab. 3) obtained in this harsh period in the forested areas mainly characterized these predatory species as scavengers. After finding an ungulate carcass, they usually stayed at the carrion until it was completely consumed. Different species of carnivores fed at the carcasses found (Tab. 4). Such carrion appeared mainly due to wolf kills (46%, n = 172) and from wild ungulates that had died due to other causes (54%), and

Table 2. Percentage of occurrence of small mammal species consumed by generalist carnivores in the warm (WS) and cold seasons (CS) in northern Belarus, 1992–1998

Species of small mammals	Badger		Red fox		Raccoon dog		Pine marten		Polecat	
	WS	CS	WS	CS	WS	CS	WS	CS	WS	CS
Clethrionomys glareolus	17.4	100	14.3	16.2	8.3	17.6	48.9	63.0	15.1	40.0
Microtus sp.	39.1	–	45.7	30.4	–	17.6	7.6	7.3	37.7	20.0
Arvicola terrestris	–	–	6.3	8.6	8.3	29.5	1.1	–	11.3	10.0
Micromys minutus	–	–	3.2	–	–	–	–	0.8	1.9	–
Apodemus sp.	43.5	–	21.0	32.4	–	–	25.0	16.9	17.0	11.4
Sorex sp.	–	–	0.8	3.8	66.7	17.6	3.3	4.0	5.7	10.0
Neomys fodiens	–	–	–	–	–	–	–	–	1.9	2.9
Talpa europaea	–	–	7.1	8.6	16.7	17.6	4.3	4.0	7.5	4.3
Dryomys nitedula	–	–	–	–	–	–	3.3	1.6	1.9	–
Sicista betulina	–	–	0.8	–	–	–	1.1	–	–	1.4
Chiroptera sp.	–	–	0.8	–	–	–	5.4	2.4	–	–
Sample size (n)	23	2	126	105	12	17	92	124	23	70

Table 3. Feeding habits (in percentage of observations) of generalist carnivores in the harshest period in late winter and early spring according to the snowtracking data (totally 1 679 km) in northern Belarus, 1992–1998

Plausible explanation of feeding habits	Badger	Brown bear	Red fox	Raccoon dog	Pine marten	Polecat
Scavenging (to find carrion or occasionally catch any prey)	49.3	55.2	46.2	20.1	62.7	37.1
Feeding on carrion (mostly of wild ungulate carcasses) and stay around	30.9	20.5	32.3	42.7	18.9	40.8
Hunting on small mammals	0.6	0	14.8	0.9	12.1	11.5
Catching of amphibians	4.7	0	0	5.9	0.1	8.6
Collecting cranberries	10.1	20.4	0.2	12.7	1.0	0
Feeding on herbs	0.8	2.3	0.1	9.2	0	0
Other feeding habits	3.6	1.6	6.4	8.5	5.2	2.0
Length of snowtracking, km	162	304	247	302	379	285

Table 4. Composition of predators (expressed in percentage of track observations) consumed the wild ungulate carcasses found (n = 172) in northern Belarus, 1989–1998

Species of wild ungulate carcasses	Badger	Brown bear	Red fox	Raccoon dog	Pine marten	Polecat	Lynx	Wolf
Elk (n = 74)	5.4	16.2	94.6	60.8	78.4	54.1	5.4	52.7
Wild boar (n = 98)	5.1	8.2	92.8	73.5	62.2	42.9	6.1	30.6

was scarce as a food resource. Usually, in various areas of 5–7 km^2, we found 1 or 2 (up to 4) elk carcasses and 1–4 (up to 9) carcasses of wild boar. Only 6 carcasses (1 elk and 5 wild boars) out of 98 carcasses found (6.1%) were negligibly eaten, 32 carcasses (32.7%) still contained a substantial amount of carrion, but the majority of carcasses (60 out of 98, 61.2%) was nearly totally eaten and mainly contained the skull, other large bones and remnants of skin. Nevertheless, all such poor remnants of wild ungulate carcasses were visited by generalist cernivores, who evidently tried to consume some carrion.

Shift in the abundance of native generalist carnivores

In figures 1 and 2, a pairwise comparison between changes in the abundance of raccoon dogs and the abundance of native species of generalist predators in the Rossony and Gorodok study areas are given. Negative correlation between the raccoon dog abundance and the abundance of polecats was statistically significant for both study areas (Rossony area: $r_s = -0.84$, $P < 0.001$; Gorodok area: $r_s = -0.67$, $P = 0.009$). Also, a statistically significant negative correlation between the raccoon dog abundance and the abundance of other native generalists was found for the Rossony area only (pine marten: $r_s = -0.91$, $P < 0.001$; red fox: $r_s = -0.71$, $P = 0.004$; badger: $r_s = -0.91$, $P = 0.002$; brown bear: $r_s = -0.66$, $P = 0.01$).

Discussion

In the warm season in the natural landscape of northern Belarus, generalist carnivores were characterized by a fairly wide food spectrum. Predominant items of their diets were fruits, small mammals, insects and birds. Although several pairs of predatory species had considerable dietary overlap, there was little evidence of resource competition during the warm season. The diets overlapped mainly concerning non-limited food resources such as

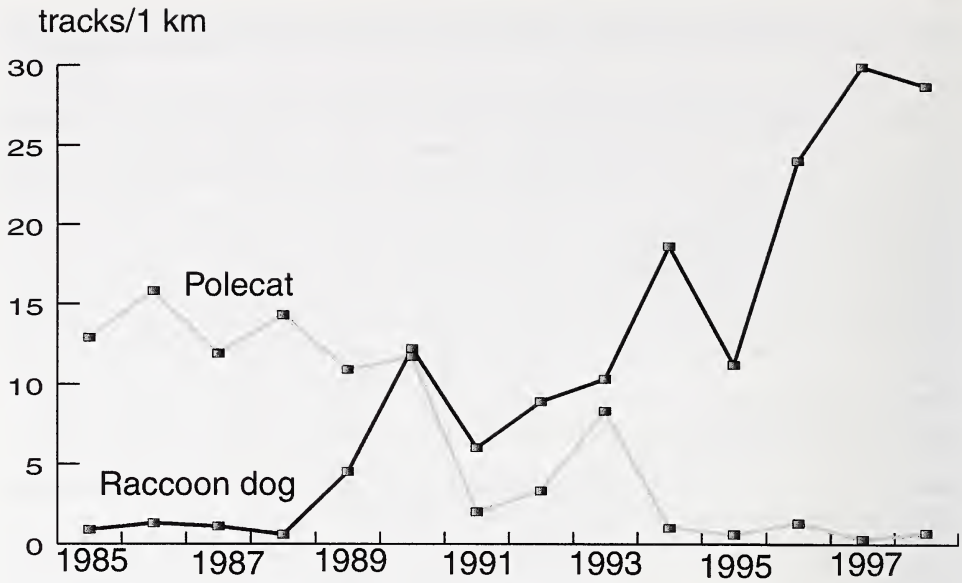

Fig. 1 a.

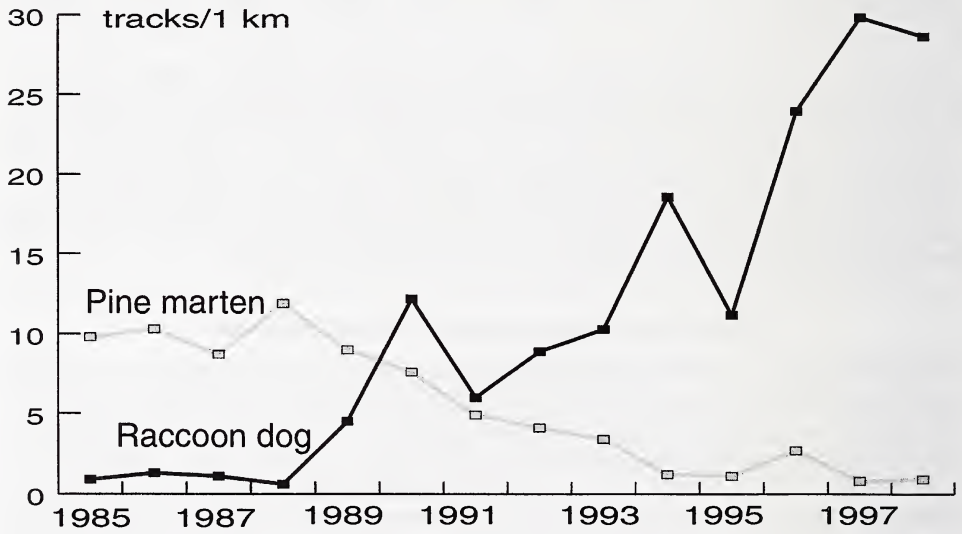

Fig. 1 b.

fruits, cereal seeds, and insects. Also, for most of the warm season, small mammals seem to be a non-limited prey (Sidorovich et al. 2000).

In the cold season, food niches of the active generalist predators became narrower and considerably overlapped, which coincided with a substantial decrease in food abundance and availability. During this period of poor food supply, the observed generalists mainly consumed wild ungulate carrion, small mammals, and fruits, which were markedly limited as a food resource. By inhabiting the same ecosystems, several pairs of predatory species may compete for food. In the harshest period of late winter and during early

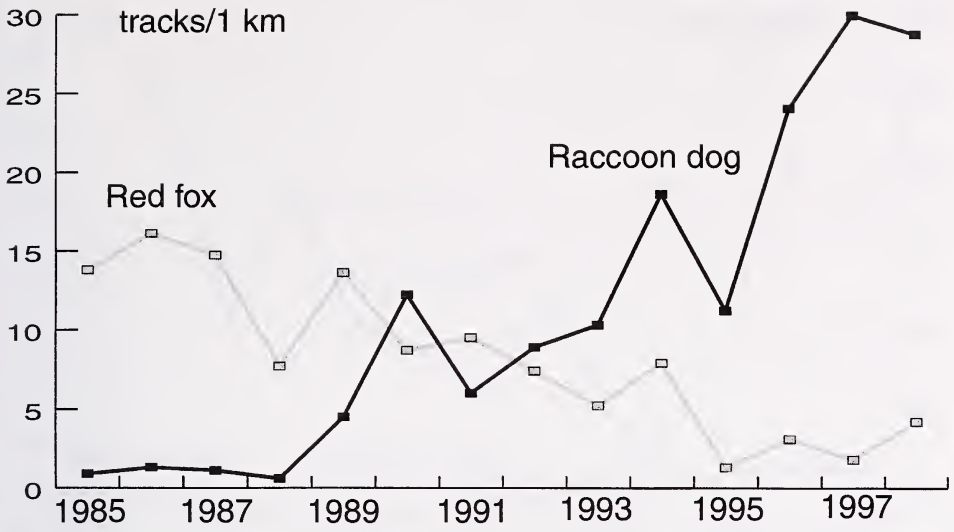

Fig. 1c.

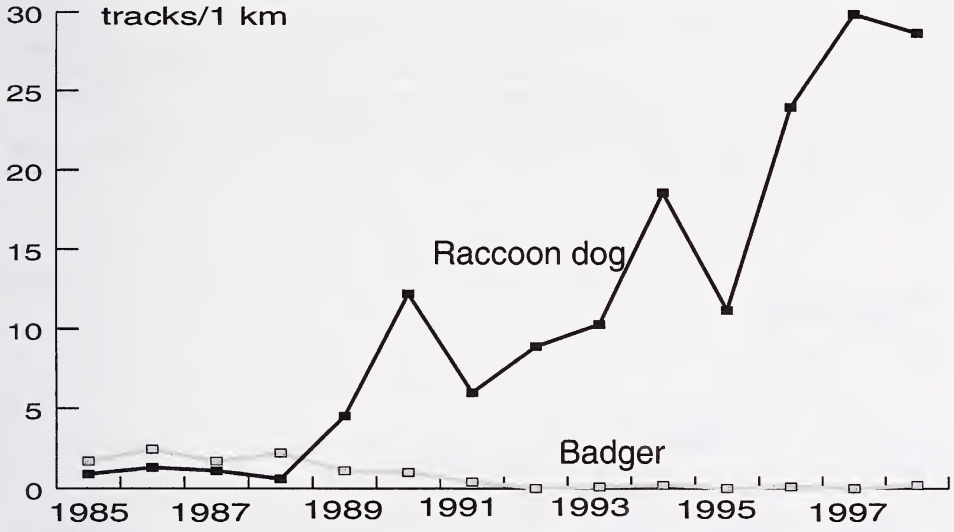

Fig. 1d.

spring, very often characterized by deep and/or soft snow cover in forests, when it is energetically expensive to move around and the majority of food items is unavailable, all generalists were forced to feed on carrion. During this period, low abundance of carrion may substantially affect all generalist carnivores, with the probable exception of the raccoon dog. This exception appears due to the raccoon dog's capability to save enough internal fat until late winter, to be inactive in harsh conditions, and to consume anything edible food including wild boar scats and herbs as a last choice. Consequently, the feeding of numerous raccoon dogs on carrion leads to a substantial decrease in this very important food resource, which should severely affect the native generalist guild inhabiting the forest ecosystems. This plausibly had a particular impact on the polecat population.

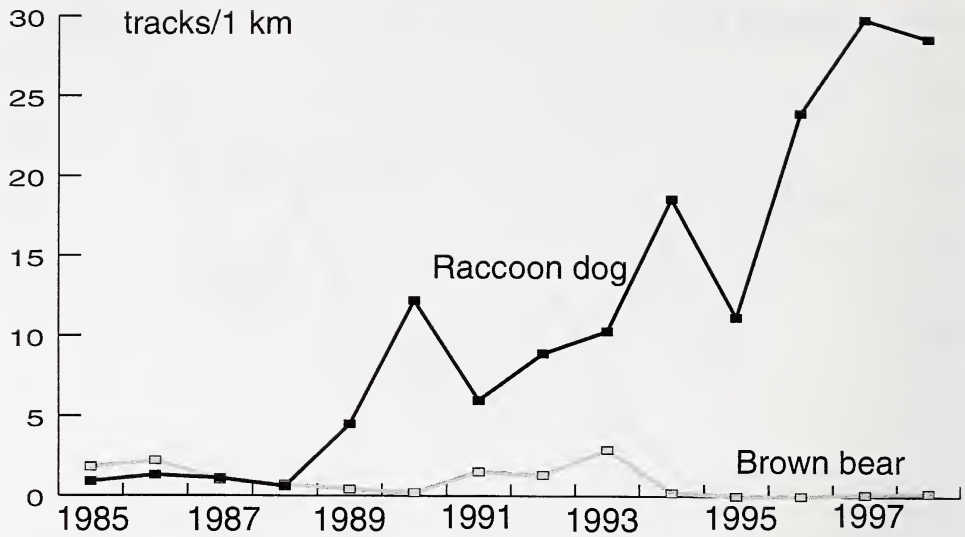

Fig. 1 e.

Fig. 1. Multiannual fluctuations of the abundance of native generalist carnivores (polecat, pine marten, red fox, badger, brown bear) in relation to change in the abundance of raccoon dogs in the Rossony study area, Rossony district, Vitebsk region, northern Belarus, late winter and early spring of 1985–1998. Average number of track trails of a predatory species which crossed 1 km of the inspected route during two days passed after the last snowfall was used as an abundance index of the species.
a) polecat – raccoon dog; b) pine marten – raccoon dog; c) red fox – raccoon dog; d) badger – raccoon dog; e) brown bear – raccoon dog

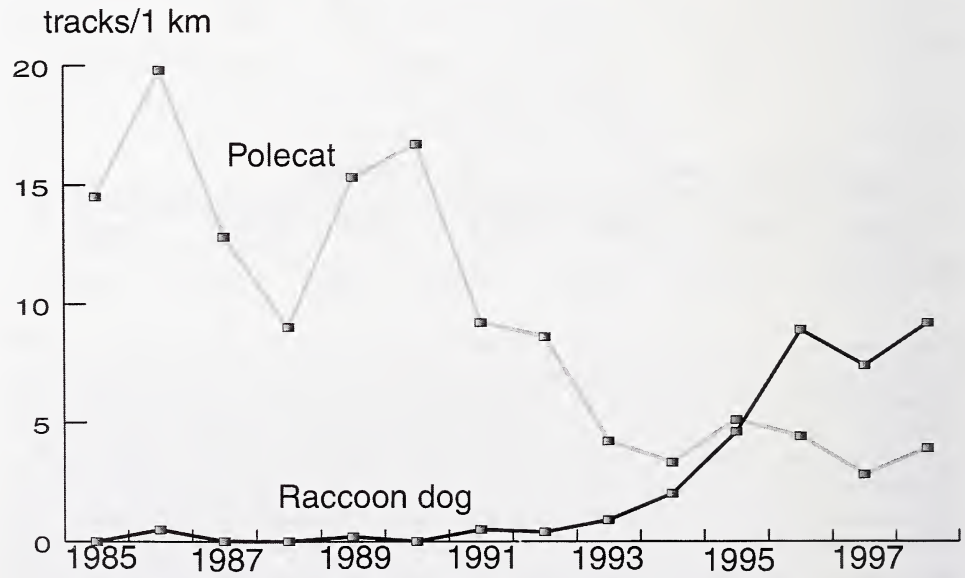

Fig. 2 a.

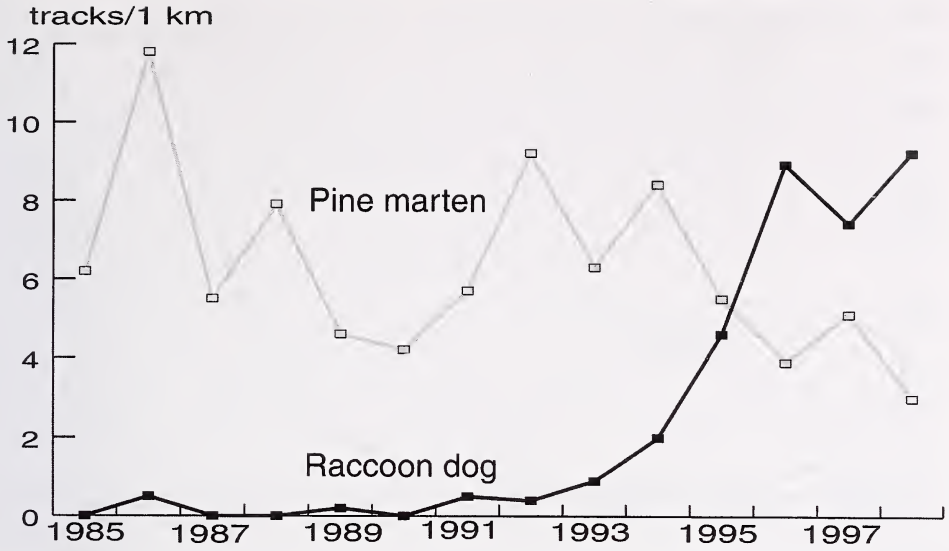

Fig. 2 b.

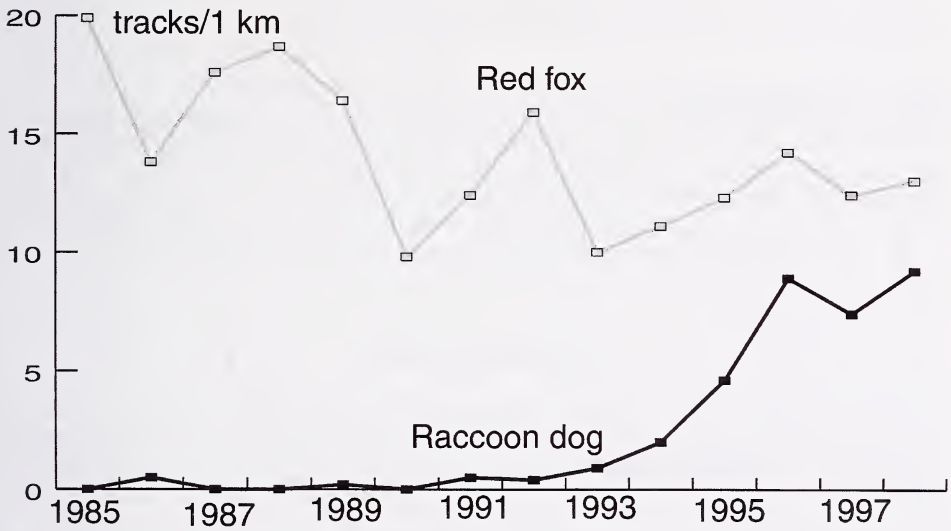

Fig. 2 c.

The obtained data also suggest that in the mixed forests of northern Belarus a specific pattern of sharing food resources between generalist carnivores has developed. Both their feeding habits and dietary overlaps are very different in comparison with those in the more southern Bialowieza Primeval Forest of eastern Poland (JEDRZEJEWSKA and JEDRZEJEWSKI 1998). As regards the differences between these two communities of vertebrate predators both inhabiting temperate forests, the following explanation might be given concerning a substantial difference in habitat conditions.

In the post-glacial landscape of northern Belarus, the soils are fairly poor because of their relatively young age and conditions of a more severe climate than of the more

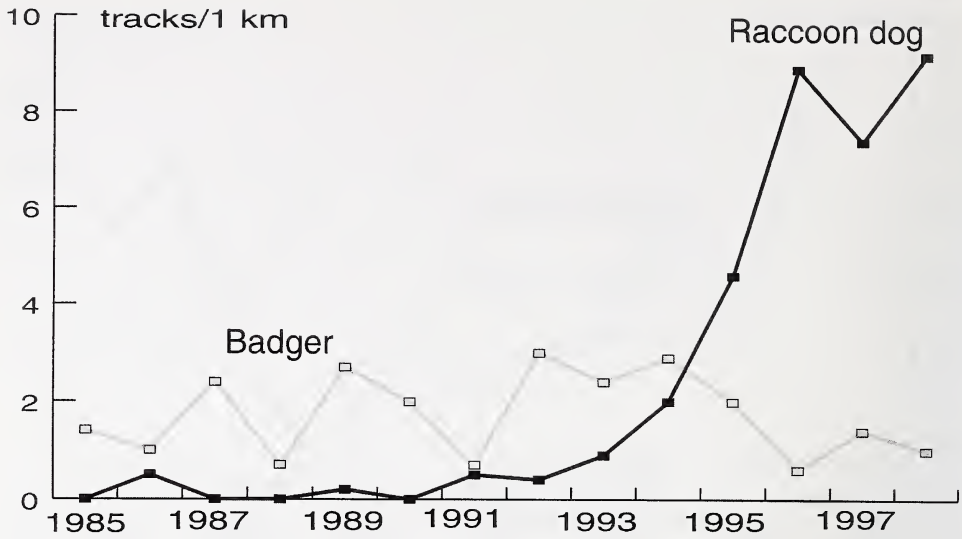

Fig. 2 d.

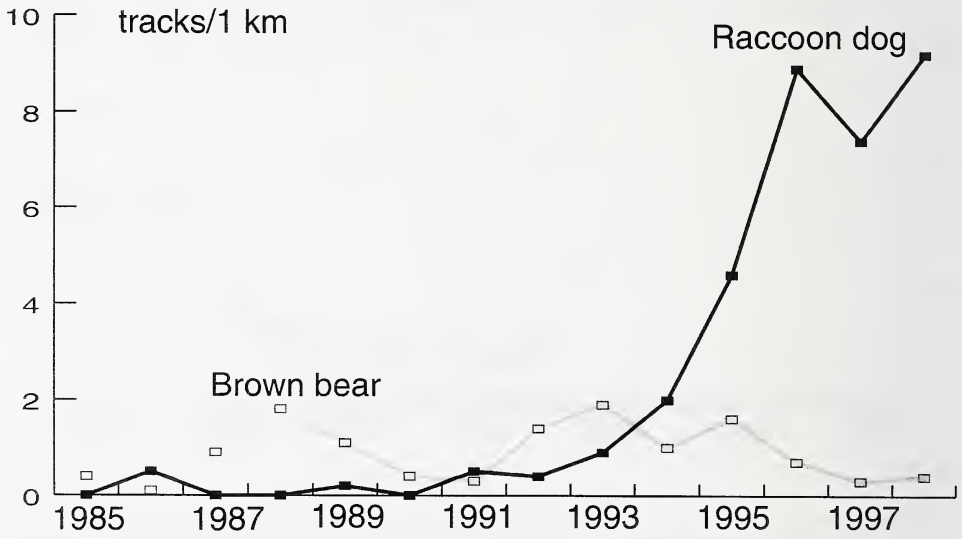

Fig. 2 e.

Fig. 2. Multiannual fluctuations of the abundance of native generalist carnivores (polecat, pine marten, red fox, badger, brown bear) in relation to change in the abundance of raccoon dogs in the Gorodok study area, Gorodok district, Vitebsk region, northern Belarus, late winter and early spring of 1985–1998. Average number of track trails of a predatory species which crossed 1 km of the inspected route during two days after the last snowfall was used as an abundance index of the species.
a) polecat – raccoon dog; b) pine marten – raccoon dog; c) red fox – raccoon dog; d) badger – raccoon dog; e) brown bear – raccoon dog

southern region of forest zone located outside the influence of the last glaciation. In these harsh environmental conditions, mixed forests contain few masting deciduous tree species such as oak and linden and mostly consist of pine, spruce, birches, alders, and aspen. This, in turn, causes a significantly lower number and biomass of small rodents (Sidorovich et al. 2000). Severe winter with strong frost and deep snow cover also makes it difficult for predators to feed on small mammals living under the snow. Therefore, in northern Belarus the habitat conditions of mammalian consumers such as red fox and pine marten are worse than those in the Bialowieza Primeval Forest. Thus, northwards these carnivores more frequently face a shortage of mammalian prey and need to supplement their diets with other food categories (carrion, fruits, birds).

Also, severe conditions of winter time substantially impede polecats from catching amphibians, whereas this predator prefers to feed on frogs in other areas where winter is milder (Weber 1989; Jedrzejewski et al. 1993; Jedrzejewska and Jedrzejewski 1998). In the harsh winter conditions of northern Belarus, polecat acts as a generalist predator feeding on small mammals, amphibians, birds, and carrion. As regards habitat conditions for badgers, invertebrate (especially earthworm) diversity and biomass are substantially lower northwards (Hotko 1993; Neal and Cheeseman 1996; Jedrzejewska and Jedrzejewski 1998). This affects the diets of badgers, which prefer to feed on earthworms (Kruuk 1989; Neal and Cheeseman 1996). In northern Belarus, low biomass of earthworms forces badgers to act as a generalist predator characterized by seasonal feeding specializations on different food items (Sidorovich 1997). This leads to a different pattern of dietary overlap between badger and other generalist carnivores in northern Belarus than in the more southern deciduous forest of the Bialowieza Primeval Forest (Jedrzejewska and Jedrzejewski 1998).

Thus, all the above-mentioned ecological conditions of the large area influenced by the last glacier have determined a different pattern of sharing food resources between forest generalist predators, as well as their feeding habits, in the natural forest ecosystems of northern Belarus compared to those in the more southern mostly deciduous forest in the Bialowieza Primeval Forest (Jedrzejewska and Jedrzejewski 1998). This points out the flexible and highly adaptive nature of the vertebrate community, and at the same time it may indicate their different responses to the influence of introduced species.

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Zusammenfassung

Nahrungsüberlappung bei generalistischen Carnivoren in Beziehung zum Einfluß des eingeführten Marderhundes (Nyctereutes procyonoides) auf die heimischen Prädatoren im nördlichen Weißrußland

Es wurden die Ernährungsgewohnheiten und deren Überlappungen zwischen waldbewohnenden, sich omnivor ernährenden Raubsäugern (Braunbär *Ursus arctos*, Rotfuchs *Vulpes vulpes*, Dachs *Meles meles*, Baummarder *Martes martes*, Iltis *Mustela putorius* und Marderhund *Nyctereutes procyonoides*) in der naturnahen Waldlandschaft Nord-Weißrußlands (Gorodok und Rossony Bezirk) untersucht. In der warmen Jahreszeit (April–Oktober) war für diese generalistisch lebenden Carnivoren ein sehr breites Nahrungsspektrum charakteristisch. Früchte, Kleinsäuger, Insekten und Vögel waren die vorherrschenden Nahrungsbestandteile. Obwohl bei einigen Artenpaaren, wie Braunbär – Dachs, Marderhund – Dachs, Baummarder – Rotfuchs und Baummarder – Marderhund, deutliche Nahrungs-

überlappungen auftraten, gab es in der warmen Jahreszeit in der Gruppe der Generalisten nur kleine Hinweise auf Konkurrenz um Ressourcen. In der kalten Jahreszeit (November–März) wurden die Nahrungsnischen der omnivoren Beutegreifer ohne Winterruhe enger und überlappten sich stärker, was auch mit einer substanziellen Abnahme der Nahrungshäufigkeit und -verfügbarkeit übereinstimmt. In dieser Periode mit schlechter Nahrungsversorgung fraßen die Generalisten meist Aas (Elch und Wildschwein), Kleinsäuger sowie Früchte. Bei Besiedlung gleicher Habitate können so einige Artenpaare, z. B. Baummarder – Rotfuchs, Iltis – Rotfuchs, Iltis – Marderhund, Iltis – Baummarder, um Nahrung konkurrieren. In der härtesten Zeit im Spätwinter und Anfang des Frühjahrs, also unter Bedingungen einer tiefen und/oder weichen Schneedecke im Wald, ist Bewegung energetisch ungünstig und viele Nahrungskomponenten nehmen ab. Dann sind alle Generalisten gezwungen sich von Aas zu ernähren, dessen Häufigkeit diese Carnivoren, mit vermuteter Ausnahme des Marderhundes, deutlich beeinflußt. Die erhobenen Daten zur Häufigkeit der Prädatoren weisen darauf hin, daß mit Erreichen einer hohen Populationsdichte des Marderhundes, die einheimischen Prädatoren seltener wurden.

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