

The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe

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Predation by wolves *Canis lupus* Linnaeus, 1758 in ungulate communities in Europe, with special reference to the multi-species system of Białowieża Primeval Forest (Poland/Belarus), was assessed on the basis results of original research and literature. In historical times (post-glacial period), the geographical range of the wolf and most ungulate species in Europe decreased considerably. Community richness of ungulates and potential prey for wolves, decreased over most of the continent from 5–6 species to 2–3 species. The wolf is typically an opportunistic predator with a highly diverse diet; however, cervids are its preferred prey. Red deer *Cervus elaphus* are positively selected from ungulate communities in all localities, moose *Alces alces* are the major prey only where middle-sized species are scarce. Roe deer *Capreolus capreolus* are locally preyed on intensively, especially where they have high density, co-exist mainly with moose or wild boar *Sus scrofa*, and red deer is scarce or absent. Wild boar are generally avoided, except in a few locations; and European bison *Bison bonasus* are not preyed upon by wolves. Wolf predation contributes substantially to the total natural mortality of ungulates in Europe: 42.5% for red deer, 34.5% for moose, 25.7% for roe deer, and only 16% for wild boar. Food niche breadth (B) of wolves in Europe, calculated only for the ungulates considered in this study, increases with the number of ungulate species in the community. There is also a significant relationship between ungulate community breadth and food niche breadth of wolves. Food niche breadth of wolves, however, does not achieve very high values even in the richest ungulate communities. Wolves easily adapt to locally abundant food of anthropogenic origin (livestock, garbage). The level of predation on livestock may be a result of different husbandry practices (eg use of livestock guarding dogs) rather than of differences in availability of wild and domestic prey. Available data from Europe suggest that wolves likely limit density of red deer and moose in some areas. Roe deer density can be decreased locally by wolves but is limited mainly by lynx *Lynx lynx*. Wild boar density is more influenced by mast crops of *Quercus* spp. and *Fagus silvatica* (and to a lesser extent by snow depth) than by wolf predation.

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Key words: *Canis lupus*, predation, prey preference, ungulates, Europe

Contents

Introduction	336
Sources of data	337
Methods	340
Forest, ungulate, and wolf distribution in Europe	341
Characteristics of forest ecosystems, ungulate communities, and large carnivores in Białowieża Primeval Forest	351

Food habits of wolves	355
Białowieża Primeval Forest	355
Wolf diet	355
Selectiveness of wolf predation	356
Variability of wolf predation	359
Role of wolves in natural mortality of ungulates	362
Other European localities	363
Core wolf populations (eastern Europe)	363
Satellite wolf populations (northern, southern, and western Europe)	365
Effects of wolf predation on ungulate communities	367
Richness and species composition of ungulate communities	367
Availability of food of anthropogenic origin	372
Factors influencing hunting success of wolves	372
Wolf predation as a possible limiting factor of ungulate density in Europe	375
References	376

Introduction

Literature on the effects of large carnivores on ungulate populations is extensive (review: Skogland 1991), and much of it deals with predation by wolves *Canis lupus* Linnaeus, 1758. Research on wolf-prey interactions in North America began in the 1940s (Murie 1944, Cowan 1947) and expanded in the subsequent decades (review: Mech 1970). Many of these studies sought to understand factors that depressed ungulate populations. Similar reasons motivated studies on wolf ecology in the former Soviet Union (review: Bibikov 1985).

A considerable body of evidence has been collected on certain aspects of wolf predation on ungulates: species, sex, and age of prey (review: Mech 1970, Bibikov 1985, Okarma 1992a). Numerous studies from North America on the effect of large carnivores (mainly wolves) on ungulates show that carnivores can limit population density of many species, eg caribou *Rangifer tarandus* Linnaeus, 1758 (Bergerud and Elliot 1986, Seip 1991), white-tailed deer *Odocoileus virginianus* Zimmermann, 1780 (Mech and Karns 1978, Potvin *et al.* 1988, Messier 1991), and moose *Alces alces* Linnaeus, 1758 (review: Ballard *et al.* 1990, Gasaway *et al.* 1992). In the former Soviet Union, predation by wolves was claimed to be the most important factor limiting density of ungulates (Filonov 1983). However, the degree to which carnivores can regulate ungulate prey is still controversial. Among North American ungulate populations, predation has been argued to exert an important element of control (Keith 1974), constitute the limiting factor (Bergerud *et al.* 1983, Bergerud and Snider 1988, Larsen *et al.* 1989), or regulate density (Messier and Crête 1985, Van Ballenberghe 1987, Ballard *et al.* 1990). Others, however, have noted that the evidence that predation regulates ungulate density is equivocal (Sinclair 1989, Boutin 1992).

Boutin (1992) argued that the evidence for predation as a primary limiting and/or regulatory factor in most moose populations was not convincing. He

classified existing hypotheses on dynamics of moose-carnivore systems (wolves, bears *Ursus arctos* Linnaeus, 1758) into four groups:

1. **Predator limitation hypothesis:** According to this hypothesis, changes in moose density are the result of many factors, but in most cases, predation is primary (Gasaway *et al.* 1983);

2. **Predator regulation hypothesis:** This hypothesis states that predation regulates moose densities around a low-density equilibrium (Van Ballenberghe 1987);

3. **Predator-pit hypothesis:** Predation is thought to regulate moose densities around a stable, low-density equilibrium, but when densities pass a threshold, populations escape this control. Then, at an upper equilibrium, densities are regulated by competition for food (Messier and Crête 1985, Bergerud *et al.* 1983, Messier 1994);

4. **Stable limit cycle hypothesis:** This hypothesis states that moose and wolves show stable limit cycles with a period of 30–40 years (Peterson and Page 1983).

Direct comparisons between Europe and North America on the influence of wolf predation on ungulate populations are difficult because of differences in habitats where wolves still survive. In Europe, rich multi-species deciduous forests dominate, whereas in most areas of North America, there are relatively simple, mainly coniferous-dominated forest ecosystems (Mityk 1978). Moreover, European forests harbour generally richer communities of ungulates, whereas in North America often one species dominates (moose, white-tailed deer, or caribou).

There have been few studies in Europe on the effect of wolves on ungulate populations, and most have been conducted in the former USSR (Filonov 1980, Filonov and Kaletskaya 1985, Filonov 1989). Researchers have focused on quantifying the impact of various predator species on ungulate populations in separate locations. These studies lacked broad geographical perspective, in contrast to the review by Jędrzejewski *et al.* (1993) of lynx predation in the Palaeartic.

The aim of this paper is to: (1) assess the role of wolves in a multi-species community of ungulates in continental Europe, using Białowieża Primeval Forest (BPF) as a comparison; (2) summarize available data on wolf predation from various European locations, and (3) estimate the influence of human activity (deforestation, extermination of wild ungulates, husbandry, etc.) on predation by wolves.

Sources of data

This paper is based on data from BPF and literature from other locations in Europe where wolves still occur. Data from BPF are unique because they have been gathered over many decades. They consist of archival data from 19th century (Kartsov 1903), results of studies on wolf ecology in the Belarussian part of BPF (Gavrin and Donaurov 1954, Bunevich 1988), unpublished data on numbers and predation by wolves in the Belarussian (courtesy of archives of State National Park "Belo-vezhskaya Pushcha" and A. N. Bunevich) and the Polish part of BPF (courtesy of L. Milkowski) from 1960 to 1990, and results of studies on the predator community in BPF (Jędrzejewski *et al.* 1989,

Table 1. Localities in Europe (54) that provided source data on wolf predation (refer to Fig. 1). Supporting references used to construct Figs 17–20 are marked with *.

Reference point in Figure 1	Geographical location	Source	Source used for Figure			
			17	18	19	20
1	2	3	4	5	6	7
1	Yamal peninsula (Russia)	Makridin 1962				
2	Pechoro-Ilycheskii Reserve (Russia)	Filonov 1989	*	*	*	*
3	Ilimskii Reserve (Russia)	Filonov 1989	*	*	*	*
4	Kostromskaya oblast (Russia)	Dubrovskii 1980				
5	Bashkirskii Reserve (Russia)	Filonov 1989	*	*	*	*
6	Gurievskaia oblast (Russia)	Zalozny 1980				
7	Kyzyl-Agach State Reservation (Azerbaijan)	Litvinov 1981		*		*
8	Caucasian Nature Reserve (Georgia)	Kudaktin 1978, Kudaktin 1986	*		*	
9	Western Caucasia	Kudaktin 1982				
10	Northwestern Caucasia	Bibikov <i>et al.</i> 1985				
11	Voronezh Nature Reserve (Russia)	Ryabov <i>et al.</i> 1992				
12	Voronezhskaya oblast (Russia)	Ryabov 1987				
13	Voronezhskaya oblast (Russia)	Ryabov 1974				
14	Voronezhskaya oblast (Russia)	Ryabov 1979				
15	Mordovskii Reserve (Russia)	Filonov 1989	*	*	*	*
16	Okskii Reserve (Russia)	Filonov 1989	*	*	*	*
17	Belarus	Rykovskii 1980, Kuchmel 1994	*			
18	Pripyatskii Reserve (Belarus)	Litvinov <i>et al.</i> 1981	*			*
19	Berezinskii Reserve (Belarus)	Litvinov <i>et al.</i> 1981	*			*
20	Central-Forest State Reserve (Russia)	Kochetkov and Sokolov 1979, Kochetkov 1988	*			*
21	Pskovskaya oblast (Russia)	Rusakov and Timofeeva 1984				
22	Novgorodskaya and Leningradskaya oblast (Russia)	Rusakov 1979b, Rusakov 1979a	*	*	*	*
23	Darvinskii Reserve (Russia)	Filonov 1989	*	*	*	*
24	Finland	Pulliainen 1965	*			**
25	Karelya (Russia)	Rusakov 1979a			*	
26	Finland	Nieminen and Leppaluoto 1988				
27	Onega peninsula (Russia)	Rukovskii and Kupriyanov 1972				
28	Murmanskaya oblast (Russia)	Rusakov 1979a			*	
29	Laplanskii Reserve (Russia)	Filonov 1989	*	*	*	*
30	Northern Sweden	Björvall and Isakson 1982				
31	Sweden	Haglund 1968				
32	Norway/Sweden	Wabbakken 1992				
33	Białowieża Primeval Forest (Poland/Belarus)	Gavrin and Donaurov 1954, Bunevich 1988, Jędrzejewski <i>et al.</i> 1992, Jędrzejewska <i>et al.</i> 1994, Okarma <i>et al.</i> 1995a			*	*
			*	*	*	*

Table 1 - concluded.

1	2	3	4	5	6	7
34	Carpathians Mountains (Slovakia)	Bubenik 1966				
35	Slovakian Carpathians	Brtek and Voskár 1987				*
36	Bieszczady Mountains (Poland)	Okarma 1984, Okarma 1991, Bobek <i>et al.</i> 1992, Śmietana and Klimek 1993	*	*	*	*
37	Carpathian Mountains (Ukraine)	Kerechun 1979	*	*	*	*
38	Romania	Almasan <i>et al.</i> 1970, Ionescu 1992				
39	Southwestern Bulgaria	Genov 1992				
40	Ihtiman Sredna Gora Mountains (Bulgaria)	Ivanov 1988				
41	Greece	Papageorgiou <i>et al.</i> 1994				
42	Abruzzo National Park (Italy)	Boitani 1982, Fico <i>et al.</i> 1993, Patalano and Lovari 1993				
43	Foreste Casentinesi National Park (Italy)	Mattiolo <i>et al.</i> 1995	*	*		*
44	La Spezia province (Italy)	Sacchi <i>et al.</i> 1994		*		*
45	Northern Apennines (Italy)	Meriggi <i>et al.</i> 1991, Matteucci 1992				*
46	Mercantour National Park (France)	Lequette <i>et al.</i> 1994				
47	Demanda Mountains (Spain)	Cuesta <i>et al.</i> 1991				
48	Old Castille (Spain)	Reig <i>et al.</i> 1985				
49	Douro Meseta (Spain)	Cuesta <i>et al.</i> 1991				
50	Leon province (Spain)	Salvador and Abad 1987				*
51	Cantabrian Mountains (Spain)	Braña <i>et al.</i> 1982, Cuesta <i>et al.</i> 1991				
52	West Galicia (Spain)	Cuesta <i>et al.</i> 1991				
53	Northern Portugal	Magalhaes and Fonseca 1982, Van Haaften <i>et al.</i> 1983, Pereira <i>et al.</i> 1985, Fonseca 1992				
54	Extremadura and Sierra Morena (Spain)	Cuesta <i>et al.</i> 1991				

Jędrzejewski *et al.* 1992, Okarma 1993b, Okarma *et al.* 1993, Jędrzejewska *et al.* 1994, 1996a, b, Okarma *et al.* 1995a). I also reviewed literature on trophic ecology of wolves from several European locations (Table 1): from the relatively compact geographical range of wolves in eastern Europe (Belarus, Ukraine, Lithuania, European part of Russia) and the central and southern part of the continent (Slovakia, Romania, Bulgaria, Greece, the former Yugoslavia), and from isolated wolf populations in Scandinavia, Spain, Portugal, and Italy (Fig. 1).

Analyses of community richness of ungulates presented in this paper are limited to the continental part of Europe. The British Isles and isles in the Mediterranean Sea are not included because of the early eradication of wolves and many ungulates, which resulted in lack of reliable data. I delimited the eastern border of Europe as follows: from the eastern shore of the Novaya Zemlya, along the eastern slopes of Ural Mountains, Emba river, the western shore of the Caspian Sea, the Kuma and

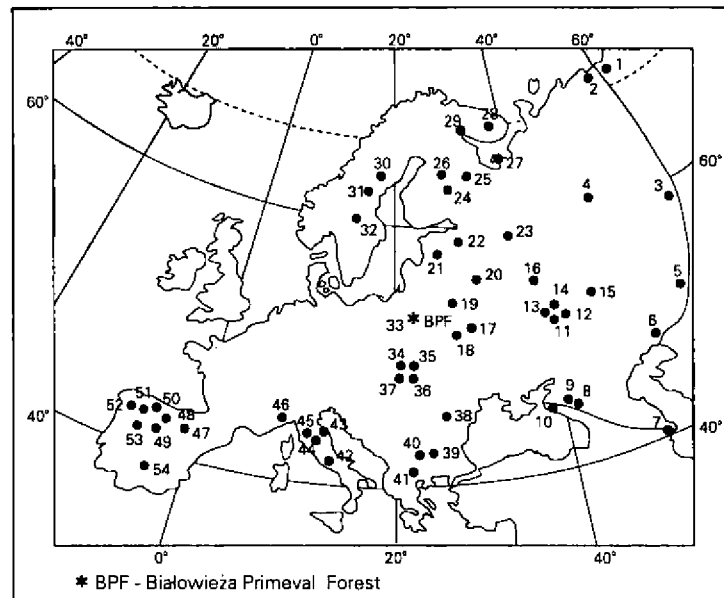


Fig. 1. Localities in Europe that provided source data on wolf predation used in this paper. Description of localities and sources are given in Table 1.

Manycz rivers to the Black Sea. The marine border went through Bosphorus to the Aegean Sea (Mityk 1978).

The distribution of plant zones (biomes) in Europe followed the Atlas Świata (1962). For the purpose of this paper, six major biome classes were distinguished: (1) tundra and woody tundra, (2) boreal forest (taiga), (3) temperate deciduous and mixed forest and mixed montane forest, (4) Mediterranean sclerophyllous scrub and evergreen oak forest, (5) forest-steppe and steppe, and (6) semidesert and desert. The current distributions of forests was taken from Geograficzny Atlas Świata (1991).

Geographical ranges of ungulates in Europe in historical times (post-glacial period) were reconstructed following Heptner *et al.* (1961). Current distribution of red deer *Cervus elaphus* Linnaeus, 1758 followed Heptner *et al.* (1961) and Bützler (1986); roe deer *Capreolus capreolus* Linnaeus, 1758 – Lehmann and Sägeser (1986) and Aragon *et al.* (1995); wild boar *Sus scrofa* Linnaeus, 1758 – Heptner *et al.* (1961) and Herre (1986a); European bison *Bison bonasus* Linnaeus, 1758 – Flerov (1979) and Pucek (1986, 1994); moose – Nygren (1986); reindeer – Heptner *et al.* (1961) and Herre (1986b); fallow deer *Dama dama* Linnaeus, 1758 – Chapman and Chapman (1975) and Heidemann (1986); saiga antelope *Saiga tatarica* Linnaeus, 1766 – Bannikov *et al.* (1961) and Zhirnov (1982).

Methods

Studies considered in this paper used various techniques for assessing wolf food habits (eg analyses of scats and/or stomach contents, recovering carcasses of ungulates killed by wolves) and different methods of determining frequency of occurrence of food items. Thus, some data were re-calculated (occurrence of each item was taken as one prey) to obtain the percentage of prey that was used for further calculations.

Food niche breadth B of wolves was calculated according to Levins (1968): $B = 1 / \sum p_i^2$, where p_i is percent of occurrence of a particular food item. Ungulate community breadth was also calculated according to the above formula, where p_i is percent of occurrence of particular species in ungulate community. Food niche breadth of wolves was later shown in relation to the number of ungulates in the community, and to ungulate community breadth for several European locations.

Information about historical and present distribution of ungulates in Europe was used to show geographical ranges of species in post-glacial times and now. Respective ranges of all species were overlaid to create isoclines of community richness.

To assess the selection of wolves for a particular species of ungulate, I used Ivlev's selectivity index D (modified by Jacobs 1974) $D = (r - p) / (r + p - 2rp)$, where r is the proportion of this species in the wolf diet, and p is the proportion of this species in the ungulate community. Ivlev's index ranges from -1 (total avoidance of a species) through 0 (selection proportional to occurrence) to $+1$ (maximum positive selection).

A number of publications (Table 1) describing trophic ecology of wolves in several European locations (Fig. 1) provided data to calculate the contribution of wolf predation to the natural mortality of ungulates, the contribution of wolf predation to the total predator-caused mortality (other predators were brown bear, wolverine, lynx, and stray or feral dogs), the food niche breadth of wolves, and the selection of wolves for a particular species of ungulate.

Forest, ungulate, and wolf distribution in Europe

Europe is a densely populated continent characterized by extensive changes to the natural environment. One may expect that the altered landscape and direct persecution by humans have affected the numbers, distribution, and food habits of wolves. In this section, comparing original and current distributions of biome classes and ungulates, I attempted to show differences in habitats and ungulate communities available to wolves in historical times and now.

In the post-glacial period, nearly all of Europe was covered with forests. The central part of the continent was covered with deciduous and mixed temperate forests (oak *Quercus* spp. as the dominant species), and the mountains contained mixed forests with a high proportion of beech *Fagus sylvatica*. The northernmost edges of the continent were occupied by tundra and woody tundra, but most of the northern part was covered with coniferous forests (pine *Pinus sylvestris*, spruce *Picea abies*). The southern part was covered with evergreen oak forests and Mediterranean sclerophyllous scrubs. The region adjacent to the Black Sea and the Caspian Sea was covered with steppe, and the area north of the Caspian Sea comprised semidesert and desert (Fig. 2A).

At present, most of Europe consists of non-forested areas (fields, pastures, urbanized and industrial areas). Areas covered with temperate deciduous forest and evergreen oak forest have decreased drastically, they have become fragmented and they are often of secondary origin. Deforestation is less extensive in the boreal forest zone in the northern part of the continent, although extant forests are typically of secondary origin (natural stands were cut down and regenerated spontaneously or via replantation). The tundra zone has changed very little, while steppes and semi-deserts have practically disappeared (Fig. 2B).

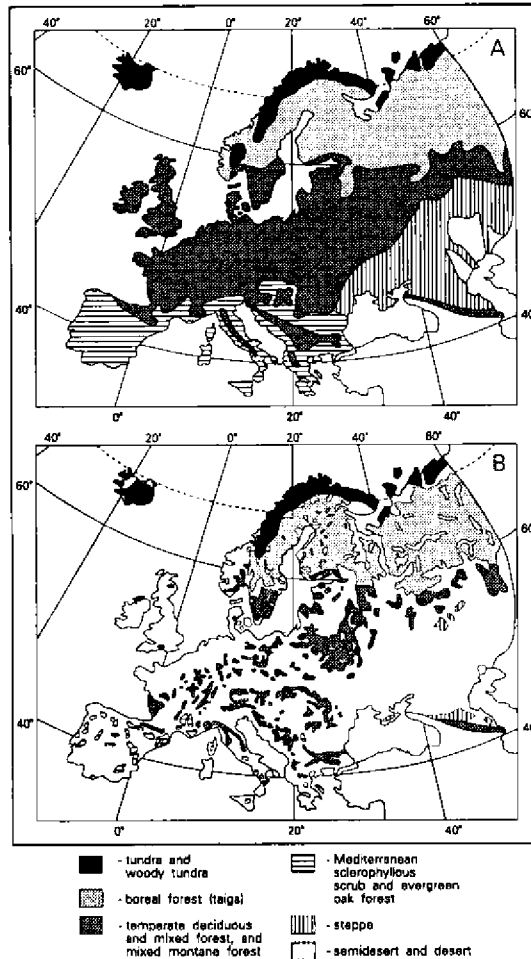


Fig. 2. Distribution of six basic biomes in Europe (A – in historical times, B – contemporary). According to Atlas Świata (1962) and Geograficzny Atlas Świata (1991), modified.

Białowieża Primeval Forest (BPF) is an exception in lowland temperate Europe. Because of very early (since the 15th century) and efficient protection as a royal hunting forest (Jędrzejewska *et al.* 1996a), BPF has changed relatively little. To a large extent, it remains a vast pristine woodland connected with other large forest tracts, mainly to the east (Pruzhana Forest in north-east, Shereshevo Forest in south-east) (Jędrzejewska *et al.* 1996a).

Only native and common species were considered in depicting the reconstructed and current composition of ungulate communities. Typical montane species that occur only in limited areas, such as chamois *Rupicapra rupicapra* Linnaeus, 1758; various ibex species *Capra ibex* Linnaeus, 1758, *C. pyrenaica* Schinz, 1838, West

Caucasian tur *C. caucasica* Gldenstaedt and Pallas, 1783, and bezoar *C. aegagrus* Erxleben, 1777 were excluded. Similarly, some species of ungulates alien to the European fauna were not considered, though they can be locally abundant. Some of these exotic species were introduced after eradication of native ungulates and have relatively extensive distributions. Sika deer *Cervus nippon* Temminck, 1838 native to the Far East, were introduced to Britain, Germany, and the former Czechoslovakia. In the former Soviet Union, they were introduced at 45 locations (Fadeev 1984). White-tailed deer, a North American species, occurs in the former Czechoslovakia, Yugoslavia, and the Soviet Union, Bulgaria, Finland. Mouflon *Ovis ammon musimon* Pallas, 1811 was present only on Corsica and Sardinia in historical times but was introduced to most European countries. Muskoxen *Ovibos moschatus* (Zimmermann, 1780) were translocated to Scandinavia.

Historical ranges of most ungulates considered in this paper (European bison, red deer, roe deer, and wild boar) in Europe occurred in the zones of deciduous temperate and evergreen forests in the central and the southern part of the continent. The northern edges of red deer, roe deer, and wild boar ranges were along the northern limit of temperate deciduous forest, whereas in the southeast these species ranged through the deciduous forest zone and to the steppe (Fig. 3A, 4A, 5A). The historical distribution of European bison was similar to other ungulates, but it did not occur in the northeastern temperate deciduous forest and eastern steppe (Fig. 6A).

Two species of ungulates were associated with the northern part of the continent. Moose inhabited the boreal forest and the northeastern part of the temperate deciduous forest. Its range was largest in the post-glacial period of the early and middle Holocene; it reached the Rhone River and Vosges Mountains to the west, the Alps to the east, the Carpathian Mountains and along the middle of the Danube River in the south (Szymczyk 1973) (Fig. 7A). Reindeer occurred in the tundra zone and secondarily in the boreal forest zone (Fig. 8A). In historical times, two more ungulate species were found at the edges of Europe. Fallow deer inhabited the southern part of the continent (evergreen forest zone) (Fig. 9A), and saiga antelope inhabited the steppe zone in the region of the Black and Caspian seas (Fig. 10A).

The original geographical ranges of ungulate species in Europe were shaped mainly by three factors:

(1) Distribution of preferred plant communities (tundra – reindeer; boreal forest – moose; deciduous forest – bison, red deer, roe deer, fallow deer, and wild boar; steppe and semi-desert – saiga antelope).

(2) Snow conditions during winter (depth and period of permanent snow cover on the ground). Formozov (1946) mentioned the importance of snow depth as a factor limiting the distribution of ungulates in the north. Critical snow depth is > 90 cm for moose, > 50 cm for roe deer, and > 30–40 cm for wild boar (Formozov 1946). Little information for European bison is available: Baskin (1979) stated that European bison survived well in winters with snow > 50 cm and can escape

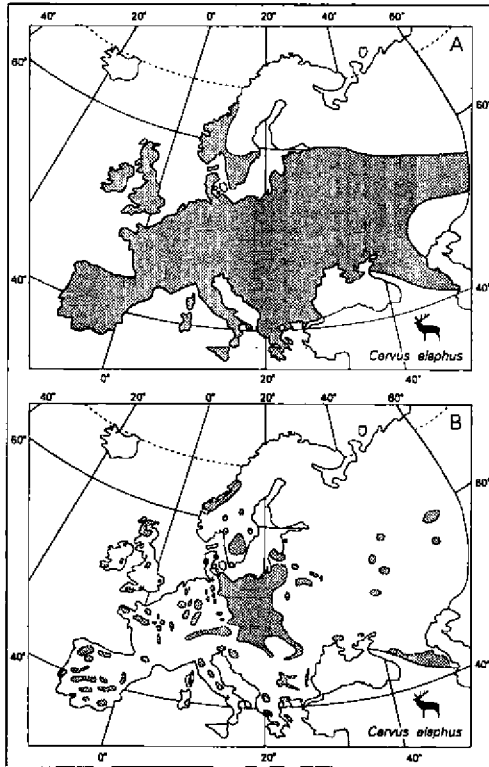


Fig. 3. Historical (A) and contemporary (B) distribution of red deer in Europe. According to Heptner *et al.* (1961) and Bützler (1986), modified.

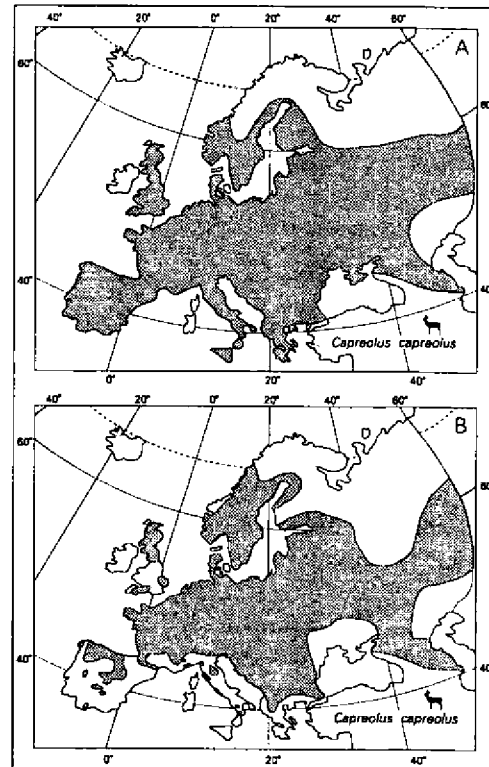


Fig. 4. Historical (A) and contemporary (B) distribution of roe deer in Europe. According to Heptner *et al.* (1961), Lehmann and Sägeser (1986), and Aragon *et al.* (1995), modified.

very fast in 1 m-deep snow. It is, however, probable that critical snow depth for European bison is similar to that for the North American analog, American bison *Bison bison* (Linnaeus, 1758) for which it is > 65 cm (Van Camp 1975). It is impossible to determine an accurate value for red deer, because it was exterminated in most of the northern part of its original range in Europe; however, Formozov (1946) suggested 50 cm as a critical value. For red deer (elk) in North America snow depth > 60 cm appear to be constraining (Houston 1982). However, not only the depth but also hardness and density of snow cover influence survival of ungulates in snow, with pronounced differences between species and between some age and sex classes within species (Telfer and Kelsall 1979, 1984). Long periods of persistent snow cover can limit the distribution of species dependent on food items found on the ground. For example, Danilkin (1989) stated that roe deer did not occur in regions where snow persisted on the ground > 230 – 240 days.

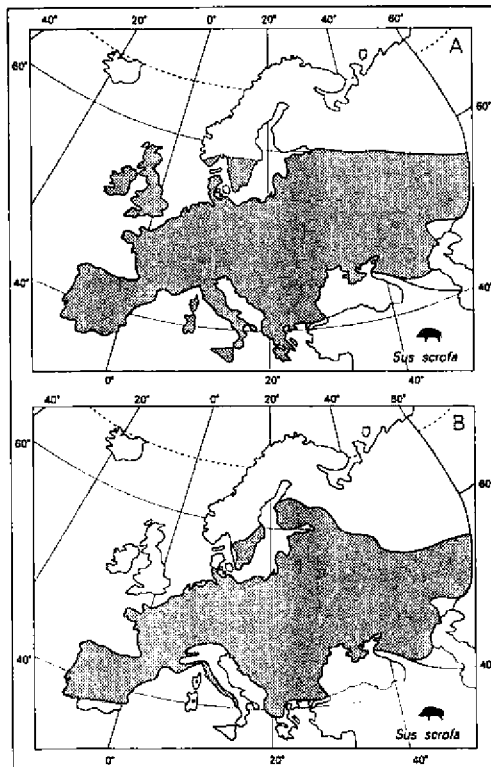


Fig. 5. Historical (A) and contemporary (B) distribution of wild boar in Europe. According to Heptner *et al.* (1961) and Herre (1986a).

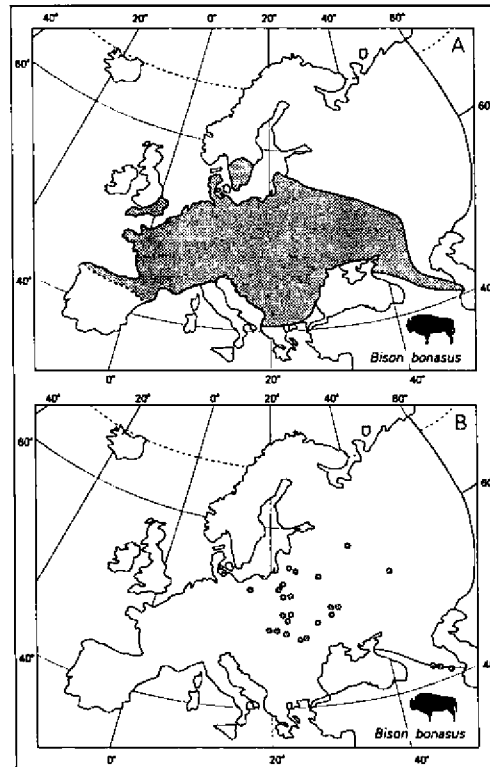
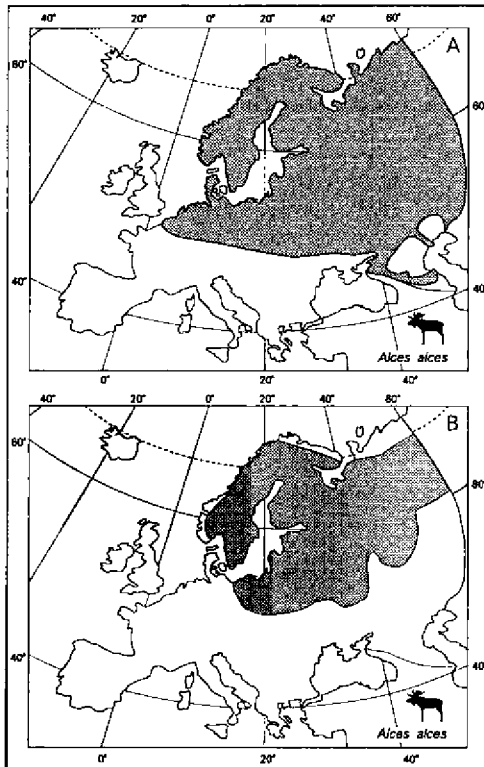


Fig. 6. Historical (A) and contemporary (B) distribution of European bison in Europe. Dashed line means an uncertain geographical limit of bison range. According to Heptner *et al.* (1961), Flerov (1979), and Pucek (1986, 1994).

(3) Deserts in the south (Heptner *et al.* 1961, Danilkin 1989). In this region low rainfall is a limiting factor on vegetation and consequently on the numbers of herbivore species. Only saiga antelope inhabited some part of the deserts adjacent to the Caspian Sea. A similar effect of dry climate was observed in Spain by Aragon *et al.* (1995), who suggested that dryness limits roe deer distribution in the south of the country.

Currently, the distributions of most ungulate species in Europe are much smaller than their original ranges. Free-ranging European bison were completely eradicated, with the exception of two populations that survived in Białowieża Primeval Forest up to 1919 and the Caucasian Mountains (up to 1927). Poaching and epizootic diseases were directly responsible for the extinction of the remnant individuals from the wild (Pucek 1994). After a successful captive breeding programme started in BPF in 1929, the first individuals were released in the wild in 1952 (Kraśniński 1983). At present, European bison occur in several locations



← Fig. 7. Historical (A) and contemporary (B) distribution of moose in Europe. According to Heptner *et al.* (1961) and Nygren (1986).

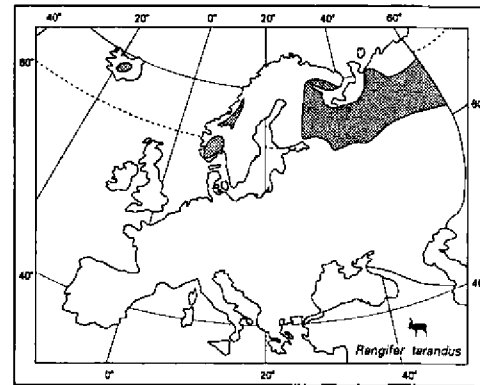


Fig. 8. Historical and contemporary distribution of reindeer in Europe. According to Heptner *et al.* (1961) and Herre (1986b).

in Poland and the former USSR (Fig. 6B), and the population size was estimated as 3281 at the end of 1993 (European bison pedigree book 1995). There are about 11 free-ranging herds of pure lowland bison and about 16 herds of the lowland-Caucasian line, mainly in the Caucasus Mountains and Ukraine (Pucek 1991, 1994).

With the exception of the European bison, the distribution of red deer has contracted to the greatest extent. Red deer are common only in central Europe and can be found only in scattered, often isolated populations in other European regions (Fig. 3B). Red deer are associated with large complexes of deciduous and mixed forests, interferred with glades, clear-cuts, and meadows along edges (Dzięciolowski 1969). Deforestation and fragmentation of extant forests reduced the range of the red deer.

Moose have survived mainly in the boreal forest zone (Fig. 7B), where low human density and difficult terrain (eg large areas of wetlands) make hunting very difficult. In the Middle Ages, moose were extirpated in most of Europe, but survived in Scandinavia, Russia, and Poland. Since the middle of the 19th century moose have steadily re-populated parts of their original range. The process of expansion has accelerated since the 1930s, and migrating individuals have been observed in

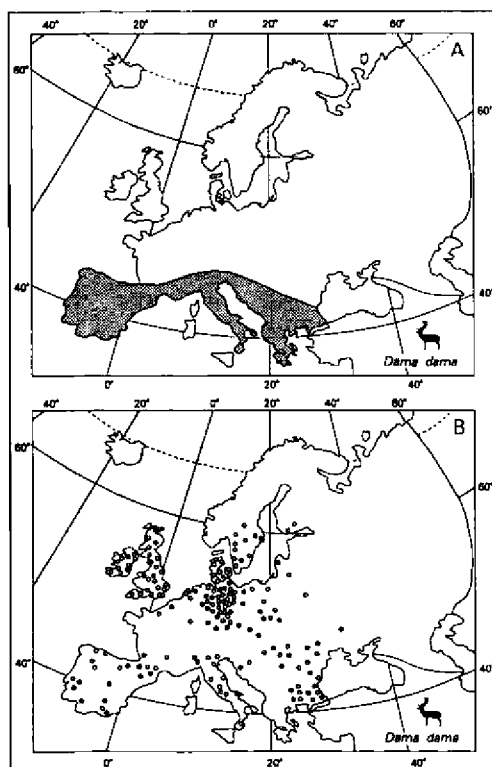


Fig. 9. Historical (A) and contemporary (B) distribution of fallow deer in Europe. According to Heptner *et al.* (1961), Chapman and Chapman (1975), and Heidemann (1986).

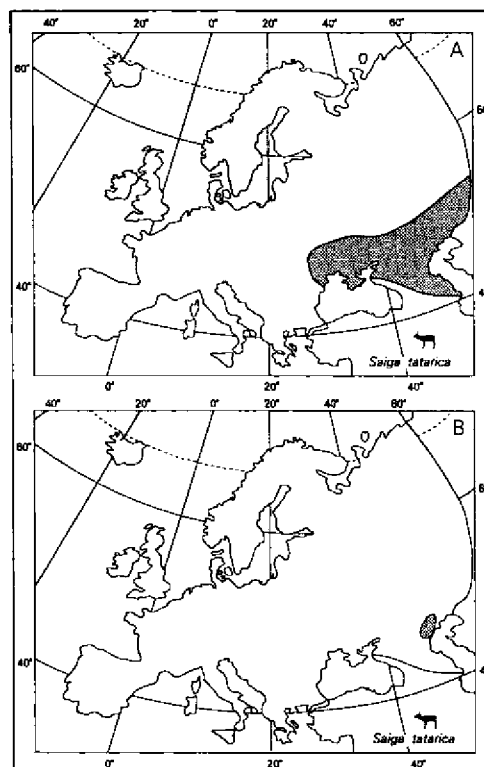


Fig. 10. Historical (A) and contemporary (B) distribution of saiga antelope in Europe. According to Bannikov *et al.* (1961), Heptner *et al.* (1961), and Zhirnov (1982).

Austria, Germany, and the former Czechoslovakia (Gyimesi 1971). Reasons for this rapid recovery (moose re-populated in Europe about 2.5 million km² in 1850–1958) (Nowak 1971) include protection in some areas and limited harvest. Population recovery was enhanced by forest management practices (eg cutting down old-growth stands, replantation with tree species preferred by moose – pine and spruce, and reforestation of abandoned fields), which considerably increased the food supply for moose, and by the extermination of large carnivores (Nowak 1971, Dzieciolowski and Pielowski 1993). The capability of moose to adapt to changing habitat conditions also helped to increase their range. Moose can also occur in small forest complexes in a “culture countryside”, suburban forests, and outskirts of large towns (Novikov and Ivanov 1970, Dzieciolowski and Pielowski 1993).

Fallow deer were nearly exterminated from continental Europe. However, fallow deer were introduced in Britain in early Roman times and in large private parks and game hunting grounds throughout Europe in the Middle Ages (Chapman

and Chapman 1975). Thus, owing to human activities, fallow deer expanded beyond their historical northern limit in recent times (Fig. 9B). Fallow deer receive supplementary feeding during winter in most locations in central and eastern Europe, but it is not necessary for their survival except in very northern locations with poor food supply and severe climatic conditions (R. Dzieciółowski, pers. comm.).

Saiga antelope were nearly exterminated by overhunting in Europe, and only two isolated populations survived in the steppe adjacent to the Caspian Sea in the early 1960s (Bannikov *et al.* 1961). In the early 1980s only one population occurred west of the Volga river (Zhirnov 1982) (Fig. 10B). Disappearance of the natural steppe habitat by conversion into monocultures of grain, and river channeling also reduced populations (Zalozny 1980, Zhirnov 1982). In the 1990s, owing to very high hunting pressure and poaching on an industrial scale, saiga antelope are at the verge of extirpation (L. V. Zhirnov, pers. comm.).

Only three species of ungulates have maintained most of their original range in Europe: reindeer (Fig. 8B), roe deer, and wild boar. The natural range of reindeer has not been reduced because important habitats are only sparsely populated and climatic conditions do not favor agriculture or livestock production. Another important factor contributing to the success of reindeer is that most occur in semi-domesticated herds (Nieminen and Leppaluoto 1988).

Ranges of roe deer and wild boar have decreased only slightly. Both species survived because they adapted to changed habitats. Roe deer distribution decreased only in the southern part of the continent (Spain, Italy) (Fig. 4B) where forests were eliminated. Olive tree plantations were established in many such areas, and large areas became semi-deserts owing to erosion. Currently in Spain, climate and anthropogenic factors (human population density and land-use practices) are the main factors limiting roe deer distribution and density (Aragon *et al.* 1995). In the central and eastern parts of the continent, overhunting caused a considerable decrease of roe deer distribution in the 19th century (Nowak 1971, Danilkin 1989). Areas originally covered with forest were converted to pastures and fields. However, roe deer have adapted well to this altered environment, and are able to live in regions without larger forest complexes (Kałuziński 1974, Pielowski 1977). This, together with moderate hunting pressure, modern forestry practices (clear-cuts and replantations), decrease in large carnivore numbers, and warming of climate contributed to the expansion of roe deer distribution in Europe since the end of the 19th century and re-population of most of its historical range (Nowak 1971, Danilkin 1989).

Wild boar disappeared from some areas of the European part of Russia owing to overhunting in the first two decades of the 20th century. However, distribution of wild boar in Russia has expanded since the 1930s as a result of protection in some areas and regulated harvest in others (Nowak 1971). Wild boar benefits from deforestation and intensive agriculture. Its current range overlaps completely with its original range (Fig. 5B). In western Poland, wild boar occupies different habitats seasonally. Scattered forests are adjacent to vast areas of potatoes, grain,

and maize fields, and wild boar leave forest cover when crops are tall enough to provide shelter. Wild boar return to forest cover after crops are harvested. In regions of intensive agriculture in Poland, the diet of wild boar consists of 70–90% crops (potatoes, maize, grains) (Genov 1981, Fruziński 1992).

On the basis of the above data one can hypothesize that a considerable decrease in the distribution of most ungulates in Europe resulted from deforestation in the temperate and evergreen zones in the southern part of the continent, exacerbated by high hunting pressure in historical times. Range restrictions were greatest for species that were easily hunted: large species (European bison, moose, red deer) or those that occurred in relatively open habitats (saiga antelope, fallow deer).

The wolf originally ranged over all of Europe (Bibikov 1985) (Fig. 11A). The wolf is typically a forest species, whose range decreased after a reduction of forested areas and wild ungulate numbers. Moreover, the wolf, unlike other animals, was systematically persecuted, which accelerated its eradication. At the end of the 19th century, wolves were exterminated in the western and southern part of the continent, and only small isolated populations survived, mainly in the mountains (Bibikov 1985).

At present, the extant range of the wolf is in Asia and in the eastern part of the European continent (the former Soviet Union) (Bibikov 1985). Relatively large populations also can be found in central and southern Europe, where they find natural refugias in remote mountains (eg the Carpathian and Balkan mountains) (Promberger and Schröder 1993). Isolated wolf populations have also survived in similar habitats in Spain, Portugal, and Italy (Blanco *et al.* 1992, Boitani 1992, Fonseca 1992). In the lowland part of the continent, the westernmost limit of the range of the wolf is in Poland (Okarma 1993a) (Fig. 11B).

The overlaid historical distributions of 8 species of ungulates in Europe, forming isoclines of ungulate community richness, revealed that the richest community occurred in the forest-steppe and steppe zone north of the Black Sea (Fig. 12A) and consisted of six species: European bison, moose, red deer, roe deer, wild boar, and saiga antelope. In the central part of the continent (temperate deciduous and mixed forest zone, west of the Rhone river), the ungulate community consisted of five species; saiga antelope did not occur in this area. Further north, the ungulate community became simplified; only reindeer occurred in the tundra zone. In southern Europe, the ungulate community consisted primarily of four species. However, in the Mediterranean region the community was enriched with fallow deer. The semidesert region adjacent to the Caspian Sea was inhabited only by the saiga antelope (Fig. 12A).

The current distributions of ungulates show that the ungulate fauna in Europe has been drastically impoverished (Fig. 12B). No species are found in the semi-deserts close to the Caspian Sea. The richest community of ungulates (five species originally occurred there) is in a limited area of northeastern Poland (including BPF), eastern Belarus, and Lithuania. Four ungulate species inhabit only a slightly larger area (European bison are missing). The diversity of ungulate

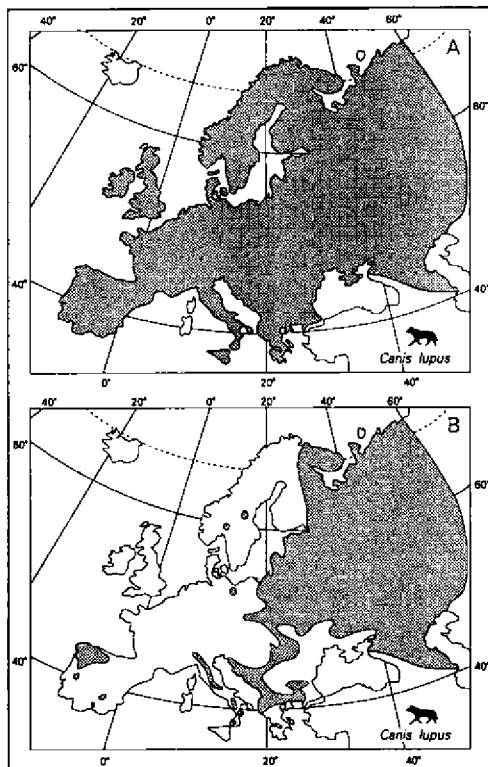


Fig. 11. Historical (A) and contemporary (B) distribution of wolves in Europe. According to Bibikov (1985) and Promberger and Schröder (1993), modified.

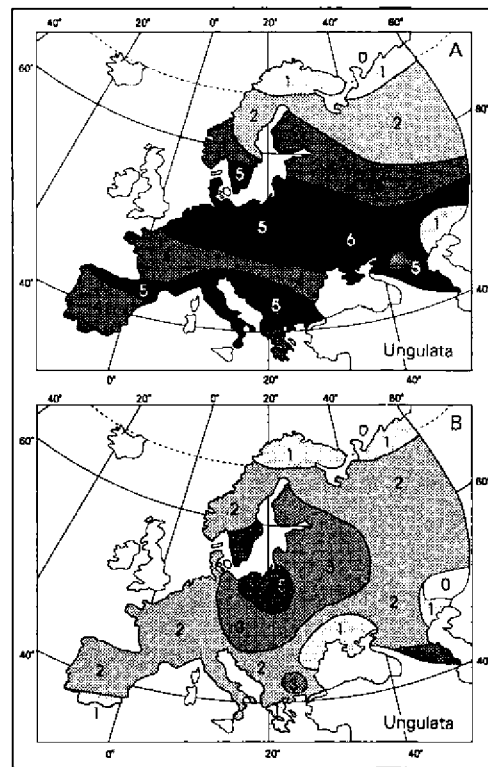


Fig. 12. Number of species (richness) in ungulate communities in the continental part of Europe (A – historical, B – contemporary).

communities decreases in all directions away from the area comprising north-eastern Poland, eastern Belarus, and Lithuania (Fig. 12B). Red deer, roe deer, and wild boar occur west of Poland; moose, roe deer, and wild boar occur east of Poland. Over most of the continent, however, only two species of ungulates co-exist: most commonly, roe deer and wild boar, and to the north, moose and roe deer, or moose and reindeer. Elsewhere, rich ungulate communities exist only in limited areas (eg lowlands of the BPF region and several mountain localities, especially the Caucasus Mountains).

Białowieża Primeval Forest (Poland/Belarus) is a unique area in Europe, where it is possible to study the impact of wolves on a pristine community of ungulates. In other areas where wolves have survived, and data on predation are available (Fig. 1), wolves mainly depend on a less diverse community of ungulates (2–3 species). Thus, BPF offers a rare opportunity to evaluate the role of wolves in ungulate communities in Europe, a relationship that once occurred over most of the European continent.

Characteristics of forest ecosystems, ungulate communities, and large carnivores in Białowieża Primeval Forest

Białowieża Primeval Forest (1451 km², 52°30'–53°N, 23°30'–24°15'E) (Fig. 13) is one of the best preserved forest ecosystems in lowland temperate Europe (Faliński 1986). It was strictly protected, as a royal hunting ground, by Polish kings to the end of the 18th century, and by Russian tsars from the 19th to the beginning of the 20th century. During the latter period, predators were intensively exterminated and measures to promote the variety and numbers of ungulates were undertaken (eg introduction of alien species like fallow deer and extensive supplementary winter feeding). During World Wars I and II, most ungulates were killed. After World War II, the forest complex was divided between Poland and the former Soviet Union (currently Belarus Republic).

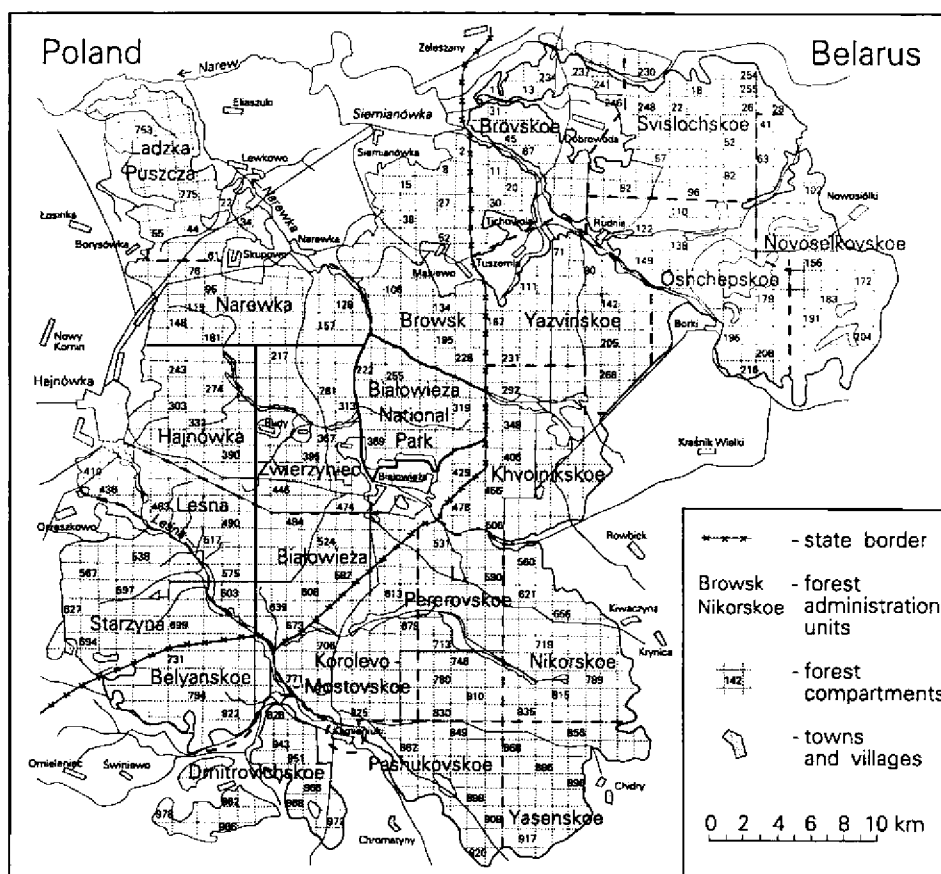


Fig. 13. Schematic map of Białowieża Primeval Forest (division into forest administration units marked).

Most of the Polish part of the forest (530 km²) is managed (ie timber exploitation and game hunting occurs). Only a small area (47 km²) has been strictly protected since 1921 as a national park, where no human activity is allowed. The whole Belarussian part of the forest (874 km²) has been designated as a state national park and a biosphere reserve (UNESCO) since 1993. No living timber is harvested, but dead and uprooted trees are removed, and no replanting is carried out (Okarma *et al.* 1995b).

In Poland, nearly all of Białowieża National Park consists of old-growth forest of natural origin (the average age of tree stands is 130 yrs). Most stands (72.5%) are dominated by deciduous species: oak *Quercus robur*, hornbeam *Carpinus betulus*, alder *Alnus glutinosa*, linden *Tilia cordata*, and Norway maple *Acer platanoides*. The richest forest communities (oak-linden-hornbeam) form 48% of tree stands (Jędrzejewska *et al.* 1994).

In the exploited area of the Polish part of BPF, most tree stands are relatively young secondary growth (replanted, average age of 72 yrs). Coniferous species, spruce *Picea abies* and Scots pine *Pinus sylvestris*, dominate (54% of tree stands). These species are considered to be economically valuable tree species and are mainly used for replanting. Oak-linden-hornbeam stands cover only 13% of the area. Large clear-cuts (up to 6 ha) have increased areas where birches (*Betula verrucosa* and *B. pubescens*) and aspen *Populus tremula* (13% of stands) dominate. There are also extensive areas of swamps and marshes, where alder (17%) and ash *Fraxinus excelsior* (3%) dominate. Other deciduous species (linden, Norway maple) have been nearly exterminated as a result of forestry practices. Timber harvest is high (3.0–4.8 m³/ha), and is sustained by intensive replantations of spruce and pine, which has devastated the natural character of the forest (Jędrzejewska *et al.* 1994, Okarma *et al.* 1995b).

In the Belarussian part of BPF, the dominant forest configuration is mixed coniferous forest (mainly pine), with a high proportion of oak. The structure of the forest has been affected by excessive clear-cutting in 1920s and 1930s. A considerable number of the Belarussian forests are of secondary origin (replanted). There also are some old-growth stands and the average age of tree-stands is 97 years. Forests of alder, aspen, birch, and ash cover 25% of the area. The annual timber harvest is low (0.8–1.7 m³/ha in 1951–1991) (Jędrzejewska *et al.* 1994, Okarma *et al.* 1995b).

BPF harbors a rich, nearly pristine community of ungulates: European bison, moose, red deer, roe deer, and wild boar (Jędrzejewska *et al.* 1994). Large carnivores are represented by wolf and lynx *Lynx lynx* Linnaeus, 1758, which in northeastern Poland are at the westernmost limits of their basic geographical range in lowland Europe (Okarma 1992b, 1993a, b). Brown bears were exterminated at the end of the 19th century (Buchalczyk 1980). Since 1981, the Polish and Belarussian parts of BPF have been separated by a border fence, which makes free movement of ungulates impossible; wolves and lynx are able to cross the fence.

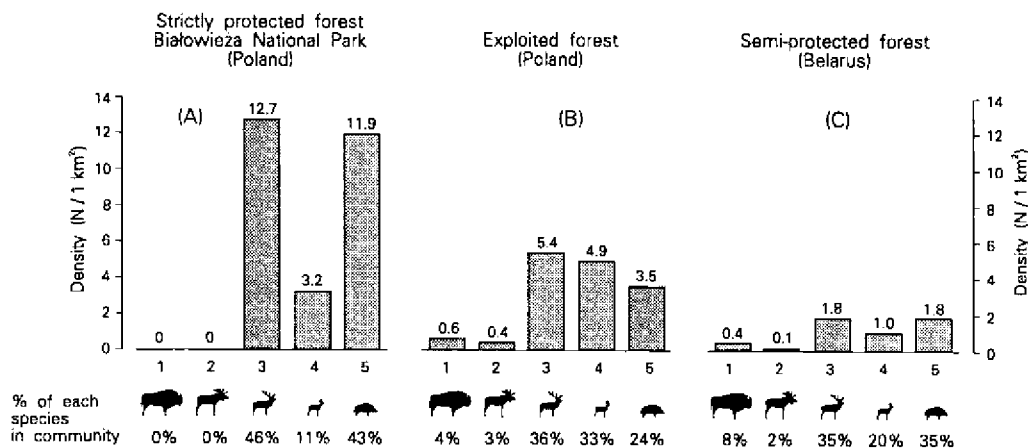


Fig. 14. Density and species composition of ungulate communities. (A) Białowieża National Park (Poland) – an average for 1991 and 1992 driving censuses, (B) exploited part of BPF (Poland) – driving census of 1991, and (C) the Belarussian part of BPF – snow-tracking of 1991, data of the State National Park “Belovezhskaya Pushcha”) (according to Okarma *et al.* 1995b). 1 – *Bison bonasus*, 2 – *Alces alces*, 3 – *Cervus elaphus*, 4 – *Capreolus capreolus*, 5 – *Sus scrofa*. N – number of individuals.

In Białowieża National Park, the ungulate community is co-dominated by red deer and wild boar – 46% and 43% of all ungulates respectively; roe deer are scarce (Fig. 14). Densities of red deer and wild boar are high: 12.7 and 11.9/km², respectively (an average density for 1991–1992) (Jędrzejewska *et al.* 1994).

In the exploited area of the BPF in Poland, red deer and roe deer dominate. Densities of red deer and wild boar are 2.4 and 3.4 times lower than in the National Park (5.4 and 3.5/km², respectively); only roe deer are more numerous (Jędrzejewska *et al.* 1994) (Fig. 14). European bison and moose have low densities: 0.6 bison and 0.4 moose/km², respectively (Jędrzejewska *et al.* 1994, Krasiński *et al.* 1994, Okarma *et al.* 1995a).

In the Belarussian part of BPF, red deer and wild boar also co-dominate the ungulate community (each species accounts for about 35% of all ungulates). Densities of ungulates are generally lower than in the Polish part of BPF (Okarma *et al.* 1995b) (Fig. 14). Ungulate density is estimated from snow-tracking in the Belarussian part of BPF, and by a driving census in the Polish part of BPF, thus results obtained in these two parts of BPF are not directly comparable. In Belarus, however, snow-tracking is often carried out for two consecutive days around forest sub-compartments 0.5 km² in size. Such a method decreases possible biases due to different travel distances of different ungulate species, producing results of similar accuracy as driving census (Sablina 1955). It is also known from Polish studies that the smaller the grid along which snow-tracking is conducted the more the results of snow-tracking are similar to results of driving censuses. Snow-tracking along a 0.25 km² grid produces results close to those of a driving census (Pucek *et al.* 1975, Z. Pucek, pers. comm.).

It has been hypothesized that differences in ungulate density between the three parts of BPF could be the result of different species and the age structure of the forest (Jędrzejewska *et al.* 1994). The total biomass of herbivorous ungulates (European bison, moose, red deer, and roe deer) per unit area was significantly correlated with the percentage area covered with tree stands dominated by deciduous trees. Biomass of omnivorous ungulates (wild boar) correlated with the percentage area covered with old tree stands (> 80 years) (Jędrzejewska *et al.* 1994), where production of seeds (mainly acorns) is highest (average yearly crop was 16 400 kg/km² in BPF). For this reason old-growth deciduous forests of BNP are inhabited by more ungulates than coniferous-dominated old-growth forests in the Belarussian part (Jędrzejewska *et al.* 1994). Even more interesting is that the density of red deer in pristine mature deciduous forests of BNP was higher than younger coniferous-dominated forests of the exploited Polish part of BPF. Bobek *et al.* (1975) found that browse supply, influencing red deer numbers is higher in thickets than in old-growth stands. The significantly higher density of red deer in BNP compared with the exploited forests of BPF is not likely to be a result of census errors (Jędrzejewska *et al.* 1994). Thus, further studies are needed to determine whether the high densities of red deer in BNP result only from the abundant browse supply.

In the exploited forests of the Polish part of BPF all ungulates, except European bison, are hunted under an annual harvest plan. Since 1991, annual harvest of ungulates has increased considerably and accounts for 50% of wild boar, and 25% of the estimated red deer population. This harvest strategy is designed to limit damage to replantations (Okarma *et al.* 1995a). Bison is a protected species and its population size is kept stable by the National Park authorities by culling several individuals per year: on average, 10% of the estimated population was culled annually in 1981–1993 (Kraśiński *et al.* 1994).

In the Belarussian part of BPF all ungulates, except bison, are hunted. Harvest is at moderate level: in the early 1990s, 6% of the estimated population sizes of red deer, 10% of roe deer, and 22% of wild boar were hunted (Okarma *et al.* 1995b). The number of free-ranging bison is about 300 (at the end of 1993), and population size is controlled by the State National Park authorities. On average, 4.7% of the population was culled annually between 1981–1993 (Kraśiński *et al.* 1994).

Large carnivores have been protected in the Polish part of BPF since 1989. Numbers of wolves are estimated by game wardens at 12 in 1993, and lynx at 16 individuals in 1994 (Jędrzejewska *et al.* 1996a, b). In the Belarussian part, the lynx was declared a protected species in 1993, and its numbers are estimated at 28 (Jędrzejewska *et al.* 1996b). The reported number of wolves is also 28; however, they are heavily hunted (16 wolves were killed in 1993) to reduce losses of ungulates (Okarma 1993b, Jędrzejewska *et al.* 1996a, b).

In the relatively well-preserved BPF, large carnivores (brown bear, wolf, lynx) have been subjected to heavy human pressure since the beginning of the 19th century (Buchalczyk 1980, Jędrzejewska *et al.* 1996a, b). The idea of hunting wolves

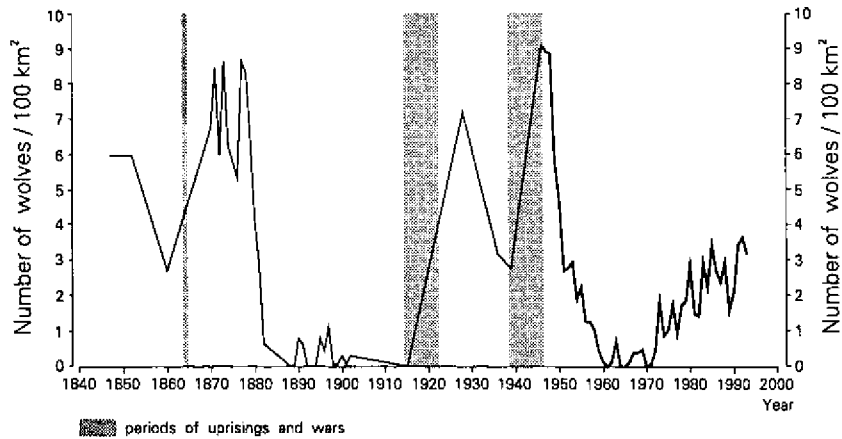


Fig. 15. Dynamics of wolf density in the whole Białowieża Primeval Forest in 1847–1993. Thin line – reconstructed density based on regression between numbers of wolves shot and population size in 1946–1971. Thick line – density reflects census by snow-tracking (according to Jędrzejewska *et al.* 1996a).

to prevent excessive damage to the livestock of local peasants was an old tradition in the region of BPF (Jędrzejewska *et al.* 1996a). During the last 150 years, as the result of efficient wolf control measures (eg driving wolves to nets, hunting young wolves with hounds, taking cubs from dens), the number of wolves in BPF fluctuated considerably (Fig. 15). Wolves were nearly extirpated twice: between 1882–1915 and 1958–1972. Always, after wars and periods of political chaos, wolves recovered and reached high densities (Fig. 15). It can be concluded that wolves have a high capacity for rebuilding their numbers, which can be attributed to high reproductive rate, flexibility in predation, accommodating social structure, and easy recovery from injuries (Jędrzejewska *et al.* 1996a). On the other hand, wolves are vulnerable to human pressure due to vocal activity that allows people to detect packs and cubs, conservative use of den sites, and fear of “fladry” (long ropes with strips of colourful material attached to them) (Okarma 1993a), which is a very effective method of wolf extermination (Jędrzejewska *et al.* 1996a).

Food habits of wolves

Białowieża Primeval Forest (BPF)

Wolf diet

In contrast to other European localities, wolves in BPF coexist with a diverse community of ungulates under relatively natural conditions. Only large carnivores (especially the wolf) have been subjected to excessive human pressure. This pressure led to the temporary eradication of wolves from BPF and subsequent

recovery during the last 150 years (Jędrzejewska *et al.* 1996a). Such unique circumstances, and the fact that the trophic ecology of the wolf in BPF has been studied for nearly 50 years, offer a rare opportunity to examine predation by wolves under varying densities of ungulates and wolves.

Gavrin and Donaurov (1954) analysed 1063 wolf faeces and 48 stomachs of killed wolves collected in 1946–1950. Bunevich (1988) analysed 32 faeces, 50 stomachs of killed wolves, and 82 carcasses of ungulates killed by wolves in 1979–1985. Jędrzejewski *et al.* (1992) analysed 144 faeces collected in 1985–1989. Results of these studies (Table 2) show that wild ungulates are the primary food of wolves in the BPF. Cervidae (mainly red deer but also roe deer) are the main prey of wolves, but wild boar also can constitute a considerable part of the wolf diet, as observed by Gavrin and Donaurov (1954) in all seasons and Jędrzejewski *et al.* (1992) in summer.

Gavrin and Donaurov (1954) found that European hare was an important dietary item for wolves. Their findings, however, have not been confirmed by other studies (Table 2). The low percentage of hare detected by Jędrzejewski *et al.* (1992) in scats collected in the Białowieża National Park can be explained by the low density of hare compared with other parts of BPF (Jędrzejewski *et al.* 1993). However, Bunevich (1988), who collected wolf scats in the same area as Gavrin and Donaurov (1954), also found few hare (Table 2). There is a possibility that some scats from large male lynx were mistakenly collected by Gavrin and Donaurov (1954) as the wolf scats, and it is known that lynx prey more intensively on hare than wolves (Jędrzejewski *et al.* 1993).

There was a high percentage of livestock in the wolf diet in the Belarussian part of BPF, especially in the late 1940s (Gavrin and Donaurov 1954). Carrion from several dumping places was the main source. Predominately middle-sized domestic animals (sheep, pigs, dogs) were actually killed by wolves (Bunevich 1988, Jędrzejewska *et al.* 1996a). In the Polish part of BPF livestock carrion is not available to wolves due to strict sanitary regulations and damage to domestic animals has occurred only sporadically (Jędrzejewska *et al.* 1996a).

Selectiveness of wolf predation

In the Polish part of BPF (pooled data for the National Park and commercial forest), the ungulate community is co-dominated by red deer and wild boar: 36 and 33% of all ungulates, respectively. Roe deer are less numerous, and European bison and moose constitute only a small percentage of the community (data from drive censuses conducted in 1991) (Fig. 16). Among ungulates killed by wolves that were found during the autumn-winter seasons of 1984/85–1993/94 (597 carcasses), red deer dominated (68%), followed by roe deer 19%, wild boar 12%, and moose 1% (Okarma *et al.* 1995a).

Ivlev's selectivity index (D) showed that wolves preferred red deer (0.68); whereas other species were killed less frequently than expected based on their availabilities. Wild boar were avoided (-0.77), which supported previous studies

Table 2. Diet of wolves in Białowieża Primeval Forest analysed by various authors in 1946–1990. W – winter (December–March), Sp – spring (April–May), Su – summer (June–August), A – autumn (September–November), Winter (October–April), Summer (May–September). ¹ Food content calculated as a percentage of prey (each occurrence of a species in a faeces sample or a stomach was calculated as 1). “–” means that a given item was not detected. ² Food content calculated as a percentage of prey (each occurrence of a species in a faeces sample or a stomach or carcase of ungulate killed by wolves was calculated as 1). “+” means < 1% of prey. Mouflon remains were also found in scats of wolves, but these mouflons were killed in an enclosure. ³ Food content calculated as percentage of biomass (%B) and percentage of occurrence (%O). * – traces (< 0.05%). ⁴ Food niche breadth (B) calculated after Levins (1968) for 12 main food groups (moose, red deer, roe deer, wild boar, European hare, squirrel, small rodents, other carnivores, carrion of cows and horses, middle-sized domestic animals, birds, amphibians and reptiles). $B = 1 / \sum p_i^2$, where p_i – percent occurrence of a particular prey group.

Food items	Source												
	Gavrin and Donaurov ¹ (1954) 1946–1951				Bunevich ² (1988) 1979–1985				Jędrzejewski <i>et al.</i> ³ (1992) 1985–1990				
	W	Sp	Su	A	W	Sp	Su	A	Winter		Summer		
	<i>n</i>	628	268	137	265	114	23	12	15	%B	%O	%B	%O
Moose	–	–	–	0.3	2.6	–	–	–	–	–	–	–	–
Red deer	6.3	4.2	5.6	6.6	59.6	52.2	33.3	46.7	31.5	29.3	38.1	31.1	
Roe deer	18.4	10.3	14.7	10.8	19.3	26.1	8.3	46.7	2.9	3.0	3.0	4.4	
Unidentified													
Cervidae	–	–	–	–	–	–	–	–	56.8	64.6	36.4	53.3	
Total Cervidae	24.7	14.5	20.3	17.7	81.5	78.8	41.6	93.4	91.2	96.9	77.5	88.8	
Wild boar	21.0	25.3	18.4	13.2	12.3	–	16.7	6.6	7.8	29.3	20.8	46.7	
European hare	15.8	16.5	19.8	14.5	–	–	8.3	–	0.2	2.0	1.4	4.4	
Squirrel	0.1	1.0	0.7	0.3	–	–	–	–	*	1.0	–	–	
Mole	0.1	–	–	–	–	–	–	–	–	–	–	–	
<i>Sorex</i> spp.	0.1	–	–	–	–	–	–	–	–	–	–	–	
Small rodents	2.9	3.4	3.6	4.6	–	–	–	–	*	5.0	*	4.4	
Raccoon dog	–	–	–	–	–	–	8.3	–	0.6	4.0	–	–	
Wolf	–	–	–	–	+	–	–	–	–	–	–	–	
Lynx	0.3	–	–	–	–	–	–	–	–	–	–	–	
Fox	0.1	–	–	–	–	–	8.3	–	–	–	–	–	
Pine marten	0.1	–	–	–	–	–	–	–	–	–	–	–	
Badger	0.1	–	–	–	–	4.3	–	–	–	–	–	–	
Cow and horse (carrion)	6.9	15.3	14.1	19.1	1.7	13.0	8.3	–	–	–	–	–	
Sheep	3.8	11.1	11.9	10.9	–	–	–	–	–	–	–	–	
Pigs	2.0	2.1	2.1	5.5	2.7	–	8.3	–	–	–	–	–	
Goats	0.1	–	0.7	0.3	–	–	–	–	–	–	–	–	
Dogs	4.7	2.4	4.2	4.5	1.7	4.3	8.3	–	–	–	–	–	
Geese	0.3	0.7	0.7	1.4	–	–	–	–	–	–	–	–	
Birds	1.0	1.0	–	–	–	–	–	–	*	2.0	0.1	4.4	
Amphibians and reptiles	–	–	–	–	–	–	–	–	*	2.0	0.1	4.4	
Invertebrates	–	–	–	–	–	–	–	–	*	1.0	–	–	
Plant material	–	1.4	2.8	2.4	+	4.3	8.3	–	0.1	24.2	0.1	24.4	
Food niche breadth (B) ⁴	6.1	5.6	5.9	5.9	2.4	2.9	5.4	2.3	2.9	–	–	2.8	

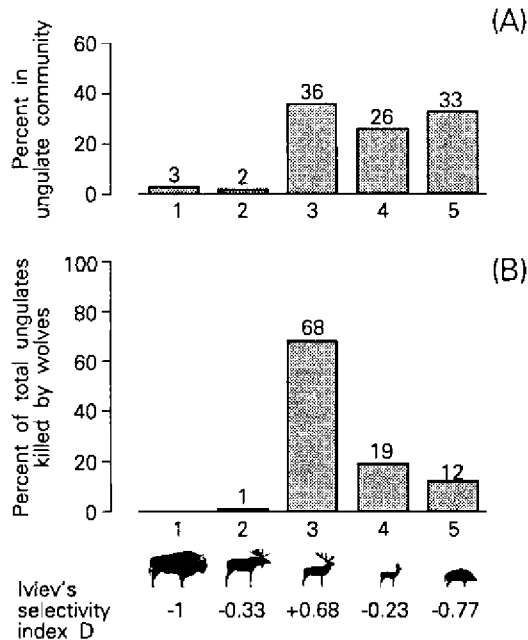


Fig. 16. (A) Species composition of the ungulate community in the Polish part of BPF (an average for 1991 and 1992 driving censuses in exploited forests and driving census of 1991 in the BNP – calculated according to data of Jędrzejewska *et al.* 1994). (B) Species composition of ungulates killed by wolves in the exploited forests of BPF in 1984–1994 (percentage of each species in the total number of ungulate carcasses, $n = 597$, identified as killed by wolves – according to Okarma *et al.* 1995a). Explanations as in Fig. 14.

by Bunevich (1988) in the Belarussian part of BPF. Negative selection of roe deer contradicted results of Bunevich (1988), who found a high degree of preference for this species. However, I suggest that such preference reflected the smaller wolf pack size in the Belarussian part of BPF in comparison to the Polish part (2.3 vs 3.6 individuals on average at the end of winter), which resulted from the intense killing of wolves at the beginning of the hunting season (Jędrzejewska *et al.* 1996a).

No European bison were found among the prey of wolves. Bison are supported by supplementary feeding during winter, and in the Polish part of BPF 80–90% of bison aggregate in winter ranges where several feeding stations are placed. Only some of the adult bulls are distributed widely (Kraśiński *et al.* 1994). Thus, calves are in relatively good physical condition and stay within large herds that shield them from wolf predation. However, in old narrative reports about BPF, a few cases of attacks by wolves and brown bears on bison were described (Kartsov 1903).

Wolf predation on a particular species of ungulates was clearly selective. Among red deer killed by wolves, stags constituted only 14% vs 27% in the living population (Okarma *et al.* 1995a). Jędrzejewski *et al.* 1992 found that wolves selected

preferably calves (61% of red deer of a known age recovered from scats of wolves in the Białowieża National Park were < 1 year old). Bunevich (1988) also showed that most red deer killed by wolves in the Belarussian part of BPF were juveniles (55%); 31% were adult females. However, Okarma *et al.* (1995a) found no preference for juveniles and females from carcasses of ungulates killed by wolves in the commercial part of the BPF in 1969/70, 1977/78, and 1984/85–1993/94. This inconsistency with results determined from scat analysis could be because the use of kills tends to underestimate the number of young in the wolf diet. This is because the small prey are often eaten completely (Ryabov 1974, Litvinov 1981, Jędrzejewski *et al.* 1992).

Among wild boar killed by wolves, juveniles prevailed (94% of wild boar in wolves' scats from Białowieża National Park were young < year old) (Jędrzejewski *et al.* 1992). Similar results were obtained from the Belarussian part of BPF (Kozlo 1975, Bunevich 1988). Few moose were preyed on by wolves, but calves and a few females are occasionally eaten. Wolves preyed randomly on different sex and age classes of roe deer (Okarma *et al.* 1995a).

Variability of wolf predation

Predation by wolves varied seasonally, particularly between winter and summer. Jędrzejewski *et al.* (1992) found that cervids (mostly red deer) constituted 91.2% of the biomass consumed by wolves in winter (October–April), and wild boar were only 7.8% of their diet. In summer (May–September), the percentage of wild boar increased to 20.8% and cervids decreased to 77.5% of prey biomass (Table 2). It is impossible to compare these values with data on wolf predation from other BPF studies, because the diet of wolves was divided in four seasons for analyses (Table 2). However, Bunevich (1988) also detected that in summer the percentage of wild boar among wolf prey was the highest while cervids was the lowest (Table 2). Similar trends were noted by Gavrin and Donaurov (1954) who found the percentage of cervids in the wolf diet was the highest in the winter, although seasonal differences were small. Wild boar was the highest in spring (even higher than cervids) (Table 2).

The pattern of wolf predation in BPF depends also on the species composition of the ungulate community. Considerable differences in density and species composition of the ungulate community (cf Fig. 14) between Białowieża National Park and the exploited forest (Jędrzejewska *et al.* 1994) have resulted in varied prey selection by wolves (Fig. 17). In the National Park where red deer and wild boar co-dominate, red deer are most common among carcasses from wolf predation, followed by wild boar. In the commercial forest, where red deer and roe deer co-dominate, red deer were also the primary prey, followed by roe deer (Fig. 17).

The diet of wolves in the Belarussian part of BPF, analysed by comparable methods, has changed over the past 30 years (1946–1985) (Gavrin and Donaurov 1954, Bunevich 1988; Table 2). Occurrence of wild ungulates in the wolf diet increased (depending on the season) from about 31–46% to 58–94%, domestic

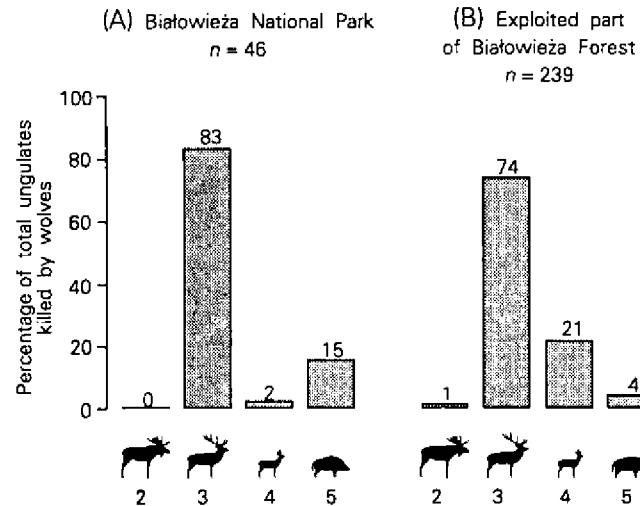


Fig. 17. Species composition of ungulates killed by wolves (percent of each species in the total number of wolf kills found) in the Białowieża National Park and exploited forests (n = number of wolf kills) in the autumn-winter seasons of 1986/87–1990/91 (according to Jędrzejewska *et al.* 1994). Explanations as in Fig. 14.

animals (mainly carrion) decreased from about 18–42% to 6–25%, and the European hare decreased to the point that it is now low in the diet (8%). Red deer have become a primary food for wolves, instead of wild boar, and their occurrence in the diet of wolves increased 10 times vs a decrease of 2 times for wild boar (Table 2). These changes in the trophic ecology of wolves, with wild ungulates as the primary food, could be explained by simultaneous and large increases in ungulate numbers, mainly red deer and roe deer. Overall density of ungulates was estimated as 1.7/km² in 1946–1948, 3.8 in 1950–1951, and 6.9 in 1988 (Bunevich 1988). Low predation on domestic animals in recent years may be the result of high numbers of wild ungulates and a moderate density of wolves. Wolves tend to prey more on domestic animals during periods of high density, or at very low densities when pack social structure breaks down due to overhunting (Jędrzejewska *et al.* 1996a).

Wolves preyed on particular species of ungulates with different intensity in various years. Gavrin and Donarov (1954) studied the role of wild boar, roe deer, and red deer in the autumn-winter diet of wolves in relation to changes of their numbers in consecutive years (Table 3). They found that density of roe deer continuously increased from 1946/47 to 1949/50, but their occurrence in the diet of wolves decreased, and concluded that high predation on roe deer was associated with severe winter conditions, which resulted in debilitating physical condition of the prey. Predation rates on wild boar differed 3-fold between two severe winters (1946–1947 and 1949–1950), despite identical densities in wild boar (Table 3).

Table 3. Percentage of wild boar, roe deer, and red deer in the diet of wolves in relation to ungulate numbers, species composition of ungulate community, age structure of population, physical status of individuals, severity of winter, and acorn crop in the Belarussian part of Białowieża Primeval Forest in autumn–winter seasons 1946/47–1949/50 (according to data from Gavrin and Donaurov 1954).

Factor	1946/47	1947/48	1948/49	1949/50
Severity of winter	Severe (deep snow and low temperatures)	Mild	Mild	Severe (shallow snow but low temperatures)
Acorn crop	Very high	Moderate	Null production	Moderate
<i>Wild boar Sus scrofa</i>				
Population numbers	506	723	1068	510
Percentage in ungulate community	42.6	46.4	49.5	25.0
% Occ. in wolf diet	7.5	16.0	25.2	23.6
Population structure	Majority of adults as a result of population crash in 1944 and 1945	Majority of juveniles and subadults	Majority of juveniles and subadults	Moderate number of juveniles and subadults
Physical condition of individuals	Strong, healthy	Strong, healthy	Debilitated, starved	Weak and late, development of young as a result of late breeding in winter 1948/49
<i>Roe deer Capreolus capreolus</i>				
Population numbers	371	475	605	849
Percentage in ungulate community	31.2	30.5	28.0	41.5
% Occ. in wolf diet	28.2	16.6	12.8	9.3
Physical condition of individuals	Debilitated, weak	Strong, healthy	Strong, healthy	Strong, healthy
<i>Red deer Cervus elaphus</i>				
Population numbers	311	360	485	684
Percentage in ungulate community	26.2	23.1	22.5	33.5
% Occ. in wolf diet	8.5	4.9	4.2	10.5
Physical condition of individuals	Weak, debilitated	Strong, healthy	Strong, healthy	Debilitated, weak
Estimated number of wolves	77	78	99	40

Such a phenomenon may be explained by a higher proportion of juveniles and subadults in the wild boar population and the weak development of young. Gavrin and Donaurov (1954) suggested that the success of wolves hunting ungulates in various years depended equally on total numbers of ungulates and the status of their populations (eg age structure, physical condition, disease) and also is influenced by the size of wolf packs. Packs were more successful in killing ungulates than solitary wolves. They also suggested that, in BPF, wild boar and roe deer were complementary species: when it was difficult to hunt wild boar successfully, wolves shifted to roe deer.

Results of recent studies in the Polish part of BPF (Jędrzejewski *et al.* 1992, Okarma *et al.* 1995a) confirmed that natural mortality of ungulates varied manifold among years and depended on climatic conditions during winter and food availability (eg acorn production). Death from starvation, cold, and disease (mainly wild boar) were related to the severity of winter. For example, during the unusually snowy and cold winter of 1969/70, at least 30% of the ungulate population (except bison) in the Polish part of BPF died (409 red deer, 1 226 roe deer, and 417 wild boar) (Okarma *et al.* 1995a). The acorn crop (up to 2 000 kg/ha in good mast years, Pucek *et al.* 1993) can determine ungulate survival in winter, especially for wild boar (Lebedeva 1956), but also for red deer and European bison (Okarma *et al.* 1995a).

Niche breadth (B) of the wolf diets, calculated from three studies in BPF, varied (see Table 2). In the 1950s, when densities of wild ungulates were low, the diet niche was relatively broad (about 6). Wolves consumed a variety of food (Gavrin and Donaurov 1954). By the late 1980s, the diet niche was narrower (Bunevich 1988, Jędrzejewski *et al.* 1992) and cervids dominated the diet of wolves. Only the summer diet niche breadth, calculated after Bunevich (1988), was similar to levels observed in the 1950s (such a high value was not necessarily accurate, because sample size from summer was small: $n = 12$). Unfortunately, diet niche breadth could not be compared to data from Jędrzejewski *et al.* (1992), who also analysed wolf diet throughout a year but divided it into only two classes: summer and winter (Table 2).

Role of wolves in natural mortality of ungulates

Populations of ungulates in BPF are affected by several mortality factors; eg hunting, weather conditions, food supply, and predation (Okarma *et al.* 1995a). Predation by wolves varies in importance for each ungulate species. Predation by wolves is the major mortality factor for red deer, accounting for 65.2% of the known natural mortality ($n = 627$ carcasses). Wolves are responsible for 26.4% of the known natural mortality of roe deer ($n = 424$). Diseases and starvation (36.3%) and lynx predation (32.1%) are more important. Predation by wolves has little effect on wild boar (only 19.1% of the known natural mortality, $n = 378$) compared to the primary mortality factors, disease and starvation (73.3%).

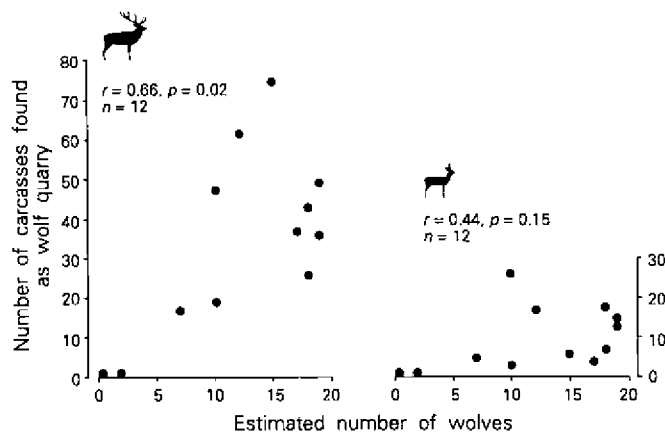


Fig. 18. Number of red deer and roe deer killed by wolves found in relation to estimated number of wolves in the Polish part of the BPF (exploited forests only, data for 1969/70, 1977/78, and 1984–1994) (according to Okarma *et al.* 1995a). Each point represents one year.

The importance of wolf predation in the natural mortality of ungulates varies considerably between years and is modified by winter climate and food supply (acorn crop). Red deer mortality also depends on the number of wolves (Okarma *et al.* 1995a), a relationship that was highly significant for red deer and non-significant for roe deer (Fig. 18). Such comparisons are possible because the number of wolves have varied considerably in the Polish part of BPF since the 1950s when their numbers were estimated at 30–40. They were extirpated in the late 1960s, and then slowly increased (owing to migration from Belarus) to about 20 individuals in recent years (Jędrzejewska *et al.* 1996a).

In summary, it is clear that wolf interaction with the nearly pristine, multi-species ungulate community in BPF is typical of an opportunistic predator. Wolves clearly prefer cervids (red deer and roe deer) and avoid wild boar. Predation by wolves is highly flexible and pressure on a particular species of ungulates changes according to the structure of the ungulate community (density and relative proportions of species), age structure and physical condition of prey, climatic conditions during winter, and abundance of food (especially acorns).

Other European localities

Core wolf populations (eastern Europe)

Most of the geographical range of the wolf in Europe is in the eastern part of the continent. It is a common belief that wolves in Russia live under natural conditions, which is only partly correct. In Russia, wolves can be divided into two ecological types: (1) “wild” wolves that occur in natural habitats and prey mainly

Table 4. Diet of wolves (% of occurrence) in the Central-Forest State Reserve (Russia) from 1975/76 to 1984/85 as revealed by scat analyses (from Kochetkov 1988). Each season = May–April next year.

Food item	1975/76 <i>n</i> = 171	1976/77 <i>n</i> = 203	1977/78 <i>n</i> = 105	1978/79 <i>n</i> = 100	1979/80 <i>n</i> = 57	1980/81 <i>n</i> = 70	1981/82 <i>n</i> = 58	1982/83 <i>n</i> = 69	1983/84 <i>n</i> = 51	1984/85 <i>n</i> = 52
Moose	50.9	43.3	52.7	33.0	53.3	66.2	64.5	63.6	66.0	92.8
Wild boar	8.5	20.3	18.2	11.0	25.0	6.8	8.1	15.6	22.7	–
Blue hare	9.6	20.3	10.9	25.7	8.3	16.1	8.1	9.1	1.9	3.6
Rodents	4.5	4.2	0.9	2.8	3.3	–	1.6	2.6	–	–
Other mammals	0.6	0.5	0.9	6.4	3.3	1.4	6.5	3.9	–	–
Livestock (sheep, cows, pigs, goats)	15.7	4.3	14.6	13.8	5.0	6.8	4.8	1.3	5.6	3.6
Birds	3.9	2.5	0.9	1.8	1.8	–	4.8	2.6	1.9	–
Plants	6.3	4.6	0.9	5.5	–	2.7	1.6	1.3	1.9	–

on wild ungulates, and (2) “synantrophic” wolves that live in anthropogenic habitat and feed on livestock, dogs, poultry, and carrion (Bibikov *et al.* 1985).

Ungulates typical of a given region or habitat are the staple food of wolves in habitats that are transformed only moderately by human activities. In tundra, reindeer constitute most of the wolf diet; in taiga – moose; in mixed and deciduous forests – red deer, roe deer, and wild boar; and in mountains – red deer, roe deer, wild boar, and various mountain sheep and ibex species; in steppes and deserts – saiga antelope (Novikov 1956, Naumov 1967, Bibikov 1985). There are, however, considerable differences in wolf predation on ungulate species between years and seasons. Kochetkov (1988) analysed the diet of wolves in a 10-year period under conditions of relatively stable moose-wild boar proportions in the ungulate community and found significant differences in the percentage of these species in the diet of wolves (Table 4). Also Rusakov (1979b), analyzing prey consumption by wolves in the northern part of Pskovskaya oblast (Russia) in 1968–1975, demonstrated considerable interannual differences in prey consumption: percentage of occurrence in wolf scats ranged between 31.2–94.6% for moose and 0–10.4% for wild boar. Several authors indicated significant differences in the effect of wolf predation on ungulate communities in various seasons (especially non-snow vs snow period) (Gavrin and Donaurov 1954, Kochetkov 1988, Jędrzejewski *et al.* 1992, Śmietana and Klimek 1993).

In reasonably “natural” locations where ungulates are not readily available or were eradicated, other food items are important to wolves. In the tundra and taiga forest zones, blue hare *Lepus timidus* constituted a major (Rukovskii and Kupriyanov 1972, Dubrovskii 1980, see Zheleznov 1994 for review) or considerable part (Rusakov 1979b, Kochetkov 1988) of the diet. In some areas of the European

Table 5. Food composition of two packs of synantrophic wolves: in eastern Caucasus and the Voronezh oblast (Russia) (according to Bibikov *et al.* 1985).

Eastern Caucasus <i>n</i> = 216 (scats)		The Voronezh oblast <i>n</i> = 43 (digestive tract contents)	
Food item	% occurrence	Food item	% occurrence
Domestic pig	71.3	Domestic pig (carrion)	47.3
Cow	21.8	Fruits and seeds	38.2
Rodents	1.8	(wild pears, blackthorn, maize, sunflower, oat)	
Plants	1.8	Sheep (carrion)	9.2
Goat	1.4	Mammal bones	2.7
Wild boar	0.9	Wild boar	1.3
Sheep	0.5	Birds	1.3
Donkey	0.5		

part of Russia, beaver *Castor fiber* are preyed on intensively (Gatikh 1979, Kazenevskii 1979). In a region adjacent to the Caspian Sea where saiga antelope is the only species of wild ungulates, wolves prey on it and livestock. In some areas of this region, however, no ungulates exist (wild boar and saiga antelope were extirpated), and wolves survive on rodents (large-toothed souslik *Citellus fulvus* and little souslik *Citellus pygmaeus*) in summer and livestock and carrion in the autumn-winter period (Zalozny 1980). These wolves can be thus classified as synantrophic (Bibikov *et al.* 1985).

Synantrophic wolves prevail in the southern part of Russia, Ukraine, and Moldova (densely populated areas of intensive agriculture) but also inhabit tundra and mountains (areas of free-grazing livestock) (Bibikov *et al.* 1985, Ryabov 1987, 1993). The degree of synantrophism varies considerably in different regions, but the primary food of such wolves is always livestock, carrion, and occasionally fruits (Table 5). Owing to specialization on carrion and livestock, synantrophic wolves do not actively hunt wild ungulates, have altered territorial behavior (Bibikov *et al.* 1985, Ryabov 1993), and often produce wolf-dog hybrids (Ryabov 1979, 1993).

Satellite wolf populations (northern, southern, and western Europe)

In the northern part of Europe, habitats and ungulate communities are relatively well preserved, but the ungulate community is simple (max 2 species: reindeer and moose). In the far north, wolves prey intensively on large herds of semi-domesticated reindeer (Makridin 1962, 1979, Pulliainen 1965, Haglund 1968, Bjärval and Isakson 1982, Nieminen and Leppaluoto 1988). Further south, wolves prey more intensively on moose (Wabbakken 1992). Locally, even at quite northern latitudes, moose may be positively selected and reindeer avoided (Filonov 1989).

In western and southern Europe, wolves have faced impoverished ecological conditions; eg destruction of habitat and reduced numbers of ungulates. Under such circumstances, wolves often survive on food resources of anthropogenic origin such as livestock (Magalhaes and Fonseca 1982, Van Haaften *et al.* 1983, Pereira *et al.* 1985, Ivanov 1988, Blanco *et al.* 1990, Cuesta *et al.* 1991, Meriggi *et al.* 1991, Genov 1992, Fico *et al.* 1993, Patalano and Lovari 1993, Papageorgiou *et al.* 1994) and garbage from unmanaged dumps (Boitani 1982, Reig *et al.* 1985, Salvador and Abad 1987). Owing to extreme differences in habitat and ungulate communities in this part of Europe, the composition of the wolf diet varies considerably. In Bulgaria, the main prey of wolves during winter and spring is roe deer, red deer, and young wild boar; domestic animals (sheep and goats) predominate during summer (Ivanov 1988, Genov 1992). In Portugal and Greece, wolves prey on domestic animals (Magalhaes and Fonseca 1982, Van Haaften *et al.* 1983, Papageorgiou *et al.* 1994). In the northeastern part of Spain (West Galicia, Cantabrian Mountains, and Douro Meseta), the wolf diet resembles that of synantrophic wolves in Russia, consisting of livestock and carrion (Cuesta *et al.* 1991). Conversely, wolves in central and southern Spain (Demanda Mountains, Extremadura and Sierra Morena) prey on wild ungulates, where they are numerous, but livestock also is important. Among wild ungulates, roe deer were more intensively preyed upon than wild boar (Braña *et al.* 1982, Cuesta *et al.* 1991). In most locations in Italy, wild boar populations are expanding (Apollonio *et al.* 1988) and are the most important wild prey (Brangi *et al.* 1991, Meriggi *et al.* 1991, Sacchi *et al.* 1994, Mattioli *et al.* 1995). Dependence of wolves on wild boar reflects availability. In many places wild boar is the only wild ungulate present (Sacchi *et al.* 1994) or, in more diverse communities, the most numerous (Meriggi *et al.* 1991). In other areas in Italy, livestock (Patalano and Lovari 1993, Sacchi *et al.* 1994), rodents, and fruits are important dietary items (Meriggi *et al.* 1991).

Recently, densities of wild ungulates in southern and western Europe have increased and, as a consequence, the importance of livestock in the wolf diet decreased considerably. In Romania, domestic animals constituted 75% and wild ungulates 25% of the wolf diet between 1954–1967, but proportions reversed in 1991 (22% and 78%, respectively) (Almasan *et al.* 1970, Ionescu 1992). In central Italy, in the late 1970s, wolves were heavily dependent on garbage (Boitani 1982), but now domestic and wild ungulates constitute the primary foods of wolves (Patalano and Lovari 1993).

On the basis of these analyses, it can be concluded that in spite of a multitude of environmental conditions resulting in highly variable trophic ecology of wolves there are certain common features of wolf predation in Europe (ie wild ungulates as the staple food, preference for cervids). Local food availability (scarcity of ungulates, abundant food of anthropogenic origin) can often temporarily destroy, disturb, or alter these features. However, after the natural prey-base has recovered, they should again become manifest after some time delay as it is under natural conditions.

Effects of wolf predation on ungulate communities

Predation by wolves is extremely variable, and diet composition and selection of ungulate species can be affected by several factors. Some of these factors occur over large geographical scale; others are important locally (Table 6).

Table 6. Most important factors influencing wolf predation within available ungulate communities.

Factors	Source
MACROSCALE – ecosystem level	
* richness and species composition of ungulate community	This study
* relative proportions in density between particular species of ungulates within ungulate community	This study
* presence and availability of food of anthropogenic origin (livestock, garbage)	Boitani 1982, Bibikov <i>et al.</i> 1985, Reig <i>et al.</i> 1985, Salvador and Abad 1987, Cuesta <i>et al.</i> 1991, Mattioli <i>et al.</i> 1995
MICROSCALE – local conditions influencing hunting success of wolves	
* climatic conditions (snow depth, low temperatures, ice-layer on the surface of snow)	Kazenevskii 1961, Kotov 1969, Okarma <i>et al.</i> 1995a
* demographic characteristics of prey populations (juveniles vs adult individuals)	Gavrín and Donaurov 1954
* physical condition of prey	Okarma 1991, Bobek <i>et al.</i> 1992
* number of individuals in a group (pairs vs. packs)	Kochetkov 1988
* individual food preference of particular packs	Kudaktin 1978, Kochetkov 1988
* learning of hunting methods for new prey species	Rusakov and Timofeeva 1984, Filonov 1989
* road network in winter	Zalozny 1980
* persecution by man	Filonov 1989, Jędrzejewska <i>et al.</i> 1996a

Richness and species composition of ungulate communities

Cervids are preferred by wolves throughout their geographical range in Europe (Fig. 19). Prey selection by wolves varies considerably with local conditions; selection indices can vary from strongly positive to strongly negative (eg +0.94 to -0.89 in moose, +0.68 to -0.66 in red deer, and +0.67 to -0.77 in roe deer) (Fig. 19). Only red deer are positively selected in all places, except a single locality in Mordovskiĭ Nature Reserve (Russia), due to the high contribution of Sika deer which are the most preferred prey of wolves there (Filonov 1989). Where wolves prey mainly on other ungulates (moose, wild boar), they will shift to red deer when the red deer density increases (Gavrín and Donaurov 1954, Jędrzejewski *et al.* 1992, Ryabov *et al.* 1992, 1994). In the southern Ural Mountains and Asia, *Cervus elaphus sibiricus* was the most important food of wolves in several locations (Lavov 1972, Fedosenko *et al.* 1978, Gromov 1979, Zavatskii 1986, Gordiyuk 1991), and was positively selected even when it constituted only a small percentage of the

ungulate community (Darman 1986). In several locations in Canada, red deer was the major prey, often positively selected from the community of ungulates (Carbyn 1983, Paquet 1992, Huggard 1993a, Weaver 1994).

Moose constitute the major prey of wolves only where other middle-size species are scarce or of limited availability (Rusakov 1979b, Kochetkov 1988, Filonov 1989). Studies in North America reported that moose are such formidable prey that wolves depend heavily on other ungulate species when available (Mech 1966 for review of older studies, Potvin *et al.* 1988, Forbes and Theberge 1992, Paquet 1992). In contrast, Gasaway *et al.* (1992) found that where moose density was similar to caribou density (in Alaska and Yukon), moose was the staple food of wolves. Roe deer, a relatively small ungulate, are preyed on intensively by wolves in some locations. Common to these areas is a high density of roe deer, a simple ungulate community (mainly with wild boar and/or moose), and absence or scarcity of red deer (Gaross 1979, Braña *et al.* 1982, Filonov 1989, Cuesta *et al.* 1991).

According to available European data, reindeer are avoided as prey (Fig. 19); however, only 3 locations were included, which likely biases this result. In contrast, caribou in North America can be the most vulnerable species in wolf-multiple prey systems (Seip 1992). Caribou are unable to fight off predators as moose can, and have a low rate of reproduction compared to deer (Seip 1991). Available data from other locations in Eurasia (Central Siberian Plateau, Russia) did not verify this conclusion but did show that wolves can be sustained locally almost exclusively by reindeer (Suvorov and Lisenko 1988, Zheleznov 1994). Hunting success of wolves can be significantly greater on wild reindeer than moose (Zheleznov 1992).

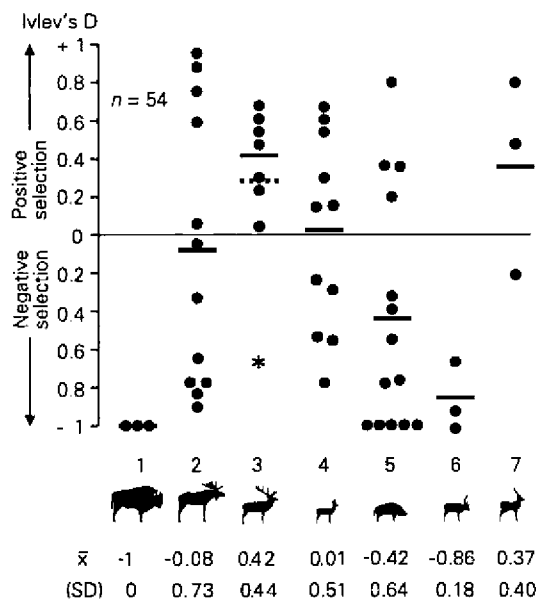


Fig. 19. Ivlev's selectivity index D for wolf predation on a given species of ungulates in several European locations. 1 – actual values of Ivlev's index for a given species in various localities, — – an average selection index for a given species, * – Ivlev's index for red deer in Mordovskii Reserve (Russia), ... – an average selection for red deer with a value for Mordovskii Reserve (*) included. Sources of data are indicated in Table 1. 1 – *Bison bonasus*, 2 – *Alces alces*, 3 – *Cervus elaphus*, 4 – *Capreolus capreolus*, 5 – *Sus scrofa*, 6 – *Rangifer tarandus*, 7 – *Cervus nippon*.

European bison are not generally preyed on by wolves. At present, bison live in small isolated populations (Pucek 1994), constitute only a small percentage of local ungulate communities, obtain supplementary feeding in winter, and form large aggregations around feeding sites (Kraśiński 1967, 1978, Kraśiński *et al.* 1994). Kudaktin (1986) reported that a small percentage of wolf scats in the Caucasian Reserve, contained hairs of European × American bison hybrids. The bison, however, may have been consumed as carrion. In historical times in Europe, wolf predation on bison was probably low, because they co-existed in mixed ungulate communities with other mid-sized and numerous ungulates that were easier prey for wolves than bison. In contrast, North America bison is a major food of wolves in Wood Buffalo National Park; calves are selected disproportionately compared to their availability. Only bison and moose occur in Wood Buffalo, and bison are more numerous (Carbyn *et al.* 1993).

Generally, wild boar are avoided by wolves (Belyanin 1979, Rykovskii 1980, Nesterenko 1988, Filonov 1989, Jędrzejewska *et al.* 1994, Okarma *et al.* 1995a) (Fig. 19). Wild boar are positively selected in only a few locations in Russia (Kudaktin 1978, Litvinov *et al.* 1981, Kochetkov 1988) and Italy (Mattioli *et al.* 1995), which may be the result of specific local conditions (eg few species of ungulates available, mainly moose and wild boar, and their relative densities). Wild boar also may be locally vulnerable to wolves (due to specific habitat conditions or a preponderance of young, or distinct prey preferences of some wolf packs). Intensive predation on wild boar in some areas may indicate the potential importance of wild boar as wolf prey throughout Europe due to the high reproduction rate and potential density of wild boar.

A preference of wolves for cervids also is evident from data on mortality of ungulates. Predation by wolves represents a major part of the total predation in all species of ungulates except European bison, which generally are not preyed on by wolves (Fig. 20). Only wild boar are affected by wolves to a relatively small extent compared to other predators (brown bear, wolverine *Gulo gulo*, lynx), except

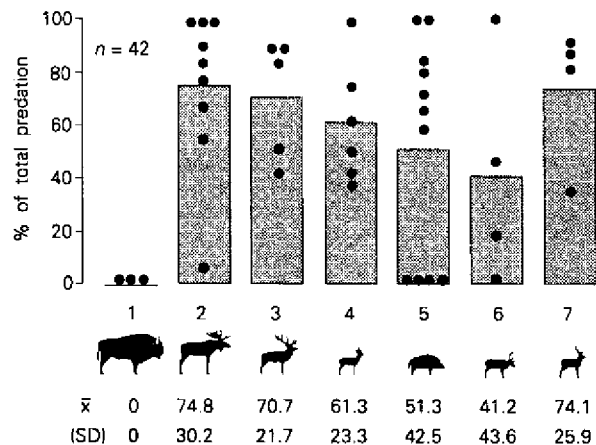


Fig. 20. Percent contribution of wolf predation to the total predator-caused mortality of 7 ungulate species in Europe. Height of bars indicate average wolf contribution for a given species, ● - actual values of wolf predation as a percentage of total predation on a given species in various localities. Sources of data are indicated in Table 1. Explanations as in Fig. 19.

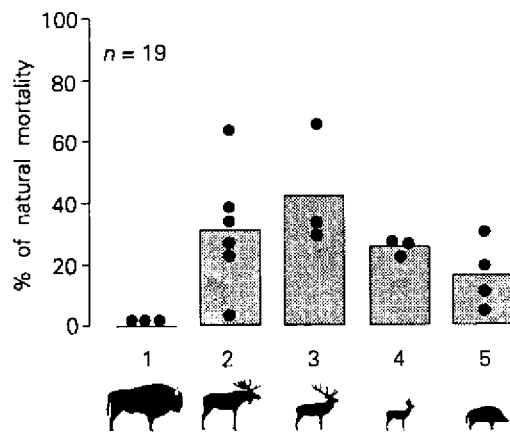


Fig. 21. Percent contribution of wolf predation to the total natural mortality of 5 ungulate species in Europe. Height of bars indicate average wolf contribution for a given species, ● – actual values of wolf predation as a percentage of total natural mortality for a given species in various localities. Sources of data are indicated in Table 1. 1 – *Bison bonasus*, 2 – *Alces alces*, 3 – *Cervus elaphus*, 4 – *Capreolus capreolus*, 5 – *Sus scrofa*.

in areas where the wolf was the only predator (Fig. 20). A similar pattern (a preference for cervids) was obtained when analyzing the contribution of wolf predation to total natural mortality of ungulates; ie 42.5% for red deer, 34.5% for moose, 25.7% for red deer, and 16% for wild boar (Fig. 21).

Predation by wolves also is selective within a given ungulate species. In all locations in Europe, wolves killed mainly young wild boar (Gavrín and Donaurov 1954, Lavov 1972, Ryabov 1974, Gatikh 1979, Rusakov 1979b, Kuzmin and Khakhin 1980, Litvinov 1981, Kudaktin 1982, Brtek and Voskár 1987, Kochetkov 1988, Jędrzejewski *et al.* 1992, Śmietana and Klimek 1993, Kuchmel 1994, Mattioli *et al.* 1995). A similar pattern of wolf predation on wild boar was reported in Asia (Abdunazarov and Taryannikov 1991). Adult wild boar are able to defend themselves effectively against wolves and occasionally kill wolves (Vyrypaev 1980) or escape into dense thickets where wolves cannot attack them easily (Kudaktin 1982).

Among moose, males are killed less often than expected, whereas calves, yearlings, and older specimens are preyed on significantly more than expected (Kaletskaya 1973, Makridin 1979, Rusakov 1979b, Kuzmin and Khakhin 1980, Rykovskii 1980, Litvinov *et al.* 1981, Filonov 1989). Similar results have been obtained in studies of wolf predation on moose in North America, which demonstrated selection for calves (Mech 1966, Fuller and Keith 1980, Peterson *et al.* 1984). Such selection is expected because moose calves are inexperienced with wolves and less dangerous and slower while escaping than adults (Mech 1970).

Red deer calves and females are usually selected (Bubenik 1966, Okarma 1991, Gordiyuk 1991, Bobek *et al.* 1992, Jędrzejewski *et al.* 1992). Only Kudaktin (1978) and Bobek *et al.* (1992) found that wolves killed disproportionately more adult males than their availability. Wolves in Asia preyed most intensively on calves of *Cervus elaphus sibiricus* (Fedosenko *et al.* 1978). However, in western Sayan Mountains (Russia) more adults than calves were killed in winter. Among adult

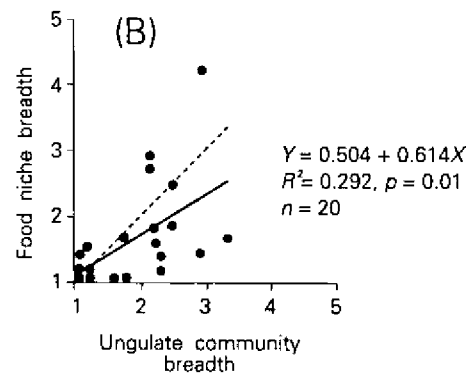
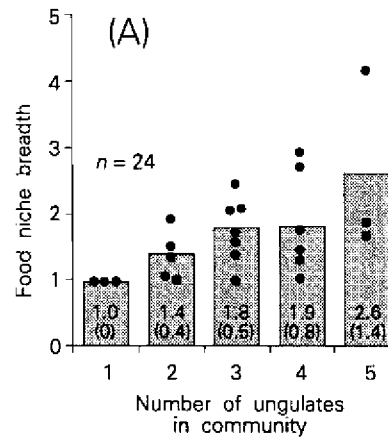


Fig. 22. Food niche breadth of wolves for 24 European locations in relation to (A) number of ungulates in the community: numbers inside bars are means and SD (in parentheses); and to (B) ungulate community breadth for 20 locations: dashed line is $y = x$ line, solid one is regression line. ● - actual values of food niche breadth in various locations. Food niche breadth B calculated after Levins (1968) for a maximum of 5 ungulate species: $B = 1 / \sum p_i^2$, where p_i - percent of occurrence of particular prey. Ungulate community breadth calculated according to identical formula, but p_i - percent of occurrence of particular species in ungulate community. Sources of data are indicated in Table 1.

animals killed by wolves males prevailed in some years (Zavatskiĭ 1986). In Canada wolves killed a higher proportion of calves and older animals than expected (Carbyn 1983, Paquet 1989, Huggard 1993b, Paquet 1993, Boyd *et al.* 1994, Weaver 1994). Nevertheless, there can be considerable seasonal and annual differences in predation by wolves on a given species of ungulate (Gavrĭn and Donaurov 1954, Kochetkov and Sokolov 1979, Kochetkov 1988, Jędrzejewski *et al.* 1992, Śmietana and Klimek 1993), which has been confirmed in North America (Mech 1970, Fuller 1989, Carbyn *et al.* 1993, Huggard 1993a).

Food niche breadth (B) of wolves in Europe, calculated only for ungulates considered in this study - European bison, moose, red deer, roe deer, and wild boar (maximum value 5) - increased with increasing number of ungulate species in the community (Fig. 22A). There was a statistically significant relationship between ungulate community breadth and food niche breadth of wolves (Fig. 22B); however, food niche breadth of wolves did not achieve maximum values even in the richest ungulate communities (5 species). The only exception was the Caucasian Nature Reserve where calculated niche breadth was as high as 4.18. It is, however, a special

locality with a high contribution of other ungulates that were not considered in this study, including chamois and West Caucasian tur (Golgofskaya 1970).

This high value may have also resulted from pooling data for different packs with diverse prey preferences (Kudaktin 1978). Low values of food niche breadth both in relation to number of ungulate species in the community and to ungulate community breadth indicated that, in spite of wide range of species available, wolves focused only on a few prey species.

Predation by wolves on alien or introduced ungulate species can be significant. Sika deer introduced to several locations in Russia became a staple food of wolves and were highly selected from ungulate communities (Ryabov 1974, Kazenevskii 1979, Filonov 1989). Fallow deer were an important prey species in some areas of Italy (Matteucci 1992, Centofanti 1994). Mouflon are heavily preyed on by wolves (Lequette *et al.* 1994, author's unpubl. data) and can be completely eradicated (M. Apollonio, pers. comm.). It can be hypothesised that these species are especially vulnerable because they did not coexist with the wolf in the recent centuries and may lack antipredatory behavior (eg mouflon); or they have been introduced to locations where ungulate communities were relatively simple and thus became a target of intense wolf predation.

Availability of food of anthropogenic origin

Wild ungulates are scarce in some European locations, but food resources for wolves created by human activities may be abundant (livestock, carcasses, and garbage). Wolves have been able to adapt to locally abundant food of anthropogenic origin (Magalhaes and Fonseca 1982, Bibikov *et al.* 1985, Reig *et al.* 1985, Salvador and Abad 1987, Cuesta *et al.* 1991, Ryabov 1993). Studies in Spain (Tellería and Sáez-Royuela 1989), Russia (Ryabov 1974), and North America (Fritts and Mech 1981) suggested that predation on livestock was usually very limited in areas with abundant natural food. However, in southern (Blanco *et al.* 1992, Patalano and Lovari 1993) and northern Europe (Nieminen and Leppaluoto 1988) where wild ungulates and unguarded livestock are widely available, losses of livestock are common. Thus, it could be suggested that the level of predation on livestock does not mainly depend on the density of natural prey, but on husbandry practices (eg using guarding dogs to defend livestock, housing livestock at night) and the location of pastures relative to wolf core areas.

Factors influencing hunting success of wolves

Several authors highlighted the effect of climatic conditions during winter on wolf predation (Formozov 1946, Gavrin and Donaurov 1954, Šmietana and Klimek 1993, Okarma *et al.* 1995a). Snow depth influences mobility and behavior of wolves and their prey (Formozov 1946, Nasimovich 1955, Telfer and Kelsall 1984, Fuller 1991). Generally, hunting success of wolves is higher in winters with deep snow (Gorbiyuk 1986, Bobek *et al.* 1992, Okarma *et al.* 1995a) because wolves are lighter than large ungulates (Nasimovich 1955, Mech *et al.* 1971, Telfer and Kelsall 1984).

Similar observations have been made in several studies in Asia (Fedosenko *et al.* 1978) and North America (Mech and Frenzel 1971, Peterson and Allen 1974, Gasaway *et al.* 1983, Nelson and Mech 1986, Paquet 1989, 1993, Huggard 1993c, Boyd *et al.* 1994).

Specific winter weather conditions (eg melting and re-freezing of snow) can limit access of ungulates to food, and as a result, their body condition deteriorates (Gavrin and Donaurov 1954) which may make hunting easier for wolves. Severe winters can lead to large die-off (mass death) of wild boar and other ungulates in large parts of Europe (Caboń 1958, Kazenevskii 1961, Kotov 1969, Gunchak 1980, Nesterenko 1988) and in mountains (Fedosenko *et al.* 1978), steppes, and semi-deserts of Asia (Sludskii 1963). Under such specific conditions many ungulate carcasses are available to wolves, although wolves may not always scavenge and prefer to hunt actively (author's unpubl. data). Demographic parameters of prey populations (eg numbers of juveniles vs adults) and physical condition of individuals within prey populations can significantly alter the hunting success of wolves. A high percentage of juveniles in wild boar populations offers an abundance of relatively easy prey for wolves (Gavrin and Donaurov 1954). Toward the end of winter, the physical condition of ungulates generally decreases, and the percentage of weakened individuals among wolf prey is higher than at the beginning of winter (Okarma 1984, 1991). In North America, wolf-killed white-tailed deer and moose are often in poor condition (Mech and Frenzel 1971, Fuller and Keith 1980, Messier and Crête 1985, Potvin *et al.* 1988, Paquet 1989, Forbes and Theberge 1992). However, wolves do not always take disproportionately more sick and weak animals than expected. Several studies revealed no differences in femur fat levels between wolf-killed individuals and those in the general population for moose (Ballard *et al.* 1987), white-tailed deer (Mech and Frenzel 1971, Fritts and Mech 1981), and red deer (Carbyn 1983).

Winter conditions not only affect ungulates during the current winter, but can also affect ungulate populations on a long-term basis. Mech *et al.* (1987) demonstrated a cumulative winter effect of previous winters on some reproductive parameters of white-tailed deer and moose and on winter vulnerability of moose calves to wolves.

Hunting success by wolves on a particular species also can be affected by wolf grouping patterns. Kochetkov (1988) found considerable differences in the diet of wolves hunting in packs or pairs. Packs consumed more moose; pairs consumed more small prey (blue hare and rodents) (Table 7).

Holleman and Stephenson (1981) suggested that particular wolf packs could exhibit distinct prey preferences. Food specialization of wolf packs depends on their size, abundance and availability of prey species, relative density or biomass of potential prey species, and environmental conditions within packs' territories. Kudaktin (1978) found significant differences in diets of three packs of wolves in the Caucasian Nature Reserve in 1972–1976 (Table 8). Kochetkov (1988) analysed the diet of eight wolf packs in a region of the Central-Forest State Reserve, Russia,

Table 7. Winter diet (% of occurrence) of wolves (packs vs pairs) in the Central-Forest State Reserve (Russia) as revealed by scat analyses from 1975 to 1985 (after Kochetkov 1988). The author collected scats from wolf packs of only two wolves and from packs of three or more wolves (number of individuals in a pack was determined by snow-tracking).

Food item	Packs <i>n</i> = 328	Pairs <i>n</i> = 98
Moose	74.1	59.7
Wild boar	9.9	10.4
Blue hare	8.3	11.7
Rodents	0.9	2.6
Other mammals	0.0	2.6
Livestock (sheep, cows, pigs, goats)	3.6	7.8
Birds	3.2	5.2

Table 8. Diet (% of occurrence) of three packs of wolves in the Caucasian Nature Reserve in 1972–1976 as revealed by scat analyses (*n* = 514) (according to Kudaktin 1978). * *p* < 0.05, *** *p* < 0.001 (*G*-test for homogeneity of percentages).

Food item	Packs			Significance level
	Urushten	Alous	Umpyr	
Red deer	39.7	60.5	41.7	<i>G</i> = 5.37 ns
West Caucasian tur	33.3	5.6	7.9	<i>G</i> = 28.27 ***
Chamois	3.2	2.8	1.8	<i>G</i> = 0.42 ns
Wild boar	6.5	19.7	20.8	<i>G</i> = 9.38 *

in 1975–1985 and found distinct differences in diet. There were wide ranges of occurrences of prey items between years: moose (30–90%), wild boar (4–25%), and blue hare (3–25%).

Preference for a particular kind of prey may be perpetuated between generations, which may help explain the lack of immediate response to new prey species. Under such conditions, new hunting behavior must be developed, so despite the presence of new prey species, wolves still tend to hunt traditional ones (Rusakov and Timofeeva 1984). Before the 1960s in the Pskovskaya oblast (northeastern Russia) wolves preyed mainly on moose and blue hare; wild boar were rare and killed sporadically. Since the early 1970s, the density of wild boar has increased considerably. The remains of wild boar have regularly occurred in wolf scats since that time but only in a small amounts. From 1977–1980 the proportion of wild boar in the wolf diet increased rapidly to > 40% (Rusakov and Timofeeva 1984) (Fig. 23). Nesterenko (1988) and Filonov (1989) stated that wolves in Darvinskiĭ Reserve (Russia) preyed mainly on moose despite the steadily

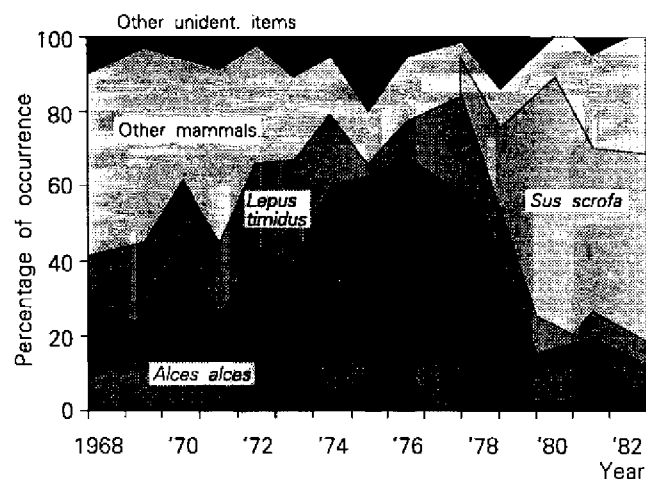


Fig. 23. Winter and early spring diet of wolves (analyses of faeces, $n = 978$) in the Pskovskaya oblast (Russia) from 1968 to 1982 (according to Rusakov and Timofeeva 1984).

increasing wild boar density to the point that they were more abundant than moose. Such "hunting conservatism" may be one of the reasons for the delayed response by wolves to changes in demographic patterns of prey species (Mech and Karns 1978, Gasaway *et al.* 1983).

Human activities, other than providing food of anthropogenic origin, also can modify wolf predation. Zalizny (1980) found that road networks that are cleared of snow allowed wolves to travel further and thereby increase access to prey over a larger area. Similar observations were made by P. Paquet (1994, pers. comm) in Banff National Park, Canada. In regions where wolves are heavily harvested, their numbers can be considerably lowered, and pack structure broken down (Bunevich 1988, Filonov 1989, Ryabov 1993). This may decrease the impact of wolf predation on ungulates (especially on red deer; Okarma *et al.* 1995a) and change the pattern of selection for particular species from the available ungulate community.

Wolf predation as a possible limiting factor of ungulate density in Europe

It is difficult to generalize on the limiting effect that wolf predation has on ungulate densities in Europe. Most forest ecosystems in Europe have been changed, and both ungulates and wolves have undergone intensive game management resulting in high densities of ungulates and low densities of wolves. Human hunting is the major mortality factor and drives the population dynamics of ungulates over most of Europe. In some years, severe winters reduce ungulate (wild boar, red deer, roe deer) densities in central and northern Europe (Caboń 1958, Kotov 1969, Okarma *et al.* 1995a).

Available data on wolf predation, particularly from relatively undisturbed areas (eg Białowieża Primeval Forest), reveal potential effects of wolf predation on

ungulate communities in Europe. Red deer are affected by wolf predation to the largest extent (Okarma *et al.* 1995a), and such predation probably can limit populations under pristine wolf-red deer relationships. The impact of wolves on moose is heavy in some European locations (> 40% of total natural mortality), focused mainly on calves and yearlings. Thus, it can be concluded that moose numbers can be limited locally if present in a simple ungulate community.

Roe deer, especially when numerous, also could be affected heavily by wolves (eg where abundant and if red deer were not present). However, lynx predation is probably the most important factor of natural mortality of roe deer (Jędrzejewski *et al.* 1993).

Wolves and other predators generally have no effect on wild boar numbers, except in localities where wild boar is the only ungulate (Litvinov 1981). Wild boar mortality is dependent basically on the acorn crop and to a lesser extent, snow depth (Okarma *et al.* 1995a). Mast production of oak is synchronized over temperate deciduous forests in Europe (review in Pucek *et al.* 1993), and therefore, population changes of wild boar originally also must have been correlated with mast production. In the mountains, beech mast has a similar effect on wild boar; high seed production of beech occurs every 3–5 years (Gunchak 1980). Currently, oak and beech forests survive only in small patches in an otherwise greatly altered European landscape, so they play a small role in shaping population demography of wild boar.

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References

- Abdunazarov B. B. and Taryannikov V. I. 1991. [Volk in the western Tien-shan]. [In: Ekologiya, okhrana i akklimatizatsiya mlekopitayushchikh v Uzbekistane. O. P. Bogdanov, ed]. Izdatelstvo AN UzSSR, Tashkent: 42–48. [In Russian]
- Almasan H., Scarlatescu G., Nesterov V. and Manolache L. 1970. Contribution a la connaissance du regime de nourriture du loup (*Canis lupus* L.) dans les Carpathes roumaines. Transactions 9th IUGB Congress, Moscow 1969: 523–529.
- Apollonio M., Randi E. and Toso S. 1988. The systematics of Italian wild boar. Bollettino di zoologia 3: 213–221.
- Aragon S., Braza F. and San Jose C. 1995. Socioeconomic, physiognomic, and climatic factors determining the distribution pattern of roe deer *Capreolus capreolus* in Spain. Acta Theriologica 40: 37–43.
- Atlas Świata [Atlas of the World]. 1962. PWN-Polish Scientific Publisher, Warszawa: 1–523.
- Ballard W. B., Whitman J. S. and Gardner C. L. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs 98: 1–54.
- Ballard W. B., Whitman J. S. and Reed D. J. 1990. Population dynamics of moose in in south-central Alaska. Wildlife Monographs 114: 1–49.
- Bannikov A. G., Zhirnov L. V., Lebedeva L. S. and Fandeev A. A. 1961. [Biology of saiga antelope]. Izdatelstvo Selskokhozyaistvennoi Literatury, Zhurnalov i Plakatov. Moskva: 1–336. [In Russian]

- Baskin L. M. 1979. Ecology and behaviour of European bison. [In: European bison, morphology, systematics, evolution, ecology. V. E. Sokolov, ed]. Izdatelstvo Nauka, Moskva: 442–470. [In Russian]
- Belyanin V. N. 1979. [Wolves in Zhigule Mountains]. [In: Ekologicheskie osnovy okhrany i ratsionalnogo ispolzovaniya khishchnykh mlekopitayushchikh]. Izdatelstvo Nauka, Moskva: 86–87. [In Russian]
- Bergerud A. T. and Elliot J. P. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* 64: 1515–1529.
- Bergerud A. T. and Snider J. B. 1988. Predation in the dynamics of moose populations: a reply. *Journal of Wildlife Management* 52: 559–564.
- Bergerud A. T., Wyett W. and Snider J. B. 1983. The role of wolf predation in limiting a moose population. *Journal of Wildlife Management* 47: 977–988.
- Bibikov D. I. (ed). 1985. The wolf. History, systematics, morphology, ecology. Izdatelstvo Nauka, Moskva: 1–606. [In Russian]
- Bibikov D. I., Kudaktin A. N. and Ryabov L. S. 1985. Synanthropic wolves: distribution, ecology. *Zoologicheskii Zhurnal* 64: 429–441. [In Russian with English summary]
- Björvall A. and Isakson E. 1982. Winter ecology of a pack of three wolves in northern Sweden. [In: Wolves of the world. F. Harrington and P. C. Paquet, eds]. Noyes Publications, New Jersey: 146–157.
- Blanco J. C., Cuesta L. and Reig S. (eds) 1990. [The wolf (*Canis lupus*) in Spain]. ICONA, Madrid: 1–118. [In Spanish with English summaries]
- Blanco J. C., Reig S. and Cuesta L. 1992. Distribution, status and conservation problems of the wolf *Canis lupus* in Spain. *Biological Conservation* 60: 73–80.
- Bobek B., Borowski S. and Dzięciolowski R. 1975. Browse supply in various forest ecosystems. *Polish Ecological Studies* 1: 17–32.
- Bobek B., Perzanowski K. and Śmietana W. 1992. The influence of snow cover on the patterns of selection within red deer population by wolves in Bieszczady Mountains, Poland. [In: Global trends in wildlife management. B. Bobek, K. Perzanowski and W. Regelin, eds]. Transactions of 18th IUGB Congress, Kraków 1987. Świat Press, Kraków-Warszawa, Vol. 2: 341–348.
- Boitani L. 1982. Wolf management in intensively used areas of Italy. [In: Wolves of the world. F. Harrington and P. C. Paquet, eds]. Noyes Publications, New Jersey: 158–172.
- Boitani L. 1992. Wolf research and conservation in Italy. *Biological Conservation* 61: 125–132.
- Boutin S. 1992. Predation and moose population dynamics: a critique. *Journal of Wildlife Management* 56: 116–127.
- Boyd D. K., Ream R. R., Pletscher D. H. and Fairchild M. W. 1994. Prey taken by colonizing wolves and hunters in the Glacier National Park area. *Journal of Wildlife Management* 58: 289–295.
- Braña F., Campo del J. C. and Palomero G. 1982. Le loup au versant nord de la Cordillère Cantabrique. *Acta Biologica Montana* 1: 33–52.
- Brangi A., Rosa P. and Meriggi A. 1991. Predation by wolves (*Canis lupus* L.) on wild and domestic ungulates in northern Italy. Proceedings of a conference "Ongules/Ungulates 91", Toulouse, France: 541–543.
- Brtek L. and Voskár J. 1987. [Feeding ecology of the wolf in Slovakian Carpathians]. *Biologia (Bratislava)* 42: 985–990. [In Slovak]
- Bubenik A. B. 1966. [Impact of lynx *Lynx lynx* L. and wolf *Canis lupus* L. on population structure of roe deer and red deer]. *Lynx* 6: 7–10. [In Czech with German summary]
- Buchalczyk T. 1980. The brown bear in Poland. [In: Bears – their biology and management. C. J. Martinka and K. L. Mc Arthur, eds]. Bear Biologists Association Conference Ser 3: 229–232.
- Bunevich A. N. 1988. [Dynamics of numbers and diet of wolf in Belovezha Primeval Forest]. *Zapovedniki Belorussii* 12: 108–113. [In Russian]
- Bützler W. 1986. *Cervus elaphus* Linnaeus, 1758 – Rothirsch. [In: Handbuch der Säugetiere Europas. Band 2/II. J. Niethammer and F. Krapp, eds]. Aula-Verlag, Wiesbaden: 107–139.

- Caboñ K. 1958. Das Massensterben von Wildschweinen im Naturstaatspark von Białowieża im Winter 1955/56. *Acta Theriologica* 2: 71–82.
- Carbyn L. N. 1983. Wolf predation on elk in Riding Mountain National Park, Manitoba. *Journal of Wildlife Management* 47: 963–976.
- Carbyn L. N., Oosenbrug S. M. and Anions D. W. 1993. Wolves, bison and the dynamics related to the Peace-Athabasca delta in Canada's Wood Buffalo National Park. Circumpolar Research Series No 4, Canadian Circumpolar Institute, University of Alberta, Edmonton: 1–270.
- Centofanti E. 1994. [Presence of the wolf *Canis lupus* L. and other wild canids in relation to ungulate populations in the Casentinesi Forests]. Unpublished report, Gruppo Lupo Italia: 1–11. [In Italian]
- Chapman D. and Chapman N. 1975. Fallow deer. Terence Dalton Limited. Lavenham-Suffolk: 1–271.
- Cowan I. McT. 1947. The timber wolf in the Rocky Mountain National Parks of Canada. *Canadian Journal of Research* 25: 139–174.
- Cuesta L., Barcena F., Palacios F. and Reig S. 1991. The trophic ecology of the Iberian wolf (*Canis lupus signatus* Cabrera, 1907). A new analysis of stomach's data. *Mammalia* 55: 240–254.
- Danilkin A. A. 1989. [Structure of geographical range of roe deer in USSR and factors responsible for its limits]. *Ekologiya* 4: 46–51. [In Russian]
- Darman Yu. A. 1986. [Wolf and ungulates in Khingansk reserve]. *Trudy 4 Sezda Vsesoyuznogo teriologicheskogo obshchestva No 3, AN SSSR, Moskva*: 45. [In Russian]
- Dubrovskii V. Yu. 1980. [Remarks on summer ecology of the wolf in taiga of the Kostromska oblast]. [In: Behaviour of the wolf. D. I. Bibikov, ed]. AN USSR, Moskva: 123–129. [In Russian]
- Dzięciółowski R. 1969. The quantity, quality and seasonal variation of food resources available to red deer in various environmental conditions of forest management. Forest Research Institute, Warszawa: 1–295.
- Dzięciółowski R. and Pielowski Z. 1993. [Moose]. Anton-5, Warszawa: 1–208. [In Polish]
- European bison pedigree book 1993. 1995. National Council for Nature – Białowieża National Park, Białowieża: 1–61.
- Fadeev E. 1984. [Sika deer in the USSR]. *Okhota i okhotniche khozyaystvo* 5: 18–21. [In Russian]
- Faliński J. B. 1986. Vegetation dynamics in temperate lowland primeval forest. Dr. W. Junk Publishers, Dordrecht. *Geobotany* 8: 1–537.
- Fedosenko A. K., Zhiryakov V. A. and Grachev Yu. A. 1978. Some data on the ecology and behaviour of wolves in the northern Tien-shan and Dzhungara Alatau. *Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii* 83(3): 5–18. [In Russian with English summary]
- Fico R., Morosetti G. and Giovannini A. 1993. The impact of predators on livestock in the Abruzzo region of Italy. *Revue scientifique et technique. Office international des epizooties* 12(1): 39–50.
- Filonov K. P. 1980. Predator-prey problems in nature reserves of the European part of the RSFSR. *Journal of Wildlife Management* 44: 389–396.
- Filonov K. P. 1983. [Variability of mortality factors in populations of wild ungulates]. *Ekologiya* 2: 57–64. [In Russian]
- Filonov K. P. 1989. Ungulates and large predators in wildlife reserves. *Izdatelstvo Nauka, Moskva*: 1–251. [In Russian]
- Filonov K. P. and Kaletskaya M. L. 1985. [Influence of wolf predation on wild ungulates]. [In: The wolf. D. I. Bibikov, ed]. *Izdatelstvo Nauka, Moskva*: 336–354. [In Russian]
- Flerov K. K. 1979. Systematics and evolution. [In: European bison, morphology, systematics, evolution, ecology. V. E. Sokolov, ed]. *Izdatelstvo Nauka, Moskva*: 8–127. [In Russian]
- Fonseca F. P. 1992. Population trends of wolves in Portugal. [In: Wolves in Europe. Ch. Promberger and W. Schröder, eds]. *Proceedings of the workshop "Wolves in Europe – current status and prospects", Oberammergau 1992. Munich Wildlife Society, Ettal*: 111–112.
- Forbes G. and Theberge J. B. 1992. Importance of scavenging on moose by wolves in Algonquin Park, Ontario. *Alces* 28: 235–241.

- Formozov A. N. 1946. [Snow cover and its importance in the life of mammals and birds of SSSR]. Izdatelstvo Moskovskogo Universiteta, Moskva: 1–287. [In Russian]
- Fritts S. H. and Mech L. D. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildlife Monographs* 80: 1–79.
- Fruziński B. 1992. [Wild boar]. *Cedrus*, Warszawa: 1–248. [In Polish]
- Fuller T. K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* 105: 1–41.
- Fuller T. K. 1991. Effect of snow depth on wolf activity and prey selection in north central Minnesota. *Canadian Journal of Zoology* 69: 283–287.
- Fuller T. K. and Keith L. B. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. *Journal of Wildlife Management* 44: 583–602.
- Gaross V. Ya. 1979. [Impact of lynxes and wolves on roe deer population in Lithuania]. [In: *Ekologicheskie osnovy okhrany i ratsionalnogo ispolzovaniya khishchnykh mlekopitayushchikh*]. Izdatelstvo Nauka, Moskva: 257–261. [In Russian]
- Gasaway W. C., Boertje R. D., Grangaard D. V., Kelleyhouse D. G., Stephenson R. O. and Larsen D. G. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs* 120: 1–59.
- Gasaway W. C., Stephenson R. O., Davis J. L., Shepherd E. K. and Burris O. E. 1983. Interrelationships of wolves, prey, and man in interior Alaska. *Wildlife Monographs* 84: 1–50.
- Gatikh V. C. 1979. [The role of wolves in biocenosis of the Belarussian Polese]. [In: *Ekologicheskie osnovy okhrany i ratsionalnogo ispolzovaniya khishchnykh mlekopitayushchikh*]. Izdatelstvo Nauka, Moskva: 94–95. [In Russian]
- Gavrin V. F. and Donaurov S. S. 1954. [Wolf in Belovezha Primeval Forest]. *Zoologicheskii Zhurnal* 33: 904–924. [In Russian]
- Genov P. 1981. Food composition of wild boar northeastern and western Poland. *Acta Theriologica* 26: 185–205.
- Genov P. 1992. The wolf *Canis lupus* L. in southwestern Bulgaria. [In: *Global trends in wildlife management*. B. Bobek, K. Perzanowski and W. Regelin, eds]. Transactions of 18th IUGB Congress, Kraków 1987. Świat Press, Kraków-Warszawa: 359–362.
- Geograficzny Atlas Świata [Geographical Atlas of the World]. 1991. Państwowe Przedsiębiorstwo Wydawnictw Kartograficznych. Warszawa-Wrocław: 1–274.
- Golgofskaya K. Yu. 1970. The growth of wild ungulate populations and the state of grasslands in the Caucasian preserve. *Byulleten Moskovskogo Obshestva Ispytatelei Prirody, Otdel Biologicheskii* 75(4): 17–21. [In Russian with English summary]
- Gordiyuk N. M. 1986. [Selectivity of wolf hunting in the southern Ural Mountains depending on depth and condition of snow layer]. [In: *Rol krupnykh khishchnikov i kopytnykh v biotsenozakh zapovednikov*]. CNIL Glavokhoty RSFSR, Moskva: 54–59. [In Russian]
- Gordiyuk N. M. 1991. Interrelations between wolves and ungulates as registered by observation of the marked wolf pack in the southern Urals. *Byulleten Moskovskogo Obshestva Ispytatelei Prirody, Otdel Biologicheskii* 96(1): 3–10. [In Russian with English summary]
- Gromov E. I. 1979. [Diet of wolves in Sikhote-Alinskii Reserve]. [In: *Ekologicheskie osnovy okhrany i ratsionalnogo ispolzovaniya khishchnykh mlekopitayushchikh*]. Izdatelstvo Nauka, Moskva: 101–102. [In Russian]
- Gunchak N. S. 1980. Diet of wild boar in the Ukrainian Carpathians. *Vestnik Zoologii* 5: 73–78. [In Russian with English summary]
- Gyimesi J. 1971. [Migrations of moose to Czechoslovakia]. *Poľovnický Zborník* 1: 217–224. [In Slovak with German summary]
- Haglund B. 1968. Winter habits of the bear (*Ursus arctos* L.) and the wolf (*Canis lupus* L.) as revealed by tracking in the snow. *Viltrevy* 5: 217–361. [In Swedish with English summary]
- Heidemann G. 1986. *Cervus dama* (Linnaeus, 1758) – Damhirsch. [In: *Handbuch der Säugetiere Europas*. Band 2/II. J. Niethammer and F. Krapp, eds]. Aula-Verlag, Wiesbaden: 140–158.

- Heptner V. G., Nasimovich A. A. and Bannikov A. G. 1961. [Artiodactyla and Perissodactyla]. [In: Mlekopitayushchie Sovetskogo Soyuza. V. G. Geptner and N. P. Naumov, eds]. Izdatelstvo Vysshaya shkola, Moskva: 1–776. [In Russian]
- Herre W. 1986a. *Sus scrofa* Linnaeus, 1758 – Wildschwein. [In: Handbuch der Säugetiere Europas. Band 2/II. J. Niethammer and F. Krapp, eds]. Aula-Verlag, Wiesbaden: 36–66.
- Herre W. 1986b. *Rangifer tarandus* (Linnaeus, 1758) – Ren, Rentier. [In: Handbuch der Säugetiere Europas. Band 2/II. J. Niethammer and F. Krapp, eds]. Aula-Verlag, Wiesbaden: 198–216.
- Holleman D. F. and Stephenson R. O. 1981. Prey selection and consumption by Alaskan wolves in winter. *Journal of Wildlife Management* 45: 620–628.
- Houston D. B. 1982. The northern Yellowstone elk, ecology and management. Macmillan Publishing Co., Inc., New York: 1–474.
- Huggard D. J. 1993a. Prey selectivity of wolves in Banff National Park. I. Prey species. *Canadian Journal of Zoology* 71: 130–139.
- Huggard D. J. 1993b. Prey selectivity of wolves in Banff National Park. II. Age, sex, and condition of elk. *Canadian Journal of Zoology* 71: 140–147.
- Huggard D. J. 1993c. Effect of snow depth on predation and scavenging by gray wolves. *Journal of Wildlife Management* 57: 382–388.
- Ionescu O. 1992. Current status and prospects for the wolf in Romania. [In: Wolves in Europe. Ch. Promberger and W. Schröder, eds]. Proceedings of the workshop “Wolves in Europe – current status and prospects”, Oberammergau 1992. Munich Wildlife Society, Ettal: 9–14.
- Ivanov V. K. 1988. Observations on the behaviour and biology of wolves (*Canis lupus* L., 1758) in the Ihtiman Sredna Gora Mountains. *Bulgarian Academy of Sciences, Ecology* 21: 25–33.
- Jacobs J. 1974. Quantitative measurements of food selection; a modification of the forage ratio and Ivlev's Electivity index. *Oecologia* 14: 413–417.
- Jędrzejewska B., Jędrzejewski W., Bunevich A. N., Miłkowski L. and Okarma H. 1996a. Population dynamics (1847–1993) and demography of wolves *Canis lupus* in Białowieża Primeval Forest (Poland and Belarus). *Mammal Review*. (in press)
- Jędrzejewska B., Jędrzejewski W., Okarma H., Schmidt K., Bunevich A. N. and Miłkowski L. 1996b. Population dynamics (1869–1994), demography and home ranges of the lynx in Białowieża Primeval Forest (Poland and Belarus). *Ecography*. (in press)
- Jędrzejewska B., Okarma H., Jędrzejewski W. and Miłkowski L. 1994. Effect of exploitation and protection on forest structure, ungulate density and wolf predation in Białowieża Primeval Forest, Poland. *Journal of Applied Ecology* 31: 664–676.
- Jędrzejewski W., Jędrzejewska B., Okarma H. and Ruprecht A. L. 1992. Wolf predation and snow cover as mortality factors in the ungulate community of the Białowieża National Park, Poland. *Oecologia* 90: 27–36.
- Jędrzejewski W., Jędrzejewska B. and Szymura A. 1989. Food niche overlaps in a winter community of predators in the Białowieża Primeval Forest, Poland. *Acta Theriologica* 34: 337–348.
- Jędrzejewski W., Schmidt K., Miłkowski L., Jędrzejewska B. and Okarma H. 1993. Foraging by lynx and its role in ungulate mortality: the local (Białowieża Forest) and the Palaearctic viewpoints. *Acta Theriologica* 38: 385–403.
- Kaletskaia M. L. 1973. [Wolf and its role as a predator in the Darwinskiĭ Reserve]. *Trudy Darvinskogo gosudarstvennogo zapovednika* 9: 41–58. [In Russian]
- Kaluźniński J. 1974. The occurrence and distribution of field ecotype of roe-deer in Poland. *Acta Theriologica* 19: 291–300.
- Kartsov G. 1903. [Belovezha Primeval Forest. Its historical description, contemporary game management, and monarchical hunts in the Forest. A. Marks, St. Petersburg: 1–414. [In Russian]
- Kazenevskii P. F. 1961. On more case of death in the wild ungulates (winters 1955/56). *Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii* 66(6): 147–148. [In Russian with English summary]

- Kazenevskii P. F. 1979. [Volk in the Khopersk Reserve]. [In: *Ekologicheskie osnovy okhrany i ratsionalnogo ispolzovaniya khishchnykh mlekopitayushchikh*]. Izdatelstvo Nauka, Moskva: 110–112. [In Russian]
- Keith L. B. 1974. Some features of population dynamics in mammals. Proceedings of 11th IUGB Congress, Stockholm 1973. National Swedish Environmental Protection Board, Stockholm: 17–58.
- Kerechun S. F. 1979. [Impact of carnivores on numbers of ungulates in a zone of the Carpathian Mountains]. [In: *Ekologicheskie osnovy okhrany i ratsionalnogo ispolzovaniya khishchnykh mlekopitayushchikh*]. Izdatelstvo Nauka, Moskva: 43–44. [In Russian]
- Kochetkov V. V. 1988. [Biology of the wolf in Verkhnevolzhe, a case of the Central-Forest State Reserve]. Ph D thesis, Gosudarstvennyy Agropromyshlennyj Komitet SSSR, Moskva 1988: 1–20. [In Russian]
- Kochetkov V. V. and Sokolov A. A. 1979. [Wolf feeding in the Central-Forest State Reserve]. [In: *Ekologicheskie osnovy okhrany i ratsionalnogo ispolzovaniya khishchnykh mlekopitayushchikh*]. Izdatelstvo Nauka, Moskva: 112–114. [In Russian]
- Kotov V. A. 1969. A hard winter for wild ungulate animals in the Caucasian preserve. *Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii* 74(1): 57–61. [In Russian with English summary]
- Kozlo P. G. 1975. [Wild boar]. Izdatelstvo Uradzhai, Minsk: 1–223. [In Russian]
- Krasiński Z. A. 1967. Free living European bisons. *Acta Theriologica* 12: 391–405.
- Krasiński Z. A. 1978. Dynamics and structure of the European bison population in the Białowieża primeval forest. *Acta Theriologica* 23: 3–48.
- Krasiński Z. A. 1983. The first 10 years of free-living bison in the Białowieża Primeval Forest 1952–1961. *Parki narodowe i Rezerваты przyrody* 4(2): 39–50. [In Polish with English summary]
- Krasiński Z. A., Bunevich A. N. and Krasińska M. 1994. Characteristics of lowland European bison populations in Polish and Belarussian parts of Białowieża Forest. *Parki narodowe i Rezerваты przyrody* 4: 25–68. [In Polish with English summary]
- Kuchmel S. V. 1994. [An assesment of wolf impact on ungulate populations]. *Materialy 7 Zoologicheskoi Konferentsii "Problemy izucheniya, sokhraneniya i ispolzovaniya biologicheskogo raznoobraziya zhivotnogo mira"*, Minsk 1994. Izdatelstvo Navuka i Technika, Minsk: 256–257. [In Russian]
- Kudaktin A. N. 1978. Selective wolf predation on ungulates in the Caucasian nature reserve. *Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii* 83(3): 19–28. [In Russian with English summary]
- Kudaktin A. N. 1982. The hunting habits of wolves in western Caucasia. *Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii* 87(1): 24–30. [In Russian with English summary]
- Kudaktin A. N. 1986. [Influence of the wolf on ungulates in the Caucasian reserve]. [In: *Ro! krupnykh khishchnikov v biocenozach zapovednikov. Sbornik nauchnykh trudov CNIL Glavokhoty RSFSR*. A. K. Fedosenko, ed]. Moskva: 21–35. [In Russian]
- Kuzmin I. F. and Khakhin G. V. 1980. [Impact of wolves on ungulates in the middle of the European part of USSR]. [In: *Kopytnye fauny SSSR*]. Izdatelstvo Nauka, Moskva: 171–172. [In Russian]
- Larsen D. G., Gauthier D. A. and Markel R. L. 1989. Causes and rate of moose mortality in southwest Yukon. *Journal of Wildlife Management* 53: 548–557.
- Lavov M. A. 1972. [Impact of wolves and lynx on wild ungulates in western Siberia]. *Materialy k nauchnoi konferentsii, posvyashchennoi 50-letiyu Instituta. VNIIOZ Kirov*: 112–115. [In Russian]
- Lebedeva L. S. 1956. [Ecological characteristics of the wild boar in Białowieża Primeval Forest]. *Uchenye Zapiski Moskovskogo Gorodskogo Pedagogicheskogo Instituta im. V. P. Potemkina* 61: 105–271. [In Russian]
- Lehmann E. von and Sägeser H. 1986. *Capreolus capreolus* Linnaeus, 1758 – Reh. [In: *Handbuch der Säugetiere Europas. Band 2/II. J. Niethammer and F. Krapp, eds*]. Aula-Verlag, Wiesbaden: 233–268.

- Lequette B., Houard T., Del Corso C., Mari F. and Boscagli G. 1994. [Wolf return to the Maritime Alps: Preliminary data]. Abstracts of 1st Italian Theriological Congress, Pisa, October 1994: 87. [In Italian]
- Levins R. 1968. Evolution in changing environment. Princeton University Press, Princeton: 1-120.
- Litvinov V. P. 1981. The wolf (*Canis lupus*) and wild boar (*Sus scrofa*) in the Kyzyl-Agach State Reservation. Zoologicheskii Zhurnal 60: 1588-1591. [In Russian with English summary]
- Litvinov V. P., Litvinov V. F. and Tikhanskiĭ A. D. 1981. [Feeding of wolves in Berezinskiĭ and Pripyatskiĭ Reserves]. Zapovedniki Belorussii 5: 98-102. [In Russian]
- Magalhaes C. Paixao de and Fonseca F. P. 1982. The wolf in Braganca country. Impact on cattle and game. Transactions of 14th IUGB Congress, Dublin 1979: 281-286.
- Makridin V. P. 1962. The wolf in the Yamal north. Zoologicheskii Zhurnal 41: 1413-1417. [In Russian with English summary]
- Makridin V. P. 1979. [Polar wolves and their impact of reindeer breeding and wild ungulates]. [In: Ekologicheskie osnovy okhrany i ratsionalnogo ispolzovaniya khishchnykh mlekopitayushchikh]. Izdatelstvo Nauka, Moskva: 122-125. [In Russian]
- Matteucci C. 1992. Preliminary data on the ecology of a wolf *Canis lupus* L. population in northern Italy. [In: Global trends in wildlife management. B. Bobek, K. Perzanowski and W. Regelin, eds]. Transactions of 18th IUGB Congress, Kraków 1987. Świat Press, Kraków-Warszawa, Vol. 2: 367-370.
- Mattioli L., Apollonio M., Mazzarone V. and Centofanti E. 1995. Wolf food habits and wild ungulate availability in the Foreste Casentinesi National Park (Italy). Acta Theriologica 40: 389-404.
- Mech L. D. 1966. The wolves of Isle Royale. Fauna of the National Parks of the United States, Fauna Series 7: 1-210.
- Mech L. D. 1970. The wolf: the ecology and behavior of an endangered species. Doubleday, New York: 1-289.
- Mech L. D. and Frenzel L. D., Jr 1971. An analysis of age, sex, and condition of deer killed by wolves in northeastern Minnesota. USDA Forest Service Research Paper NC-52: 35-50.
- Mech L. D., Frenzel L. D., Jr and Karns P. D. 1971. The effect of snow conditions on the vulnerability of white-tailed deer to wolf predation. USDA Forest Service Research Paper NC-52: 51-59.
- Mech L. D. and Karns P. D. 1978. Role of the wolf in a deer decline in the Superior National Forest. USDA Forest Service Research Paper NC-148: 1-23.
- Mech L. D., McRoberts R. E., Peterson R. O. and Page R. E. 1987. Relationship of deer and moose populations to previous winters' snow. Journal of Animal Ecology 56: 615-627.
- Meriggi A., Rosa P., Brangi A. and Matteucci C. 1991. Habitat use and diet of the wolf in northern Italy. Acta Theriologica 36: 141-151.
- Messier F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. Journal of Animal Ecology 60: 377-393.
- Messier F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75: 478-488.
- Messier F. and Crête M. 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia 65: 503-512.
- Mityk J. 1978. [Physical geography of the parts of the world]. PWN-Polish Scientific Publisher, Warszawa: 1-503. [In Polish]
- Murie A. 1944. The wolves of Mt. McKinley. U. S. Dept. Interior, U.S. National Park Service, Fauna Ser. No 5: 1-238.
- Nasimovich A. A. 1955. The role of the regime of snow cover in the life of ungulates in the USSR. Izdatelstvo Akademii Nauk SSSR, Moskva: 1-403. [In Russian]
- Naumov N. P. 1967. [The wolf]. [In: Mlekopitayushchie Sovetskogo Soyuza, vol. 2. V. G. Heptner and N. P. Naumov, eds]. Izdatelstvo Vysshaya shkola, Moskva: 123-193. [In Russian]
- Nelson M. E. and Mech L. D. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. Journal of Wildlife Management 50: 471-474.

- Nesterenko V. V. 1988. [The role of wolves in ecosystems of nature reserves]. [In: Populyatsionnye issledovaniya zhyvotnykh v zapovednikakh. V. E. Sokolov, ed]. Izdatelstvo Nauka, Moskva: 139–144. [In Russian]
- Nieminen M. and Leppaluoto J. 1988. Predation in the reindeer husbandry area in Finland during 1976–1986. *Rangifer* 8: 25–34.
- Novikov G. A. 1956. [Mammalian predators of USSR fauna]. Izdatelstvo AN SSSR, Moskva-Leningrad: 42–52. [In Russian]
- Novikov G. A. and Ivanov P. D. 1970. The appearance of elks (*Alces alces* L.) in the precincts of Leningrad. *Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii* 75(6): 27–35. [In Russian with English summary]
- Nowak E. 1971. The range expansion of animals and its causes. *Instytut Ekologii PAN, Zeszyty Naukowe* No 3: 1–255. [In Polish with English summary]
- Nygren K. 1986. *Alces alces* (Linnaeus, 1758) – Elch. [In: *Handbuch der Säugetiere Europas*. Band 2/II. J. Niethammer and F. Krapp, eds]. Aula-Verlag, Wiesbaden: 173–197.
- Okarma H. 1984. The physical condition of red deer falling prey to the wolf and lynx and harvested in the Carpathian Mountains. *Acta Theriologica* 29: 283–290.
- Okarma H. 1991. Marrow fat content, sex and age of red deer killed by wolves in winter in the Carpathian Mountains. *Holarctic ecology* 14: 169–172.
- Okarma H. 1992a. [The wolf – monograph of a species]. *Białowieża*: 1–168. [In Polish with English chapter]
- Okarma H. 1992b. Status, distribution and numbers of lynx in Poland. Proceedings of a seminar on the situation, conservation needs and reintroduction of lynx in Europe. Neuchâtel, Switzerland, October 1990. Council of Europe Press, *Environmental Encounters* No 11: 23–25.
- Okarma H. 1993a. Status and management of the wolf in Poland. *Biological Conservation* 66: 153–158.
- Okarma H. 1993b. Protection and management of large carnivores (wolf, lynx) in the Białowieża Primeval Forest, Poland. Proceedings of the seminar on the management of small populations of threatened mammals, Sofia, Bulgaria, October 1993. Council of Europe Press, *Environmental Encounters* No 17: 56–59.
- Okarma H., Jędrzejewska B. and Jędrzejewski W. 1995b. Białowieża Primeval Forest: habitat and wildlife management. Proceedings of a conference "Biodiversity conservation in transboundary protected areas", Bieszczady-Tatry 1994. US National Academy of Sciences, Washington. (in press)
- Okarma H., Jędrzejewska B., Jędrzejewski W., Miłkowski L. and Krasiński Z. 1995a. Roles of hunting, predation, and few other factors in the winter mortality of ungulates in Białowieża Primeval Forest, Poland. *Acta Theriologica* 40: 197–217.
- Okarma H., Miłkowski L., Jędrzejewska B. and Jędrzejewski W. 1993. Importance of wolf predation among several factors of ungulate mortality in the exploited part of Białowieża Primeval Forest, Poland. *International Symposium on the Wolf of the Wolf Specialist Group SSC-IUCN*. Leon 1993, Spain: 51–52.
- Papageorgiou N., Vlachos Ch., Sfougaris A. and Tsachalidis S. 1994. Status and diet of wolves in Greece. *Acta Theriologica* 39: 411–416.
- Paquet P. C. 1989. Behavioral ecology of sympatric wolves (*Canis lupus*) and coyotes (*C. latrans*) in Riding Mountain National Park. Ph D thesis, University of Alberta: 1–198.
- Paquet P. C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. *Journal of Mammalogy* 73: 337–343.
- Paquet P. C. 1993. Summary reference document – ecological studies of recolonizing wolves in the Central Canadian Rocky Mountains. Parks Canada, Banff National Park Warden Service, Banff, Alberta: 1–215.
- Patalano M. and Lovari S. 1993. Food habits and trophic niche overlap of the wolf *Canis lupus*, L. 1758 and the red fox *Vulpes vulpes* (L. 1758) in a mediterranean mountain area. *Revue d'Ecologie (Terre et Vie)* 48: 279–294.

- Pereira M., Fonseca F. and Magalhaes C. 1985. Wolf ecology in Portugal. Actas 1 Simposio de Predadores, Lisboa: 122–167.
- Peterson R. O. and Allen D. L. 1974. Snow conditions as a parameter in moose-wolf relationship. *Naturaliste Canadien (Que.)* 101: 481–492.
- Peterson R. O. and Page R. E. 1983. Wolf-moose fluctuations at Isle Royale National Park, Michigan, USA. *Acta Zoologica Fennica* 174: 251–253.
- Peterson R. O., Woolington J. D. and Bailey T. N. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs* 88: 1–52.
- Pielowski Z. 1977. Das Rehwild – Wild der Zukunft in der Agrarlandschaft. *Beiträge Jagd- und Wildforschung* 10: 193–200.
- Potvin F., Jolicœur H. and Huot J. 1988. Wolf diet and prey selectivity during two periods for deer in Quebec: decline versus expansion. *Canadian Journal of Zoology* 66: 1274–1279.
- Promberger Ch. and Schröder W. (eds). 1993. Wolves in Europe – status and perspectives. Proceedings of the workshop “Wolves in Europe – current status and prospects”, April 1992, Oberammergau. *Münich Wildlife Society, Ettal*: 1–136.
- Pucek Z. 1986. *Bison bonasus* (Linnaeus, 1758) – Wisent. [In: *Handbuch der Säugetiere Europas*. Band 2/II. J. Niethammer and F. Krapp, eds]. Aula-Verlag, Wiesbaden: 279–315.
- Pucek Z. 1991. History of the European bison and problems of its protection and management. [In: *Global trends in wildlife management*. B. Bobek, K. Perzanowski and W. Regelin, eds]. *Transactions of 18th IUGB Congress, Cracow 1987*. Świat Press, Kraków-Warszawa: 19–39.
- Pucek Z. 1994. [Progress in and threats to the European bison restitution]. *Kosmos* 43(1): 147–169. [In Polish with English summary]
- Pucek Z., Bobek B., Łabudzki L., Miłkowski L., Morow K. and Tomek A. 1975. Estimates of density and number of ungulates. *Polish Ecological Studies* 1: 121–136.
- Pucek Z., Jędrzejewski W., Jędrzejewska B. and Pucek M. 1993. Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop, and predation. *Acta Theriologica* 38: 199–232.
- Pulliainen E. 1965. Studies on the wolf (*Canis lupus* L.) in Finland. *Annales Zoologici Fennici* 2: 215–259.
- Reig S., Cuesta L. and Palacios F. 1985. The impact of human activities on the food habits of red fox and wolf in Old Castille, Spain. *Revue d'Ecologie (Terre et Vie)* 40: 151–155.
- Rukovskii N. N. and Kupriyanov A. G. 1972. Some peculiarities of distribution and ecology of *Canis lupus* in the Onega peninsula. *Zoologicheskii Zhurnal* 51: 1593–1596. [In Russian with English summary]
- Rusakov O. S. 1979a. [Carnivores as a factor in dynamics of ungulate numbers in the northwestern USSR]. [In: *Ekologicheskie osnovy okhrany i ratsionalnogo ispolzovaniya khishchnykh mlekopitayushchikh*. Izdatelstvo Nauka, Moskva: 61–62. [In Russian]
- Rusakov O. S. 1979b. [Peculiarities of wolf feeding in the northern part of Pskovskaya oblast]. [In: *Ekologicheskie osnovy okhrany i ratsionalnogo ispolzovaniya khishchnykh mlekopitayushchikh*. Izdatelstvo Nauka, Moskva: 132–134. [In Russian]
- Rusakov O. S. and Timofeeva E. T. 1984. [Wild boar]. *Izdatelstvo Leningradskogo Universiteta, Leningrad*: 1–204. [In Russian]
- Ryabov L. S. 1974. The attitude of wolves towards domestic animals and wild ungulates in the region of the Khopersk nature reserve. *Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii* 79(3): 6–15. [In Russian with English summary]
- Ryabov L. S. 1979. *Canis lupus* in the east of the Voronezh district. *Zoologicheskii Zhurnal* 58: 564–569. [In Russian with English summary]
- Ryabov L. S. 1987. On the wolf synanthropy in the central Black Earth Belt. *Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii* 92(1): 3–12. [In Russian with English summary]

- Ryabov L. S. 1993. [Wolves of the Black Earth Belt]. Izdatelstvo Voronezhskogo Universiteta, Voronezh: 1–167. [In Russian]
- Ryabov L. S., Likhackii Yu. P. and Nikitin N. M. 1992. [The wolf in the Voronezh Nature Reserve (feeding interactions)]. [In: Krupnye khishchniki. Sbornik nauchnykh trudov Glavokhoty RSFSR]. Moskva: 42–47. [In Russian]
- Ryabov L. S., Likhackii Yu. P. and Nikitin N. M. 1994. [Interactions of wolves (*Canis lupus* L.) of the Voronezh Reserve with wild and domestic ungulates]. *Ekologiya* 94(1): 53–59. [In Russian]
- Rykovskii A. S. 1980. [Observations on peculiarities of wolf behaviour in Belarus]. [In: Behaviour of the wolf. D. I. Bibikov, ed]. AN USSR, Moskva: 103–110. [In Russian]
- Sablina T. B. 1955. [Ungulates of the Białowieża Forest]. *Trudy Instituta Morfologii Zhivotnykh AN SSSR* No 15. Izdatelstvo Akademii Nauk SSSR, Moskva: 1–191. [In Russian]
- Sacchi O., Alieri F. and Cesaris C. 1994. [Wolf *Canis lupus* diet in an area with high availability of domestic ungulates]. Abstracts of 1st Italian Theriological Congress, Pisa, October 1994: 150. [In Italian]
- Salvador A. and Abad P. L. 1987. Food habits of a wolf population (*Canis lupus*) in León province, Spain. *Mammalia* 51: 45–52.
- Seip D. R. 1991. Predation and caribou populations. *Rangifer*, Special Issue No 7: 46–52.
- Seip D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70: 1494–1503.
- Sinclair A. R. E. 1989. Population regulation in animals. [In: Ecological concepts: the contribution of ecology to an understanding of the natural world. J. M. Cherrett, ed]. Blackwell Scientific Publications, Oxford: 197–241.
- Skogland T. 1991. What are the effects of predators on large ungulate populations? *Oikos* 61: 401–411.
- Sludskii A. A. 1963. [Mass death of ungulates in steppes and deserts of Eurasia]. *Trudy Instituta Zoologii AN Kazakhskoi SSR* 20: 5–88. [In Russian]
- Suvorov A. P. and Lisenko E. V. 1988. [Some peculiarities of wolf ecology in spring-summer period]. *Sbornik Nauchnykh Trudov, VASKHNIL, Sibirskoe otdelenie, Novosibirsk*: 45–50. [In Russian]
- Szymczyk W. 1973. Occurrence of moose in Europe in Holocene. *Przegląd zoologiczny* 17(1): 89–93. [In Polish with English summary]
- Śmietana W. and Klimek A. 1993. Diet of wolves in the Bieszczady Mountains, Poland. *Acta Theriologica* 38: 245–251.
- Telfer E. S. and Kelsall J. P. 1979. Studies of morphological parameters affecting ungulate locomotion in snow. *Canadian Journal of Zoology* 57: 2153–2159.
- Telfer E. S. and Kelsall J. P. 1984. Adaptation of some large North American mammals for survival in snow. *Ecology* 65: 1828–1834.
- Tellería J. C. and Sáez-Royuela C. 1989. [Ecology one Iberian population of wolves (*Canis lupus*)]. *Doñana Acta Vertebrata* 16: 105–122. [In Spanish]
- Van Ballenberghe V. 1987. Effects of predation on moose numbers: a review of recent North American studies. *Swedish Wildlife Research Suppl.* 1: 431–460.
- Van Camp J. 1975. Snow conditions and the winter feeding behavior of *Bison bison* in Elk Island National Park. *Canadian Wildlife Service Report*: 1–91.
- Van Haaften J. L., Peireira M. R. and Fonseca F. P. 1983. A wolf study in Portugal. *Proceedings of 16th IUGB Congress, Strbske Pleso 1983, Czechoslovakia*: 550–554.
- Vyrypaev V. A. 1980. On hunting behaviour of the wolf in Tien-shan. *Zoologicheskii Zhurnal* 59: 1870–1874. [In Russian with English summary]
- Wabbakken P. 1992. Wolves in Sweden and Norway. [In: Wolves in Europe. Ch. Promberger and W. Schröder, eds]. *Proceedings of the workshop "Wolves in Europe – current status and prospects"*, Oberammergau 1992. Munich Wildlife Society, Ettal: 9–14.
- Weaver J. L. 1994. Ecology of wolf predation amidst high ungulate diversity in Jasper National Park, Alberta. Ph D thesis, University of Montana, Missoula: 1–166.

- Zalozny D. V. 1980. [Some peculiarities of wolf ecology in Gurievskoi oblasti]. [In: Behaviour of the wolf. D. I. Bibikov, ed]. AN USSR, Moskva: 77–89. [In Russian]
- Zavatskiĭ B. P. 1986. [The role of wolves in biocenoses of Sayano-Shushenskii zapovednik]. Sbornik nauchnykh trudov CNIL Glavokhoty RSFSR, Moskva: 35–54. [In Russian]
- Zheleznov N. 1992. Ecology of the grey wolf *Canis lupus* L. on Chukotka. [In: Global trends in wildlife management. B. Bobek, K. Perzanowski and W. Regelin, eds]. Transactions of 18th IUGB Congress, Kraków 1987. Świat Press, Kraków-Warszawa, Vol. 2: 381–384.
- Zheleznov N. K. 1994. [Data on wolf *Canis lupus* L. ecology in northeastern USSR]. Sbornik nauchnykh trudov "Teriologicheskie issledovaniya v Yakutii", Sibirskoe otdelenie AN SSSR, Irkutsk: 28–50. [In Russian]
- Zhirnov L. V. 1982. [Brought back to life: ecology, conservation, and utilization of saiga antelope]. Izdatelstvo Lesnaya promyshlennost, Moskva: 1–223. [In Russian]

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