PREY SELECTION AND PREDATION BY WOLVES IN BIAŁOWIEŻA PRIMEVAL FOREST, POLAND

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Relationships of wolves (*Canis lupus*) and ungulates were studied in the Polish part of Białowieża Primeval Forest with high densities of prey. The number of wolves ranged from 7 to 19, and the number of packs ranged from 2 to 4. Average densities were 2.3 wolves/100 km². Red deer (*Cervus elaphus*) was the main prey of wolves. Roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), moose (*Alces alces*), and European bison (*Bison bonasus*) were hunted less than expected based on their abundance. Mean mass of ungulates killed by wolves was 55 kg. Prey were consumed quickly, with 57% of kills completely eaten on the 1st day after killing. Average killing rate by wolves was 0.78 ungulate per wolf pack per day (0.14 prey item per wolf per day). Results of this study combined with the data obtained in the Belarussian part of Białowieża Primeval Forest in 1946–1985 allowed for analysis of dietary response of wolves to changes in densities of ungulates. Wolves showed a response to abundance of red deer. The amount of other ungulates in their diet depended on the densities of red deer. From 1991 to 1996, wolves annually removed 57–105 red deer, 19–38 wild boar, 19–25 roe deer, and 0–2 moose per 100 km². Those amounts were equivalent to 9–13% of spring–summer densities of red deer, 4–8% of wild boar, 3–4% of roe deer, and 0–29% of moose. Additionally, hunters annually harvested 131–140 red deer, 44–114 roe deer, 1–7 moose, and 45–142 wild boar per 100 km². Effects of predation and harvest by hunters on ungulate mortality were likely additive and caused declines in ungulate populations during our study.

Key words: *Canis lupus*, *Cervus elaphus*, hunter harvest, killing rate, Poland, predation impact, prey selection

In Białowieża Primeval Forest (BPF) of eastern Europe, wolves (*Canis lupus*) coexist with 5 species of wild ungulates: European bison (*Bison bonasus*), moose (*Alces alces*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*). Our study was directed at es-

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timating the impact of wolves on wild ungulates and defining elements and mechanisms of predation, including dietary responses by wolves to changes in ungulate densities and killing rates. In earlier investigations (Jędrzejewski et al. 1994; Jędrzejewska et al. 1992), we showed that wolves selected red deer and hunted other species less often than expected from their avail-

ability. Also, we documented that the relative effect of wolf predation among all causes of deaths was small in bison, moose, and wild boar and more significant in red deer and roe deer (Okarma et al. 1995).

Under conditions of a diverse prey base, wolves may be expected to show complicated and locally varying patterns of prey selection and functional responses. Messier (1995a) suggested that wolves preying on 2 species of ungulates would respond to changes in numbers of both species, with a more vulnerable prey evoking type 2 or asymptotic response (according to classification of Holling 1959) and less vulnerable prey evoking a type 3 or sigmoid response. Reaction by wolves to changes in availability of >2 sympatric prey has not been studied theoretically or empirically. Based on data obtained in Eurasian multiprey systems, we predicted that wolves would respond functionally to the main preferred prey, the red deer. Fluctuations of deer numbers also may determine predation of wolves on other coexisting species of ungulates.

Our goal was to assess components of predation: wolf numbers, their diet composition, prey consumption and selection, dietary responses to changes in ungulate numbers, and average killing rate—all based on data accumulated over ≥10 years. We calculated the magnitude of wolf predation over 4 years and compared this number with densities of ungulates and other major factors of ungulate mortality, specifically harvests by hunters and predation by lynx (*Lynx lynx*—Okarma et al. 1997). During our study, densities of ungulates were high but declining, and wolves were relatively undisturbed by humans (no legal hunting, occasional poaching—B. Jędrzejewska et al. 1996).

Materials and Methods

Study area.—The BPF (at present 1,450 km²) is the best preserved woodland of its size in lowland temperate Europe. It is located on the Polish–Belarussian border (52°45′N, 24°E) in the boreal nemoral zone and is composed of rich mixed and multispecies stands of trees. The most characteristic forest association in BPF is oak–lime–hornbeam (*Quercus robur–Tilia cordata–Carpinus betulus*) with admixtures of maple (*Acer platanoides*) and spruce (*Picea abies*) growing on brown and podzolic soil. Drier sandy soils are overgrown with coniferous and mixed coniferous forest dominated by pine (*Pinus silvestris*) and spruce with admixtures of oak. Wet places with stagnated water are covered by black alder (*Alnus glutinosa*). Small forest rivers and brooks are lined by alder and ash (*Fraxinus excelsior*) and admixtures of elm (*Ulmus glabra*). The only open areas within the woodland are marshes of sedges (*Carex*) and reeds (*Phragmites*) in narrow river valleys and several glades with small villages. Further information on vegetation was given by Faliński (1986). The Polish part of BPF, where this study was conducted (580 km²), consisted of exploited (530 km²) and strictly protected (47 km²) regions. The exploited forests (average age, 72 years) had timber harvest, reforestation, and game hunting. In the protected part of Białowieża National Park, most of the stands of trees (average age, 130 years) were of natural origin. Neither exploitation of timber nor game hunting was allowed in Białowieża National Park. In 1996, Białowieża National Park was expanded to 100 km².

The bison is a protected species, and its population size is kept stable by yearly culling. The other 4 species of ungulates are hunted in the exploited part of BPF but not in Białowieża National Park. The guild of large carnivores was impoverished in the 19th century by extermination of the brown bear (*Ursus arctos*), and currently it contains the wolf and the lynx. During the past 150 years, numbers of wolves and lynxes ranged from temporary exterminations for predator control to very high densities (B. Jędrzejewska et al. 1996; W. Jędrzejewski et al. 1996). In the Polish part of BPF, wolves were harvested at low rates after 1970 but have been protected from 1989 to the present. In the Belarussian part of BPF, wolves continue to be heavily hunted (on average, 16 wolves/year or ≤80% of recorded winter numbers—B. Jędrzejewska et al. 1996). In 1981, a wire fence was constructed on the border, but both wolves and lynxes are known to cross it in some places.

Wolf and ungulate population trends.—Data

on wolf numbers were collected by snowtracking (Game Department of Forestry Administration directed by L. Miłkowski—B. Jędrzejewska et al. 1996) and by snowtracking, radiotracking, and visual observations (our team). We combined those data and analyzed numbers of wolves and wolf packs each winter. The largest number of wolves in 1 group seen or identified from snowtracking in 1 wolf territory was accepted as the size of the wolf pack in a given season. Detailed analysis of wolf numbers and their home ranges for the period of radiotracking was repoted by Okarma et al. (1998).

We used the data on ungulate numbers in 1985–1993 from the Game Department of Białowieża Forestry Administration (Jędrzejewska et al. 1997) and in 1991–1993 from drive censuses (Jędrzejewska et al. 1994, 1997; Okarma et al. 1997). Drive censuses were not conducted in 1994. Information on ungulate densities in late winter 1995 was given by Kossak (1995; drive census), and it was corrected for the uncensused area of Białowieża National Park. All censuses of ungulates were conducted in late winter.

The calculations of spring–summer populations of ungulates were based on their densities in late winter, the percentage of adult females in the populations, and the number of juveniles per female. To estimate juveniles per female red deer, we used our visual observations collected in BPF in 1987–1995. Of 276 adult females and young seen (only counting observations for which sex and age of individuals could be determined), mean number of fawns per adult female was 0.9 in July and declined steadily to 0.58 in January–February and 0.35 in March–April. These findings were consistent with data obtained by drive censuses; in the late winters of 1991–1993, 0.43–0.59 juveniles/adult female red deer were recorded. For roe deer, we used the data of Sablina (1955), who found that an average of 95% of the adult females were with fawns in early summer (means of 1.52 juveniles/ mother and 1.45 juveniles/adult female). For wild boar, we distinguished years of poor reproduction after the failure of seed crop of oak (1991–1992—Jędrzejewska et al. 1997) when 3.2 juveniles/mother were reported and years of moderate conditions (1992–1993, 1993–1994, and 1995–1996) when, on average, 5.9 juveniles/mother were seen (Lebedeva 1956; Jędrzejewski et al., in litt.). On average, 1 calf/female

moose was recorded during driving censuses and in 17 observations of moose. Percentages of adult females in all ungulate species were recorded during driving censuses. Data on annual harvest of ungulates by hunters were provided by the Game Departments of Białowieża, Browsk, and Hajnówka Forest Administration offices and the Regional Headquarters of the State Forests in Białystok.

Analysis of diet composition and prey of wolves.—In 1985–1996, we collected 411 wolf fecal samples. The results presented here include earlier data from 144 fecal samples described by Jędrzejewski et al. (1992). Analysis of feces followed the standard method of drying and washing through a 0.5-mm-mesh sieve (Goszczyński 1974; Lockie 1959). Prey were identified by bone, hair, and feather remains according to the taxonomic keys of Pucek (1981) and Debrot et al. (1982) and by comparison with our own reference material. Relative amounts of various prey were presented as the percentage of occurrence in the total number of fecal samples and the percentage of biomass consumed by wolves. To obtain the biomass of each prey species, the weight of prey remains recovered from feces was multiplied by coefficients of digestibility (Goszczyński 1974). Roe deer and red deer were distinguished only in cases where bone or hoof remains were found in feces. Microscopic analysis of hair allowed some differentiation (Teerink 1991) but did not allow for unambiguous identification of deer species. Thus, in many cases, deer material in feces was classified as Cervidae. Nonetheless, the proportions of various Cervidae species among wolf kills was determined based on a large sample of remnants of kills found in the forest.

In 1986–1996, we found 136 carcasses of ungulates killed by wolves by deliberately searching along wolf trails in snow and occasionally during other field work. We searched most intensively during the winter when students and volunteers participated in field work for 1–2 weeks and snow improved detection of carcasses. When a carcass was found, we determined the species, age, and sex (cf. Jędrzejewski et al. 1992, 1993; Okarma et al. 1995). To analyze consumption rates, we described the degree of prey use by wolves and grouped all carcasses into 4 classes: I = 25% of a carcass consumed by wolves (only a small part of prey eaten), II = 50%, III = 75%, and IV = 100% (only large

bones, skin, legs, head, and intestines left). For 85 fresh carcasses, the date and approximate time of killing by wolves were estimated from signs on snow and known recent weather conditions. All tracks of scavengers also were noted (cf. Jędrzejewski et al. 1993). Because it was difficult to assess how much was eaten by wolves or scavengers, carcasses with large portions of meat that apparently were consumed by scavengers (mainly wild boars) were excluded from the analysis of consumption rate.

We also included 513 carcasses of ungulates killed by wolves and registered by game wardens in the exploited part of BPF in the winters of 1985–1986 through 1993–1994 (Okarma et al. 1995). For the purpose of this report, data on wolf prey collected by us and game wardens were combined for each winter season and percentages of each prey species in the total sample were calculated. For the analysis of wolf predation, we also used percentages of prey recalculated from wolf scats.

Prey selection and dietary response.—To assess the selection by wolves of particular species of ungulates, Ivlev's selectivity index (D; modified by Jacobs 1974) was calculated: $D = (r - p)/(r + p - 2rp)$, where r is a fraction of a species among prey of wolves (649 kills found in 1985–1996) and p is the fraction of a species in an ungulate community. D ranged from -1 (total avoidance of a species) to 0 (selection proportional to occurrence) to 1 (maximum positive selection).

Dietary response of wolves to changes in ungulate densities was analyzed based on our data from 1985–1993 (carcasses of ungulates killed by wolves) and earlier information on wolf diets obtained in the Belarussian part of BPF by Gavrin and Donaurov (1954), who covered years 1947–1950 and Bunevich (1988) who studied wolves in 1979–1985. The relative proportion of each species in wolf diet was documented.

Estimation of killing rate by wolves.—From all ungulates killed by wolves, we selected 53 that were found during our intensive searches, combined with snowtracking and, in 1995–1996, with radiotelemetry. Those kills were concentrated in 15 time sequences, each including 2 or more fresh kills (≤ 10) found within the same territory of wolves but separated by <5 days and thus presumed to have been killed in succession. Prey of unmarked wolves (found in 1987–1994) originated largely from 1 pack and in most cases

was located, as confirmed by radiotracking in subsequent years, in the core area of its territory (ca. 50 km^2 of Białowieża National Park). All prey of 1 sequence were arranged according to the estimated date and time of the wolf kill. For all sequences covering 70 days, mean number of days per prey item was calculated as a measure of killing rate by 1 pack. That method yielded a single averaged estimate of the killing rate for all years and seasons for 1987–1996. Multiannual variation in killing rates could not have been tracked.

As an auxiliary check of the accuracy of the estimate of kill rate, we examined our radiotracking data for 4 radiocollared wolves (2 breeding females and 2 subadult females) belonging to 2 packs, from 1994 to 1996 (Okarma et al. 1998). We radiotracked wolves for 5–7 days/week by traveling forest roads with a car or bicycle. In addition to a daily search for wolves, we radiotracked a selected wolf continuously for 5 consecutive days once each month. Radiocollared wolves were followed within a distance of 1–2 km. Depending on our distance from wolves and their activity, the estimated accuracy of locations was 100–500 m. Sixteen sessions of continuous radiotracking were performed, of which 11 contained data suitable for assessing killing rates. We mapped wolf movements with notations of date and time of wolf movements and rests and deduced the minimum number of ungulate prey items used by wolves during each session. In most cases, we did not try to find wolf prey during continuous radiotracking, but we assumed that the locality of a new prey item was marked by a long stay of wolves in the same place at night. Wolves would either kill a new individual or come back to the remains of a previous kill. If wolves stayed in a new location and did not return to any place they had visited on earlier days, we presumed that they fed there on a fresh kill. We were able to identify locations of permanent dens or resting sites known from our long-term radiotracking data, and they were not mistaken for kill sites. Although the continuous radiotracking data allowed only for indirect assessment of killing rate, it corroborated results obtained by kill search.

Calculation of the total predation impact of wolves on ungulates was based on the number of wolf packs detected in each year and the size of their home ranges, the relative amounts of

TABLE 1.—Numbers of wolves in the Polish part of Białowieża Primeval Forest (580 km^2) in the winter seasons of 1985–1986 through 1995–1996. Data on wolf numbers were estimated by game wardens (Jędrzejewska et al. 1996) and obtained from radiotracking (Okarma et al. 1998). Number of wolves in each pack was determined by mapping the results of game inventories and snowtracking. Where these 2 estimates differ, the latter is given in parentheses. Corrected numbers of wolves are the sums of wolf numbers in each pack (in cases of 2 values for the Białowieża National Park [BNP] pack, the higher value is taken). Because the game warden estimates did not account for large territories of wolves and double-counted 1 pack in some years, their estimates are higher than the corrected numbers of wolves.

| Winter season | Number of wolves in Polish BPF | | Number of wolves/pack | | | | Corrected number of wolves | Number of packs |
	Game warden estimates	Radio-tracking	BNP pack	Leśna pack	Ladzka pack	Other packs		
1985–1986	17		5 (6)	6			12	2
1986–1987	18		6	6	1		13	3
1987–1988	19		6 (7)	5	4		16	3
1988–1989	7		4	3			7	2
1989–1990	10		4	5	3		12	3
1990–1991	18		7	5	3		15	3
1991–1992	19		8	7	2	2	19	4
1992–1993	12		6	4	2		12	3
1993–1994	10	12	6	4	2		12	3
1994–1995		14	7	5	2		14	3
1995–1996		15	5	6	4		15	3
Mean	14.3		6.0	5.1	2.6		13.4	2.9
SD	4.05		1.26	1.14	1.01		3.04	0.54

prey species killed, the average killing rate of ungulates per wolf pack, and ungulate densities. Predation impact was analyzed for 1991–1993 and 1995, years with the estimates of ungulate densities obtained by drive censuses.

RESULTS

Wolf numbers.—In 1985–1996, wolf numbers in the Polish part of BPF did not show any trends (Table 1). Game inventories recorded from 7 to 19 wolves (mean, 14.3). Our radiotracking data gave similar results but suggested that in some years game wardens may have counted 1 pack as 2 packs. The corrected (by excluding double counting of a pack) numbers of wolves averaged 13.4. All data indicated the permanent presence of 2 packs in the central part of BPF (Białowieża National Park and Leśna packs) and fairly regular occurrence of a small pack in the northwestern part of BPF (Ladzka pack—Okarma et al. 1998).

In 1991–1992, a 4th pack was recorded. In 1985–1996, the mean size of the 3 most stable packs varied from 2.6 to 6 wolves. The average density of wolves in the Polish part of BPF was 2.31 wolves/100 km^2.

Wolf diet composition and prey selection.—The most important prey of wolves were wild ungulates, making up 97–98% of biomass consumed (Table 2). Cervids comprised 84% of total biomass eaten by wolves in autumn–winter and 79% in spring–summer. The 2nd most important item was wild boar (13–17%). Other prey, ranging in size from shrews to European bison, comprised only small percentages of the total biomass eaten by wolves in either season. Remains of domesticated animals (cows and horses) were found in only 4 fecal samples. In one-third of all fecal samples, we detected grasses and sedges. There was very little seasonal variation in wolf

TABLE 2.—Diet composition (based on fecal analysis) of wolves in the Polish part of the Białowieża Primeval Forest in spring–summer (1 May–30 September) and autumn–winter (1 October–30 April), 1985–1996.

	Spring–summer		Autumn–winter	
Item	% occurrence in feces	% total biomass consumed[a]	% occurrence in feces	% total biomass consumed[a]
Eastern hedgehog, *Erinaceus concolor*			0.3	0.2
Common shrew, *Sorex araneus*			0.9	+
Insectivora total			1.2	0.2
Bank vole, *Clethrionomys glareolus*	1.5	+	1.5	+
Undetermined vole, *Microtus*			1.7	0.1
Undetermined mouse, *Apodemus*	1.5	+		
Undetermined small rodent	1.5	+	0.6	+
Small rodents total	3.0	+	3.2	0.1
Brown hare, *Lepus europaeus*	3.0	0.9	1.2	0.1
Beaver, *Castor fiber*	3.0	2.3		
Red squirrel, *Sciurus vulgaris*			0.3	+
Raccoon dog, *Nyctereutes procyonoides*			1.2	0.2
Medium-size mammals total	6.0	3.2	2.7	0.3
Wild boar, *Sus scrofa*	43.3	17.4	35.2	12.7
Red deer, *Cervus elaphus*	20.9	24.5	9.3	10.7
Roe deer, *Capreolus capreolus*	4.5	1.9	3.2	3.9
Undetermined cervids	68.7	52.8	80.2	69.0
European bison, *Bison bonasus*			0.6	1.8
Wild ungulates total	100.0	96.6	98.6	98.1
Cattle carcass			0.6	0.7
Horse carcass			0.6	0.5
Livestock carcass total			1.2	1.2
Great spotted woodpecker, *Dendrocopos major*			0.3	+
Nuthatch, *Sitta europaea*			0.3	+
Tawny owl, *Strix aluco*			0.6	+
Undetermined large bird	1.5	0.1		
Undetermined medium-size bird			0.9	+
Bird egg	1.5	+		
Birds total	3.0	0.1	1.7	+
Undetermined reptile	1.5	+	0.3	+
Undetermined anuran	4.5	+	0.3	+
Plant material	28.4	+	32.6	0.1
Total number of fecal samples or total grams of biomass consumed per fecal sample	67	1,466	344	1,506

[a] + = <0.05%.

diet. In spring–summer, wild boars (mainly young animals) were hunted more often than in autumn–winter (Table 2).

Among 649 remnants of wolf kills found in BPF, red deer was the dominant species (Table 3). It also was the only species positively selected among wild ungulates. All other prey, especially the bison, were killed less often than expected from their abundance. Wolves hunted young individuals of all species, except for roe deer (the smallest species), more often than adults (Table 3). The known sex and age structure of ungulate prey allowed for calculation of average body mass of wolf prey. With young animals prevailing among wolf kills, the mean masses of prey were rather small (Table 3). Mass of an average ungulate killed by

TABLE 3.—Species and age structure of ungulates killed by wolves in 1985–1996 in Białowieża Primeval Forest. Percentage of each species in the living community is the mean for 1985–1995 (Jędrzejewska et al. 1997; Kossak 1995; Okarma et al. 1997). Selectivity index *D* ranges from −1 (total avoidance) to 1 (the strongest positive selection). Data for sex and age structure of moose killed by wolves are from Okarma et al. (1995). For other ungulates, the averaged values from the following sources are given: red deer—Bunevich (1988), Jędrzejewski et al. (1992), Okarma et al. (1995); roe deer—Jędrzejewski et al. (1992), Okarma et al. (1995); wild boar—Jędrzejewski et al. (1992, in litt.). Mean body masses of ungulates killed by wolves were calculated as the weighted mean from average masses in each sex and age class of given species (Bobek et al. 1992; Dzię-ciołowski 1969; Dzięciołowski and Pielowski 1993; Fruziński 1992; Miłkowski 1970; Pielowski 1988) and respective proportions of these sex and age classes among wolf prey.

| Species | Mean percentage in community | Wolf kills | | *D* index | Sex and age structure of wolf kills (%) | | | Mean body mass of prey (kg) |
		n	%		Adult male	Adult female	Juvenile	
European bison	3.7	1	0.2	−0.90				
Moose	1.3	4	0.6	−0.37	0	25	75	122.5
Red deer	38.5	445	68.6	0.55	13	36	51	69.0
Roe deer	31.7	111	17.1	−0.38	15	64	21	18.1
Wild boar	24.8	88	13.5	−0.36		32	68	44.1
Total	100	649	100					55.0

wolves in 1985–1996 was 55 kg (weighted mean).

Two sources of data (feces and carcasses) for species of ungulates killed by wolves showed similar patterns of variation among years (Fig. 1). The percentage of red deer in wolf kills decreased from 82% in 1986 to 53% in 1994 whereas that of roe deer remained fairly constant and low (17% on average). Analysis of feces also revealed that the percentage of cervids in wolf diet decreased. The opposite trend was observed in the share of wild boar among ungulates killed by wolves. In 1986–1991, wild boars constituted on average 6% of carcasses, but in 1992–1994, they increased to 22%. Similarly, analysis of feces revealed an increase of wild boar from 4% of biomass consumed in 1986–1987 to 24% in 1995–1996 (Fig. 1).

Dietary response.—Wolves showed a strong dietary response to the increase in densities of red deer (Fig. 2). With the 14-fold change of densities of red deer between 1947 and 1991 (0.4–5.7 individuals/km²), the percentage of this species among wolf prey items varied from ca. 10% to nearly 80%. With growing density of red deer, wolves hunted fewer roe deer and wild boar. However, there was a negative response of wolves to increase of densities of these 2 species (Fig. 3). Availability of red deer determined the proportions of other ungulates in wolf diet.

The rate of decrease in hunting pressure by wolves on alternative prey with growing density of red deer was faster for wild boar than for roe deer (Fig. 2). In 1946–1991, the mean percentage of wild boar (calculated from regression equations) among wolf prey items decreased from 37% to 3%, whereas that of roe deer decreased from 29% to 11%. Thus, roe deer was a more commonly sought as prey than was wild boar.

Prey consumption rate.—For 85 carcasses (65 red deer, 16 wild boar, and 4 roe deer), we were able to estimate the amount of time that elapsed since the wolf kill. Of all prey items found on the 1st day after killing (*n* = 39), 57% were class IV, 15% were class III, 18% were class II, and 10% were class I. Of ungulates found on the 2nd day after killing (*n* = 24), 83% were class
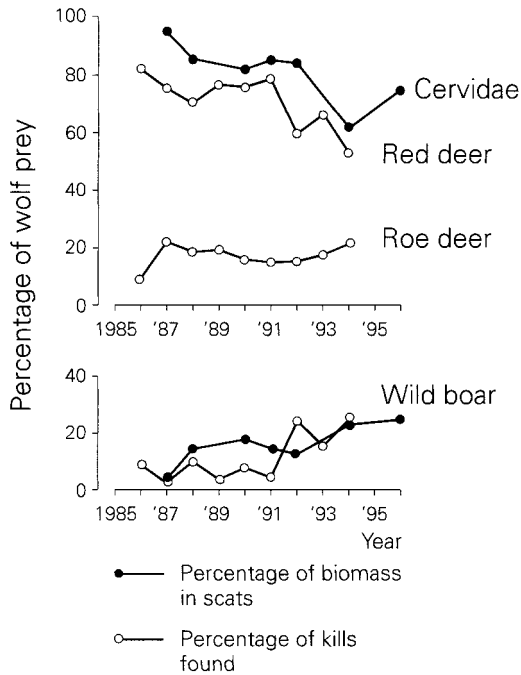
FIG. 1.—Changes in percentages of cervids and wild boar in wolf diets, as revealed by fecal analysis and search for wolf kills in Białowieża Primeval Forest from 1985–1986 to 1995–1996. Because remains of red deer, roe deer, and moose recovered from feces rarely were identified to species, only 1 line for all cervids is given.

III or IV and 17% were class II. Of 22 prey items found on the 3rd day or later after killing, most (64%) were completely eaten, and all others (36%) were class III. Wolves utilized a mean of 91% of the edible parts of ungulate prey. No significant difference between consumption rate of young and adult ungulates by wolves was detected. The mean consumption of carcasses found on the 1st or 2nd day after killing was 82% in young ungulates and 79% in adult animals (G-test for homogeneity of percentages, $G = 0.056$, $d.f. = 1$, $P > 0.50$).

Killing rate.—Each of the prey sequences ($n = 15$) used to calculate killing rate contained from 2 to 10 ungulates, presumed to have been killed consecutively by wolves. The sequences covered 70 days and included 53 carcasses (40 red deer, 12 wild boar,
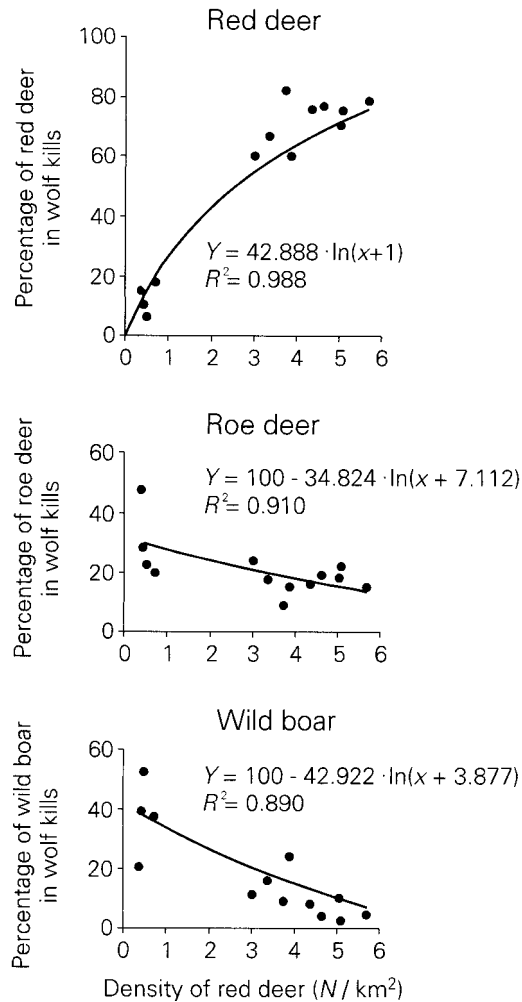

FIG. 2.—Dietary responses of wolves to changes in densities of red deer. Each point denotes 1 year or a mean value for several years. Data from Gavrin and Donaurov (1954) and Bunevich (1988) for the Belarussian part of Białowieża Primeval Forest (4 seasons for 1946–1947 through 1949–1950 and 1 averaged value for 1979–1985) were combined with data on carcasses analyzed in this study for winter only, 1985–1986 through 1992–1993. Red deer densities for adequate years and parts of Białowieża Forest are from Jędrzejewska et al. (1997).

and 1 roe deer). On 56% of the days, wolves killed 1 ungulate, and on 10% of the days, they killed 2 ungulates. On 30% of days, we found no ungulates killed by
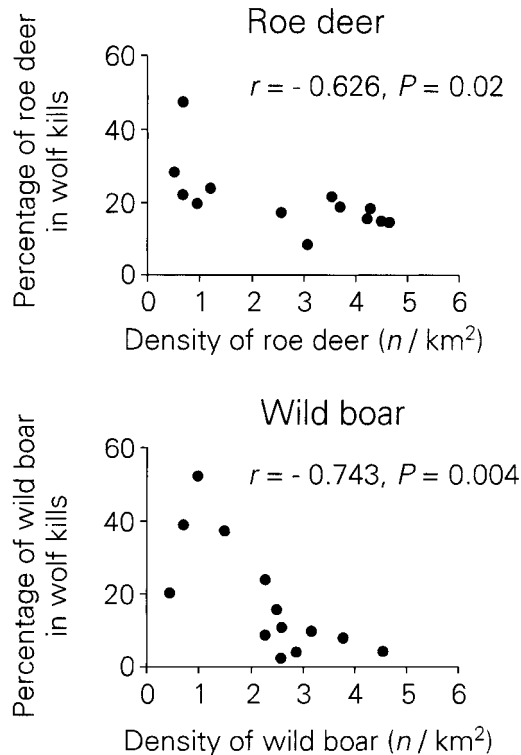
FIG. 3.—Percentages of roe deer and wild boar among ungulate prey of wolves in relation to population densities of these ungulates. Each point denotes 1 year or a mean value for several years; *r* is Pearson's correlation coefficient (sources as in Fig. 2).

wolves. Based on those data, the killing rate varied from 0.6 to 1.0 prey per wolf pack per day, with a killing rate of 0.78 ± 0.15 ($\bar{X} \pm SD$) prey items per pack per day or 1 prey item every 1.32 ± 0.23 days. Given the mean pack size of 5.6 wolves (Białowieża National Park and Leśna packs in 1985–1996), that was equivalent to 0.14 ungulate prey killed by 1 wolf per day.

Another estimate of killing rate by wolves came from 11 continuous radiotracking sessions that covered 47 days and included 33 locations of presumed prey and 3 prey items found. In each session, the killing rate could have ranged from 0.4 to 1.0 ungulates per pack per day. The killing rate would be 0.78 ± 0.22 ungulates per wolf pack per day or 1 prey item every 1.4

± 0.49 days. That assessment was nearly identical with that based on carcass sequences from snowtracking.

With mean body mass of wolf prey estimated as 55 kg, the average biomass used by 1 wolf was 7.7 kg/day, but that included remains left by wolves. If 75% was assumed as a consumable fraction of prey (Messier and Crete 1985) and an average degree of utilization of edible parts (91%) was accounted for, food consumption by 1 wolf was 5.3 kg/day.

Predation impact.—In 1991–1996, wolves killed 117–160 ungulates/100 km^2 annually (Table 4). The highest predation was on red deer (57–105 individuals/100 km^2), then wild boar (19–38 individuals/100 km^2) and roe deer (19–25 individuals/100 km^2). Number of moose killed by wolves was always very low (0–2 individuals/100 km^2). In 1991–1996, wolf predation on red deer expressed as a percentage of deer numbers was fairly stable. It constituted 9–13% of the spring–summer (seasonally highest) numbers of deer and 32–47% when compared with annual production of young (Table 4). During the study, harvest of red deer by hunters was high (average of 21% of spring–summer numbers of deer and 72% of their annual increase). Combined predation by wolves and lynxes (the latter estimated by Okarma et al. 1997) and harvest by hunters exceeded yearly production of red deer and caused a population decline (Fig. 4). Compared with the annual mortality of red deer (measured as the difference between spring–summer and subsequent late winter densities), harvest by hunters appeared more important (average of 45% of the total mortality) than wolf predation (29%).

Wolf predation on roe deer accounted for 3–4% of its spring–summer numbers and 8–10% of the yearly increase due to reproduction. It played a small role in the annual mortality of roe deer (average of 5.5%), less than the impact of harvest by hunters and lynx predation (Table 4; Fig. 4). Thus, wolves contributed little to the decline of

TABLE 4.—Predation impact by wolves on red deer, roe deer, moose, and wild boar in Białowieża Primeval Forest in 1991–1996. Calculations of yearly predation by wolves was based on number of packs (except for Ladzka pack, see Table 1), respective areas utilized by each pack, proportions of each prey species among wolf kills, and the average killing rate (1.32 days/ungulate prey/wolf pack). Pack size in the years listed was 5.33 ± 1.80 ($\bar{X} \pm SD$). Proportions of each prey species are based on carcasses found in 1992–1993 or recalculated from percentages of biomass of each prey group in wolf feces and mean body masses of prey in 1991–1992, 1993–1994, and 1995–1996.

Parameter	Years (late winter to late winter)				Mean (SD) or estimated average
	1991–1992	1992–1993	1993–1994	1995–1996	
WOLF POPULATION					
Area used for calculation (km²)	520	470	470	470	483 (25)
Number of wolf packs	3	2	2	2	2.25 (0.5)
RED DEER POPULATION DYNAMICS					
Density in March (number of deer/ 100 km²)	607	416	359	463	461 (106)
Percentage of adult females	46	44	48	47	46 (2)
Number of juveniles per adult female	0.9	0.9	0.9	0.9	0.9
Juveniles born in spring (number of deer/100 km²)	251	165	155	196	192 (43)
Density in May (number of deer/100 km²)	858	581	514	659	653 (149)
Annual mortality (number of deer/100 km²)	442	222			250
Wolf predation					
Percentage of red deer among wolf prey	66.1	66.7	48.6	52.6	59 (9)
Total yearly predation (number of deer/100 km²)	105	78	57	62	76 (22)
Predation as percentage of					
Spring–summer density of red deer	12	13	11	9	11 (2)
Red deer increase due to breeding	42	47	37	32	39.5 (6)
Annual mortality of red deer	24	35			29
Harvest by hunters					
Annual harvest (number of deer/100 km²)	133	131	131	140	134 (4)
Harvest as percentage of					
Spring–summer density of red deer	16	23	25	21	21 (4)
Red deer increase due to breeding	53	79	85	71	72 (14)
Annual mortality of red deer	30	59			45
ROE DEER POPULATION DYNAMICS					
Density in March (number of deer/ 100 km²)	492	425	288	324	382 (93)
Percentage of adult females	46	45	51	41	46 (4)
Number of juveniles per adult female	1.45	1.45	1.45	1.45	1.45
Juveniles born in spring (number of deer/100 km²)	328	277	213	193	253 (62)
Density in May (number of deer/100 km²)	820	702	501	517	635 (153)
Annual mortality (number of deer/100 km²)	395	414			300
Wolf predation					
Percentage of roe deer among wolf prey	15.4	17.6	18.2	15.9	17 (1)
Total yearly predation (number of deer/100 km²)	25	21	21	19	22 (2)

TABLE 4.—Continued.

Parameter	Years (late winter to late winter)				Mean (*SD*) or estimated average
	1991–1992	1992–1993	1993–1994	1995–1996	
Predation as percentage of					
Spring–summer density of roe deer	3	3	4	4	3.5 (1)
Roe deer increase due to breeding	8	8	10	10	9 (1)
Annual mortality of roe deer	6	5			5.5
Harvest by hunters					
Annual harvest (number of deer/100 km²)	85	114	102	44	86 (31)
Harvest as percentage of					
Spring–summer density of roe deer	10	16	20	21	14 (5)
Roe deer increase due to breeding	26	41	48	23	35 (12)
Annual mortality of roe deer	22	28			25
MOOSE POPULATION DYNAMICS					
Density in March (number of moose/ 100 km²)	37	12	14	2.5	16 (15)
Percentage of adult females	42	39	50	44	44 (6)
Number of juveniles per adult female	1.0	1.0	1.0	1.0	1.0
Juveniles born in spring (number of moose/100 km²)	15	5	7	1	7 (6)
Density in May (number of moose/ 100 km²)	52	17	21	3.5	23 (20)
Annual mortality (number of moose/ 100 km²)	40	3			21
Wolf predation					
Percentage of moose among wolf prey	1.2	0	0.7	0.8	0.7 (0.5)
Total yearly predation (number of moose/100 km²)	2	0	1	1	1 (1)
Predation as percentage of					
Spring–summer density of moose	4	0	5	29	10 (13)
Moose increase due to breeding	13	0	14	100	32 (46)
Annual mortality of moose	5	0			2.5
Harvest by hunters					
Annual harvest (number of moose/100 km²)	7	4.5	5.5	1	4.5 (2)
Harvest as percentage of					
Spring–summer density of moose	13	26	26	29	24 (7)
Moose increase due to breeding	47	90	79	100	79 (23)
Annual mortality of moose	18	150			
WILD BOAR POPULATION DYNAMICS					
Density in March (number of boar/ 100 km²)	458	209	308	225	300 (114)
Percentage of adult females	15	16	16	16	16 (1)
Number of juveniles per adult female	3.2	5.9	5.9	5.9	5.2 (1.4)
Juveniles born in spring (number of boar/100 km²)	220	197	291	212	230 (42)
Density in May (number of boar/100 km²)	678	406	599	437	530 (130)
Annual mortality (number of boar/100 km²)	469	98			

TABLE 4.—Continued.

Parameter	Years (late winter to late winter)				Mean (*SD*) or estimated average
	1991–1992	1992–1993	1993–1994	1995–1996	
Wolf predation					
Percentage of wild boar in wolf prey	17.3	15.7	32.5	30.7	24 (9)
Total yearly predation (number of boar/100 km²)	28	19	38	36	30 (9)
Predation as percentage of					
Spring–summer density of wild boar	4	5	6	8	6 (2)
Wild boar increase due to breeding	13	10	13	17	13 (3)
Annual mortality of wild boar	6	19			12.5
Harvest by hunters					
Annual harvest (number of boar/100 km²)	142	90	45	48	81 (45)
Harvest as percentage of					
Spring–summer density of wild boar	21	22	8	11	16 (7)
Wild boar increase due to breeding	65	46	15	23	37 (23)
Annual mortality of wild boar	30	92			61

roe deer, which was caused by hunting and lynx predation.

In wild boar, harvest by hunters was more important than wolf predation, compared with spring–summer densities of boar (average, 16% harvested by hunters and 6% taken by wolves) or their yearly increase due to reproduction (37% and 13%, respectively). At the highest boar densities in 1991–1992, the 2 mortality factors combined had smaller impact on the wild boar population (36% of annual mortality) than at lower densities, after population decline (100% of mortality; Fig. 4). Wolf predation on moose was most variable; it was low (0–5%) at high densities of moose but increased to 29% of spring–summer numbers (≤100% of annual production of young) at low densities, which were caused by harvest by hunters (Table 4).

DISCUSSION

Our study revealed the main features of wolf predation on ungulates in the temperate forests of Europe under conditions of fairly high densities of ungulates. First, we documented a strong link between wolves and red deer. Red deer were the preferred prey of wolves; changes in population size of red deer caused dietary response from wolves. Opposite to predictions by Messier (1995a), wolves did not respond to growing densities of any other prey species. Their consumption of other ungulates, particularly the wild boar, was shaped by densities of red deer. Roe deer, the smallest ungulate of BPF, was a fairly stable component of wolf diet, always captured less often than expected from its prevalence in ungulate community. Very small groups and a secretive and elusive style of life in forests (Jędrzejewska and Jędrzejewski 1998) make roe deer a difficult prey for wolves.

The mutual relationship between wolves and red deer was evident also from the analysis of the 100-year series of data on ungulate and wolf densities in BPF (Jędrzejewska et al. 1997). Numbers of red deer and wolves were correlated negatively, which resulted from substantial increase in the deer population in periods of persecution and extermination of wolves. Furthermore, the rate of annual population growth of red deer was correlated negatively with combined densities of wolves and lynxes. The densities of none of the other ungulate
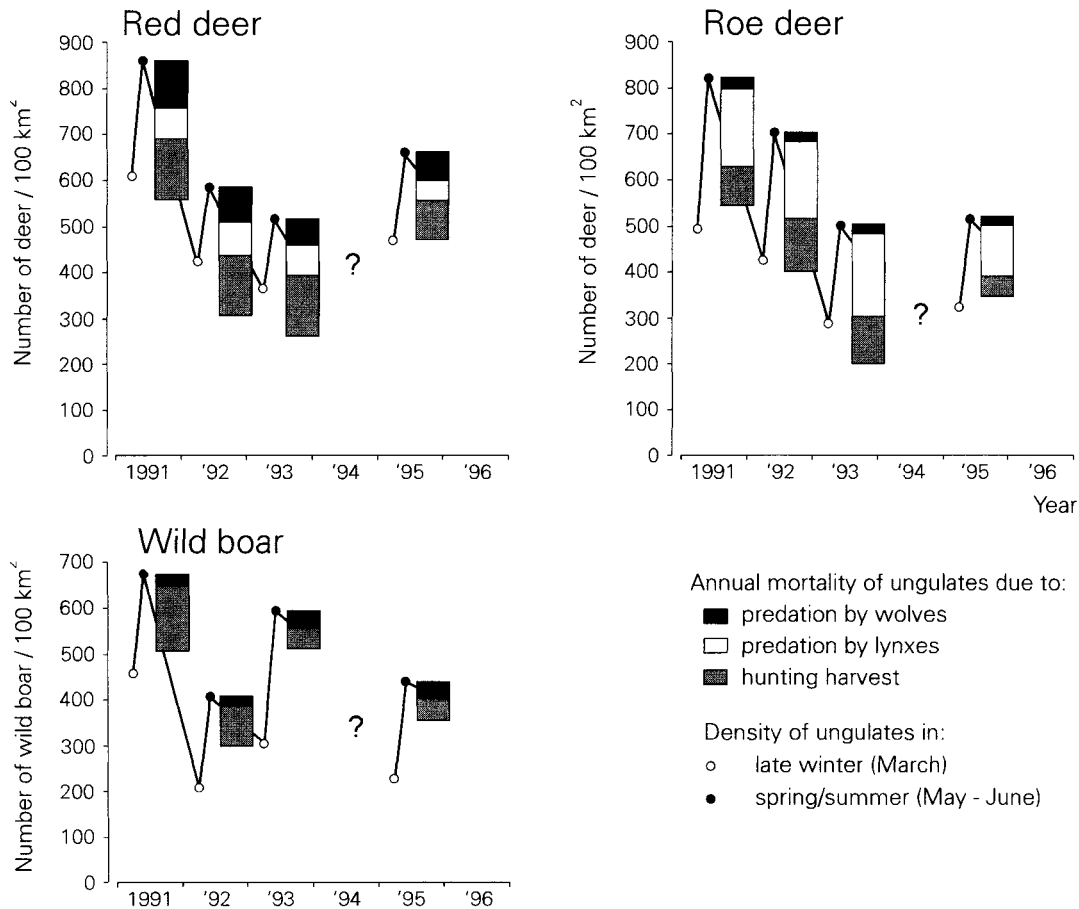
FIG. 4.—Total annual predation by wolves and lynxes and annual harvest by hunters compared with densities of red deer, roe deer, and wild boar in Białowieża Primeval Forest from 1991 to 1995–1996. Late winter (March) densities of ungulates were surveyed by drive censuses; spring–summer (May–June) densities were calculated based on the proportion of adult females in populations in late winter and mean number of juveniles per adult female in spring. Data on lynx predation from Okarma et al. (1997).

species were correlated with wolf densities as markedly as were those of red deer (Ję-drzejewska et al. 1997).

The 1st estimate of kill rates by European wolves, as directly measured in Białowieża, was 0.14 ungulate prey items per day per wolf. This figure is higher than that usually reported from North America. In Isle Royale National Park, wolves hunted moose at a rate 0.01–0.05 prey items per wolf daily (Messier 1991). Moose, however, are about 3–4 times heavier than the average prey item in BPF (recalculated from Messier and

Crete 1985; Thurber and Peterson 1993). Our results are similar to data on wolves hunting caribou (*Rangifer*) or deer (*Odocoileus*). In Alaska, wolves killed caribou with the rate of 0.03–0.11 ($\bar{X} = 0.09$—Dale et al. 1994; Stephenson and James 1982). In Ontario, a kill rate of 0.06 deer per wolf per day was recorded by Kolenosky (1972). Furthermore, high availability of ungulates and low densities of wolves in our study area have contributed to the high killing rate we observed.

On Isle Royale, Thurber and Peterson

(1993) related killing rate to the size of wolf packs. With pack size growing from 2 to 8 wolves, the daily killing rate of a pack increased from 0.09 to 0.16 ungulates/day. For 5–6 wolves in a pack (typical pack size in our study), the daily killing rate of Isle Royale wolves would have been 0.12 moose/pack or 0.02 moose/wolf (calculated from regression equation of Thurber and Peterson 1993). In our study, wolf packs ranged in size from 2 to 8 animals, but mean pack size (used in calculations of predation impact) varied little among years. Thus, possible variation in killing rate due to varying pack size had little influence on accuracy of calculations of predation impact in our study.

Potential prey consumption rates by European wolves were calculated by Głowaciński and Profus (1997) based on metabolic rates of wolves calculated from laboratory experiments. These authors arrived at estimates of 1.7–2.8 kg of prey biomass per wolf per day. This is only one-half of the value obtained in our study, which suggests that the total impact of wolves on ungulates calculated by Głowaciński and Profus (1997) from energy requirements of wolves is seriously underestimated.

In BPF, wolves exerted highest predation impact on red deer. They took more deer than lynxes did but fewer than did human hunters. For the seasons 1991–1992 through 1995–1996, mortality due to these 3 factors usually exceeded the yearly production of young and caused decline of deer population. This decline accelerated in 1996 and 1997 (Jędrzejewski et al. 1999). The results of our study suggest that effects of predation and harvest by hunters on the total mortality of ungulates are additive. Hunting in BPF is most intense from October through February. At this time, wolf and lynx predation is determined largely by the existing density of adults and number of young. In 1991, forestry personnel began intense reduction of ungulates to protect forest plantations from browsing. When added to this culling process, predation contributed significantly to the decline of ungulate numbers.

There are still many unanswered questions about wolves in European biomes. Variation in kill rates in relation to seasons and to changes in ungulate abundance remains unknown. Also, dietary responses of wolves to changes in ungulate abundance in localities where red deer are scarce or absent need to be investigated. The role of predation, whether in regulating or limiting (sensu Messier 1995b; Sinclair 1989) populations of European ungulates, needs further study.

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