Wolf Canis lupus numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990–2000

Authors: Sidorovich, Vadim E., Tikhomirova, Larisa L., and Jędrzejewska, Bogumiła

Source: Wildlife Biology, 9(2) : 103-111

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2003.032

Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990-2000

Vadim E. Sidorovich, Larisa L. Tikhomirova & Bogumiła Jędrzejewska

Sidorovich, V.E., Tikhomirova L.L. & Jędrzejewska, B. 2003: Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990-2000. - Wildl. Biol. 9: 103-111.

Wolf *Canis lupus* relationships with wild ungulates, domestic animals and humans were studied in an area of ca 800 km^2 at the head of the Lovat River in northeastern Belarus during 1990-2000. The region was dominated by natural habitats (78%) consisting mainly of forests and bogs, but also lakes and rivers. The abundance of wild ungulates, such as moose *Alces alces*, wild boar *Sus scrofa*, and roe deer *Capreolus capreolus*, as censused by snow tracking and assessed by game wardens, declined 5 to 6-fold between 1990 and 1996, most probably due to uncontrolled exploitation and poaching. During 1997-2000, the numbers of ungulates began to recover. Wolves responded to the shortage of wild ungulates by a strong shift in feeding habits. When wild ungulates were numerous, wolf diet as studied by scat analysis was composed of wild ungulates (80-88% of consumed biomass), with small additions of medium- and small-sized wild animals (7-13%), mainly beaver *Castor fiber* and hare *Lepus* sp., and domestic animals (4-6%), mainly cattle. In the years when the recorded numbers of wild ungulates were at their lowest, wolves preyed on domestic animals (38% of biomass consumed), wild ungulates (32%), and medium- and small-sized wild prey (29%). Wolf damage to domestic animals (28 head of cattle and 247 dogs killed) and wolf-human interaction (100 observations of wolves in and near villages, including one attack by a rabid wolf on 11 people) were recorded in 14 villages. The rate of wolf predation on domestic animals and their appearances in villages increased exponentially with the declining biomass of wild ungulates and ceased again when wild ungulates began to recover; a one-year time lag in wolf response to changes in ungulate abundance was observed. The numbers of wolves as estimated by snow tracking and assessed by game wardens played a weaker role in shaping wolf-livestock and wolf-human interaction. The wolf population was strongly affected by hunting during the study. Wolves responded numerically with a 1 to 2-year time lag to the varying intensity of harvest by humans. Our study showed the role of the human factor in shaping wolf numbers and wolf-livestock interaction in eastern Europe. The three major components of this relationship were: 1) the manifold decline in wild ungulate abundance, which was most probably caused by uncontrolled exploitation by humans in the years of political transformation and economic regress, made wolves shift to predation on domestic animals; inevitably, wolves were frequently seen in the rural areas; 2) people interpreted the growing rates of wolf damage and appearances near the settlements as an effect of greatly increasing numbers of wolves, and demanded that authorities and hunters fight the 'wolf plague'; 3) hunting impact on wolves increased and led to a marked reduction in wolf numbers and a decline in wolf-human conflicts. This scenario was most probably repeated in many areas of eastern Europe during 1990-2000, which was a decade of political and economical transformation. From

a management perspective, we suggested that predation levels and wolf-human conflicts could be reduced not only by increased wolf harvest but also by enhancing the density and diversity of wild ungulates.

Key words: Canis lupus, feeding habits, livestock depredation, moose, roe deer, wild boar, wolf-human interaction

Vadim E. Sidorovich & Larisa L. Tikhomirova, The Vertebrate Predation Research Group, Institute of Zoology, National Academy of Sciences of Belarus, Akademicheskaya Str. 27, 220072 Minsk, Belarus - e-mail address: vadimsid@mustbel.open.by
Bogumiła Jędrzejewska, Mammal Research Institute, Polish Academy of Sciences, 17-230 Białowieża, Poland - e-mail: bjedrzej@bison.zbs.bialowieza.pl

Corresponding author: Vadim E. Sidorovich

Received 10 October 2001, accepted 20 September 2002

Associate Editor: Henryk Okarma

The relationships of European wolves *Canis lupus* with their main prey, wild ungulates, have long been affected by the events in human history and economy. First and most important, domestic animals kept in rural areas, from small poultry to horses, offered an important alternative prey to wolves, the more so as wild ungulates declined in range and abundance. Secondly, hunting harvest of both ungulates and wolves affects wolf numerical responses to variation in ungulate abundance. Meriggi & Lovari (1996), having analysed data on wolf diets in 15 localities in southern Europe, showed that the shares of wild and domestic ungulates in wolf diets were strongly negatively correlated. Indeed, in the whole continent, species composition of wolf prey varied from almost exclusively wild ungulates belonging to five native species in the Białowieża Primeval Forest, eastern Poland (Jędrzejewski, Jędrzejewska, Okarma, Schmidt, Zub & Musiani 2000) to domestic ungulates of five species in Greece (Papageorgiou, Vlachos, Sfougaris & Tsachalidis 1994). Meriggi, Brangi, Matteucci & Sacchi (1996) documented that, in Italy, the use of livestock species was lower wherever the richness and diversity of wild ungulate guild increased. The same pattern, but in the temporal scale, was described by Jędrzejewska & Jędrzejewski (1998) from central-eastern Europe. As pasturing of cattle in the woodland ceased and numbers of wild ungulates recovered, wolves easily shifted from frequent hunting on livestock to preying on wild ungulates only. Ryabov (1974) reported that, in the Voronezh region in Russia, wolves caused little damage to numerous goats and other livestock, because free-living sika deer *Cervus nippon* (introduced to the Khopersk Nature Reserve) were very abundant.

Livestock predation by wolves may also be affected by human-imposed changes in the abundance of wild ungulates. Jędrzejewska, Jędrzejewski, Bunevich, Miłkowski & Krasiński (1997) analysed the population dynamics of five species of wild ungulates in the Białowieża Primeval Forest in eastern Poland and western Belarus based on data covering >100 years and found that during periods of war, military and political unrest and economical regress, wild ungulates served as food resources for humans and suffered heavy poaching that could even lead to extermination of the largest, and most slowly reproducing species, e.g. European bison *Bison bonasus*. In such situations, wolves may have to compensate for the decline in wild prey by hunting domestic ungulates where and whenever available (Osmolovskaya & Priklonskii 1975).

In this paper, we report 11 years of monitoring data on the relationship between wolves, wild ungulates and livestock in natural woodlands interspersed with rural areas in northeastern Belarus. The study period (1990-2000) was characterised by profound political changes and economical regress. This situation favoured uncontrolled exploitation of wild ungulates, which led to their fast, many-fold decline. In this paper, we analyse: 1) dietary response of wolves to changes in wild ungulate abundance, 2) effect of harvest by humans on wolf numbers, and 3) frequency of wolf attacks on domestic animals.

Study area

The study was carried out in an area of about 800 km^2 at the head of the Lovat River (55°45'N, 30°20'E) in the Gorodok district, Vitebsk region, northeastern Belarus (Fig. 1). The study area is characterised by large forests and bogs on rough glacial terrain, fairly natural network of rivers and glacial lakes. Natural habitats comprise about 78% of the area, and man-transformed land (i.e. fields, pastures, meadows, human settlements and roads) covers 22%, in some localities up to 31%. Agricultural land is dominated by dry meadows (16% of the entire region, and 73% of the agricultural land). The average density of the human population is about 3 people/km^2.

The study area belongs to the transitional region of temperate mixed forests. Spruce *Picea abies* and pine *Pinus sylvestris* are the dominant species among the coniferous trees. Alder *Alnus glutinosa* and *A. incana*, birch *Betula pendula* and *B. pubescens*, and aspen *Populus tremula* are the most common deciduous trees. Masting deciduous trees such as oak *Quercus robur* and lime *Tilia cordata* are rare. The guild of large predators includes wolf, lynx *Lynx lynx*, and brown bear *Ursus arctos*. The community of wild ungulates consists of three species: moose *Alces alces*, roe deer *Capreolus capreolus*, and wild boar *Sus scrofa*. Other possible prey species of wolves were beavers *Castor fiber*, blue hare *Lepus timidus*, and brown hare *L. europaeus*.

The terrain is flat to undulating with altitudes lying within 100-200 m a.s.l. Mean temperature in July is 18°C, and in January -6°C. Winters are variable, but usually snow cover persists for at least 1.5-2 months, with a maximal depth of 30-90 cm. Maximum duration of the snow period is about six months, i.e. from late October till mid April. During winter, periods of severe frost (below -20°C) alternate with thaws lasting for some weeks.

Material and methods

In 1990-2000, abundance of wolves and wild ungulates was estimated by snow tracking. Each year in late winter (January-March), the same 36-km transect, located in the natural habitats, was walked, and the number of animal trails crossing the transect was counted. The route crossed various forest types, river valley, lake shore and open marshes as well as rural areas. It was representative of the landscape structure and composition in the whole study area. The abundance index of each species was calculated as the number of tracks divided by the number of kilometres walked and the number of days passed from the last snowfall, and multiplied by 2 (number of tracks/ km/2 days).

As an additional source of data, estimates of wolf and ungulate numbers from the local department of the Belarusian hunting organisation (Gorodok Raisovet BOOR) were also used for analysis. The estimates come from game wardens and forest guards, who inspect their districts many times during each winter (e.g. before and during hunts for ungulates and wolves, when hunting for furbearers, and when inspecting the signs of poaching activities) and - by recording tracks, visual observations, and other signs of animal activities - estimate the number of ungulates and wolves in their districts (covering a total of 728 km^2). Number of wolves and ungulates ob-

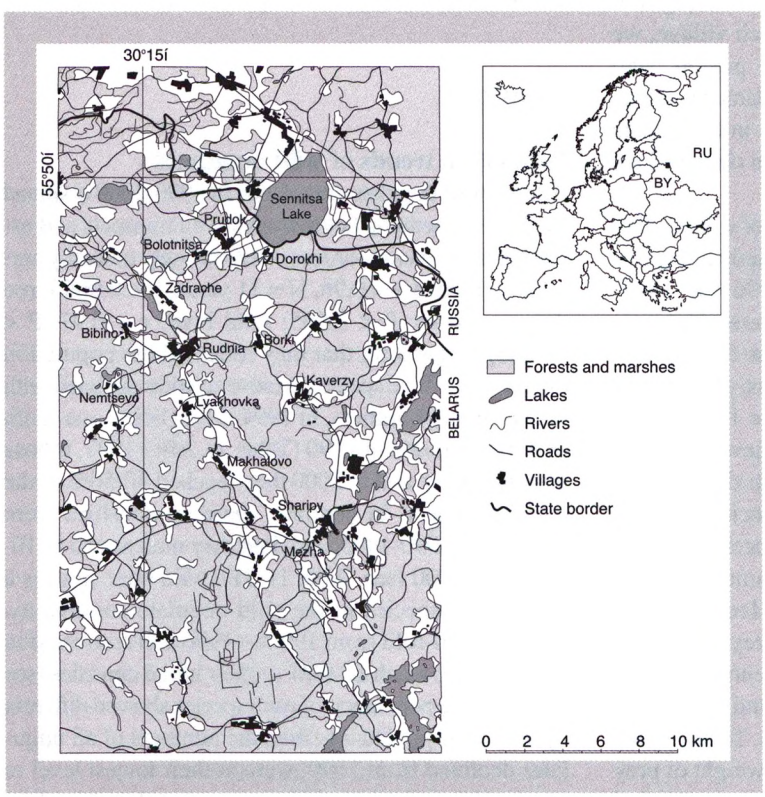

Figure 1. The study area is located in the basin of the Lovat River in the Gorodok district, Vitebsk region, northeastern Belarus. Names of villages are those from which data on wolf sightings and predation on domestic animals were collected.

tained from the hunters' organisation was recalculated per 100 km^2. Based on personal experience of game wardens rather than on methodical surveys, this estimate is an index of abundance and not the actual density. We believe, nonetheless, that it well reflects the multiannual trend in numbers as the data were gathered in the same way throughout the study period. For calculation of crude biomass of wild ungulates the following body masses were applied: for moose 200 kg, for wild boar 80 kg, and for roe deer 20 kg.

Wolf predation on livestock and wolf sightings by humans around villages were monitored in an area of about 240 km^2 located at the centre of the whole study region, and populated by humans more densely than the other parts of it. Large patches of natural habitats were interspersed with the 14 villages Bibino, Bolotnitsa, Borki, Dorokhi, Kaverzy, Lyakhovka, Makhalovo, Mezha, Morozovo, Nemtsevo, Prudok, Rudnia, Sharipy and Zadrache (see Fig. 1). The majority of these villages were small (5-26 houses and 9-67 inhabitants), but two were fairly large (49 and 84 houses, 147 and 242 inhabitants). Farmers mostly kept cows, pigs, hens, dogs and cats, whereas horses, sheep and geese were less common. Two collective farms ('kolkhoz') operated in the two large villages, and they had many cows (110 and 280), pigs (50 and 120), and horses (15 and 40). In each village, we contacted an experienced and reliable person, who gathered information about cases of wolf damage on livestock and other observations on wolves in the village and its surroundings. A total of 377 such observations were collected during 1990-2000.

In order to analyse the diet composition of wolves, their scats were collected in the study area, mainly along forest paths. During 1990-1992, 1994-1996 and 1999-2000, a total of 1,185 scats were gathered and analysed. Almost equal numbers of scats came from spring-summer and autumn-winter seasons. Analysis of scats followed the standard procedure (Lockie 1959, Goszczyński 1974, Jędrzejewska & Jędrzejewski 1998); they were washed through a 0.5-mm mesh sieve and the remaining contents were identified to species based on bone and tooth fragments (according to Pucek 1981) and microscopically, using the keys for mammalian hair (Debrot, Mermod, Fivaz & Weber 1982, Teerink 1991). The relative amounts of the various prey species in wolf diet were given as percentage of occurrence in the total number of analysed scats (%Occ) and percentage of biomass consumed (%Bio) by wolves. To assess the consumed biomass of each species, the weight of prey remains recovered from faecal samples was multiplied by coefficients of digestibility. Since no such digestibility factors for wolves are available, data for the related canid species, the red fox *Vulpes vulpes*, were applied (after Goszczyński 1974, Jędrzejewska & Jędrzejewski 1998). Food niche breadth (B index; after Levins 1968) was calculated for the percentage of biomass consumed in five food categories:

$$B = 1/\sum p_i^2,$$

where p_i is the fraction of a given food category in the total prey biomass consumed by wolves. B could vary from 1 (the narrowest niche) to 5 (the broadest niche possible). To assess wolf preferences for the three species of wild ungulates, Ivlev's selectivity index D (after Jacobs 1974) was calculated:

$$D = (r - p)/(r + p - 2rp),$$

where r is the fraction of the species among wild ungulates consumed by wolves (total number of findings of wild ungulate remains in all scats was taken as 100 to calculate the fractions), and p is the fraction of the species in the wild ungulate community (calculated from pooled data of track counts). D can range from -1 (total avoidance of a species) to 0 (selection proportional to occurrence) to 1 (maximum positive selection).

Results

Population trends of wild ungulates

Estimates of ungulate abundance in 1990-2000 obtained by the two methods (snowtracking on transects and assessments by game wardens) were strongly mutually correlated (moose: $r = 0.96$, $N = 11$ years, $P < 0.0005$; roe deer: $r = 0.94$, $P < 0.005$; wild boar: $r = 0.97$, $P < 0.0005$), suggesting that they reflected the population trends of the three species. Moose steadily declined with the minimum numbers, in 1994-1996, being one-tenth of those recorded in 1990 (Table 1). After 1997, moose numbers grew, and in 2000 they reached 40-50% of the initial numbers. In contrast, roe deer densities were low during 1990-1995, and then they increased 5 to 10-fold until 2000 (see Table 1). The wild boar, always a dominating species in the wild ungulate community, declined >10-fold from 1990 to 1996 and recovered in 1997-2000 to reach 60-80% of their initial densities (see Table 1). The population of each species showed different dynamics. If pooled together, the numbers of all ungulates declined from 1990, were at their lowest level in 1994-1996, and started to increase after that time (Fig. 2). During the 11 years of our study, the amplitude of variation was very large: 4 to 5-fold in estimated num-

Table 1. Index of wild ungulate winter abundance (tracks/1-km transect/2 days), index of estimated ungulate winter abundance (individuals/100 km^2), index of wolf winter abundance and hunting harvest, and wolf interaction with livestock and humans in the head region of the Lovat River (Gorodok district, Vitebsk region, NE Belarus) during 1990-2000.

	Year										
Species/records	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
Index of ungulate winter abundance											
Moose	12.7	10.1	7.6	2.1	0.9	1.3	1.2	2.8	3.7	4.5	7.1
Roe deer	1.3	0.9	1.1	1.0	1.5	1.1	2.9	8.2	10.6	16.2	13.6
Wild boar	25.1	27.4	18.1	10.1	4.2	2.1	1.5	6.1	10.0	18.1	20.9
Estimate of ungulate winter abundance											
Moose	61	52	34	16	7	7	9	20	17	28	23
Roe deer	12	20	18	24	36	32	38	54	96	124	132
Wild boar	238	201	154	98	51	48	24	56	96	142	110
Index of wolf winter abundance and wolf harvest											
Wolf tracks[a]	1.4	0.6	1.0	0.3	0.7	1.1	2.3	1.6	0.5	0.4	0.6
Wolf numbers[b]	2.2	1.3	1.5	0.9	1.6	3.6	2.1	3.0	0.5	0.8	1.7
Wolves shot[c]	24	20	28	7	9	5	27	19	15	10	12
Wolf interaction with livestock and humans											
Wolves seen in village	1	2	4	0	2	5	29	37	12	3	5
Cattle killed by wolf	0	0	1	0	2	5	12	4	1	2	1
Dogs killed by wolves	2	1	2	6	24	44	72	55	21	13	7

[a] Number of tracks/1-km transect/2 days;
[b] Number of wolves/100 km^2 based on game wardens' assessment of the numbers of wolves in winter;
[c] Number of wolves shot by hunters in the Gorodok district.

bers of wild ungulates, and 7-fold in their crude biomass.

The species structure of the community also varied during the study period. The share of moose in the total numbers of wild ungulates declined from 20% in 1990 to 13% in 1996 and 9% in 2000. The proportion of roe deer grew from 4% in 1990 to 50-53% in 1996-2000, and the share of wild boar declined from 76% in 1990 to 34% in 1996, and then increased to 41% in 2000. However, in terms of biomass, the wild boar dominated throughout the study period (percentage shares in 1990, 1996 and 2000 were 60, 43 and 55%, respectively), followed by moose (39, 40 and 29%, respectively). Roe deer contributed the least to the total crude biomass of wild ungulates (1, 17 and 16% in 1990, 1996 and 2000, respectively).

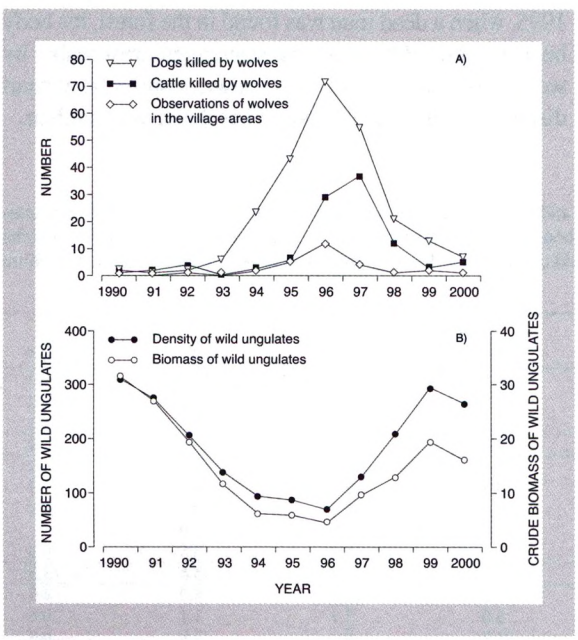

Figure 2. Number of dogs (▽) and cattle (■) killed by wolves, and observations of wolves in and near villages (◇; A) in relation to the abundance expressed as density (●; number of individuals/100 km^2) and crude biomass (○; in tonnes/100 km^2) of wild ungulates (B) pooled for moose, roe deer and wild boar, and censused in an area of 728 km^2. Wolf-livestock and wolf-human interaction were monitored in an area of 240 km^2 embracing the 14 villages (data as in Table 1).

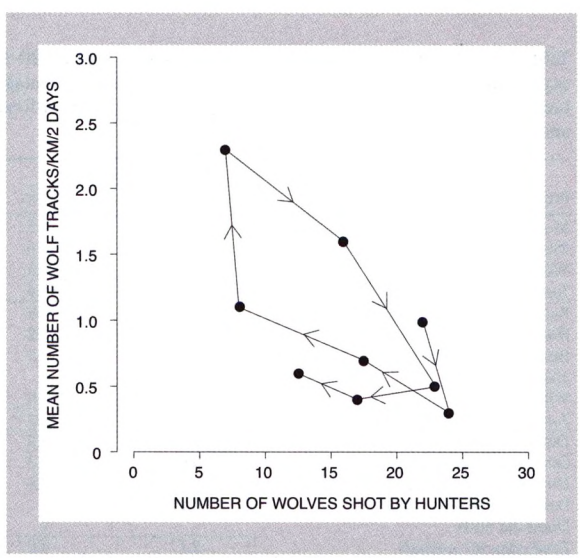

Figure 3. Numerical response of wolves expressed as mean number of wolf tracks/km/2 days in relation to the mean number of wolves shot by hunters in the region (with a 1 to 2-year lag) in 1990-2000 (data as in Table 1). The arrows show the time sequence of events.

Table 2. Roles of ungulate abundance (with 1-year lag) and wolf numbers in shaping wolf interaction with domestic animals and humans. The results of the multiple regression analyses are based on data from Table 1; N = 10 years, *** P < 0.001, ** P < 0.01, * P < 0.05, ns - not significant. Semipartial correlations squared (sr_i^2) show the contribution of each dependent variable to the total variation explained (Tabachnick & Fidell 1983).

Dependent variable log-transformed, ln(x+1)	Total variation explained R^2	Contributions of independent variables to the total variation explained (sr_i^2)		
		Biomass of wild ungulates in year n-1	Index of wolf abundance in year n	
Number of dogs killed	0.991***	0.587***	0.020**	(Tracks)
	0.976***	0.695***	0.007 (ns)	(Numbers)
Number of cattle killed	0.896***	0.180**	0.274**	(Tracks)
	0.713**	0.310*	0.091 (ns)	(Numbers)
Number of observations of wolves in the village area	0.682**	0.069 (ns)	0.301*	(Tracks)
	0.412 (ns)	0.215 (ns)	0.031 (ns)	(Numbers)

Wolf response to hunting harvest by humans and abundance of wild ungulates

Estimates of wolf numbers obtained by snowtracking and game wardens' assessments were mutually correlated (r = 0.63, N = 11 years, P = 0.04). The mean estimate of wolf density during the study was 1.75 individuals/100 km^2 (SD: 0.94). Changes in wolf numbers were not correlated with the variation in wild ungulate densities, neither directly nor with 1 or 2-year time lags (P > 0.1). The most important factor shaping the variation in wolf numbers was the mean hunting harvest of wolves by humans in the preceding two years (R^2 = 0.43, N = 9 years, P = 0.05 for wolf tracks, and R^2 = 0.50, P = 0.03 for estimated wolf densities; see data in Table 1). Thus, wolves responded to the changing rate of persecution with a 1 to 2-year time lag (Fig. 3).

However, variation in wild ungulate numbers did have a strong impact on prey searching and hunting behaviour of wolves. As wild ungulates declined, wolves were more likely to approach the vicinities of human settlements in search for domestic animals (see Fig. 2). During 1990-2000, 28 cows and 247 dogs were reported to have been killed by wolves. Among the dogs, 117 (47%) were hunters' dogs attacked by wolves when roaming in the field or forest away from the village, and 130 (53%) were watch dogs, often chained, killed by wolves near the houses. Moreover, in 1990-2000, wolves were observed 100 times in the village areas. These observations include the case of a rabid wolf that, in 1997, came into one of the villages and bit 11 people before it was killed by locals. The only other possibly direct interaction of wolves and humans happened in 1995, when a dead man was found in the forest, his body bearing signs of having been scavenged presumably by wolves. As the man had been known to suffer from heart disease, the ultimate cause of his death was unclear.

Table 3. Diet composition of wolves in the periods of high (1990-1992 and 1999-2000) and low (1994-1996) abundance of wild ungulates expressed as percentage occurrence in scats (%Occ), and percentage of consumed biomass (%Bio). + = contribution of <0.05%. Food niche breadth B (after Levins 1968) calculated for four categories of food: wild ungulates, wild medium and small-sized prey, domestic medium and small-sized animals and plant material.

Prey category	1990-1992		1994-1996		1999-2000	
	%Occ	%Bio	%Occ	%Bio	%Occ	%Bio
Moose *Alces alces*	42.7	32.5	19.8	10.8	14.9	9.7
Roe deer *Capreolus capreolus*	6.5	3.6	10.5	4.0	20.3	10.2
Wild boar *Sus scrofa*	87.7	52.3	26.2	17.3	85.3	60.1
Total wild ungulates	*96.1*	*88.4*	*54.0*	*32.1*	*93.3*	*80.0*
Raccoon dog *Nyctereutes procyonoides*	2.9	0.9	25.1	5.9	15.5	3.2
Hare *Lepus* sp.	5.8	2.2	53.4	17.2	18.9	4.7
Beaver *Castor fiber*	6.3	3.3	22.6	5.1	10.7	4.8
Micromammalia	1.1	+	10.5	0.3	1.9	+
Wild birds *Aves*	4.7	0.9	6.5	1.0	3.5	0.3
Total wild medium and small-sized prey	*17.9*	*7.3*	*70.5*	*29.5*	*36.8*	*13.0*
Domestic cattle	6.3	3.4	35.8	23.6	8.0	4.7
Other domestic ungulates	0.6	0.3	5.0	3.1	1.1	0.8
Domestic dog *Canis familiaris*	0.9	0.3	21.2	9.1	2.9	0.9
Domestic cat *Felis catus*	0.2	+	10.7	1.9	0.8	0.1
Domestic birds	-	-	0.8	0.1	-	-
Total domestic animals	*8.1*	*4.0*	*74.9*	*37.8*	*12.8*	*6.5*
Fruits and seeds	1.6	0.2	2.8	0.5	2.9	0.4
Other plant material	1.1	0.1	2.5	0.1	1.3	0.1
Food niche breadth B	1.27		3.65		1.52	
Mean number of prey/scat	1.69		2.37		1.88	
Number of scats analysed	447		363		375	

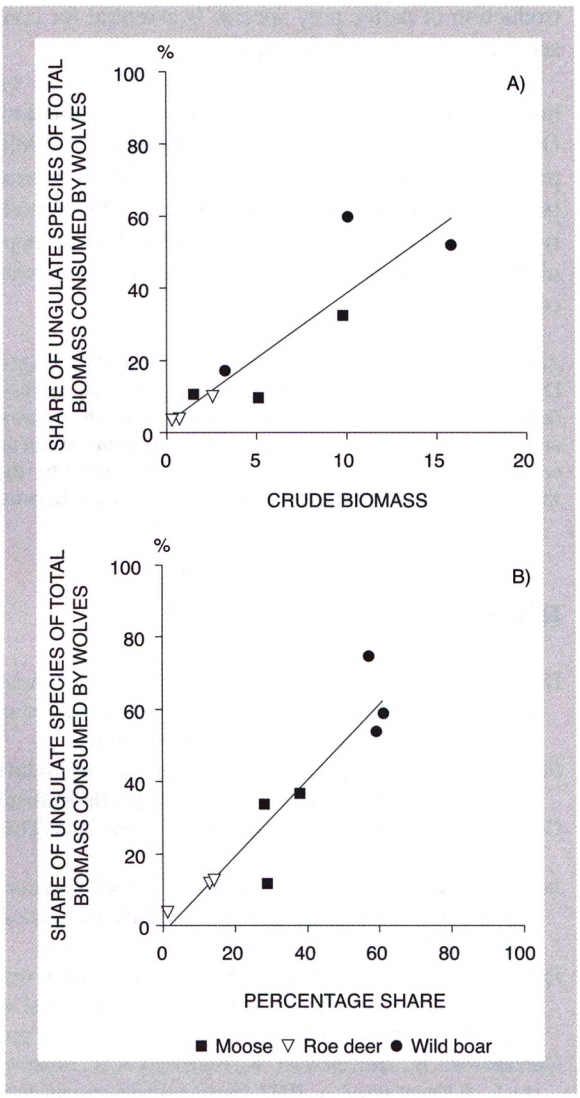

Figure 4. Shares of the ungulate species moose (■), roe deer (▽) and wild boar (●) in the total biomass consumed by wolves (in %) in relation to the crude biomass of the respective species (A; in tonnes/100 km^2) and as their percentage share of the total biomass of all ungulates (B). The three points for each species denote mean values for the periods 1990-1992, 1994-1996 and 1999-2000, respectively. For A): $y = 2.64 + 3.59x$; $R^2 = 0.811$. $P = 0.001$, and for B): $y = 1.90 + 1.06x$, $R^2 = 0.865$, $P < 0.0005$.

The number of cattle and domestic dogs killed by wolves, as well as observations of wolves around the villages increased exponentially with the decline in wild ungulates and the highest number of such incidences was recorded during 1995-1997. Indeed, the between-year variation in wolf interaction with domestic animals and humans were best explained by two factors: abundance (biomass) of wild ungulates with a 1-year time lag and index of wolf abundance (multiple regression analyses: R^2 from 0.991 to 0.412, P from <0.0005 to 0.15, N = 10 years). Semipartial correlations squared calculated for each regression model showed that the abundance of wild ungulates (acting with a 1-year lag) was a far more important factor than wolf numbers (Table 2).

The diet composition of wolves also reflected the fall and rise of wild ungulates in the study period. Wild ungulates constituted 88% of food biomass consumed by wolves during 1990-1992, 32% in 1994-1996, and 80% during 1999-2000 (Table 3). The most important buffer prey compensating for the shortage of wild ungulates was domestic animals (mainly cattle) and wild medium-sized mammals (predominantly hare, but also raccoon dog *Nyctereutes procyonoides* and beaver).

Wolves preyed on the three wild ungulates opportunistically, with no consistent preferences for any species. Their percentage shares in the total food biomass consumed by wolves were proportional to the amount of crude biomass of wild ungulates available (Fig. 4A). Also, the species structure of ungulates preyed upon reflected that in the living community (Fig. 4B). Food niche breadth calculated for five groups of prey (see Table 3) was the narrowest in 1990-1992, when wild ungulates were most numerous (B = 1.27) and the widest in 1994-1996 (B = 3.65), when they were rare.

Discussion

In Europe, the numerical response of wolves to variation in ungulate abundance is even more disturbed by humans than their dietary, functional response. Until very recently, deliberate control or eradication of wolves has been an indisputable, widely accepted way of wolf 'management'. The only periods when wolves could recover in numbers and regain some of their original range were the times of war and uprisings (Osmolovskaya & Priklonskii 1975, Jędrzejewska, Jędrzejewski, Bunevich, Miłkowski & Okarma 1996). In effect, in many regions of central and eastern Europe the negative correlation between wolf numbers and ungulate densities was observed (Filonov 1989, Jędrzejewska et al. 1997) instead of a typical positive numerical response. In our study, both wolf and ungulate dynamics were shaped predominantly by human harvesting. Though we have no precise data on ungulate hunting quotas and poaching intensity, the information obtained by interviewing the local hunters as well as our observations on the remnants of the poached moose and wild boar in the study area allowed us to roughly estimate that, since 1992, the killing rate of ungulates by humans could have increased 5 to 10-fold in com-

parison with earlier years and it remained heavy until 1995. Thus, uncontrolled exploitation by humans was the most probable cause of the ungulate decline in the 1990s. Conducive to this was the political transformation and economical regress in Belarus (before 1991 - the Belarusian Socialist Soviet Republic).

Our study evidenced that a manifold decline in wild ungulate abundance was an essential factor responsible for the increased predation on domestic animals by wolves. Interestingly, however, our interviews with local people revealed that they interpreted the observed changes as resulting from presumed growth of the wolf population. In 1990-1993, when wolves only rarely killed cattle or dogs, local people forgot about wolf danger to livestock and even started to think that wolves must have been rare in the area. When wolves began to appear in and near the villages, the local citizens believed that this was the result of a marked increase in wolf numbers. Such interpretation of wolf-livestock interaction was a common opinion in many areas of Belarus in the decade 1990-2000, and was the main reason for intensified hunting of wolves after 1996.

The number of wolves did not decline with reduced abundance of wild ungulates, because the wolves had access to numerous domestic animals. In the early 1990s, wolves were relieved from heavy control but few years later, when heavy damage to livestock caused complaints from farmers, hunting on wolves intensified. Worth attention is the shape of the wolf's numerical response to hunting by man. It occurred with a substantial (1-2 years) time lag as could be expected from the reproduction and maturation rate of wolves. Also, a one-year lag was observed in the dietary shifts of wolves to domestic animals when wild ungulates declined. The wolves continued to prey on declining wild ungulates, but then again, when wild ungulates began to recover, wolves for some time continued their rallies to the villages before they shifted back to wild prey. This suggests substantial conservationism in wolf hunting habits.

The described situation of ungulate-human-wolf relationship seems typical for the large regions of Belarus in the 1990s and most probably occurred in many areas of eastern Europe during 1990-2000, as this was a decade of profound political and economical transformation. From a management perspective, we suggest that predation level and human-wolf conflicts could be reduced not only by increased wolf harvest in agricultural areas (Mech 2001), but also by enhancing the density and diversity of wild ungulates. A similar conclusion was drawn in a study on Portugese wolves (Vos 2000) which fed exclusively on livestock because of the scarcity of wild prey. Vos (2000) emphasised that reintroduction of native prey species is essential for conservation of wolves in Portugal.

Finally, the controversial issue of wolf attacks on humans still awaits serious analysis and explanation. Osmolovskaya & Priklonskii (1975) and Ryabov (1988) proposed that such incidences were more likely to happen, when wolves became numerous and suffered deadly shortage of food, when rabies spread in the wolf population, and when hybridisation with stray dogs was common.

Acknowledgements - we are grateful to Vyacheslaw Budny, Dmitrii Petrov, Genadii Lauzhel and Aleksei Polozov for their help in the field work, to Karol Zub for drawing the figures, and to Dr Włodzimierz Jędrzejewski for his comments on an earlier draft of this paper. The study was financed by the Institute of Zoology, National Academy of Sciences of Belarus.

References

Debrot, S., Mermod, C., Fivaz, G. & Weber, J-M. 1982: Atlas des poils de mammiferes d'Europe. - Universite de Neuchatel, Peseux, Switzerland, 208 pp. (In French).

Filonov, K.P. 1989: Ungulates and large predators in wildlife reserves. - Izdatelstvo Nauka, Moskva, 246 pp. (In Russian)

Goszczyński, J. 1974: Studies on the food of foxes. - Acta Theriologica 19: 1-18.

Jacobs, J. 1974: Quantitative measurements of food selection: a modification of the forage ratio and Ivlev's selectivity index. - Oecologia (Berlin) 14: 413-417.

Jędrzejewska, B. & Jędrzejewski, W. 1998: Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. - Springer Verlag, Berlin, Germany, 450 pp.

Jędrzejewska, B., Jędrzejewski, W., Bunevich, A.N., Miłkowski, L. & Krasiński, Z.A. 1997: Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. - Acta Theriologica 42: 399-451.

Jędrzejewska, B., Jędrzejewski, W., Bunevich, A.N., Miłkowski, L. & Okarma, H. 1996: Population dynamics of wolves Canis lupus in Białowieża Primeval Forest (Poland and Belarus) in relation to hunting by humans, 1847-1993. - Mammal Review 26: 103-126.

Jędrzejewski, W., Jędrzejewska, B., Okarma, H., Schmidt, K., Zub, K. & Musiani, M. 2000: Prey selection and predation by wolves in Białowieża Primeval Forest, Poland. - Journal of Mammalogy 81: 186-202.

Levins, R. 1968: Evolution in changing environments. - Princeton University Press, USA, 132 pp.

Lockie, J.D. 1959: The estimation of the food of foxes. - Journal of Wildlife Management 23: 224-227.

Mech, L.D. 2001: Managing Minnesota's recovered wolves. - Wildlife Society Bulletin 29: 70-77.

Meriggi, A. & Lovari, S. 1996: A review of wolf predation in

southern Europe: does the wolf prefer wild prey to livestock? - Journal of Applied Ecology 33: 1561-1571.

Meriggi, A., Brangi, A., Matteucci, C. & Sacchi, O. 1996: The feeding habits of wolves in relation to large prey availability in northern Italy. - Ecography 19: 287-295.

Osmolovskaya, W.I. & Priklonskii, S.G. 1975: The Middle Russian wolf (its distribution, abundance and interrelations with man). - Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologii 80(1): 117-130. (In Russian with an English summary).

Papageorgiou, N., Vlachos, C., Sfougaris, A. & Tsachalidis, E. 1994: Status and diet of wolves in Greece. - Acta Theriologica 39: 411-416.

Pucek, Z. (Ed.) 1981: Keys to vertebrates of Poland. Mammals. - PWN, Polish Scientific Publishers, Warszawa, Poland, 368 pp.

Ryabov, L.S. 1974: The attitude of wolves towards domestic animals and wild ungulates in the region of the Khopersk Nature Reserve. - Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologii 79(3): 6-15. (In Russian with an English summary).

Ryabov, L.S. 1988: Osobennosti razmnozheniya volkov (Canis lupus L.) v Centralnom Chernozeme [Characteristics of wolf (Canis lupus L.) reproduction in the Central Black Earth region]. - Ekologiya 1988(6): 42-48. (In Russian).

Tabachnick, B.G. & Fidell, L.S. 1983: Using multivariate statistics. - Harper & Row, New York, 509 pp.

Teerink, B.J. 1991: Hair of West-European mammals. Atlas and identification key. - Cambridge University Press, Cambridge, UK, 232 pp.

Vos, J. 2000: Food habits and livestock depredation of two Iberian wolf packs (Canis lupus signatus) in the north of Portugal. - Journal of Zoology (London) 251: 457-462.