

Food Niche Overlaps in a Winter Community of Predators in the Białowieża Primeval Forest, Poland

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The preliminary results of studies on food niches of predators in the Białowieża National Park, the last remnant of European virgin lowland forests, are presented. The winter diet of seven native species (wolf, lynx, red fox, pine marten, polecat, stoat, and tawny owl) and one introduced species (raccoon-dog) was determined by scat analysis. Pianka's index α of niche overlap was calculated. Three groups of predators were distinguished: (1) large specialists (the wolf and the lynx; they rely on red deer, roe deer and wild boar), (2) small specialists (the polecat, the stoat and the tawny owl; rodents form a bulk of their diet), (3) generalists (the medium size predators, the fox, the marten and the raccoon-dog; they widely consume rodents and scavenge on the carcasses of large prey). The extensive food niche overlaps occurred within each group of specialists ($\alpha > 0.8$ for pairs wolf-lynx, stoat-tawny owl). Minute overlaps took place between large and small specialists ($\alpha < 0.2$ for wolf-stoat, lynx-polecat). Generalists extensively overlapped with all other species ($\alpha > 0.6$ for fox-lynx, fox — raccoon-dog, marten-tawny owl) and their mean α 's were the highest. The pattern of resource partitioning between species is based on (1) the common use of rodents. This prey category determined the degree of overlapping (except the pair wolf-lynx), (2) some specialization of every species in a different food resource (usually of second importance in the diet). The raccoon-dog's (a newcomer) food niche was characterized by extensive overlaps with those of all the natives. The overlaps of winter food niches indicate the possible competition in resource use.

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1. INTRODUCTION

More and more often it has been realized that the best way of managing plant and animal communities is to preserve them in their natural state as far as possible. Many seeming improvements applied to altered ecosystems have failed. Recently there has been a growing interest in the reintroduction of formerly extinct animal species, including predators. This requires a good knowledge of how natural communities function. However, there are few places in Europe where it is

possible to study the interactions between different predatory species and the predator-prey relationships. Most research on predation has been carried out in intensively settled countries and has analyzed impoverished or non-native assemblages of predators (Pearson, 1966; Ryszkowski *et al.*, 1973; Boonstra, 1977; Goszczyński, 1977; Erlinge *et al.*, 1983).

This paper reports on the winter diet (determined from scats) of predators in the Białowieża National Park, the last remnant of European virgin forests, that supports an exceptionally rich in species community of mammalian and avian predators. We present the preliminary results on sharing the food resources by seven native and one introduced species in winters 1985/86 and 86/87.

2. STUDY AREA

Data were gathered in the Białowieża National Park, eastern Poland (23°55'E, 52°45'N). The park includes about 50 square km of diverse deciduous, mixed and coniferous forest with oak *Quercus robur*, linden *Tilia cordata*, maple *Acer platanoides*, hornbeam *Carpinus betulus*, spruce *Picea abies*, pine *Pinus silvestris*, and many other tree species. No commercial nor sanitary cuttings take place in the park area. Hunting is not allowed and man penetration is restricted to a few pedestrian paths.

The spatial and age structure of tree stands are typical of primeval forests. The swampy, river-flooded, fresh and fairly dry forest associations with many decaying wind-fallen trees make the habitat extremely varied in macro as well as in microscale. On the southern border the Park meets the Białowieża Glade with its open fields and meadows whereas from the north, east and west it joins continuous forests. Three small rivers flow through the study area. For a detailed description of forest habitats see Faliński (1986).

3. PREDATORS AND PREY

Predators breeding in the park area consisted of over 20 species of mammals and birds. In winter, when several migratory raptors were gone and badgers *Meles meles* were asleep, about a dozen species occurred. Of these the following were studied: the wolf *Canis lupus*, the lynx *Felis lynx*, the red fox *Vulpes vulpes*, the pine marten *Martes martes*, the polecat *Mustela putorius*, the stoat *Mustela erminea*, the tawny owl *Strix aluco* and the raccoon-dog *Nyctereutes procyonoides*. The latter species colonized Białowieża forests in the early 1950s. They migrated from Byelorussia (the Soviet Union) where they had been previously introduced. Raccoon-dogs spend much of the winter time asleep, but they often wake and forage.

The weasel *Mustela nivalis*, the most common predator in the forest, is not presented due to lack of data. Weasels deposit scats in the toilet-chamber of their dens (Ternovski, 1977) thus data on diet are particularly difficult to get. The river otter *Lutra lutra* as well as the American mink *Mustela vison*, which has replaced an extinct European mink *Mustela lutreola*, were very rare and no scats were collected.

The winter assemblage of raptors consisted of few species. Most breeding raptors were gone. Some others, like the long-eared owl *Asio otus* or the wintering rough-legged hawk *Buteo lagopus* do not enter the forest.

Primeval forest associations support a great diversity of prey species. To facilitate analy-

ses of predator diets, the prey items identified from scats were grouped into 11 ecologically meaningful categories of food. The prey groups are listed here in order of magnitude.

(1) **Large mammals** included the most abundant red deer *Cervus elaphus*, wild boar *Sus scrofa*, and the less common roe deer *Capreolus capreolus* and moose *Alces alces*.

(2) **Hares** *Lepus europaeus* sparsely inhabited the forest, but occurred more frequently in nearby meadows and fields.

(3) **Squirrels** *Sciurus vulgaris* (combined with sporadically found arboreal dormice *Gliridae*).

(4) **Birds** preyed upon in winter were mostly year round residents (jay *Garrulus glandarius*, hazel hen *Tetrastes bonasia*, woodpeckers and small *Passeriformes*) and passerine visitors from the north.

(5) **Forest rodents** included two most abundant species: the bank vole *Clethrionomys glareolus* and the yellow-necked mouse *Apodemus flavicollis*. Both were numerous during the study period (authors' own data from trapping). Occasional *Pitymys subterraneus* were found.

(6) **Swamp and shrub rodents** included abundant root voles *Microtus oeconomus* inhabiting river valleys and forest marshes, much less common field voles *Microtus agrestis* and occasional *Micromys minutus*.

(7) **Field rodents**, i.e. the common vole *Microtus arvalis* and the striped field mouse *Apodemus agrarius* (the latter less abundant) lived on meadows and fields adjacent to the forest edge.

(8) **Insectivores** included the common shrew *Sorex araneus*, the water shrew *Neomys fodiens* and the mole *Talpa europaea*.

(9) **Amphibians** were represented by *Rana temporaria* and *R. arvalis*. Accidental reptiles (i.e. *Lacerta* sp. and *Emys* sp.) were added here.

(10) **Invertebrates** (mostly earthworms *Lumbricus* sp. and insects).

(11) **Plant material** consisted of seeds and fibrae (mushrooms were incorporated here).

The last two kinds of food (invertebrates and plant material) were impoverished and hardly accessible in winter as compared with the vegetation season.

4. METHODS AND MATERIAL

Scats of predatory mammals and pellets of tawny owl were collected in the period of permanent snow cover that lasted from 17 December 85 to 30 March 86 and from 15 December 86 to 5 April 87, i.e. 103 and 111 days, respectively. The maximal depth of snow cover reached 54 cm in 85/86 and 47 cm in 86/87.

Most feces were collected during the snow tracking of particular animals. Furthermore, forest roads were surveyed for wolf and fox scats, fallen trees for marten feces and hollow trees for owl pellets. Winter dens of raccoon-dogs, polecats and stoats were searched and the scats deposited there were collected after the snow-melt. The entire material consisted of 37 scats of wolf, 15 of lynx, 142 of fox, 46 of raccoon-dog, 94 of pine marten, 32 of polecat, 8 of stoat, and 94 tawny owl pellets.

The analysis of scats and pellets followed standard procedure of drying and then washing through a sieve of 0.5 mm mesh. Prey items were identified by fragments of bones, claws, feathers and exoskeletons of insects. The microscopic examination of mammalian hair and soft-bodied invertebrate remains was performed.

The contribution of each group of prey to the diet was presented as percentage occurrence in the scats. Food niche overlaps were expressed as Pianka's symmetrical matrix of α 's (Pianka, 1973; Slobodchikoff & Schulz, 1980). Index α varies from 0 (complete isolation) to 1 (identity of niches).

Some data from winter 1985/86 were given a more detailed description by Reig and Jędrzejewski (1988).

5. RESULTS

5.1. Diet Composition

Utilization of food resources by predators is shown in Fig. 1. Ungulates and rodents were the basic food maintaining the winter community of predators in the Białowieża National Park. The analyzed eight

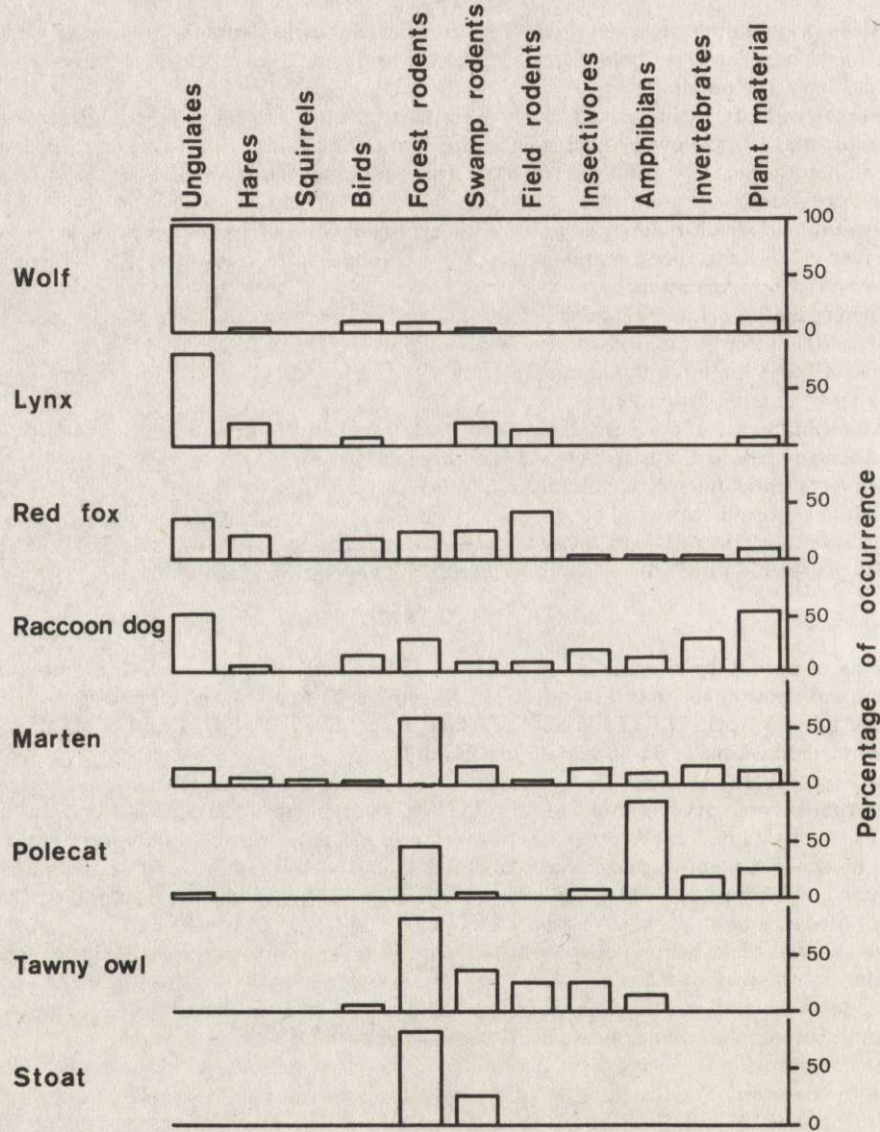


Fig. 1. Percentage occurrence of different categories of food in the scats of predators in the Białowieża National Park in winter. For description of food types and sample sizes see text.

species can be divided into three groups according to diet composition. The first group of large specialists includes the wolf and the lynx. They rely on red deer and wild boar as a basic and nearly exclusive prey. The second group contains the medium-size predators: the fox, the raccoon-dog and the marten. These are generalists, which widely consume rodents and scavenge on the carcasses of large herbivores either killed by wolves and lynxes or which have died from severe winter conditions. The third group comprises the three smallest species: stoat and tawny owl, which are rodent specialists, and the polecat, which is an amphibian specialist.

Except one sheep found in a scat of a wolf no domestic animals (cattle, poultry, etc.) were detected in the scats of any predator.

Some predators probably experience the danger of being potential prey of larger species. A raccoon-dog was a quarry of a wolf (scat analysis), a tawny owl was found killed by a marten (snow tracking) and a red fox fell as a victim to lynx (Kossak, 1988).

5. 2. Food Niche Overlaps

The extensive food niche overlaps (Fig. 2) occurred within both groups

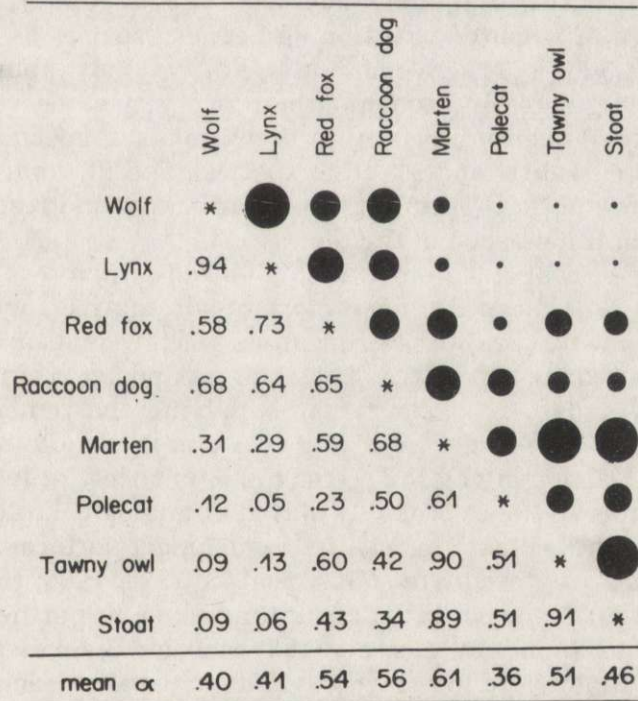


Fig. 2. Food niche overlaps (expressed as Pianka's index α) in winter community of predators; α varies from 0 (complete separation) to 1 (identity of niches).

of specialists, *e.g.* between wolf and lynx or stoat and tawny owl. Large and small specialists are well separated: minute overlaps take place for instance between wolf and stoat, or lynx and polecat. Medium-sized generalists extensively overlapped with all other species.

The marten, the raccoon-dog and the red fox had the highest mean values of α 's. The lowest mean α value was that of the polecat (Fig. 2). Mean α for the whole community equalled 0.48.

6. DISCUSSION

The examined eight species comprise the gross of the community of terrestrial and avian predators present in the study area in winter. The weasel, which lacks data in this work, is a rodent specialist throughout its range (Erlinge, 1975; Brugge, 1977; King, 1980; Delattre, 1984). Therefore it can be assumed that also in the Białowieża forest the winter food niche of the weasel is similar to that of the stoat.

The small number of lynx and stoat scats does not allow great accuracy in determining their diets, but the possible error is minimized by the fact that these two species are specialists with a narrow spectrum of food consumed (*cf.* Haglund, 1966; Debrot *et al.*, 1984).

The pattern of resource partitioning between species as drawn here is based on (1) an extensive common use of two most abundant types of prey, *i.e.* ungulates and rodents (these two prey categories determine the degree of overlapping within both groups of specialists as well as between generalists and all other species); and (2) some inclination (specialization) of most species towards different food resources, usually of second importance in the diet.

To several species of medium- and small-sized carnivores the carcasses of deer and wild boar are an important alternative food that promotes their survival during severe winters when rodents are hardly accessible (deep snow) or scarce. Thus wolves and lynxes may support generalistic predators by constantly supplying the remains of their kills. This may have some stabilizing effect on the whole community.

Extensive scavenging by fox seems to be its ancestral feeding habit. Foxes in temperate zones probably played an analogical role as hyaenas and jackals in hot climates a role that is no longer performed whenever larger killers are exterminated (Goszczyński, 1974, 1986; Harris, 1981). Haglund (1966) reported on lynxes killing foxes in northern Sweden. The same was found by Kossak (1988) in the Białowieża National Park. In the Białowieża forest wolves and lynxes often cache their killings by covering them with snow, grass and leaves or dirt (authors' own data). This makes sense as a protection against scavengers. In the

Swedish wilderness, where foxes were rare lynxes did not cache their prey (Haglund, 1966).

The raccoon-dog's (a newcomer in the community) scavenging habits seem to be even more strongly pronounced. The generalistic diet of the raccoon-dog certainly promotes its colonizing of new ranges and may also, as it was in the case of the red fox, lead to the sinurbization of this species in the near future.

Some separation of niches is due to feeding by each species of predator on different types of less abundant prey. Lynx hunts hares, red fox catches hares and birds, raccoon-dog forages on plants and invertebrates (mainly earthworms), and tawny owl eats a substantial number of insectivores.

The polecat's specialization in amphibians makes its niche well separated from all other species. This is, however, partially due to lack of data on other semi-aquatic species of predators, *i.e.* mink and otter, which may also have substantial amounts of amphibians in their diets (Ternovski, 1977; Erlinge & Jensen, 1981). One can expect these three species living close to water flows to overlap with each other.

The polecat's role in the predatory community is somewhat surprising. The feeding ecology of this species has primarily been known from studies done in rural landscapes, where domestic poultry, other birds and rabbits made up a bulk of this animal's diet (Rzebik-Kowalska, 1972; Brugge, 1977; Erlinge *et al.*, 1982). This led to a misunderstanding that in its ancestral habitats the polecat was primarily a bird-eater (Ewer, 1973). In fact its place in an undisturbed community is more similar to that of the mink than of any other mustelids.

The absence of domestic animals from the predators diets was the striking feature of this community, authenticating its primeval character. This results from both an adequate supply of natural food sources and the very isolated nature of the studied forests. Though many predators inhabit the Park they cause practically no damage to domestic animals. This undesirable aspect has commonly been a complaint in most of Europe (Rzebik-Kowalska, 1972; Harris, 1981; Salvador & Abad, 1987, and others).

Erlinge *et al.* (1982) who studied the whole community of vertebrate predators in an open field area in southern Sweden found much different pattern of resource partitioning and food niche overlaps. They presented data from autumn, when several species of breeding raptors and badgers were present. Large predators (wolf, lynx) were absent from the study area and domestic cats *Felis catus* occurred there. The most important prey animals were rabbits *Oryctolagus cuniculus* which formed a staple food for generalistic predators, *e.g.* red foxes

and polecats, thus separating their niches very well from the niches of small specialists feeding on rodents (*e.g.* stoats and long-eared owls).

This paper shows only the winter aspect of food sharing. The seasonal dynamics of niches certainly occur in most, if not all, species, as a result of seasonal changes in prey abundance and an influx of some other predators absent from the area in winter.

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NAKŁADANIE SIĘ NISZ POKARMOWYCH W ZIMOWYM ZESPOLE DRAPIEŻNIKÓW W PUSZCZY BIAŁOWIESKIEJ

Streszczenie

Przedstawiono wstępne wyniki badań nad składem pokarmu drapieżników w Białowieżskim Parku Narodowym, ostatnim fragmencie pierwotnych lasów nizinnych Europy. Zimowy pokarm 7 rodzimych gatunków (wilk *Canis lupus*, ryś *Lynx lynx*, lis *Vulpes vulpes*, kuna leśna *Martes martes*, tchórz *Mustela putorius*, gronostaj *Mustela erminea* i puszczyk *Strix aluco*) i jednego obcego gatunku (jenot *Nyctereutes procyonoides*) określono metodą analizy kału. Użyto wskaźnik podobieństwa Pianki (α) do przedstawienia stopnia nakładania się nisz pokarmowych.

W zimowym zespole drapieżników wyróżniono 3 grupy: (1) duże drapieżniki wyspecjalizowane (wilk i ryś polujące na jelenie, dziki i sarny); (2) małe drapieżniki wyspecjalizowane (gronostaj, puszczyk i tchórz, które w dużej mierze żywią się gryzoniami); (3) drapieżniki oportunistyczne (gatunki średniej wielkości: lis, kuna i jenot, które polują na gryzonie oraz żerują na kopytnych padłych i zabitych przez wilki i rysie) (Ryc. 1).

Nisze pokarmowe drapieżników wewnątrz obu grup specjalistów nakładały się w znacznym stopniu ($\alpha > 0.8$ dla par wilk-ryś, puszczyk-gronostaj). Najmniejsze podobieństwo nisz wystąpiło między dużymi i małymi specjalistami ($\alpha < 0.2$ dla par wilk-gronostaj, ryś-tchórz). Skład pokarmu gatunków oportunistycznych wykazywał znaczne podobieństwo do wszystkich drapieżników ($\alpha > 0.6$ dla par lis-ryś, lis-jenot, kuna-puszczyk), a ich średnie wskaźniki nakładania się nisz były najwyższe (Ryc. 2).

Pokarmowe współistnienie drapieżników w lasach pierwotnych Białowieskiego Parku Narodowego oparte jest na (1) szerokim wykorzystaniu gryzoni jako podstawowego pokarmu; decyduje to o wysokim podobieństwie nisz pokarmowych różnych gatunków (z wyjątkiem pary wilk-ryś); (2) pewnej specjalizacji każdego gatunku drapieżnika w innej grupie ofiar o drugorzędym znaczeniu w diecie. Duże nakładanie się nisz pokarmowych w zimowym zespole drapieżników może wskazywać na istnienie konkurencji o zasoby pokarmowe.