Wolf predation and snow cover as mortality factors in the ungulate community of the Białowieża National Park, Poland

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Summary. Wolf-ungulate interactions were studied in the pristine deciduous and mixed forests of the Białowieża National Park in 1985–1989. The study period included two severe and two mild winters. The community of ungulates inhabiting Białowieża National Park consisted of red deer Cervus elaphus, 55% of all ungulates; wild boar Sus scrofa, 42%; and roe deer Capreolus capreolus, moose Alces alces, and European bison Bison bonasus, about 1% each. The average size of red deer groups increased from 2.7 (SD 2.35) in spring and summer to 6.9 (SD 6.84) in autumn and winter. In winter the group size of red deer was positively correlated with the depth of snow cover and negatively correlated with the mean daily temperature. Average group size of wild boar did not change significantly between seasons; it was 6.8 (SD 5.16) in spring and summer and 5.7 (SD 4.67) in autumn and winter. Analysis of 144 wolf scats showed that wolves preyed selectively on red deer. In October-April, Cervidae (mostly red deer) constituted 91% of biomass consumed by wolves, while wild boar made up only 8%. In May-September deer formed 77% of prey biomass, and the share of wild boar increased to 22%. In all seasons of the year wolves selected juveniles from deer and boar populations: 61% of red deer and 94% of wild boar of determined age recovered from wolves' scats were young <1 year old. Analysis of 117 carcasses of ungulates found in Białowieża National Park showed that predation was the predominant mortality factor for red deer (40 killed, 10 dead from causes other than predation) and roe deer (4 killed, none dead). Wild boar suffered most from severe winter conditions (8 killed, 56 dead). The percentage of ungulates that had died from undernutrition and starvation in the total mortality was proportional to the severity of winter.

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Most of our knowledge of wolf-ungulate relationships comes from two sources: extensive studies conducted in the United States and Canada during the last decades (e.g. Mech 1970; Peterson 1977; Fritts and Mech 1981; Nelson and Mech 1981; Messier and Crête 1985; Ballard et al. 1987; Mech et al. 1987; Carbyn 1987) and numerous investigations performed in the Soviet Union (review in Bibikov 1985; Pavlov 1990). These two groups of studies most often report on relatively pristine interactions of wolves and wild ungulates. In contrast, Europe's wolves, which survive in scattered populations, often depend on garbage dumps and domestic animals (Gavrin and Donaurov 1954; Boitani 1982; Salvador and Abad 1987). Natural communities of ungulates and their large predators have been absent for centuries from most temperate forests of Europe.

This paper describes wolf-ungulate interactions in the Białowieża National Park, which protects the last surviving remnant of former pristine woodlands of lowland continental Europe. We present 4 years of studies on wolf feeding habits as part of a long-term project on predatorprey relationships in the Park.

We tried to answer the following questions: (1) What is the species structure of the ungulate community? (2) How do wolves utilize that community as potential prey? (3) How much do winter conditions affect mortality of different ungulate species?

Study area

Białowieża National Park (47.5 km²) lies in the middle of the extensive woodlands (Białowieża Primeval Forest) of 1250 km² on the border of Poland and the Soviet Union. Rich oldgrowth of the Park represents the lowland type forests of boreal zone and is comprised of oak *Quercus robur*, hornbeam *Carpinus betulus*, linden *Tilia cordata*, maple *Acer platanoides*, birches *Betula pubescens* and *B. verrucosa*, alder *Alnus glutinosa*, spruce *Picea abies*, pine *Pinus sylvestris*, and several other tree species. The structure of the forest is typical of the virgin wood-land unaltered by management, hunting or tourism (Faliński 1986). The fresh, fairly dry, swampy, and riverflooded forest associations with living trees ranging in age from seedlings to over 500 years, as well as with many decaying uprooted trees, make the habitat extremely varied.

As evidenced by the earliest written reports, Białowieża Forest was protected as the royal hunting forest of Polish kings and Lithuanian dukes from the 15th century until the end of the 18th century. Then the Russian occupation (19th century) brought the deliberate increase of ungulate numbers by introduction of alien species and through predator removal and supplementary winter feeding. In the 20th century, two world wars had disastrous effects on Białowieża Forest: native game species were decimated, the European bison was exterminated, and the introduced fallow deer *Dama dama* died out. In 1944, the Białowieża Primeval Forest was divided by the Polish–Soviet border. Since then, the Polish part of the forest has undergone a fast healing process due to conservation and special forest management rules. The European bison was saved from extinction and the first individuals were released to the wild in 1952 (Krasiński 1967). Other game recovered their status and numbers.

In the 20th century, wolves lived continuously in the Forest except for 1960–1980, when the severe predator control both in Poland and in the Byelorussian Soviet Republic (by baiting and shooting) temporarily deprived the Polish borderland of wolves (Miłkowski 1986).

The contemporary community of ungulates comprises red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, wild boar *Sus scrofa*, moose *Alces alces*, and European bison *Bison bonasus*. In historical times two species have become extinct: auroch *Bos primigenius* (17th century in central Poland, but probably earlier in Białowieża Forest) and forest horse *Equus gmelini* (18th century). The guild of large predators contains wolf *Canis lupus* and lynx *Lynx lynx*, and was impoverished in 19th cen-



Fig. 1. Mean daily temperatures and depth of snow cover during the four winters (October 1-April 15, 1985/86 to 1988/89) in Białowieża forest, eastern Poland

tury by extermination of brown bear Ursus arctos. Detailed information about the entire community of predators and prey resources can be found in Jędrzejewski et al. (1989).

Climatically, the continental features prevail, but its transitional character makes it rather variable. During four years of studies (1985/86–1988/89) winters differed greatly in temperature and snow cover (Fig. 1).

Methods and material

Surveys of the ungulate community

Surveys of ungulates were aimed at determining the proportions of each species in the entire community. From winter 1985/86 through winter 1989/90 during any daytime field work on the predator-prey project, all observations of ungulates were recorded. Observers encountering ungulates determined their species, group size, and whenever possible the presence of young in the group, and mapped the position of observed animals. A total of 283 observations including 1580 animals were made.

Twice in February 1987 and twice in March 1987, censuses of ungulates by snow tracking were conducted on a grid of transects of total length 59,246 m, which covered 11.2 km². This area was representative of the forests of the National Park. The transects were walked by observers within 1–2 days after fresh snowfall. The number of tracks were noted for each 50 m section, but for further calculations the summed values for longer sections (usually 500 m) were used. The index of ungulate abundance used in this paper is the mean number of tracks crossing 1 km of transect per day (*n* tracks per day per 1 km) calculated as a mean for all longer sections.

Determination of wolf feeding habits

The study of wolf diet was based on the analysis of 144 scats collected between winter 1985/86 and autumn 1989. Analysis of scats followed standard procedures (Lockie 1959; Goszczyński 1974). Prey were identified on the basis of bony remains according to the key by Pucek (1984). Whole skeletons of wild boar and roe deer and parts of red deer skeletons were used as reference material for discrimination of ungulate species. Microscopic analysis of hair was done according to the keys by Dziurdzik (1973) and Debrot (1982).

The age of ungulates recovered from wolf scats was determined by (1) analysis of bony remains (hooves, teeth, ossification of sutures, porosity of joint bones) in comparison to reference materials (skeletons), and (2) macroscopic comparison of hair recovered from scats with the reference material (hair of farmed red deer, roe deer and wild boar of known age). Two age classes were distinguished: juveniles (fawns and piglets <1 year of age) and adults (deer and boar >1 year). Wild boar piglets molt when 12-14 months old and their juvenile coat is clearly distinct from adult hair (Pucek 1984). In roe deer, only juveniles up to 3-4 months old could be distinguished by hair from older animals (cf. Pucek 1984). In red deer, the juvenile hair was a good identification feature in spring and summer till the first molt in autumn. In autumn and winter, the difference between juvenile and adult coat is less pronounced (Pucek 1984); age determination by hair was then used only in connection with the bone identification method.

The biomass of prey consumed by wolf was obtained by using the coefficients of digestibility from Goszczyński's (1974) work on foxes. (Coefficients for roe deer carcasses were used here for all species of ungulates.)

From winter 1986/87 to spring 1989 the western part of the Białowieża National Park (about 15 km²) was searched for carcasses of ungulates either killed by wolves and lynxes or dead due to other causes. The area searched included the tracking transects (11.2 km², see above). Searching was done on foot during any field work such as snow tracking, scat collecting, tracking of individual predators. Whenever possible the cause of death and the species of predator involved were identified by tracks and signs on snow at the carcass. Since autumn 1987, the sex and age of ungulates found dead or killed were also determined. Out of 31 ungulates determined as wolf kills, 16 were found 1-5 days after the wolves had killed them; visible tracks on snow or ground clearly indicated that wolves actually chased and killed these animals and did not feed at carcasses of animals that had died from other causes. Therefore, we assumed that all 31 wolf kills were the results of wolves' hunts for live ungulates.

Meteorological data were provided by the Białowieża Meteorological Station and included mean daily temperatures and depth of snow.

Results

Structure of ungulate community

Red deer and wild boar were the most abundant ungulates, accounting for over 95% of all ungulates documented in the forest (Table 1). The smallest ungulate, roe deer, and the large ones, moose and European bison, were rare.

The grouping pattern of red deer varied seasonally. In spring and summer, solitary deer were more commonly seen than any other groups (Fig. 2). In autumn and winter, the most frequently observed group consisted of 5 red deer. The group mean size grew significantly from 2.7 in spring and summer to 6.9 in autumn and winter

 Table 1. Species composition of the ungulate community in Białowieża National Park, Poland

Species	Body mass (kg)		Obser of liv	rvations e animals	Snowtracking in Feb-Mar			
	Adult	Adult	1987-	-1989	1987	1987		
	females	males	n^1	%	n^2	%		
Red deer	80-134	126-224	875	55.4	7.66	51.7		
Wild boa	r 85–140	90-176	668	42.3	6.58	44.4		
Roe deer	21	25	19	1.2	0.52	3.5		
Moose European	195–230	265–382	10	0.6	0.05	0.4		
bison	300–540	400-920	8	0.5	-	_		
Total			1580	100	14.81	100		

n = number of observations during daytime field work

 $^{2} n$ = mean number of tracks crossing 1 km of transect per day

Observations and snow tracking yielded statistically similar results (G=0.59, df=2, P>0.5, G-test for homogenity of percentages). Sources of data on body masses: red deer (min-max), Dzięciołowski (1969); wild boar (min-max), Pucek (1984); roe deer (mean), dressed carcass weight after Miłkowski (1970) increased by 1/3 according to Pielowski (1988); moose (min-max), Pucek (1984); European bison (min-max), Krasińska (1988)



Fig. 2. Frequency distribution of group size in red deer in springsummer (*above*) and autumn-winter (*below*) in Białowieża National Park. Data for 1986/87–1989 pooled



Group size (N boar)

Fig. 3. Frequency distributions of group size in wild boar in springsummer (*above*) and autumn-winter (*below*) in Białowieża National Park. Data for 1986/87–1989 pooled

 $(t=3.444, P<0.001, \text{ test for equality of means with une$ qual variances; Sokal and Rohlf 1981).

In winter, red deer tended to form larger aggregations during periods with deep snow and low temperature. Group size was positively correlated with snow depth (Kendall $\tau = 0.230$, n = 109, P < 0.0002) and negatively correlated with the average daily temperature (Kendall $\tau = -0.244$, n = 109, P < 0.0002).

The grouping pattern of wild boar did not distinctly vary seasonally (Fig. 3). The slight decrease of the mean herd size from 6.8 in spring and summer to 5.7 in autumn and winter was not significant (t=1.13, P>0.2, test for equality of means with unequal variances). The size of winter groups of wild boar did not vary with the depth of snow (Kendall $\tau=0.040$, n=73, P>0.5) or temperature (Kendall $\tau=-0.054$, n=73, P>0.5).

In spring and summer, most groups of wild boar that included 6 and 7 individuals, and all groups including 8 and more individuals, were families with piglets. Two or more sows with their offspring often formed one large group. The average groups with piglets comprised 2.2 adults (individuals > 1 year) (SD 1.3, range 1–5) and 7.8 piglets (SD 4.4, range 2–17).

Roe deer seen in spring and summer were lone individuals (n=4). In autumn and winter, mean group size in roe deer was 2.5 (SD 2.23, range 1-7, n=6). The difference between mean group size in summer and winter was not significant (t=1.65, P>0.1).

Wolf diet and feeding habits

Deer (both red and roe) were the staple food of wolves in all seasons, exceeding 77% of biomass consumed, and increasing to 93% in severe winters (Tables 2 and 3). The remains of Cervidae were identified to species in 50% of cases in summer and 30% in winter. Nonetheless, the red deer was obviously predominant in wolf diet, and the proportion of roe deer was low. In spring and summer, the proportion of wild boar biomass in wolf diet increased to 21%, nearly treble that of autumn and winter (Table 2). These seasonal changes in per cent biomass of red deer and wild boar in wolf diet were significant (G=8.16, df=1, P < 0.005, G-test for homogeneity of percentages). A similar change, though less pronounced, was observed when food composition during two severe winters was compared to diet during two mild winters (G = 5.084, df = 1, P < 0.025) (Table 3).

The total number of scats with Cervidae remains was 140 and of those with wild boar remains 51. We assumed that they represented 140 deer and 51 wild boar specimens killed by wolves. (The scats were collected over the 4-year period, and were separated by an average time interval of about 6–7 days. In some cases, however, more than one wolf scat was collected from the National Park in the same day. If we take all scats collected during any day as one sample, then there were 73 occurrences of deer and 36 of wild boar, the proportion very close to 140 deer versus 51 boar.)

We compared these figures (73% deer and 27% wild boar among wolf prey recovered from scats) to the numbers of deer (red and roe deer) and boar from observations (data from Table 1). Ivlev's electivity index Dmodified by Jacobs (1974) was calculated to quantify

 Table 2. Composition of wolf diet (% biomass consumed and % occurrence in scats), 1 May-30 September and 1 October-30 April in Białowieża National Park, Poland

Item	May-Se	pt $(n = 45)$	Oct–Apr $(n=99)$		
	% Bio	% Occ	% Bio	% Occ	
Red deer	38.1	31.1	31.5	29.3	
Roe deer	3.0	4.4	2.9	3.0	
Undet. Cervidae	36.4	53.3	56.8	64.6	
Total Cervidae	77.5	91.1	91.2	97.0	
Wild boar	20.8	46.7	7.8	29.3	
Lepus europaeus	1.4	4.4	0.2	2.0	
Sciurus vulgaris		_	+	1.0	
Small rodents	+	4.4	+	5.0	
Nyctereutes					
procyonoides		_	0.6	4.0	
Birds	0.1	4.4	+	2.0	
Amphibians and					
reptiles	0.1	4.4	+	2.0	
Invertebrates		_	+	1.0	
Plant material	0.1	24.4	0.1	24.2	
Mean biomass consu	imed				
per 1 scat (g)	139	94.5	148	31.3	

Data for 1985/86–1989 pooled. n = number of scats

Table 3. Composition of wolf diet (% biomass consumed and % occurrence in scats) in Białowieża National Park in severe winters (December-April 1985/86 and 86/87) and mild winters (December-April 1987/88 and 88/89) (see Fig. 1)

Item	Mild with $(n=32)$	nters	Severe winters $(n=47)$		
	% Bio	% Occ	% Bio	% Occ	
Red deer	15.3	15.6	31.6	25.5	
Roe deer	1.6	3.1	0.6	2.1	
Undet. Cervidae	69.2	78.1	61.1	68.1	
Total Cervidae	86.1	96.9	93.3	95.7	
Wild boar	13.7	46.9	4.6	19.1	
Lepus europaeus	0.1	3.1	0.4	2.1	
Sciurus vulgaris	0.1	3.1	_	_	
Small rodents	+	3.1	0.1	4.2	
Nyctereutes					
procvonoides		_	1.1	4.2	
Birds	~		+	6.4	
Amphibians and					
reptiles		_	0.3	2.1	
Plant material	+	31.2	0.2	19.1	
Mean biomass consu	ımed				
per 1 scat (g)	187	76.8	12:	59.7	

n = number of scats

wolves selectiveness towards these two major prey species. D varies from 1 (strongest preference), to 0 (random removal of both prey), to -1 (strongest negative selection). Deer were clearly preferred by wolves (D=0.36), and wild boar were taken less often than might have been expected from their proportion in the community (D=-0.34).

Among 140 cervid remains, 43 were indentified as red deer, 7 as roe deer, and 90 as undetermined Cervidae.

Table 4. Numbers of juvenile (<1 year of age) and adult (>1 year) ungulates found in wolf scats in Białowieża National Park

Prey	N	Aay-Sept	ember	October-April		
	Juv	Adult	Undet.	Juv	Adult	Undet.
Red deer	9	5	_	11	8	10
Roe deer	1	2	_		3	1
Undet. Cervidae	10	9	6	28	12	25
Total Cervidae	20	16	6	40	22	36
Wild boar	8	1	13	8		21

The delicate bones of roe deer were very conspicuous and distinctly easier to identify than those of red deer. Therefore, we accepted 7 roe deer remains (3.7% of all ungulate remains) as a conservative, but reliable number of roe deer in the wolf diet; the rest was classified as red deer. It approximates the proportion of roe deer in the entire community of ungulates (compare Table 1).

Age classes of ungulates determined from bone and hair remains in wolf scats are shown in Table 4. In red deer, wild boar and in undetermined cervids, the young were most intensely preyed upon by wolves. Sixty deer (61% of all determined cases) were young <1 year of age, and 38 were older (39%). The proportions of fawns among deer killed by wolves in spring-summer and in autumn-winter were similar (Table 5). All except one wild boar of determined age (94%) were young <1 year of age (Table 5). In roe deer killed by wolves, no prevalence of young was noted.

Data on age of ungulates killed by wolves (carcasses found in the forest) are scarce: 7 out of 15 red deer and 2 out of 5 wild boar were juveniles <1 year old.

The roles of predation and snow cover in winter mortality of ungulates

The search for carcasses conducted from winter 1986/87 to spring 1989 yielded over 120 ungulate remains. Nearly all (117) were found between November and the end of April (Table 5). In red deer the most important cause of death was predation, predominantly by wolves: 40 out of 50 red deer carcasses (80%) were of animals killed by predators. Predation was the only recorded mortality factor in roe deer (Table 5). In wild boar, 56 out of 62 carcasses found (90%) were of animals that had died from undernutrition and/or disease. Most dead boar were found in their lairs, sometimes 2–3 (max. 7) dead boar in the same lair at a time. Young boar were most vulnerable to death from undernutrition. Out of 47 boar carcasses of estimated age, 40 were <1 year old (87%).

Death caused by factors other than predation (most often undernutrition) acted selectively on the wild boar population (Ivlev's electivity index D=0.748) and negatively on red deer population (D=-0.753).

Species composition of ungulates killed by predators (wolf and lynx) and recovered from wolf scats did not differ (G=5.74, P>0.05, df=2). However, they both differed significantly from species composition of ungu-

13 8	2 1	- 1	
21 2	3 29	1	
11 2 5	3 - 1	- 1	
18	4 21	1	
1 7	1	$\frac{-}{2}$	
8 1	1 4	2	
25 2 20	6 - 2	- - 4	
47 3	8 54	4	
	$ \begin{array}{r} 13 \\ 8 \\ 21 \\ 2 \\ 11 \\ 2 \\ 5 \\ 18 \\ - \\ 1 \\ 7 \\ 8 \\ 1 \\ 25 \\ 2 \\ 20 \\ 47 \\ 3 \\ \end{array} $	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$

One moose poached in winter 1986/87 was not included in the table

lates observed (scats: G=9.62, df=3, P<0.025; kills: G=26.9, df=3, P<0.001) (Fig. 4).

Species composition of ungulates that had died from undernutrition and/or disease differed significantly from those observed (G=74.04, df=3, P<0.001) and those killed by predators (G=155.86, df=2, P<0.001) (Fig. 4).

The carcasses of ungulates were more difficult to find in snowless, mild winters (lack of tracks). Therefore, the changes in numbers of carcasses found in consecutive winters reflect not only the changes in mortality rate but the survey bias due to different conditions as well. However, we believe the likelihood of finding killed versus dead ungulates was equivalent in the same winter. Therefore, their relative abundances during each winter show the importance of predation and snow cover as mortality factors. During the extremely severe winter of 1986/87 (compare Fig. 1), death caused by factors other than predation accounted for 55% of all ungulates found dead in the Park. During milder winter of 1987/88 this proportion was 48%, and during the warm, snowless winter of 1988/89 only 31%.

Discussion

Prey choice by wolves

In 1985/86–1988/89, Białowieża National Park was intensely utilised by a pack of wolves (including up to 5



Fig. 4. Percentage of red deer, wild boar, and roe deer in the total number of ungulates observed in the Białowieża National Park (year round), recovered from wolf scats (autumn-winter), killed by large predators (autumn-winter), and dead from undernutrition and/or diseases (autumn-winter)

individuals). The wolves were frequently recorded by tracks and sporadically seen. The territory of the pack embraced also the managed forests outside the National Park. Though wolves moved freely between the managed forests and the protected primeval forests, we believe that the material collected by us in the National Park represents the wolf-ungulate relationships in the natural forests of the Park. In addition to mature tree stands, the managed parts of the Białowieża Forest are characterized by the presence of small clearcuts, small forest plantations, and young age-classes of tree stands. The species composition of ungulates in those forests differs, including a much greater proportion of roe deer. Wolves' kills collected in the managed part of Białowieża Forest contained up to 30% of roe deer and a very low proportion of wild boar (L. Miłkowski, M.Sc., Eng., unpubl. data from game inventories). Therefore, both the structure of the ungulate community and the wolf-ungulate relationships presented in this paper are representative of the natural forests of the Białowieża National Park.

The pack of wolves penetrating the National Park was spatially isolated from anthropogenic sources of food and at the same time it enjoyed plentiful natural food resources. We think that the results of this study describe the pristine wolf-ungulate interactions that once occurred widely in lowland continental Europe. The species composition of the ungulate community in Białowieża National Park differs from that in managed forests and agricultural habitats of Poland and Central Europe: red deer and wild boar were dominant species, and roe deer had a surprisingly low abundance. No contemporary data are available to assess how much the ungulate assemblage of Białowieża National Park reflects the primeval potential of this forest, but some confirmation is provided by excavations of late Palaeolithic and Mesolithic sites. Jarman (1972, cited in Clutton-Brock 1987) reviewed 165 such sites throughout Europe and reported that the bone remains of red deer were found at more than 95% of all sites, of wild pigs at slightly less than 85%, roe deer at approximately 60%, moose at less than 15% and European bison at less than 5%.

Wolves inhabiting Białowieża National Park and facing the diverse community of ungulates tended to specialize in hunting red deer. Their preference for deer was exceptionally pronounced during severe winters when they hunted deer intensively, and disregarded numerous wild boar carcasses. In mild, snowless winters and in summer, red deer were less susceptible to wolf predation. Wolves then had to hunt more wild boar. Nonetheless, boar were clearly avoided by wolves compared to their share in the community of ungulates. Roe deer were preyed upon by wolves more or less proportionally to their – rare – occurrence in the Park.

Selective preving on red deer and discarding wild boar seem to be a typical hunting strategy of wolves in vast regions of lowland forests in the European part of the Soviet Union. Filonov (1989) analyzed the choice of prey by large predators in Soviet nature reserves. Six reserves harboured communities of ungulates consisting of the same species as Białowieża Primeval Forest, but without European bison and occasionally with introduced sika deer Cervus nippon. Data given by Filonov (1989) are compared to the material obtained in Białowieża (Table 6). In all cases where red deer occurred in the community, the preference for them by wolves was clearly shown. In regions where red deer were absent from or rare in the ungulate community, wolves selected moose, roe deer, or introduced sika deer. Wild boar were always avoided by these predators (Table 6). A high contribution of wild boar to wolf diet (66.7% of all prey items) was reported by Litvinov (1981) in Kyzyl-Agach Reserve (by the Caspian Sea) where wild boar were the only species of ungulate.

In Białowieża, wolves selected fawns from the red deer population. No data on age structure of red deer in Białowieża Forest are available. It is, however, possible to compare the data of this study to studies conducted by Dzięciołowski (1979) in other extensive forests of Poland. In four populations of red deer, young <1 year of age composed on average 24% of all individuals (18–38%). Therefore, 66% of fawns <1 year among all deer taken by wolves means strong selective predation on red deer fawns in Białowieża National Park. Prevalence of fawns among red deer killed by wolves was also reported by Okarma (1991) in the Bieszczady Mountains (Eastern Carpathians), Poland. Analysis of remains of wolf kills, however, underestimates the number of fawns and piglets in the wolf diet, because the smallest prey is eaten completely (Litvinov 1981, and authors own data).

33

Table 6. Selectivity of wolves preying on ungulate species in Białowieża National Park (this paper) and forests of six nature reserves ('zapovednik') in the European part of the Soviet Union (after Filonov 1989)

Reserve		Moose	Red deer	Roe deer	Sika deer ^a	Wild boar
Białowieża NP $(n=191)$	L K	1	55 70	1 3.5		42 26.5
Darvinskii (n=393)	L K	75 99	- -	+ 0.1	-	25 0.9
Bashkirskii (n=202)	L K	53 11	41 71	5 18	-	1 _
Pripiatskii (n=47)	L K	31 11	_	12 55	-	57 34
Berezinskii $(n=252)$	L K	54 65	4 11	1 1	_ _	41 23
Okskii $(n=259)$	L K	73 71	_		12 29	15 -
Mordovskii $(n=174)$	L K	45 15	13 3	?	34 82	8 -

^a alien, introduced species

L – animals that lived in the study area (in %), K – animals killed by wolves (in %). n=number of wolf kills (in the reserves in the Soviet Union; mulli-year data) and number of prey recovered from wolf seats (in Białowieża National Park

With this in mind, we again refer to Filonov's (1989) data from the Soviet reserves. In the Bashkirskii Reserve, fawns <1 year composed 23% of the living population of red deer and 49% of deer killed by wolves. In the Altai Reserve, the figures were 8% and 15% respectively. No selection of fawns was recorded in the Sayan-Shushenskii Reserve, where fawns constituted only 8% of the deer population.

Wolf selection of wild boar piglets in Białowieża was obvious: 94% of boar remains in wolf scats were those of young < 1 year of age. A census taken by Miłkowski and Wójcik (1984) in the managed part of the Białowieża Primeval Forest in March showed that piglets formed 57% of the population of boar. In the Slovak Carpathian Mountains 80% of wild boar taken by wolves were piglets <1 year (Brtek and Voskar 1987). Litvinov (1981) reported that 50% of wild boar taken by wolves in the Kyzyl-Agach Reserve were piglets <1 year. Aerial censuses revealed that piglets constituted 32.1% of the boar population in spring. Litvinov (1981) commented that wolves' selectivity towards piglets had been underestimated because "it was determined by tracking of wolf packs, that the newborns and piglets to 6 months of age were completely eaten by these predators". Older boars, both males and females, are a difficult, if not invulnerable, prey to wolves due to their tusks and active defence behaviour.

Predation risk and herd size in ungulates

In many mammals and birds, the group size increases with the increase of predation risk (review in Elgar 1989). The seasonal changes in grouping pattern in red deer do

Predators present	Percent of groups with				
	1 ind	2–7 inds	8+inds		
wolf, lynx	19	60	21		
wolf, lynx, hunters	16	74	10		
wolf, lynx, hunters	28	59	13		
wolf, hunters	26	67	7		
hunters	25	73	2		
hunters	49	49	2		
	wolf, lynx wolf, lynx, hunters wolf, lynx, hunters wolf, lynx, hunters hunters hunters hunters	Predators presentPercent ofwolf, lynx19wolf, lynx, hunters16wolf, lynx, hunters28wolf, hunters26hunters25hunters49	Predators presentPercent of groups with 1 indwolf, lynx19wolf, lynx, hunters1674wolf, lynx, hunters2859wolf, hunters2667hunters2573hunters49	Predators presentPercent of groups with 1 ind2–7 inds $8 + inds$ wolf, lynx196021wolf, lynx, hunters167410wolf, lynx, hunters285913wolf, hunters26677hunters25732hunters49492	

^a Wolves and lynxes exterminated after World War II

^b Wolves and lynxes exterminated in the first half of 19th century

Data for Plaska, Józefów, Iława and Kobiór forests taken from Dzięciołowski (1979), Borki Forest after Dzięciołowski (1991). Białowieża National Park – data for all seasons and years pooled

occur in deer populations regardless of the presence or absence of predators (compare Dzięciołowski 1979). However, the presence of predators may promote relatively larger groups both in summer and winter. We compared our data from Białowieża National Park with the data collected in the same way by Dzieciołowski (1979, 1991) in five extensive forests of Poland, three of them with predators and two without predators (Table 7). With the presence of wolves and lynx in the forest, the proportion of groups including eight or more individuals was the highest, and reached 10-21% compared with 2% in areas with no large predators. The proportion of 'groups' comprised of solitary individuals was the highest in the population that had lived without predators for over 100 years (Godyń 1937). Additionally, it is likely that "predation" exerted by human hunters (who search for deer visually), would cause deer to disperse and stay solitary or in small groups.

Therefore, it seems that predation was the primary factor leading to large groups of red deer in areas with predators present in comparison to areas without predators.

Predation risk is also the most likely explanation for the increase of group size in red deer as the snow depth increases, which was observed in Białowieża National Park.

The groupings of wild boar were fairly stable year round (slightly bigger in summer though). Larger groups of wild boar seem to be fairly safe from wolf attacks. It was observed that the vigilant group of adult boar forms a circle, with tusks facing outwards, and they do not flee (S. Wąsik, pers. comm.). During the winter of 1985/86, Dr. S. Reig observed a pack of five wolves interacting with a herd of several wild boar in Białowieża National Park. Both species seemed to pay no attention to each other, but most probably the wolves were "testing" the boars. Kudaktin (1982) described an active defence of small piglets by the mother boar against wolves' attack.

Grouping patterns of wild boar in the Camargue, France, where no large predators are present, differred greatly from those in Białowieża National Park (Dardaillon 1988). In the Camargue the most common 'groups' were single individuals (47% of groups), followed by groups of 2–5 individuals (41%) and groups including 6 or more individuals (19%). In Białowieża, single boars formed only 17% of all groups, herds of 2–5 individuals formed 40%, and groups > 6 were most numerous (43%, data pooled for all seasons and years). Similar grouping tendencies in wild boar were observed by Dzięciołowski (1991) in Borki Forest (north-eastern Poland) where wolves, lynxes, and hunters act as predators. Lone individuals formed 12% of all groups, 29% were groups containing 2–5 animals, and 59% of groups consisted of 6 and more animals. Therefore, predation risk is a factor contributing to the larger groups in wild boar.

Roe deer live solitarily or in small families. Average group size in Białowieża (data pooled) was 1.9. In Kobiór forest (Dzięciołowski 1979), where no large predators have been present for over 100 years, the average group size of roe deer was 1.5 – very similar to the population living under constant predation risk.

Winter mortality of ungulates – relative importance of predation and snow cover

It was not possible to determine the regulating effect of wolves on the populations of ungulates in Białowieża National Park because the densities of prey were not censused and predation impact not quantified. Nevertheless, predation proved to be the most important winter mortality factor in red deer. It also seems to be a typical feature of wolf-deer interactions in Europe. Filonov (1989) presented data on red deer mortality in six reserves in the Soviet Union (data collected by search for carcasses). Predation was the cause of death in 78% of located red deer carcasses in the Altaiskii Reserve, 93% in Berezinskii, 87% in Bashkirskii, 83% in Kavkazskii, 28% in Mordovskii, and 20% in the Voronezhskii Reserve (mean = 65%).

The mortality of wild boar in Białowieża National Park, mostly caused by factors other than predation, was related to the severity of winters. Deep snow makes foraging by boar energetically costly and difficult, causing starvation, rapid deterioration and possibly fast spread of diseases. Caboń (1958) reported mass death of wild boar in Białowieża Forest during the extremely severe winter of 1956. Jezierski (1977) analyzed the mortality rate in a population of wild boar inhabiting Kampinos National Park in central Poland where large predators were absent. The mortality rate of boar was very high: 84% of young died within the first two years of life. Wolves may exert high pressure on the youngest wild boar, but it seems that generally, mortality from causes other than predation prevails in populations of wild boar, with or without predators. In four reserves in the Soviet Union (Filonov 1989), factors other than predation caused an average of 79% of mortality in wild boar (34–100%). Wolf predation may be a major cause of boar mortality in special cases, e.g. in the Kyzyl-Agach Reserve, where wild boar was the only species of ungulate and it constituted nearly 70% of wolf prey (Litvinov 1981).

Information on roe deer, which was uncommon in Białowieża National Park, is scarce but it deserves a few comments. Only 4 carcasses of roe deer were found. All of them, however, were killed by large predators. Roe deer were preferred prey to wolves whenever they occurred (Table 6). According to Filonov (1989), predation accounted for 100% of roe deer mortality in the Bashkirskii reserve, 97% in Altaiskii, 94% in Il'menskii, and 74% in the Berezinskii Reserve (mean = 91%). It suggests that predation may be an important factor regulating roe deer numbers.

No carcasses of dead or killed European bison were found in our studies. Since the reintroduction of the bison into the wild in 1952, the population has been followed by direct observations and tracking. No case of a bison killed by wolves or lynxes has been found (Drs Z. Krasiński and M. Krasińska, pers. comm.). In old written reports about bison in the Białowieża Primeval Forest, a few cases of wolves' attacks on bison were recorded (Karcev 1903). Bunevich (1988) found no remains of European bison in 50 stomachs, 32 scats, and 82 prey remains of wolves in the Byelorussian part of the Białowieża Primeval Forest in 1979-1985. In the Caucasian Biosphere Reserve which harbours a free-living population of European × American bison hybrids, this large ungulate was found in only 2% of wolf scats (Kudaktin 1986). In North America, wolves are successful predators of both calves and adults of American bison (Carbyn and Trottier 1988). However, European bison survive in small isolated populations, and always form a small percentage of the local ungulate communities. Given the choice, wolves and lynxes prefer to hunt smaller and more numerous species. Therefore, predation cannot be a limiting factor for an exponentially growing population of European bison that has now been saved from extinction.

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