

KILL RATES AND PREDATION BY WOLVES ON UNGULATE POPULATIONS IN BIAŁOWIEŻA PRIMEVAL FOREST (POLAND)

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Abstract. Wolf (*Canis lupus*) kill rates, factors affecting their variation, and predation impact on ungulates were studied in the Polish part of Białowieża Primeval Forest (580 km²). With the mean size of hunting groups being 4.4 individuals, wolves killed, on average, 0.513 ± 0.04 prey·(pack)⁻¹·d⁻¹ (mean \pm 1 SE); 63% of prey were red deer (*Cervus elaphus*), 28% were wild boar (*Sus scrofa*), and 4% were roe deer (*Capreolus capreolus*). Per capita kill rate averaged 0.116 ungulates·(wolf)⁻¹·d⁻¹, and daily food intake was 5.58 ± 0.32 kg·(wolf)⁻¹·d⁻¹. Kill rate on red deer was affected by snow cover ($P < 0.001$). A pack of wolves killed, on average, 0.264 deer/d in seasons with no snow and 0.587 deer/d when snow was 17 cm deep. The increase in kill rates coincided with a decline in the condition of juvenile (but not adult) deer in late winter (mean marrow fat content in the femur 66% in October–January vs. 27% in February–March). Per capita kill rates decreased slightly (not significantly) with the increasing size of wolf hunting group. However, the amount of food acquired per wolf did not differ among groups containing 2–6 individuals, because larger packs killed bigger prey more often and small prey less frequently than did small packs. Wolf kill rates on wild boar were higher in spring–summer (0.242 ± 0.06 boar·(pack)⁻¹·d⁻¹), when piglets were present, than in autumn–winter (0.106 ± 0.04 boar·(pack)⁻¹·d⁻¹). Annually, wolves killed on average 72 red deer, 16 roe deer, and 31 wild boar over a 100-km² area. Compared to prey densities, wolves were an important agent of mortality for red deer only, taking annually 12% of spring–summer (seasonally highest) numbers of deer, which was equivalent to 40% of deer annual increase due to breeding and 40% of their annual mortality. Compared to winter densities (3–6 deer/km²), percentage predation by wolves was inversely density dependent; thus wolves limited deer numbers but did not regulate prey population. By eliminating a substantial proportion of the annual production of the deer population, wolves hamper its growth and prolong the time until it reaches carrying capacity of the habitat. However, wolf predation alone is a poor predictor of deer population dynamics, because deer are also subject to lynx (*Lynx lynx*) predation and hunting harvest.

Key words: *Canis lupus*; *Capreolus capreolus*; *Cervus elaphus*; deer population; density dependence of predation; European pristine forests; hunting group size; snow cover; *Sus scrofa*; wolf kill rates.

INTRODUCTION

The rate at which wolves kill their prey in relation to prey density, known as functional response (Holling 1959), is an essential component of their predation on ungulates. With different types of functional responses and various numerical reactions of wolves to changes in prey densities, the role of predation can range from regulatory (density-dependent predation rates), to limiting (density-independent predation), to depensatory (inversely density-dependent predation rates) (Sinclair 1989, Messier 1991, 1995). However, both scarcity and high variability of the available empirical data on wolf kill rates often make it difficult to distinguish between type II (asymptotic) and type III (logistic) functional

responses, especially in the low range of prey densities (Messier 1994, Boyce 2000, Hayes and Harestad 2000). Aside from sampling errors, this variation in empirically assessed kill rates stems from the fact that the rate at which wolves capture prey is governed by a set of factors much more complex than just prey density. Among these factors are snow cover (Huggard 1993), wolf group size (Thurber and Peterson 1993, Hayes et al. 2000), vulnerability of prey (Peterson and Allen 1974), and availability of alternative prey (Dale et al. 1994). All such external factors can add substantial variation to wolf predation rates, independent of prey density.

Unknown is the seasonal variation in kill rates by wolves, especially the response to prolific abundance of newborn ungulates in spring–summer. This results from the restrictions of the method of detection used (search for kills from aircraft), which is effective during

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snowy periods (e.g., Mech et al. 1995, Hayes et al. 2000). Finally, the rarely studied aspect of wolf–ungulate relationships is wolf kill rate in multispecies prey communities. Most North American studies were conducted in ecosystems where wolves coexisted with one or two prey species (e.g., Fritts and Mech 1981, Gasaway et al. 1983, 1992, Messier 1991). In Eurasia, however, wolves usually coexist with three or four, and exceptionally with up to five or six species of ungulates (Okarma 1995). Moreover, the unique feature of Eurasian ungulate communities is the presence of the wild boar (*Sus scrofa*), which are fertile animals, producing large numbers of vulnerable young every spring (Jędrzejewska and Jędrzejewski 1998). Estimating kill rates in such communities is difficult, because small prey, such as wild boar piglets, are usually eaten completely by wolves. Thus, techniques other than aircraft search for kill remains must be applied, especially in spring and summer.

Kill rates of Eurasian wolves have not yet been studied directly, but data on wolf prey selection and diet composition suggest that densities of red deer (*Cervus elaphus*), wolves' preferred prey, may be governing kill rates on both deer and other co-occurring species of ungulates (Jędrzejewski et al. 2000). The influence of physical environment, wolf sociality, and other extrinsic factors on kill rates of Eurasian wolf remains unknown.

The role of predation in shaping ungulate populations has been discussed within the conceptual framework that distinguishes between density-dependent factors involved in population regulation and other limiting factors that may influence the population rate of increase but cannot have any regulatory impacts (Sinclair 1989, Messier 1991, 1994, 1995, Boutin 1992). In North America most research done on moose (*Alces alces*) evidenced that wolf predation rates were density dependent at low moose densities and changed to depensatory at moderate to high ungulate densities (Messier 1991, 1994, Hayes and Harestad 2000). Some research on caribou (*Rangifer tarandus*) showed that wolf predation rates were inversely density dependent over the whole range of prey densities (Dale et al. 1995). Furthermore, in multipredator ecosystems, the overall trend of prey population dynamics depends on the combined (usually additive) effects of all predators (e.g., Gasaway et al. 1992, Kunkel and Pletscher 1999).

The role of predation in shaping the numbers of European ungulates was assessed indirectly, by analysis of ungulate responses to wolf and lynx (*Lynx lynx*) control by humans in the series of 100-yr population dynamics of predators and ungulates (Jędrzejewska and Jędrzejewski 1998). The red deer irrupted in the absence of wolves, and the roe deer (*Capreolus capreolus*) in the absence of lynxes. Co-occurring European bison (*Bison bonasus*), moose, and wild boar responded to predator eradication weakly or not at all. Those unintended but well replicated "experiments" provide ev-

idence for predation acting as a major limiting factor for deer populations in Europe. Whether predators can also regulate their prey remains yet unknown.

The study presented in this paper was conducted in the last remnant of the natural temperate forests typical of European lowlands (Białowieża Primeval Forest, Poland), where wolves coexist with five species of ungulates (European bison, moose, red deer, roe deer, and wild boar) and with the Eurasian lynx. The aims of our study were as follows. (1) Based on a three-year (1996–1999) intensive radio-tracking study of three to four wolf packs, we endeavored to determine the kill rates by wolves and to show how they were affected by the following: a) social features of wolves, such as pack size and coherence; b) ambient conditions, especially severity of winter; c) characteristics of prey (prey size and availability); and d) seasonal and between-year variation in prey abundance and vulnerability. (2) We calculated the magnitude of wolf predation on three species of ungulates, and having combined the new data with the earlier (1991–1995) information on wolf predation rates (Jędrzejewski et al. 2000), we attempted to explain the role of wolves in the ungulate community of European temperate forests.

MATERIALS AND METHODS

Study area

Białowieża Primeval Forest (BPF; at present ~1450 km²) is located on the Polish–Belarussian border (52°45' N, 24° E). Due to centuries-long protection as a royal forest of Polish kings, Lithuanian dukes, and Russian czars, BPF is the best preserved woodland of its size, typical for the European lowland temperate forests. The Polish part of BPF, where this study was conducted (580 km²), consisted of exploited (480-km²) and protected (100-km²) regions. The exploited part (mean age, 72 yr) had timber harvest, reforestation, and game hunting. In the protected area (Białowieża National Park [BNP]), most tree stands were of natural origin (mean age, >100 yr). Neither exploitation of timber nor game hunting was allowed in BNP. It has been a Man and Biosphere Reserve of the United Nations Education, Scientific, and Cultural Organization (UNESCO) since 1977 and a World Heritage Site since 1979.

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*). Vicinities of small forest rivers and brooks are habitats of riverside forests of alder and ash (*Fraxinus excelsior*) with admixture of elm (*Ulmus glabra*). The only open areas within the

woodland are marshes of sedges (*Carex*) and reeds (*Phragmites*) in narrow river valleys (0.1–1 km wide) and several glades with small villages. There are only five bituminous roads of a total length ~50 km accessible for public transportation in the Polish part of BPF. More information on BPF was given by Faliński (1986) and Jędrzejewska and Jędrzejewski (1998).

Of five species of Białowieża's ungulates, the bison is a protected species, but its population is kept stable by yearly culling. The other four species are hunted in the exploited part of BPF, but not in BNP. In the 1990s, the mean winter densities of ungulates (all species pooled) were ~10 individuals/km², equivalent to ~820 kg crude biomass per square kilometer (Jędrzejewski et al. 2000). The guild of large predators was impoverished in the 19th century by extermination of brown bear (*Ursus arctos*), and currently it contains the wolf and the lynx. During the past 150 yr, the wolf population ranged from temporary extermination due to predator control to very high densities (Jędrzejewska et al. 1996). In the Polish part of BPF, wolves have been protected since 1989, though some poaching does occur. In the Belarussian part, wolves are still heavily hunted. In 1996–1999, 5–16 wolves/yr were shot, which constituted 10–64% of their estimated winter numbers. In 1981, a wire fence was constructed in BPF on the Polish–Soviet state border, but wolves are known to cross it in some places. In the 1990s, typical home ranges of wolf packs covered 100–300 km², and wolf densities were 2–2.6 individuals/100 km² (Okarma et al. 1998).

The climate of BPF is transitional between Atlantic and continental types, but continental features prevail. During our study (1996–1999), mean daily temperature in January was –3.9°C and 19.1°C in July. Snow cover persisted on the ground for 60–157 d (mean, 96 d), and maximal depth ranged 13–63 cm in the three study winters. Mean annual precipitation was 622 mm.

*Estimating the kill and consumption rates,
and predation impact by wolves*

In 1996–1999, radio-tracking of 12 wolves belonging to four packs was conducted in the Polish part of BPF. Wolves were captured with “fladry” and nets (Okarma and Jędrzejewski 1997) or with foot snare traps (Aldrich foot snare traps for black bears, modified by authors). Foot snare traps were equipped with a radio-alarm system (A. Wagener, Köln, Germany), which allowed us to release the animal within 1–2 h after capture. Wolves were immobilized with 1.2–1.8 mL of a xylazine–ketamine mixture (583 mg of Bayer's Rompun [Bayer, Leverkusen, Germany] dissolved in 4 mL of Parke-Davis Ketavet 100 mg/mL [Parke-Davis, Munich, Germany]) and were fitted with radio collars (models MOD500 and MOD505, Telonics, Mesa, Arizona, USA; model LM Activity Collar, AVM Instruments, Livermore, California, USA; model LT14-2TS-HD-MS, Telemetry Systems, Mequon, Wisconsin,

USA; model 9D Advanced Telemetry Systems, Isanti, Minnesota, USA). Most radio collars were equipped with head position activity sensors, which helped to identify if wolves were feeding, resting, or traveling. Radio-collared wolves were located by following forest roads with vehicle or bicycle. Sessions of two to nine days (usually six) of continuous radio-tracking (24 h/d, usually done by three to six people working in 8-h shifts) were conducted for eight radio-collared wolves belonging to four packs. The other four wolves were tracked for periods too short to yield data suitable for estimating kill rates, due to dispersal or death from poaching. During continuous radio-tracking the mean distance (± 1 SD) between the observer and the wolves was 938 ± 577 m, and the presence of an observer had no effect on wolves' activity or movements (J. Theuerkauf and W. Jędrzejewski, *unpublished manuscript*).

In 1996–1999, we conducted 43 sessions of continuous radio-tracking, which together covered 234 d (from 2–9 d/session; mean ± 1 SD, 5.4 ± 1.8) and were combined with searching for prey remains and wolf scats. During the sessions, we strove to locate all potential sites of kills and prey consumption by wolves (based on their activity and duration of stay). After the wolves had left such places, regular searches for prey remains and wolf scats were conducted. In winters, snow tracking was also conducted in an attempt to cover as long a portion of wolves' trail as possible. When prey were found, the species, sex, and age were determined, percentage consumption by wolves was assessed visually, and jaws were extracted for a more detailed age estimation. In 47 red deer killed by wolves, marrow samples of 2–5 cm³ were taken from the femur ($n = 34$), tibia ($n = 13$), metatarsus ($n = 7$), or mandible ($n = 19$). The marrow samples were oven-dried at 50°C to constant mass. The percentage of fat in a sample was calculated as dry mass/fresh mass $\times 100$ (Neiland 1970). Based on highly significant correlation between marrow fat in femur and all other bones sampled (r , 0.96–0.97, P , <0.0005–0.002), we scaled the samples for all deer to represent fat content in the femur.

Information from radio-tracking, tracks on snow, and general appearance (freshness) of prey allowed us to estimate when the prey had been killed by wolves (the date and often the time of kill). If the prey was estimated to have been killed before our radio-tracking session, it was also included in the analysis, and an adequate time (maximally 5 d) was then added to that series.

As finding prey was usually difficult (due to inadequate precision of wolf localization, dense vegetation, and inaccessible terrain in many places of BPF), we applied an auxiliary method of prey detection based on scat analysis. The assumptions were based on the work by Floyd et al. (1978), who found that wolves defecated the undigested prey remains 8–56 h (0.3–2.3 d) after consumption. In BPF, wolves usually consumed a large

prey within not longer than three days (Jędrzejewski et al. 2000), so the time elapsed from killing a deer or another large prey to depositing scats from the last meals on that prey would be maximally five days. The freshness of scats was estimated in the field and verified by radio-tracking data. All scats found during radio-tracking sessions and searches for prey were dried, masses measured, washed through a 0.5-mm sieve, and then dried and weighed again. Species, age (as adult or juvenile), and number of prey individuals were identified whenever possible, based on undigested bone, hoof, and hair remains according to methods specified by Pucek (1981) and our own comparative procedures. Microscope analysis of hair was conducted according to Debrot et al. (1982) and Teerink (1991).

Based on radio-tracking data and scat freshness, the date of defecation was estimated for each scat. Then, in accordance with Floyd et al. (1978), we assumed that all small prey (newborn deer, wild boar piglets, hare, fox, beaver, dog) were killed and consumed 8–56 h (0.3–2.3 d) prior to defecation, but for calculations we applied a conservative estimate of two days for all small prey to prevent an overestimate of the killing rate. In the cases of larger prey detected in scats, we considered the “wash-out” index, i.e., the ratio of a scat mass before washing through a sieve to the mass of washed, undigested prey remains. This index depends on the proportion of amorphous mass (remains from digestion of meat and other soft tissues), which the scat contained. The wash-out index can vary from one (if a scat contained only hard undigested parts, such as bones and hair) to positive infinity (if wolves consumed only soft tissues of a freshly killed prey). To find out which values of the wash-out index indicate consumption of a newly killed (fleshy) prey, we compared two subsamples of wolf scats, both found in situations when the wolves were known to have recently fed on a kill: (1) scats deposited 0.5–2 d after killing that prey ($n = 103$), and (2) scats deposited ≥ 3 d after killing ($n = 14$). Scats in subsample (1) had the wash-out index varying within the range 1.2–140.7 (mean \pm 1 SE, 8.4 ± 1.5), whereas those in subsample (2) spanned 1.5–7.4, only (3.2 ± 0.5). Therefore, we accepted a conservative criterion that prey recovered from a scat with wash-out index > 7 had been killed and consumed two days prior to scat deposition. A prey recovered from scat with index 1–6 was assumed to have been killed five days prior to scat deposition. If the kill date was estimated to be earlier than the beginning of radio-tracking session, we added the appropriate number of days to that session for calculation of wolf kill rate to prevent its overestimate.

The list of wolf kills found during any session of radio- and snow tracking was supplemented with the prey recovered from scats only in those cases when prey specimens found in scats differed in species or age from the prey remains already found by us in the forest. Also, remains of prey of the same species and

age recovered from two or more scats, which had been found in one session of radio-tracking, were conservatively counted as one prey individual. In all, during the continuous radio-tracking sessions, we found the remains of 127 animals killed or scavenged upon by wolves. In addition, we collected 328 scats. In 188 of them, undigested prey remains were of the same species and age class of prey as the prey already found in the forest. In 174 scats, a total of 90 new prey were revealed, half of them being of small size (e.g., wild boar piglets, hare), which were completely eaten by wolves. All prey analyzed ($n = 217$) were estimated to have been killed (or scavenged upon) by wolves during 323 d, in 43 sessions of 4–15 d (mean \pm 1 SD, 7.5 ± 2.1 d); 66 d in 10 sessions represented the spring–summer season (1 May–30 September), and 257 d in 33 sessions covered the autumn–winter season (1 October–30 April). Any other prey of wolves found by us or by the forestry personnel outside the time frames of the continuous radio-tracking and prey searching were not included in the calculation of wolf kill rates, but were added to the whole sample of prey remains found or recovered from scats, and were used for calculating species structure of wolf prey.

Kill rates by wolves were estimated by two methods: (1) based on 46 time intervals between consecutive kills (only the prey found in the forest were used in this analysis); and (2) based on wolf kills found in the forest and prey detected from wolf scats, both estimated to have been killed and consumed by wolves during a total of 323 d. In the first method, we considered only those kills that we were reasonably sure had not been separated in time by any other undetected prey. The second method, relying on a much bigger sample than the first one, gave us an opportunity to analyze variation in wolf kill rates.

During the field work, tracks of wolves on snow and mud, cases of howling, and visual observations were recorded, and attempts were made to count the number of wolves in each pack and the number of wolves engaged in hunting and utilization of a kill. In 89 kills (47% of the total sample) an actual size of a hunting group was determined. In other cases, we assumed that the whole pack took part in a hunt and consumption of prey, an exception being the BNP pack in the winter season 1996–1997. That pack consisted of seven wolves that had not been observed hunting together; instead, that pack regularly split into fractions of three and four individuals.

Food consumption by wolves was estimated based on the degree of prey utilization by wolves (assessed visually in the forest), body mass of prey, and mass of uneaten remains. Body masses of various species, along with sex and age classes of prey, were taken from the following sources, reporting measurements from Białowieża Forest or other Polish populations of ungulates: Miłkowski (1970), Kozłowski (1975), Pucek (1981), Miłkowski and Wójcik (1984), Pielowski

(1988), Bobek et al. (1992), and Dzieciółowski and Pielowski (1993).

In 13 cases of prey visually assessed as completely eaten by wolves (7% of all kills analyzed), we were able to measure the mass of the discarded parts. Based on the mass of leftovers, we calculated that in large prey (body mass >65 kg live mass) wolves consumed 65% of their live mass; in medium-sized prey (20–65 kg), 75%; and in small prey (<20 kg body mass) a complete consumption by wolves meant the utilization of 90% of their live mass. If the prey was visually assessed as incompletely consumed by wolves (i.e., <100%), we calculated the actual consumption accordingly.

In the cases of wolves' scavenging on full corpses of dead ungulates (bison, domestic cow, and domestic pig), we estimated that the daily consumption was ~4.5 kg/wolf (data obtained in the research on scavenging in BPF; N. Selva, W. Jędrzejewski, unpublished data). On days when wolves returned to finish up the remains of their old prey, we estimated (based on the mass of leftovers, $n = 6$ cases) that they consumed 0.65 kg/wolf daily.

The number of red deer, roe deer, and wild boar killed by wolves annually was calculated based on mean kill rates of each pack in spring–summer and autumn–winter of each year. In two cases where we lacked measures of kill rates, mean estimates from the same respective seasons, but from different years, were substituted.

Estimating the abundance of ungulates

Winter densities of red deer, roe deer, and wild boar come from drive censuses conducted in the whole Polish part of BPF (580 km²), where the wolves were studied (see details in Jędrzejewska et al. [1994], [1997], Kossak [1997], [1998], [1999], Okarma et al. [1997]). Spring–summer numbers of ungulates were calculated based on their densities in late winter, percentage of adult females in the population, and number of juveniles per female (details in Jędrzejewski et al. [2000]). Also, we obtained the index of ungulate abundance by documenting all observations of animals encountered during our fieldwork. Having recorded the time spent in the forest by human observers, we were able to calculate the encounter rates of ungulates (number of animals encountered per one hour spent in the forest by a human observer). In all, during 1996–1999, 4889 ungulates were seen during 8722 h in the forest. Meteorological data were obtained from the meteorological station located in the Białowieża village, which lies in the center of BPF.

RESULTS

Kill rates and consumption of prey by wolves

In 1996–1999, three to four packs of wolves, 15–18 individuals total (numbers collected in winter), lived in the study area. Altogether, 269 ungulates killed by

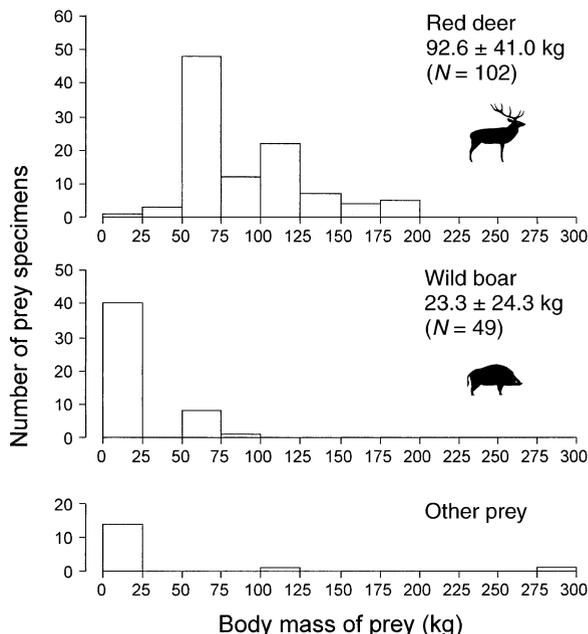


FIG. 1. Frequency distributions of body masses of 167 prey specimens killed by four wolf packs in Białowieża Primeval Forest in 1996–1999. Means \pm 1 SD reported for red deer and wild boar.

wolves were found, mostly red deer (72%) and wild boar (22%), rarely roe deer (4%), moose (1%), and domestic cow (1%). Compared to the mean species structure of wild ungulate community in the three years (red deer 35.4%, wild boar 37.8%, roe deer 20.8%, European bison 5.6%, and moose 0.4%), the red deer appeared strongly selected by wolves, which confirmed earlier findings (Jędrzejewska et al. 1994, Jędrzejewski et al. 1992, 2000). During 323 d of our observations, wolves killed 167 new prey, visited 22 remnants of their own, previously killed prey, and scavenged on carcasses of 28 dead animals (total $n = 217$). Among animals killed by wolves during that period ($n = 189$), we recorded red deer (63%), wild boar (28%), roe deer (4%), brown hares (2%), beavers (1%), red foxes (1%), and single specimens of moose, domestic cow, and domestic dog. The wolves scavenged predominantly on discarded carcasses of domestic animals (cattle and pigs, 39% of all cases of scavenging, $n = 28$), and carcasses of wild boar and European bison (32% and 25%, respectively). Based on approximate age of killed ungulates, we prescribed them to classes of body mass (Fig. 1). The mean body mass of a red deer killed by wolves was 93 kg, and that of wild boar 23 kg. Generally, the mean body mass of all wolf prey was 67.2 kg (1 SD, 52.2; mode, 63 kg; range, 2–300 kg).

Mean kill rate (estimated based on time intervals between consecutive kills found by us in the forest) was, on average, one prey per 1.9 d per pack (1 SD, 1.5), i.e., 0.526 prey animals·(pack)⁻¹·d⁻¹. Prey-to-prey time interval ranged from one hour to six days. Fur-

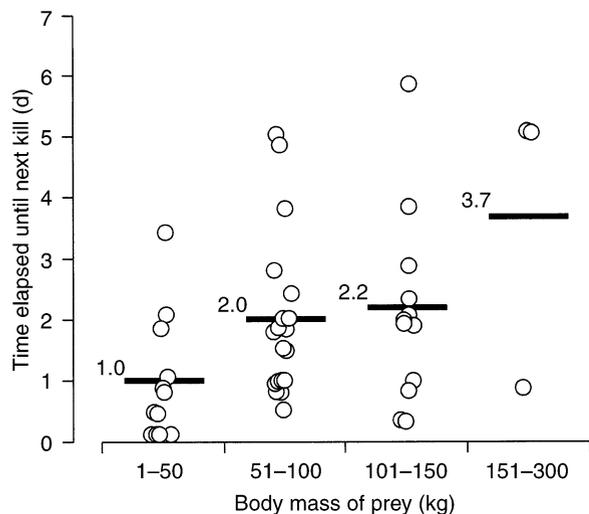


FIG. 2. Time elapsed until the next kill in relation to the body mass of prey. Open circles show time intervals ($n = 46$) between consecutive kills by wolves as documented by accurately dated prey remains found in the forest. Horizontal bars and numbers indicate mean values. Frequency distributions of time intervals significantly differed among the four classes of prey body mass (Kruskal-Wallis ANOVA, $H = 9.53$, $df = 3$, $P = 0.03$).

thermore, the time that elapsed from wolves' killing prey n to killing prey $n + 1$ markedly increased with growing body mass of prey n (Fig. 2). The second method of estimating kill rates (based on kills found and prey detected from scats) yielded very similar results (Table 1). On average, each pack killed 0.513 prey animals/day, including 0.486 ungulates and 0.027 small animals (e.g., hare, beaver). Those figures are equivalent to one prey killed per two days. As regards various species of prey, a pack of wolves killed one red deer every 3.2 d, plus one wild boar every 6.8 d, one

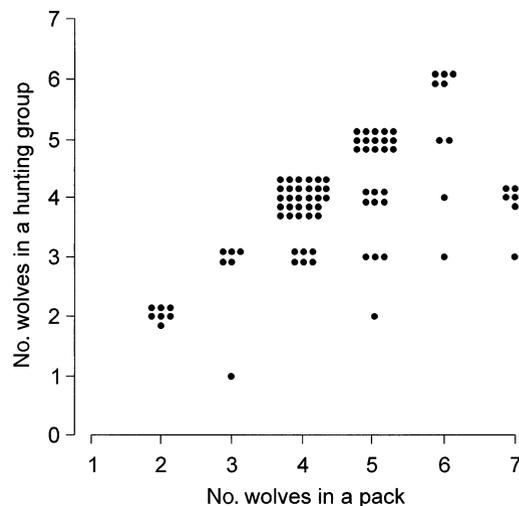


FIG. 3. Number of wolves in a hunting group as recorded at 89 instances of prey killed or carrion scavenged upon, compared to a total number of wolves in a pack.

small prey once a month, a roe deer every 44 d, and one moose or domestic cow once per 8 mo. Moreover, each pack of wolves visited the remnants of its own previously killed prey once per 13 d and scavenged on dead animals once per 12 d (Table 1). During the study, the mean hunting group included, on average, 4.4 wolves (1 SD, 1.0; mode, 4; range, 2–6). The appropriate per capita kill rates are given in Table 1.

In 1996–1999, the studied packs of wolves varied from two to seven individuals (Fig. 3). A pair of wolves was always traveling and feeding together. Packs consisting of three to four wolves split into smaller subgroups for 18% of hunts, and those of five to six wolves split on 41% of hunts. The largest pack (seven wolves) was not observed hunting together. Instead, it regularly

TABLE 1. Kill rates, scavenging rates, and consumption by wolves (*Canis lupus*) in Białowieża Primeval Forest (eastern Poland), 1996–1999.

Prey	Kill/scavenging rate per pack (no. prey·[pack] ⁻¹ ·d ⁻¹)		Kill/scavenging rate per wolf (no. prey·[wolf] ⁻¹ ·d ⁻¹)		Crude biomass of prey per pack (kg·[pack] ⁻¹ ·d ⁻¹)		Consumption rate per wolf (kg·[wolf] ⁻¹ ·d ⁻¹)	
	Mean	1 SD	Mean	1 SD	Mean	1 SD	Mean	1 SD
Live prey killed by wolves								
Red deer	0.312	0.157	0.075	0.044	29.28	15.56	4.31	2.14
Wild boar	0.147	0.214	0.034	0.052	3.38	4.62	0.54	0.70
Roe deer	0.023	0.061	0.006	0.015	0.56	1.46	0.10	0.27
Moose	0.002	0.010	<0.001	0.002	0.46	3.05	0.06	0.40
Cattle	0.002	0.015	<0.001	0.003	0.26	1.68	0.02	0.14
Small prey	0.027	0.068	0.008	0.023	0.28	0.80	0.07	0.20
Subtotal	0.513	0.261	0.124	0.073	34.22	14.99	5.10	2.01
Utilization of own, old prey, and scavenging on carrion of dead animals								
Old prey	0.078	0.104	0.019	0.028	3.02	4.19	0.04	0.06
Carrion	0.086	0.121	0.021	0.029	10.59	20.16	0.44	0.81
Subtotal	0.164	0.144	0.040	0.038	13.61	19.79	0.48	0.80
Total	47.83	25.10	5.58	2.11

Note: Small prey included beavers, hares, red foxes, and a domestic dog; carrion were dead European bison, wild boar, domestic cow, and domestic pig.

TABLE 2. Percentage distribution of prey, in four classes of body mass, killed by wolf hunting groups of various sizes.

No. wolves in group	No. prey specimens	Percentage of prey by body mass (kg)			
		1–50	51–100	101–150	151–300
4	85	45	40	14	1
5	34	26	44	15	15
6	26	19	46	23	12

Notes: Samples of prey killed by fewer than four wolves were too small for analysis (eight prey killed by one or two wolves; 14 prey killed by three wolves). Differences in prey frequencies among wolf hunting groups of various sizes were statistically significant ($G = 30.62$, $df = 6$, $P < 0.001$; G test).

divided into two subgroups (three and four wolves) each hunting on its own. Still, however, the whole pack lived and traveled together and held one territory. We examined the frequency distributions of ungulate prey killed by groups of various sizes. With increasing size of a hunting group, wolves killed significantly fewer small-sized prey and seized large prey more often (Table 2).

Red deer, wild boar, and carrion of dead ungulates made up 95% of wolves' food biomass, so we analyzed in detail wolves' kill rates for deer and boar and their scavenging rates. The densities of red deer were rather stable in Białowieża Forest during 1997–1999, which

was reflected by small between-year variation in wolf hunting for red deer (Fig. 4). However, wolf kill rates for red deer were constantly lower in spring–summer (0.211 ± 0.04 deer·(pack)⁻¹·d⁻¹, mean \pm 1 SE,) than in autumn–winter (0.355 ± 0.026), the difference being statistically significant (Mann-Whitney U test, $U = 305.5$, $P = 0.003$). This was opposite to the seasonal pattern of population dynamics of prey: deer numbers were always higher in summer than in winter, so factors other than deer number alone must have influenced wolf hunting rates. Interestingly, the encounter rates of deer by human observers were also lower in spring–summer (on average 0.183 deer seen per hour) than in autumn–winter (0.325 deer/h), which might have resulted from lower visibility of animals in the period of full development of vegetation. Between-pack variation in wolves' kill rates for deer was negligible (Kruskal-Wallis ANOVA, $H = 0.698$, $df = 3$, $P > 0.8$), but it should be noted that we had only four packs with relatively small variation in size (two to six individuals).

An important factor affecting wolf kill rate for red deer was the depth of snow cover (Table 3). It is worth noting that it was indeed the depth of snow, and not the advance of winter, that affected wolf kill rates; in the analyzed material, snow depth was not correlated with the consecutive day of winter (November 1 = day 1; $r = 0.02$, $P > 0.9$). The number of wolves in a

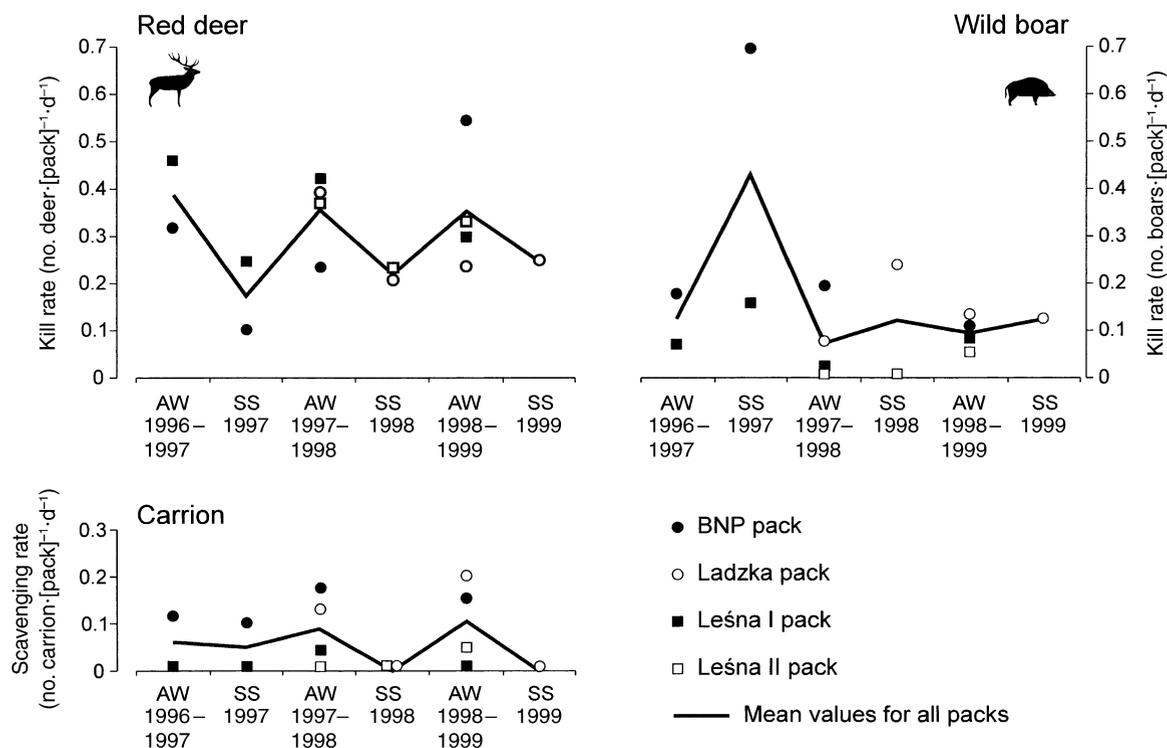


FIG. 4. Seasonal, between-year, and between-pack variation in wolf kill rates for red deer and wild boar and scavenging rate in Białowieża Primeval Forest. Abbreviations: AW, autumn–winter (1 October–30 April); SS, spring–summer (1 May–30 September).

TABLE 3. Effects of snow cover and size of wolf hunting group on kill rates and consumption of red deer by wolves; results of multiple regression analysis and ranking the set of alternative hypotheses.

Dependent variable	Multiple regression analysis				Model selection (AIC method)	
	Total variation explained (R_{adj}^2)	Contributions by independent variables (r^2)		Best model	Aikake's weight ω_i	
		Snow cover (S)	No. wolves in group (N)			
No. deer killed per pack per day (DP)	0.218**	(+) 0.263***	(+) 0.055	DP = $f(S, N)$	0.512	
Crude biomass of deer acquired per pack daily (CBP)	0.236**	(+) 0.253***	(+) 0.188*	CBP = $f(S, N)$	0.654	
No. deer killed per wolf per day (DW)	0.343***	(+) 0.264***	(-) 0.031	DW = $f(S)$	0.513	
Deer biomass consumed per wolf daily (BW)	0.365***	(+) 0.344***	(-) 0.004	BW = $f(S)$	0.687	

Notes: Variation in snow cover, wolf hunting group, and the four dependent variables are shown in Figs. 5 and 6. The r^2 values for contributions by each independent variable to the total variation explained (Tabachnick and Fidell 1983) are also presented. A "plus" symbol (+) indicates positive correlation and a "minus" symbol (-) indicates negative correlation. The best model was selected from the set of four alternative models (each of the dependent variables as a function of S , N , $S + N$, or $S \times N$) by using the Aikake's information criterion (AIC) method. Aikake's weight (ω_i) is the probability that a given model is the best model in the set (Anderson et al. 2000).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

hunting group appeared to predict a small amount of variation in kill rates (Table 3). If we held the group size constant (at the mean level of 4.4 individuals), then on average kill rates for deer would increase 2.2-fold (from 0.264 to 0.587 deer·[pack] $^{-1}$ ·d $^{-1}$) and daily consumption of deer biomass per wolf 2.4-fold (from 3.5 to 8.7 kg·[wolf] $^{-1}$ ·d $^{-1}$) with snow cover varying 0–17 cm (Fig. 5). If, in turn, snow cover were held constant (mean depth, 2.53 cm), it appeared that, with wolf hunting group growing from two to six wolves, the number of deer killed daily by the group did not increase significantly, but the crude biomass of deer acquired by them grew 2.3-fold (from 16.5 to 37.6 kg·[pack] $^{-1}$ ·d $^{-1}$) (Fig. 6). This was caused by the fact that larger groups killed large prey more often (see Table 2). In effect, per capita kill rates and consumption

of deer biomass did not decline significantly among groups of two to six wolves (Fig. 6).

What was the mechanism of higher kill rates by wolves in periods with deep snow cover? We tested whether the physical condition of killed deer, as approximated by marrow fat content, changed with an advance of winter and severe ambient conditions. In adult deer killed by wolves in October–March, fat content in femurs did not decline significantly ($P > 0.5$) throughout the cold season (Fig. 7). They all had >50% fat in bone marrow (80% \pm 15%, mean \pm 1 SD; $n = 18$). In contrast, fat reserves of young deer (<1 yr old) killed by wolves declined drastically throughout autumn and winter (Fig. 7). Among 18 young deer killed during October–January, 16 (89%) had >50% fat, and the mean level for all was 66% \pm 18% ($n = 18$). Of

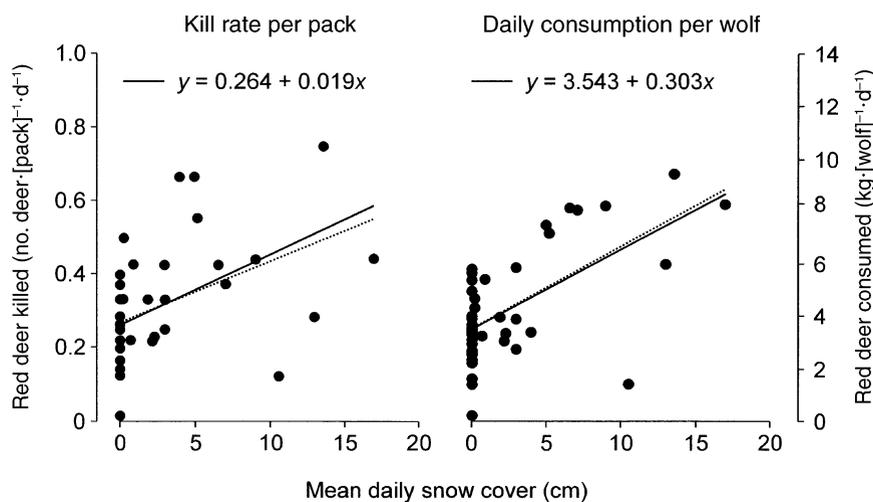


FIG. 5. Wolf kill rate and daily consumption of red deer in relation to depth of snow cover. Points are values for 43 sessions of observations, each covering 4–15 d. Dotted lines show simple linear regressions. Solid lines and regression equations show the influence of snow cover with the covarying impact of wolf group size held constant at its mean value (4.4 wolves). See Table 3 for statistical significance.

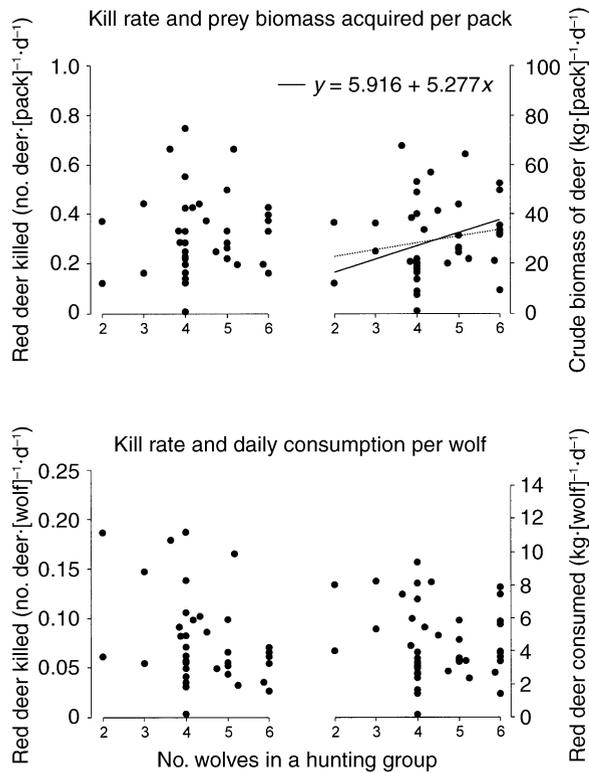


FIG. 6. Wolf kill rates and daily consumption of red deer in relation to number of wolves in a hunting group. The dotted line shows a simple linear regression; the solid line and regression equation show the influence of group size with the co-acting role of snow cover held constant (at its mean value of 2.53 cm). Statistical significance is given in Table 3. Scatterplots with no lines are shown when regressions were statistically nonsignificant. Other details are as in the Fig. 5 legend.

11 deer killed in February–March, only 2 (18%) had marrow fat content exceeding 50%, and mean for all was $27\% \pm 21\%$ ($n = 11$). That change was highly significant (G test, $G = 15.5$, $df = 1$, $P < 0.001$). Indeed, the advance of winter (consecutive days; D) and ambient temperature (T), with an interaction of these two factors, explained 46% of the total variation in the marrow fat (MF) of young deer ($R^2_{adj} = 0.455$, $n = 28$, $P < 0.0005$). When ranked by Aikake’s information criterion (AIC) method (Anderson et al. 2000), the model $MF = f(D, T, D \times T)$ was the best (Aikake’s weight $\omega = 0.671$) among seven alternative models involving consecutive days of winter, snow cover, ambient temperature, and the combinations as well as interactions of these factors.

During the study, the wild boar population underwent fluctuations in numbers, caused primarily by superabundant crop of oak seeds in autumn 1996 (see Hansson et al. 2000). Wild boar responded to extra food supply by very early and prolific reproduction in spring 1997, which resulted in high abundance of piglets, a segment of boar population most vulnerable to wolf predation (see Fig. 1). However, wolves’ response by higher kill rates for boar was manifested only in the pack inhabiting Białowieża National Park (BNP pack; Fig. 4), where mature oak stands were widespread and boar densities were much higher than in other parts of Białowieża Primeval Forest (BPF; see Jędrzejewska et al. 1994). Also, from spring 1997 through autumn–winter of 1997–1998, the encounter rates of wild boar by human observers were much higher in BNP (0.79 boar/h) than in other parts of BPF (0.13 boar/h).

Encounter rates of wild boar were generally somewhat higher in spring–summer (on average, 0.307 boar seen per hour) than in autumn–winter (0.190 boar/h). Correspondingly, wolf kill rates for wild boar were higher in spring–summer (0.242 ± 0.058 boar·[pack]⁻¹·d⁻¹,

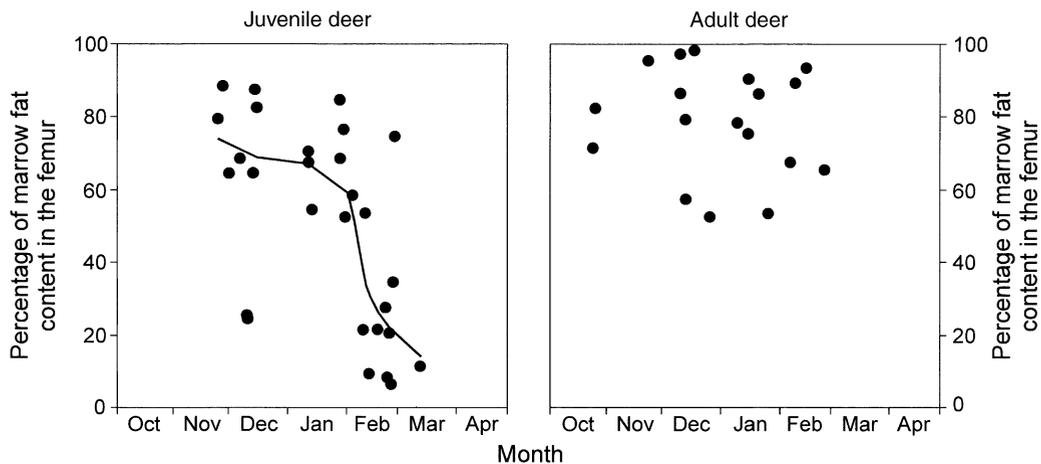


FIG. 7. Marrow fat content in the femur of young and adult red deer killed by wolves in Białowieża Primeval Forest. Each point denotes one individual, and all animals are plotted against the dates when killed. Scatterplot data of young deer were smoothed (solid line) by Lowess method (Cleveland 1979) to show the most probable temporal pattern of fat depletion. In adult deer no significant decline in marrow fat content was detected.

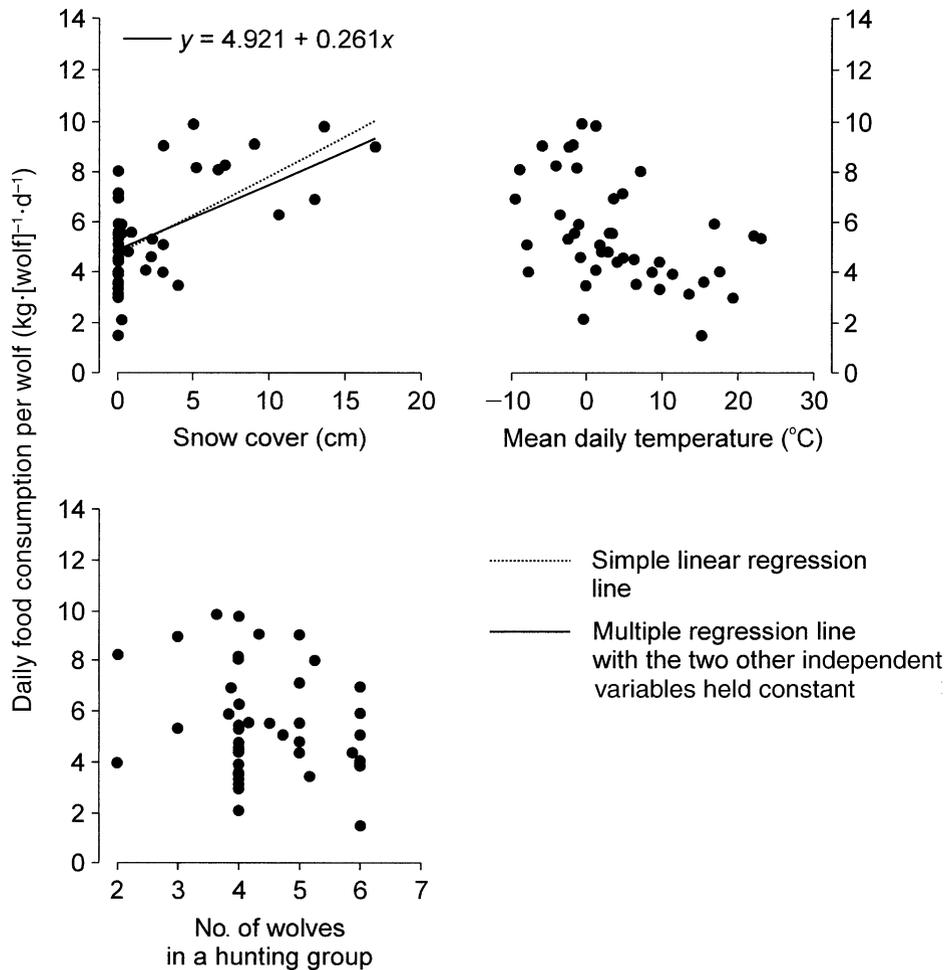


FIG. 8. Daily food consumption (kg) per wolf in relation to snow cover, ambient temperature, and number of wolves in a hunting group. Multiple regression analysis: $y = 5.288 + 0.261(\text{snow}) - 0.042(\text{temp}) - 0.099N_{\text{wolves}}$; $R_{\text{adj}}^2 = 0.374$; $n = 43$, $P < 0.0005$. Snow cover was the most significant factor shaping wolf food intake; the thick line and regression equation show the influence of snow with the two other independent variables held constant (at their mean values; temperature, 4.0°C; no. wolves, 4.4). Other details are as in the Fig. 5 legend.

mean ± 1 SE) than in autumn–winter (0.106 ± 0.038 boar·(pack) $^{-1}$ ·d $^{-1}$), albeit the difference was not significant due to the large variation among various packs and between years (Fig. 4). Frequency of wild boar killing by wolves positively correlated with the encounter rates of wild boars by human observers ($r = 0.434$, $P = 0.004$), but it was not related to snow cover or the number of wolves in a hunting group ($P > 0.6$). Wolf kill rates for red deer and those for wild boar in the 43 series of intensive several-day samplings were negatively correlated ($r = -0.37$, $P = 0.01$). Wolves scavenged on carrion more readily in cold seasons than in spring–summer (Mann-Whitney U test, $U = 289$, $P = 0.006$; Fig. 4). Furthermore, differences among packs in the frequency of scavenging were significant (Kruskal-Wallis ANOVA, $H = 12.07$, $df = 3$, $P = 0.007$).

The total daily food intake by wolves was extremely variable (Fig. 8). In multiple regression analysis, two

environmental factors (depth of snow cover and ambient temperature) and a social factor (size of wolf hunting group) explained 37% of the total variation observed. If we stabilized the covarying factors and separated the sole impact of each of the three factors, it appeared that snow cover had the strongest influence: mean daily food consumption by a wolf increased by 80% (from 4.9 to 9.4 kg·[wolf] $^{-1}$ ·d $^{-1}$) with snow depth ranging 0–17 cm (Fig. 8). Ambient temperature had weaker impact; in the observed range of mean temperatures from 20°C to –10°C, daily food intake by wolves increased by 26% (from an average of 4.9 to 6.2 kg·[wolf] $^{-1}$ ·d $^{-1}$; Fig. 8). The effect of group size on wolf daily rations was negligible. The leading role of snow in shaping the variation in daily food intake by wolves was supported by the AIC method (Anderson et al. 2000), which showed that food intake as a function of snow cover had the highest probability of being the best model (Aikake's weight $\omega = 0.459$) among

TABLE 4. Predation impact by wolves on red deer, roe deer, and wild boar in Białowieża Primeval Forest (BPF) in 1991–1999, in relation to densities and population increases of prey (estimated no. young born annually).

Year†	Ungulate density (no. individuals/100 km ²)		Annual predation by wolves (no. killed/ 100 km ²)	Annual predation on ungulates (%)‡		
	Late winter	Spring– summer		Spring density	Annual increase	Annual mortality
<i>Red deer (Cervus elaphus)</i>						
1991–1992	607	858	105	12	42	24
1992–1993	416	581	78	13	47	35
1993–1994	359	514	57	11	37	...
1995–1996	463	659	62	9	32	...
1997–1998	286	440	57	13	37	40
1998–1999	296	458	72	16	45	60
1999–2000	337	515
1991–2000	395 ± 113	575 ± 145	72 ± 18	12 ± 2	40 ± 6	40 ± 15
<i>Roe deer (Capreolus capreolus)</i>						
1991–1992	492	820	25	3	8	6
1992–1993	425	702	21	3	8	5
1993–1994	288	501	21	4	10	...
1995–1996	324	517	19	4	10	...
1997–1998	115	229	5	2	4	11
1998–1999	182	313	4	1	3	5
1999–2000	240	414
1991–2000	295 ± 132	499 ± 208	16 ± 9	3 ± 1	7 ± 3	7 ± 3
<i>Wild boar (Sus scrofa)</i>						
1991–1992	458	678	28	4	13	6
1992–1993	209	406	19	5	10	19
1993–1994	308	599	38	6	13	...
1995–1996	225	437	36	8	17	...
1997–1998	217	486	38	8	14	63
1998–1999	426	617	26	4	14	9
1999–2000	338	577
1991–2000	312 ± 102	543 ± 101	31 ± 8	6 ± 2	13 ± 2	24 ± 26

Notes: Data for 1991–1996 were presented by Jedrzejewski et al. (2000); data for 1997–1999 represent the current study. No data were available for 1994–1995 and 1996–1997.

† Measurements span March of the first year until the following February. Year entries of 1991–2000 indicate means ± 1 SD for the entire period of study, but see Notes.

‡ Predation values are given as percentages of spring density, annual increase, and annual mortality, respectively.

seven alternative models testing the effects of pack size, snow cover, temperature, as well as combinations and interactions of these factors.

Predation by wolves in relation to ungulate densities

Data on predation impact by wolves on red deer, roe deer, and wild boar were available for the seven years 1991–1999 (Table 4; three years from this study and four years from Jedrzejewski et al. [2000]). In 1991/1992–1995/1996, ungulates were subject to strongly elevated hunting harvest aimed at substantial reduction of their numbers. Since 1996/1997, the harvest was markedly lower (Kossak 1999). The wild boar dynamics was affected by two years of superabundant crop of oak seeds (in 1989 and 1996, which resulted in high densities in late winters and spring–summer seasons of 1990 and 1997, respectively).

Wolf predation was most important in the case of red deer. Annually wolves took, on average, 72 deer from 100 km², which constituted 12% of spring (seasonally highest) densities of deer, and was equivalent

to 40% of their annual increase due to breeding, and 40% of the annual mortality of deer (Table 4). Within the observed range of red deer abundance, the number of deer killed by wolves per annum was positively related to deer densities ($R_{\text{adj}}^2 = 0.556$, $n = 6$ yr, $P = 0.05$ for spring densities, and $R_{\text{adj}}^2 = 0.517$, $P = 0.06$ for winter densities). In 1991–2000, we observed a two-fold decline of deer numbers (difference between max and min recorded numbers: $G = 118.03$, $df = 1$, $P < 0.001$, G test), followed by smaller (1.5–1.8-fold) decline in the number of deer killed by wolves annually. In effect, percentage predation (number of deer killed by wolves annually as percent of deer density) showed a tendency to decline with growing density of red deer, although the relationship was not statistically significant ($r = -0.404$, $P > 0.4$ for spring densities; $r = -0.542$, $P > 0.2$ for late winter densities of deer).

In red deer, the estimated number of young born annually increased with growing population density ($R_{\text{adj}}^2 = 0.847$, $P = 0.006$), but the rate of population increase (number of young as percent of winter density)

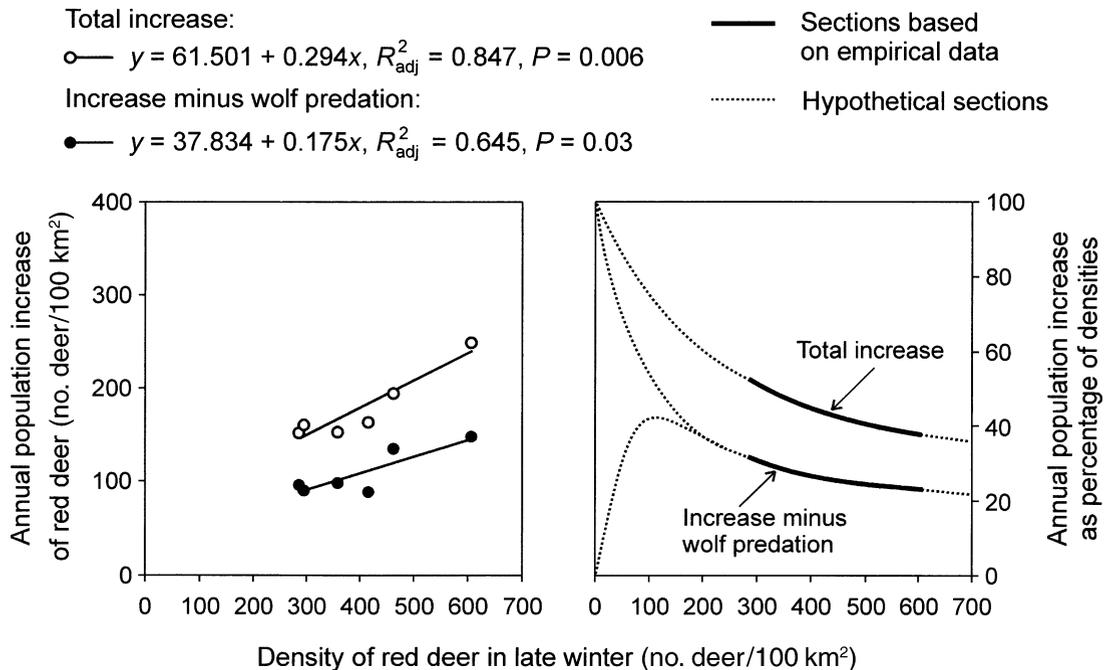


FIG. 9. Left panel: Annual population increase of red deer due to reproduction (no. young born per 100 km² per year), and increase minus annual predation by wolves (number of deer killed per 100 km² per year), in relation to late winter densities of red deer population. Right panel: percentage population increase of red deer in relation to late winter densities. Annual predation by wolves is marked as a factor reducing increase rates of prey populations. Solid lines are mathematically derived from the appropriate regression equations in the left panel. Dotted lines mark the hypothetical relationships beyond the empirical range of prey densities. The bifurcated curve shows the range of all possible outcomes of wolf–deer interactions (see *Results: Predation by wolves* for further explanations).

was inversely density dependent ($R_{adj}^2 = 0.442$, $P = 0.09$). Wolf predation on deer (number of deer killed) was positively related to deer population increase ($r = 0.826$, $P = 0.04$), and wolves exploited a fairly stable proportion (32–47%) of deer population increase (Fig. 9). Thus, wolves notably lowered the rate of population increase in red deer.

Annually wolves took, on average, 16 roe deer/100 km², a number constituting only 3% of the roe deer spring densities, 7% of their annual increase, and 7% of the average yearly mortality (Table 4). During the observed 4.3-fold decline of roe deer numbers (difference between maximum and minimum recorded densities: $G = 252.16$, $df = 1$, $P < 0.001$), the number of roe deer killed by wolves per year declined faster (over six times). This produced a positive correlation between the number of deer killed by wolves per annum and roe deer densities ($R_{adj}^2 = 0.789$, $n = 6$ yr, $P = 0.01$ for spring densities; and $R_{adj}^2 = 0.783$, $P = 0.01$ for winter densities). However, percentage predation on roe deer was always small with not much variation (1–4%), and it was not related to roe deer density ($P > 0.4$). In roe deer, the estimated number of young born annually grew with increasing density of population ($R_{adj}^2 = 0.953$, $P = 0.001$), but the percentage rate of increase showed a tendency to be inversely density dependent ($R_{adj}^2 = 0.419$, $P = 0.1$). Predation,

amounting to 3–10% of roe deer annual production of young, could only slightly lower the rate of population increase in roe deer.

From the wild boar population, wolves annually took a mean value of 31 animals/100 km², which constituted 6% of the average spring densities of wild boar, and was equivalent to 13% of their yearly increase due to reproduction and 24% of their annual mortality (Table 4). The number of wild boar killed by wolves annually was not related to boar densities ($P > 0.9$ for spring densities, and $P > 0.6$ for winter densities), but it showed a tendency to grow with higher annual production of young ($r = 0.78$, $n = 6$ yr, $P = 0.07$). Percentage predation was inversely related to densities, although the relationship was not significant ($r = -0.527$, $P > 0.2$ for spring densities; and $r = -0.783$, $P = 0.07$ for winter densities of wild boar). Wolves took a fairly stable and small proportion of wild boar annual production of young (10–17%).

In summary, wolves exerted the strongest impact on red deer population and much smaller impacts on roe deer and wild boar. In all species, however, percentage predation was either inversely density dependent or did not vary with changing densities of prey.

DISCUSSION

Kill rate estimates from Białowieża cannot be easily compared to measures obtained in numerous North

American studies (because kill rates strongly varied with prey size and wolf pack size), but per capita amount of food eaten by wolves can be compared. The value from Białowieża Primeval Forest (BPF; 5.6 kg·(wolf)⁻¹·d⁻¹) is similar to or higher than those reported elsewhere (4.4–6.3 kg·[wolf]⁻¹·d⁻¹, Mech [1966]; 0.5–7.0 kg·[wolf]⁻¹·d⁻¹, Fritts and Mech [1981]; 1.6–2.8 kg·[wolf]⁻¹·d⁻¹, Messier and Crete [1985]; 4.5–14.9 kg·[wolf]⁻¹·d⁻¹, Ballard et al. [1987]; 2 kg·[wolf]⁻¹·d⁻¹, Fuller [1989]; 4.4–7.8 kg·[wolf]⁻¹·d⁻¹, Thurber and Peterson [1993]; 4.1–6.4 kg·[wolf]⁻¹·d⁻¹, Hayes et al. [2000]). According to Schmidt and Mech (1997), the lowest of the values listed here represent underestimates. In the United States and Canada, data on predation rates were usually collected by locating wolf kills from aircraft. The accuracy of that method strongly depends on visibility (the aerial search for prey would be inapplicable in closed forests) and prey size (large prey, such as moose, are more probable to be detected than small prey). In our study area, a substantial number of prey were those of small size, often completely eaten by wolves. Searching for prey remains alone would not reveal the true kill rate, especially in spring–summer. By combining ground radio-tracking, prey searching, and identification of prey in scats, we were able to better estimate the kill rate and its seasonal variation. As many as 41% of wolf prey were traced out in scats only, and most of them were small prey (e.g., wild boar piglets, young deer, beavers). Although this method may still somewhat underestimate the kill rates (two or more prey of the same species and age, killed and consumed by wolves in a short time sequence, would be counted as one prey if recovered from scats only), it is highly recommended or even necessary to supplement the search for prey remains with the analysis of scats in studies on wolf predation in dense woodlands and in regions where wolves consume many small and medium-sized ungulates (roe deer, piglets of wild boar). Our method also yielded reliable data for all seasons, and not only for the period with snow cover. Higher kill rates in winter than in summer did not result from higher probability of detecting prey on days with snow. First, kill rates on deer increased but those on wild boar declined during winter. Secondly, wolf kill rates were similar in seasons with no snow (spring, summer, autumn) and in winter periods with shallow snow cover, which already enabled us to do snow tracking.

In North America, major factors affecting kill rates by wolves were prey density, depth of snow cover, and wolf pack size. Having reviewed more than a dozen studies on wolf kill rates on moose, Messier (1994) found that per capita kill rate was positively related to moose abundance within the observed densities of 0.2–2.5 moose/km² (~40–500 kg crude biomass/km²). Compared to those data, winter densities of ungulates in Białowieża during our study were much higher and less variable (6.2–10 individuals/km² and 500–800 kg/

km², three species pooled). Interestingly, the density of wolves in BPF (2–2.6 wolves/100 km²) was within the range of densities cited by Messier (1994) for the United States and Canada (0.2–7.8 wolves/100 km², mean 1.75). Thus, we think that in our study wolves were not limited by prey resources. Low rates of wolves' scavenging on carrion (although carrion was very abundant in the cold season; Jędrzejewska and Jędrzejewski 1998; N. Selva and W. Jędrzejewski, *unpublished data*) support this conclusion. We did observe, however, some variation in wolf kill rates due to changing prey availability. Wolves killed more wild boar in a year when piglets were very abundant, and nearly left off hunting roe deer when roe deer numbers declined. These cases, however, concerned secondary prey of wolves and not their main prey, red deer.

Positive influence of deep snow cover on wolf kill rates is well documented. Huggard (1993) reported that in Banff National Park, Canada, kill rates by wolves increased from 0.185 wapiti/d in periods with no snow to 0.910 wapiti/d when snow was 60 cm deep. Peterson and Allen (1974), who observed the same phenomenon in a wolf–moose system in Isle Royale, USA, proposed that lower mobility of moose and, thus, their poorer access to forage in deep snow brought about a higher incidence of malnutrition (especially in calves) and, in consequence, greater vulnerability to predation. On the other hand, Post et al. (1999) showed that the mean size of wolf packs increased during snowy winters, and Fuller (1991) evidenced that in severe, snowy winters wolves spent more time with other pack members than during mild winters. As kill rates per pack normally increase with pack size (Thurber and Peterson 1993, Schmidt and Mech 1997), the observed relationship between snow depth and wolf kill rates can result from two factors: higher vulnerability of prey and stronger coherence of wolf packs in periods with deep snow cover.

In this study, we attempted to disentangle the roles of snow and pack size. In Białowieża Primeval Forest, snow appeared the most important factor affecting wolf kill rates on deer, and it acted through greater vulnerability to predation of young deer with depleted fat reserves. Earlier studies on food habits of wolves in Białowieża Forest documented that the share of red deer in wolf diet increased in severe, snowy winters (Jędrzejewski et al. 1992). These findings are in agreement with other studies on European red deer, which showed that even in the absence of large predators, severe winter is a critical time for calf survival. In Norway, Loison et al. (1999) found that body masses of red deer calves decreased with increasing snow depth in winter. Okarma (1991) revealed that in Bieszczady Mountains (southeastern Poland), fat reserves of red deer calves (but not adults) killed by wolves were markedly smaller in late winter (February–March) than in early winter (December–January).

In Białowieża, per capita kill rates by wolves de-

clined slightly (and not significantly) with the growing size of wolf hunting group, whereas the amount of food acquired per wolf practically did not decline, because larger groups tended to select large-sized prey more often than smaller groups. This finding is intriguing, as the studies conducted in North America showed that albeit large packs exhibited higher kill rate, the amount of food acquired per wolf declined significantly with growing pack size (Thurber and Peterson 1993, Schmidt and Mech 1997, Hayes et al. 2000). There are, however, two essential differences between wolf situation in European temperate forests and in the boreal zone of North America. First, in European deciduous and mixed forests, wolves coexist with and prey on three to five species of ungulates ranging in size from <2 kg (wild boar piglets in spring) to >300 kg (moose, European bison) (review in Okarma [1995]). Thus, the richness of species and size classes of prey allow for great flexibility in prey choice and kill rates by wolves in order to satisfy food demands of all pack members. Second, the mean size of wolf hunting groups (4.4 wolves in this study) and the maximal recorded pack size (seven wolves) were small compared to North American packs, which usually comprised more than six (and up to 20) individuals (Thurber and Peterson 1993, Schmidt and Mech 1997, Hayes et al. 2000).

We propose that it is the size of the most frequently taken prey that sets the upper limit for wolf pack size. Wolves neither guard nor hide their kill (as the lynx do; Jędrzejewski et al. 1993), so the optimal utilization of a kill (i.e., with minimal losses to scavengers) would be to consume the kill immediately. In Białowieża, a 63-kg deer calf, the most common prey of wolves, would be eaten completely by four to five wolves within few hours. By contrast, a killed moose would support a pack of 15–20 wolves with daily food rations. This explains why packs of six to seven wolves began to disintegrate in Białowieża Forest, and packs of more than eight individuals were practically not recorded during recent decades (Jędrzejewska et al. 1996). In BPF, scavenging on ungulate carcasses (by >30 species of birds and mammals) was widespread, and scavengers were able to usurp a fair proportion of wolf kills (Jędrzejewska and Jędrzejewski 1998; N. Selva and W. Jędrzejewski, *unpublished data*). Thus we think that group living in wolves cannot be explained by simply easier acquisition of larger prey by bigger groups. (In Białowieża, wolves were able to seize adult male deer even when hunting singly.) Instead, we propose that the upper limit for a social group size is set by the need to optimally utilize a dominant class of prey.

What is the role of wolf predation in functioning of ungulate populations, especially red deer, in European temperate forests? There is historical evidence that, in BPF, wolves and lynxes limited deer numbers (Jędrzejewska et al. 1997, Jędrzejewska and Jędrzejewski 1998). During the period 1850–2000, wolves had been exterminated twice, and in both periods red deer pop-

ulation irrupted and reached densities at which further growth was halted by intraspecific competition for food. Furthermore, in the whole series of >100-yr data, the percentage population increase of deer from year to year was negatively correlated with combined densities of wolves and lynxes (Jędrzejewska et al. 1997). Notably, however, wolf numbers were negatively correlated with red deer densities (Jędrzejewska and Jędrzejewski 1998), a situation opposite to those reported for wolf–moose or, generally, wolf–ungulate systems in North America, where positive correlation of wolf numbers and ungulate density or biomass was found (Keith 1983, Fuller 1989, Messier 1994). In BPF, the negative relationship resulted from human impelling the fluctuations of wolves (via control) and partly also deer (by heavy poaching in years of political instability and economic regress) (Jędrzejewska et al. 1997).

Worth noting is the fact that Białowieża's wolves were able to maintain high densities (up to 7–9 individuals/100 km²) even when red deer were scarce or temporarily absent from the community (Jędrzejewska et al. 1996). This situation may only occur where wolves are sustained by several prey species, and then, as suggested by Seip (1992) for a wolf–moose–caribou system, the most vulnerable prey species may suffer heavy compensatory predation or even become completely eliminated. In European temperate forests, wild boar seem very important in maintenance of wolf populations. Piglets and young boar are the most important alternative prey to wolves, and they are most numerous and vulnerable to predation in spring–summer, when wolves have pups.

Messier (1994), having analyzed moose–wolf interactions over a broad spectrum of moose densities in North America, concluded that percentage predation by wolves was density dependent in the range 0–0.65 moose/km² and inversely density dependent at higher moose densities. Based on a detailed analysis of the historical data of wolf and deer population numbers in BPF, Jędrzejewska and Jędrzejewski (1998) proposed that, with a negative numerical relationship between wolf and deer and a type II (logarithmic) functional response, percentage predation by wolves on deer should be density dependent at low densities of deer (<1 individual/km²) and inversely density dependent at higher densities. In this study, as expected, percentage predation by wolves was inversely density dependent over deer densities 3–6 individuals/km². Thus, wolves limited deer numbers, but were unable to regulate their prey (*sensu* Sinclair 1989, Messier 1991). By eliminating a fair number of deer relative to their annual production, wolves can hamper population growth of red deer and prolong the time until they reach the carrying capacity of habitat.

Empirical data on wolf–deer interactions at low densities of deer are not yet available. The range of possible outcomes of those interactions is shown by a bifurcated curve in Fig. 9. They can vary from heavy,

compensatory predation, leading eventually to elimination of deer by wolves (descending section of a curve in Fig. 9), to declining predation rates at low densities of deer ensuring coexistence of predator and prey (ascending section of a curve, Fig. 9). We think that in the Palearctic region, where deer is the most preferred prey to wolves (Okarma 1995), both situations may happen, depending on a set of extrinsic factors. The most important of them are as follows: (1) abundance of alternative prey species, which can support high densities of wolves, (2) unfavorable climatic conditions (severe winters), and (3) heavy exploitation by humans, which causes elevated mortality of deer, additive to that inflicted by wolves.

Yet wolf predation alone is a poor predictor of deer population dynamics in BPF. Jędrzejewski et al. (2000) and Okarma et al. (1997) documented that predation by lynx and hunting harvest by humans were also important factors limiting deer numbers in Białowieża Forest. Those three agents of deer mortality were additive (Jędrzejewski et al. 2000). This study documented that only in the case of deer fawns were wolf predation and mortality caused by severe winter conditions found to be partly compensatory. Wolves killed fawns with very poor fat reserves, some of which might have died anyway.

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