

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/223384965>

Potential impact of wolves *Canis lupus* on prey populations in eastern Poland

Article in *Biological Conservation* · April 1997

DOI: 10.1016/S0006-3207(96)00067-5

CITATIONS

59

READS

181

2 authors:



Zbigniew Głowiński
Polish Academy of Sciences

1 PUBLICATION 59 CITATIONS

[SEE PROFILE](#)



Piotr Profus
Polish Academy of Sciences

33 PUBLICATIONS 501 CITATIONS

[SEE PROFILE](#)

POTENTIAL IMPACT OF WOLVES *Canis lupus* ON PREY POPULATIONS IN EASTERN POLAND

Zbigniew Głowaciński* & Piotr Profus

Institute of Nature Conservation, Polish Academy of Sciences, Lubicz 46, 31-512, Cracow, Poland

(Received 23 July 1994; accepted 17 January 1996)

Abstract

A 7000 km² study area in eastern Poland supported c.50 wolves *Canis lupus* in 1989 and 40 in 1992, and high numbers of game constituting the staple food of these predators. This paper assesses the energetic requirements of the wolf population as well as potential resources of its preferred prey. On the basis of basal metabolism rate (BMR) and daily food consumption (DFC), we calculate that an average wolf (35 kg) needs 13 421 kJ daily, which corresponds to 1.74 kg of prey biomass. Calculations based on field metabolism rate (FMR2-for non-herbivorous mammals) yielded a 60% higher value, i.e. 2.77 kg of meat per day. The yearly requirements of the study population, using these two methods, ranged from 242 GJ (40 individuals, BMR and DFC) to 389 GJ (50 individuals, FMR2), i.e. 31.5–51.0 tonnes of meat and edible tissues. Wolves preyed chiefly on red deer *Cervus elaphus* and roe deer *Capreolus capreolus* (70–85% of the total biomass consumed), wild boar *Sus scrofa*, hare *Lepus europaeus*, moose *Alces alces* and small rodents. The total biomass of wolf prey, censused from snow tracking and year-long observations, and corrected from drive censuses, was assessed at 879–943 tonnes. These data suggest that wolves remove no more than 10% (6.3–9.0%) of the total available biomass of ungulates which may not seriously affect resources of local game owners. © 1997 Elsevier Science Ltd. All rights reserved

Keywords: wolf, population, energy requirements, prey preference, biomass, Poland.

INTRODUCTION

Opinions on the role of wolves in regulating deer and other prey are divergent and not well documented, though many papers on the diet and food habits of this predator have been published (Mech, 1970; Bibikov,

1985; Messier & Crête, 1985; Fuller, 1989; Jędrzejewski et al., 1992; Śmietańska & Klimek, 1993; Messier, 1994). However, it is very important to determine this role in the context of conservation and rational management of living natural resources. In Poland, wolves occur on the western boundary of its central European range, following, more or less precisely, the line of the Vistula river, but varying with changes in wolf population (Fig. 1).

During the present century, at least two periods of strong increase in wolf population (in the 1930s and in the early 1950s) were observed in Poland followed by drastic declines due to severe persecution of the species by all possible means (Buchalczyk, 1992; Okarma, 1993). In the last 15 years, wolves were protected by game-laws with a close season in April–July. It seems that this protection has contributed to the recent recovery of wolves (see Okarma, 1993), after a regressive period in 1960–1975, and their return to some forests to the west of the Vistula (Pielowski, 1993). Official data show that the wolf population in Poland has increased to 800–950 individuals, despite regular shooting of up to 20% of the population yearly (Okarma, 1993; Pielowski, 1993). Wolves have also increased behind our eastern border, e.g. in Byelorussia where c.2000 wolves have been reported (Banad & Kozłowski, 1992). Some of these animals migrate to the west, reinforcing the Polish population.

The decline of the wolf in Europe has caused local societies to develop conservation initiatives on behalf of this ecologically important predator. The species was included in the IUCN Red List of Threatened Animals as well as in the checklists of some international conventions—Bern and Washington (CITES; see World Conservation Monitoring Centre, 1993; also Delibes, 1990; Buchalczyk, 1992). In Poland there has also been growing pressure for extending the protection of wolves, and since 1 April 1995 the species has been taken under strict protection in the whole of Poland, except for three administrative regions in the eastern part of the country. Nevertheless, there is anxiety that too high numbers of wolves will seriously reduce ungulate populations, causing losses to game management.

The aim of this paper was to assess the trophic impact of the wolf on populations of its prey in the province of

*Institute of Nature Conservation, Polish Academy of Sciences, 46 Lubicz St, 31-512 Kraków or 1 Ariańska St, 31-505 Kraków, Poland. Tel and Fax: 0048 (12) 210348.

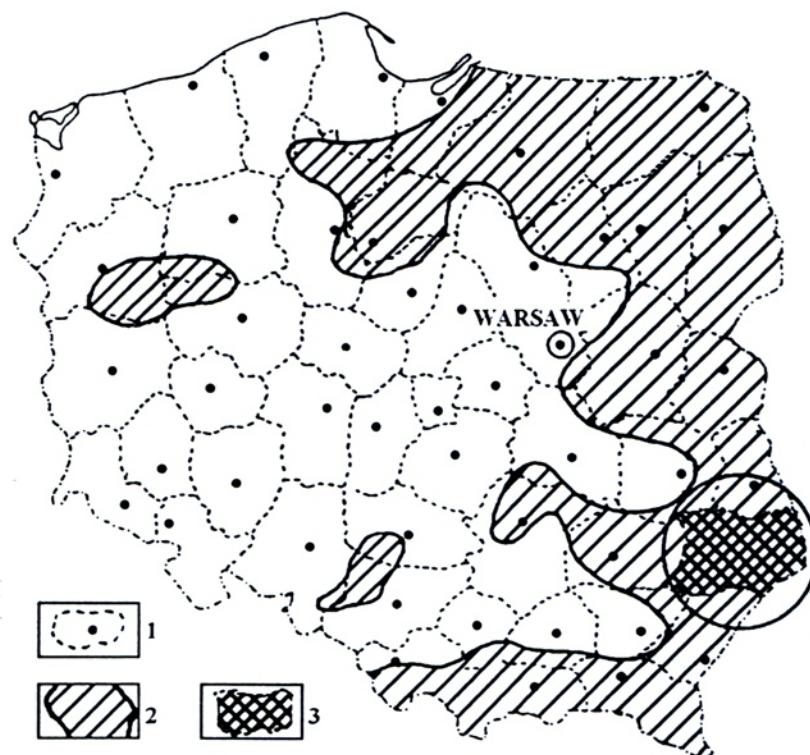


Fig. 1. Present range of wolf *Canis lupus* shown on the administrative map of Poland. 1, boundaries of provinces and their chief towns; 2, area of regular wolf occurrence; 3, study area encircled.

Zamość (Fig. 1). This administrative area lies within the range of regular occurrence of the species; its ecological conditions and fauna are fairly typical of eastern Poland. A preliminary discussion of these problems was published by Głowaciński and Profus (1992).

STUDY AREA

The province of Zamość lies in the south-eastern part of Poland, bordering on Ukraina. It covers c. 7000 km², of which 71% is agricultural land (cultivated fields, meadows, pastures, orchards etc.) and 23% forest. It is devoid of great industry and large urban agglomerations. A characteristic feature of the area is the large geomorphological differentiation: upland xerothermic habitats adjoin basins and wet meadows extending chiefly in river valleys (Taniec, Por, Huczwa, Sołokija, Wieprz, Bug). The largest forest complex is the Solska Pristine Forest/Puszcz Solska (1000 km² within Zamość), dominated by pine woods in swampy areas and on dry sandy dunes. In other parts of the region, forests are fragmented and greatly transformed. The most valuable forest areas are included in the Roztocze National Park (7905 ha) and some nature reserves. A few landscape parks covering 55 km² have also been created.

METHODS

Data on the number of wolves and their prey were obtained from the Provincial Hunting Union in Zamość

and, independently, from particular local forest districts. Estimates were also made by the agencies of the Ministry of Environmental Protection, Natural Resources, and Forestry (GUS, 1993). The data on ungulate numbers were corrected on the basis of results yielded by a more precise alternative method (see Pucek *et al.*, 1975).

Field methods

The data on animal numbers used in this paper were obtained from tracks in fresh snow or mud (NT). However, the method cannot be applied in the spring-summer period when packs/families of wolves and herds of ungulates are dispersed. Results from snow-tracking methods are therefore usually supplemented with year-long observations. Comparison of results obtained by this method with those produced by a drive census (ND; Pucek *et al.*, 1975), or by a method based on censusing roaring stags and recognizing social structure of red deer populations (Langvatn, 1977; Bobek *et al.*, 1986), shows that, in certain cases (e.g. censuses of roe deer in lowlands), the tracking method may yield results as much as 3·5 times lower. In this paper, data on ungulate numbers, obtained from a drive census, were accepted as more reliable, so the coefficients based on this method (ND) were used to correct starting data estimated by means of the NT method.

Energy requirements of wolves

Data from eastern Poland (H. Okarma, pers. comm.) give an average body weight of 41·2 kg for an adult wolf (male = 44·2 kg, n = 70; female = 38·4 kg, n = 49). In a sample

of 152 wolves killed in winter c.28% were young individuals (18 males and 15 females) with an average body mass of 27 kg. Taking into account the sex ratio in packs (1.3 males:1 female) and the seasonally high proportion of pups with an accepted average body mass of 20 kg (see also Voskár, 1993), we estimate the overall average body mass of wolves in the investigated area at 35 kg.

Calculations based on basal rate of metabolism

The daily energy requirements of wolves were first calculated under the assumption that in homiothermic vertebrates metabolism is related to body mass by an allometric function (e.g. Kleiber, 1932, 1961; Nagy, 1987; McNab, 1989; Weiner, 1989). The lowest level of energy use, characteristic of inactive animals kept at ambient temperature is the basal metabolic rate (BMR). This was calculated according to the Kleiber equation (Kleiber, 1932) for mammals:

$$\text{BMR} = 70 \text{ kcal} \times W^{0.75} = 293.13 \text{ kJ} \times W^{0.75} \quad (1)$$

where BMR is expressed in kJ per animal per day; and W is body mass in kg.

For walking, running or hunting terrestrial mammals metabolism may increase by 2–4 times (Weiner, 1987). Estimates of real energy requirements of wolves in the wild were based on data by Heptner & Naumov (1967; see Goszczyński, 1986), showing that a 37 kg free-living wolf consumes food with an energy value of 14 000 kJ daily, i.e. c.2 kg of meat. Thus, the daily food or energy consumption (DFC) is 3.18 times as high as the BMR value (4400 kJ).

The BMR may also be calculated from the oxygen used by an animal (Okarma & Koteja, 1987; Weiner, 1987; McNab, 1989), but the results are almost identical to those calculated from Kleiber's formula and differences are within the range of methodological errors.

Estimates based on the use of doubly labelled water

Recent studies on the metabolism of animals have used an isotope method of doubly labelled water, also known as the heavy water method using $D_2^{18}O$ (Nagy, 1987; Weiner, 1987, 1989). This allows indirect estimates of the total daily energy expenditure of a free-living animal. The field metabolic rate (FMR) for all eutherian mammals is closely correlated with body mass, and the allometric equation given by Nagy (1987) was used:

$$\text{FMR1 (kJ/day)} = 3.35 W^{0.813} \quad (2)$$

where W is body weight in g (see also Bozinovic & Medel, 1988).

However, for non herbivorous mammals, FMR values are higher and should be derived from Nagy's (Nagy, 1987) formula:

$$\log \text{FMR2} = 0.412 + 0.862 \log W, \quad (3)$$

which can be transformed into

$$\text{FMR2 (kJ/day)} = 2.58 W^{0.862}. \quad (4)$$

Average body weight of prey

The mean body weight of different kinds of prey was based on data from eastern Poland as well as on data from the literature cited; in the calculations sex and age structure of populations were taken into account. Values of average body mass of ungulates, taken for calculations, were reduced by 10% for juveniles and 25% for adults (after Fuller, 1989; Okarma, 1992) on account of inedible and indigestible parts of their bodies (large bones, hair and stomach).

For the red deer the population structure was generally well known for the area adjacent to the region of Zamość (Bobek *et al.*, 1992). Here the average body mass of adult red deer was estimated at 112 kg and the edible part at 92 kg. The weighted average consumption was therefore 72 kg (detailed calculations in Głowaciński & Profus, unpublished data). We assumed that wolves used on average 80% of the biomass of ungulates killed.

RESULTS

Wolf population in Zamość region

Official data, supported by independent estimates by the local forest and hunting service, indicate that the wolf population of the province of Zamość numbered 30–55 individuals in 1981–1993. The first few years were a period of increase in population here and throughout Poland, followed at the end of the 1980s by a slight decrease (Głowaciński & Profus, 1992; Okarma, 1993; see also Environmental Protection/Ochrona Środowiska-GUS, 1993). In the Roztocze National Park itself, 10 wolves (2–3 pairs + 3–6 one year-old young) were observed each year (Profus & Tomek, 1994). In 1989 and 1992 the studied population thus can be estimated at about 50 and 40 individuals, respectively. This gives an average density of wolves of c.3 individuals (3.3 in 1989 and 2.7 in 1992) per 100 km² of forest. Every year five to 20 wolves were shot. Winter wolf packs in the surveyed area consisted of three-eight individuals. These data concur with those given by Bibikov (1985), Bunjevic (1988) and Voskár (1993) on the wolf population from East and Central Europe.

Food composition and prey choice

An analysis of the diet of wolves from the eastern Poland (e.g. Miłkowski, 1986; Jędrzejewski *et al.*, 1992; Śmiertana & Klimek, 1993) shows that the main prey of wolves in this geographic region are red deer *Cervus elaphus* and roe deer *Capreolus capreolus*. Depending on the season, the proportion of deer biomass consumed by wolves varies from 65 to 96%. Red deer are usually taken more often, but in the Zamość region, roe deer are about 10 times as numerous (Table 1), and therefore their frequency in the diet of wolves was c.3 times as high (Sumiński & Filipiak, 1977). We accept that the

Table 1. Number and density of the main wolf prey in the Zamość study area from year-long tracking observations (NT). Data verified on the basis of drive censuses (ND)^a are given in bold

Species of prey	Average number of individuals per 10 km ²							
	Number of individuals		Total experimental area (6900 km ²)		Forests (1550 km ²)		Fields and meadows (4840 km ²)	
	1989	1992	1989	1992	1989	1992	1989	1992
Moose ^b	162	120	0.23	0.17	1.55	0.77	—	—
Red deer	1150	1190	1.67	1.72	7.42	7.68	—	—
	1725	1785	2.51	2.58	11.13	11.52		
Roe deer ^c	11960	13400	17.33	19.42	64.30	72.05	4.12	4.61
	17940	20100	26.00	29.13	96.45	108.06	6.18	6.92
Wild boar	740	990	1.07	1.44	4.77	6.39	—	—
	1110	1485	1.61	2.16	7.16	9.59		
Hare	51000	50520	73.91	73.22	85.14	84.34	85.14	84.34

^aAccepted correction indices ND/NT (after Pucek *et al.*, 1975, selected data) for red deer, roe deer and wild boar — 1.5.

^bIn 1989: 70 males, 60 females, 32 juveniles; in 1992: 50 males, 50 females, 20 juveniles (official data supported by the authors' own estimations, see Głowaciński *et al.*, 1992).

^cAccording to official data (GUS, 1993) the ratio of forest-living of roe deer to field roe deer in the study area is c.5:1.

Table 2. Average body weight and estimated total biomass for major wolf prey in the Zamość region. Calculations based on tracking data (NT), in bold of ungulates based on drive census (ND)

Species and mean body weight (kg)	Biomass (tonnes)		Biomass (kg/ha)				
			Forests		Fields and meadows		
	1989	1992	1989	1992	1989	1992	
Moose ^a	225	36	27	0.23	0.14	—	—
Red deer ^b	112	129	133	0.83	0.86	—	—
	193	200		1.25	1.29		
Doe deer ^c	20.5	245	275	1.26	1.47	0.10	0.12
	368	412		1.89	2.21	0.15	0.18
Wild boar ^c	66	49	65	0.32	0.42	—	—
	74	98		0.48	0.63		
Hare ^c	4.1	208	206	0.33	0.33	0.33	0.33
Total		667	706	2.97	3.22	0.43	0.45
		879	943	4.18	4.60	0.48	0.51

^aAfter averages for males ≈ 300 kg, females ≈ 200 kg, calves ≈ 100 kg.

^bAverages for 4–7 year-old males (155 kg), females (114 kg), and calves (65 kg) from Bobek *et al.* (1992); see also text.

^cAfter Ryszkowski (1982).

most probable overall proportion of red deer and roe deer biomass here is 70–85%, the proportions of these two species being more or less equal.

Wild boar *Sus scrofa* constitute 8–22% of the biomass consumed by Polish wolf populations (e.g. Jędrzejewski *et al.*, 1992). For the study population we estimate this consumption at 10–20%, taking into account a high uptake of piglets (up to 94%).

Other prey form a small proportion of the diet. Data from Poland show that domestic animals account for <6% of the biomass consumed, mainly in autumn and winter when the carcasses of these animals are used as a bait for wolves by hunters (Śmietana & Klimek, 1993). Moose *Alces alces* account for c.1% (Okarma, 1992) and hares *Lepus europaeus* usually do not exceed 3.5% (e.g. Jędrzejewski *et al.*, 1992; Śmietana & Klimek, 1993) though this figure may be 3–5 times as great in

Lithuania, Byelorussia and Ukraine (Bibikov, 1985). Smaller prey such as rodents, birds, amphibians and reptiles, are of relatively small importance though their frequency in scats is probably underestimated (Sumiński & Filipiak, 1977).

Population size and biomass of wolf prey

The number and densities of ungulates and hares estimated to occur in the study area are given in Table 1, from which the calculated biomass of all prey types was 667–879 tonnes in 1989 and 706–943 tonnes in 1992 (Table 2). Most of these resources (87%) are associated with forests; every 100 ha of woods yielded, respectively, 297–418 and 322–460 kg of biomass. The corrected higher values, obtained from drive censuses (ND), are considered more reliable and are used for further calculations.

Table 3. Daily (24 h) wolf demand for food and energy in relation to body weight

Body weight (kg)	BMR ^a	DFC ^b kJ/wolf × 24 h	FMR2 ^c	Daily edible biomass needed (g)		
				Deer/hare (7.8 kJ/g)	Wild boar (7.34 kJ/g)	Rodents (6.4 kJ/g)
20 ^d	2774	8 821	13 156	1687	1792	2142
30	3760	11 957	18 659	2392	2542	3039
35	4220	13 421	21 311	2732	2903	3471
37	4400	14 000	22 357	2866	3046	3641
40	4665	14 835	23 911	3066	3258	3894
50	5515	17 538	28 982	3715	3949	4720
60	6323	20 107	33 915	4348	4620	5524

^aBMR, basal metabolic rate.^bDFC, daily food consumption.^cFMR2, field metabolic rate. Calorific values after Weiner (1973), Górecki (1975), Jezierski & Myrcha (1975).^dFood intake for rapid growth of pups excluded.

Table 4. Field metabolic rate (FMR) for wolves of different weight categories calculated with the help of doubly labelled water method and percentage relations between values FMR and DFC. Average body weight of wolf in bold

Weight (kg)	FMR1 (kJ/day)	FMR2 (kJ/day)	FMR1:DFC (%)	FMR2:DFC (%)
30	14 620	18 659	122.3	156.0
35	16 572	21 311	123.5	158.8
37	17 338	22 357	123.8	159.7
40	18 472	23 911	124.5	161.2
50	22 147	28 982	126.3	165.3
60	25 685	33 915	127.7	168.7

Table 5. Food requirements per wolf (35 kg) in the study population-variant I. Estimates based on FMR2

Percentage prey in wolf diet	Meat consumption (kg)		Numbers of prey
	Daily	Yearly	
85 Deer ^{a,b}	2.322	848	4.3 fawns and 2.8 adult red deer + 28.3 roe deer
10 Wild boar ^a	0.290	106	3.8 young and c.0.2 adult specimen
2 Hare	0.055	20	5 adult specimens
2 Rodents	0.070	26	c.1300 small rodents
1 Moose and other prey	0.027	10	c.0.1
Food requirements:			
of one wolf	2.764	1010 = 7.78 GJ	Yearly consumption of total wolf population
of 40 wolves	110.560	40 400 = 311.2 GJ	284 fawns and 110 adult red deer + 1100 roe deer + 151 young and 9.4 adult wild boars + 200 hares + c.40 000 rodents + 3 young moose
of 50 wolves	138.200	50 500 = 389.0 GJ	215 fawns and 137 adult red deer + 1415 roe deer + 188 young and 11.8 adult wild boars + 250 hares + c.65 000 rodents + 5 young moose

^aValues of edible body mass of prey accepted here are as follows: red deer — adult 92 kg, calf 40; roe deer 15; wild boar—adult 50, young 25.^b50% of red deer and 50% of roe deer biomass (Sumiński & Filipiak, 1977; see also text).

Impact of wolves on prey

Food requirements of one wolf

As shown by estimates from Table 3 the food consumption (DFC) of a wolf correlates strongly with its body mass. The energy taken by an average wolf (35 kg), estimated by the BMR and DFC method, is c.13 420 kJ/day, which corresponds to 1.74 kg meat/day. Energy requirements based on the FMR2 method were higher and amounted to c.21 300 kJ/day, which

corresponds to 2.77 kg of meat/day, with an average energy value of 7.7 kJ/g. This gives an annual consumption of 1010–1019 kg, or 7.8 GJ.

The energy demand for a wolf calculated by the FMR technique (eqns 2 and 4) is therefore higher than that based on the BMR and DFC method, and the difference increases with body mass. The relative difference for an average wolf (35 kg) is 23.5% (FMR1) or 58.8% (FMR2) (Table 4). The estimated food and energy

Table 6. Food requirements of one wolf (35 kg) in the study population-variant II. Estimates based on FMR 2

Percentage prey in wolf diet	Meat consumption (kg)		Numbers of prey
	Daily	Yearly	
70 Deer ^{a,b}	1.913	699	3.5 fawns and 2.3 adult red deer + 23.3 roe deer
20 Wild boar ^a	0.580	212	7.5 young and c.0.5 adult specimen
5 Hare	0.137	50	12.5 adult specimens
3 Rodents	0.104	38	c.1900 small rodents
2 Moose and other prey	0.054	20	c.0.2
Food requirements			
of one wolf	2.789	1019 ^c	Yearly consumption of total wolf population
of 40 wolves	111.560	40760	142 fawns and 91 adult red deer + 932 roe deer + 301 young and 19 adult wild boars + 500 hares + c.76 000 rodents + 6 young moose
of 50 wolves	139.450	50950	177 fawns and 113 adult red deer + 1165 roe deer + 377 young and 24 adult wild boars + 625 hares + c.95 000 rodents + 10 young moose

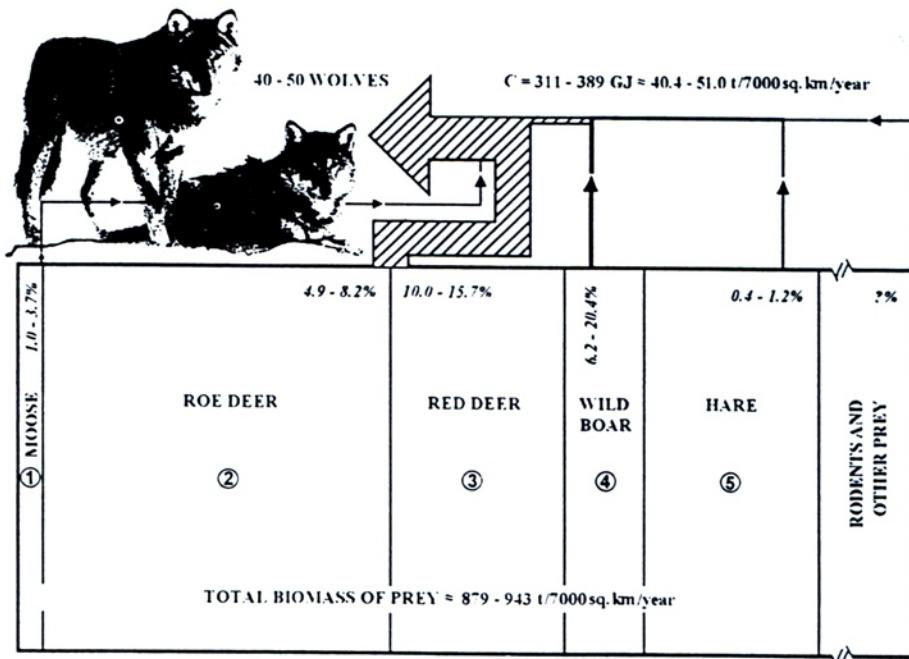
^aEdible biomass of prey as in Table 5, see also text.^b50% of red deer and 50% of roe deer biomass as in Table 5.^cEquivalent data energy units as in Table 5.

Fig. 2. Estimated edible biomass and energy consumption (C) of the wolf population in the study area. Areas of rectangles 1-5 indicate the share of particular species in the total biomass of wolf prey-average value for 1989 and 1992. Percent values refer to uptake of biomass of different kinds of prey, including inedible parts of body.

uptake from animal populations, constituting the wolf diet, will also increase by those values.

Effect on prey populations

As a basis for assessing the impact of wolf predation on other wild animals in the province of Zamość, the two most probable variants of the uptake of prey were accepted: In variant I (Table 5), a high proportion of ungulates in the diet of wolf was assumed and in variant II (Table 6), higher proportions of other prey were adopted.

Calculations based on FMR2 value and uptake of prey according to variant I (strongly differentiated diet) show that the Zamość population of wolves took at least 311 and 389 GJ per year, i.e. 40.4 and 50.5 tonnes of meat and edible tissues (see also Fig. 2).

In variant II (more evenly distributed diet), the values obtained approximate, in general, the previous ones but differ significantly in the impact on different species. The FMR2 technique gives an estimated consumption here of 40.8-51.0 tonnes/year. The most probable share of particular prey species in these totals, expressed as numbers of individuals taken, is shown in Tables 5 and 6.

Relating the estimated food requirements of wolves to numbers of prey in the study area (Tables 1 and 4), we obtain the total uptake of prey: 5.7-5.8% in 1989 and 4.3% in 1992 (FMR2 value). Simplified, the uptake of prey by wolves in the studied population is about 5% of the edible biomass of prey constituting the staple food of this predator, or 6% of the whole prey biomass including inedible parts. The uptake of ungulates

themselves as a proportion of their total biomass—671 tonnes in 1989 and 737 tonnes in 1992—was 8.7–9.0% and 6.3–6.5%, respectively.

DISCUSSION

It is very difficult to estimate the role of polyphagous predators such as wolves in complex biocenoses, where they adapt their hunting behaviour to local fluctuations in prey populations (Mech, 1970; Bibikov, 1985; Fuller, 1989; Okarma, 1992). Certain simplifications and assumptions are, therefore, necessary. In the above calculations, it is particularly important to estimate correctly: (1) the daily food requirements of wolves and (2) numbers and population structure of their prey.

Our estimate of average meat consumption per 35 kg wolf per day is 2.77 kg similar to that were obtained by other authors (e.g. Kolenosky, 1972; Peters, 1993). According to Russian data (Vyrupayev, 1979; Bibikov, 1985), yearly meat requirements per individual are 500–800 kg, a daily requirement of 1.4–2.2 kg. The FMR method, in general, underestimates food requirement because it does not consider wastage and unconsumed carcasses. Furthermore, starving wolves can consume several times as much meat as usual during a successful hunt, up to 9.2 kg according to Bibikov (1985), which is not fully digested. The killing of large herbivores by wolves therefore can be a little greater (e.g. 3 kg of meat/wolf/day) than that resulting from our calculations. However, the error should be quite small since we take a relatively high value (25% for adult ungulates) of inedible biomass. Other field studies suggest a higher average consumption by these predators. For example, Fuller and Keith (1980) estimated food intake rate at 0.15 kg of meat per kg of wolf per day, while Mech (1966, in Okarma, 1992) estimated 0.13–0.19 kg. Fuller (1989) estimated winter consumption rates of ungulates from 14 sites in North America as 2.1–7.7 kg/day for a 35 kg wolf. Messier and Crête (1985) assessed the consumption of moose (almost the only prey in Quebec) at 1.6–2.8 kg/day and recognized a food intake rate of 0.09 kg to be associated with starvation.

The accepted methods of estimating ungulate numbers are cautious and realistic. In 1989 detailed censuses of ungulates were made in the smaller forest area (125 km^2) of the region of Zamość (Tomek, 1994). Their results concerning red deer were similar to ours (11.28 individuals/ 10 km^2), but much lower in the case of roe deer and wild boar.

The results of this work suggest that the trophic impact of wolf on the relatively abundant population of ungulates and other prey in eastern Poland may be rather small. All calculations show that wolves at the density of 2.7–3.3 individuals/ 100 km^2 of forested area (0.6–0.7/ 100 km^2 of total area) remove only a few per cent of their total prey biomass and no more than 10% of relatively abundant ungulates (111–115 individuals

per 100 km^2 ; Table 1), affecting the resources of the local game owners only slightly.

However, the effect upon different kinds of prey varies. In the course of a year wolves take mostly wild boars and red deer, in extreme cases up to 20% and 16% of their population biomass, respectively (Table 5 and Fig. 2). The impact is more significant when one considers that the bulk of this biomass are young animals <1 year old. Data from neighbouring areas (to the north and south of the region of Zamość) indicate that young individuals constituted 66–91% of the wild boars killed by wolves and c.60% of the red deer killed (Jędrzejewski *et al.*, 1992; Śmiertana & Klimek, 1993). Therefore, one may expect that the regulating role of the wolf manifests itself mostly in reduction of the young generation of ungulates.

Rough estimates suggest that wolves take up to 30–53% of the annual production of red deer and 14–45% of the wild boars (Głowaciński & Profus, unpublished data). This loss of natural population growth does not seem sufficient to threaten the reproduction and stability of ungulate populations. The exploitation of the investigated ungulate populations by hunters is over twice as great (GUS, 1993) as that by wolves, but hunting pressure is exerted mainly on adult specimens, and the natural growth of ungulates is affected only slightly.

Furthermore, the results of our study and some other authors (e.g. Śmiertana & Klimek, 1993) show that, in eastern Poland, wolves mostly feed on wild animals, and they are independent of anthropogenic sources of food. The losses of livestock are nowadays, so small that even they are not registered (Okarma, 1992). Apart from the fact that wolves are competitors with hunters, they do not create any social problem here. In the light of these findings there are no reasons for demonizing the role of the wolf in hunting grounds, much less in protected areas where possibly natural ecological relations should be maintained. It seems also justifiable to enable the controlled come back of this predator to at least some forest areas (e.g. Mech, 1995) in Central/West Europe, where it once occurred.

ACKNOWLEDGEMENTS

We are very grateful to Dr François Messier from the University of Saskatchewan, Canada and to the two anonymous reviewers for their valuable comments and critical reading of the manuscript. We also wish to thank Dr Małgorzata Makomaska-Juchiewicz for the translation of the text into English as well as Dr Brian N. K. Davis for his corrections to the text and editorial remarks.

REFERENCES

- Banad, E. B. & Kozlo, P. G. (1992). Scientific principles for the increased efficiency of game management on the example of ungulates in Byelorussia. In *Global trends in wildlife*

- management, ed. B. Bobek, K. Perzanowski & W. Regelin. Trans. 18th U.K. Un. Game Biol. Congr., Krakow 1987, Swiat Press, Krakow-Warszawa, pp. 573–576.
- Bibikov, D. J. (1985). *Volk. Proischoždenie, sistematika, morfologia, ekologiya* (The wolf. History, systematics, morphology, ecology). Isdat. Nauka, pp. 1–606, Moskva (in Russian).
- Bobek, B., Morow, K., Perzanowski, K. & Kosobucka, M. (1992). *The red deer (Cervus elaphus)—its ecology and management*. Wyd. Świat, Warszawa, pp. 1–200 (in Polish).
- Bobek, B., Perzanowski, K. & Zieliński, J. (1986). Red deer population census in mountains: testing an alternative method. *Acta theriol.*, 31, 432–434.
- Bozinovic, F. & Medel, R. G. (1988). Body size energetic and foraging mode of raptors in central Chile, an inference. *Oecologia (Berl.)*, 75, 456–458.
- Buchalczyk, T. (1992). Wolf *Canis lupus*. In *Polish red data book of animals*, ed. Z. Głowaciński, PWRIŁ, Warszawa, pp. 73–76 (in Polish with English summary).
- Bunevic, A. N. (1988). Dynamika čislennosti i питание волка в Беловежской Пуще. In *Zapovedniki Belorussii* (Dynamics of population and food habits of wolf in Białowieża Primeval Forest. In *Nature reserves of Byelorussia*), Uražday, Minsk, pp. 108–113 (in Russian).
- Delibes, M. (1990). Status and conservation needs of the wolf (*Canis lupus*) in the Council of Europe member states. Council of Europe, Strasbourg. *Nature and Envir. Ser.*, 47, 1–46.
- Fuller, T. K. (1989). Population dynamics of wolves in north-central Minnesota. *Wildl. Monogr.*, 105, 1–41.
- Fuller, T. K. & Keith, L. B. (1980). Wolf population dynamics and prey relationships in northeastern Alberta. *J. Wildl. Manage.*, 44, 583–602.
- Głowaciński, Z., Kosior, A. & Profus, P. (1992). Distribution and impact of moose *Alces alces* (L.) on forest communities in the Zamość region (in Polish with English summary). *Studia Ośr. Dokument. Fizjogr.*, 20, 273–285.
- Głowaciński, Z. & Profus, P. (1992). Number and importance of the wolf *Canis lupus* L. in hunting management in the Zamość region (in Polish with English Summary). *Studia Ośr. Dokument. Fizjogr.*, 20, 287–308.
- Górecki, A. (1975). Calorimetry in ecological studies. In *Methods for ecological bioenergetics*, ed. W. Grodziński, R. Z. Klekowski & A. Duncan, Blackwell Scientific Publications, Oxford, pp. 275–281.
- Goszczyński, J. (1986). Locomotor activity of terrestrial predators and its consequences. *Acta theriol.*, 31, 79–95.
- GUS (1993). *Ochrona Środowiska. Informacje i opracowania statystyczne* (Environmental protection. Information and statistics). Warszawa (in Polish).
- Heptner, V. G. & Naumov, N. P. (eds) (1967). *Mlekopitajućkiye Sovetskovo Soiuza. II. Morskiye krov i hiščnye*. Vyžaya Škola, Moskva, pp. 1–1004 (in Russian).
- Jezierski, W. & Myrcha, A. (1975). Food requirements of a wild boar population. *Polish Ecol. Studies*, 1, 61–63.
- Jędrzejewski, W., Jędrzejewska, B., Okarma, H. & Ruprecht, A. L. (1992). Wolf predation and snow cover as mortality factors in the ungulate community of the Białowieża National Park, Poland. *Oecologia (Berl.)*, 90, 27–36.
- Kleiber, M. (1932). Body size and metabolism. *Hilgardia*, 6, 315–353.
- Kleiber, M. (1961). *The fire of life*. John Wiley, New York.
- Kolenosky, G. B. (1972). Wolf predation on wintering deer in east-central Ontario. *J. Wildl. Manage.*, 36, 357–369.
- Langvatn, R. (1977). Social behavior and population structure as a basis for censusing red deer population. *Proc. 12th Congress Game Biol.* Atlanta, pp. 77–89.
- McNab, B. K. (1989). Basal rate of metabolism, body size, and food habits in the order Carnivora. In *Carnivore behavior, ecology, and evolution*, ed. J. L. Gittleman. Cornell University Press, Ithaca, New York, pp. 335–354.
- Mech, L. D. (1970). *The wolf. The ecology and behavior of an endangered species*. Natural History Press, Gordon City, New York.
- Mech, L. D. (1995). The challenge and opportunity of recovering wolf populations. *Conser. Bio.*, 9, 270–278.
- Messier, F. (1994). Ungulate population models with predation a case study with the North American moose. *Ecology*, 75, 478–488.
- Messier, F. & Crête, M. (1985). Moose-wolf dynamics and the natural regulation of moose populations. *Oecologia (Berl.)*, 65, 503–512.
- Milkowski, L. (1986). Wilk i ryś w Puszczy Białowieskiej (Wolf and lynx in the Białowieża Primeval Forest) (in Polish). *Łowiec Pol.*, 10, 18–19.
- Nagy, K. A. (1987). Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.*, 57, 111–128.
- Okarma, H. (1992). *Wilk. Monografia przyrodniczo-łowiecka* (The wolf in Poland). Privately published, Białowieża, pp. 1–168 (in Polish with English summary).
- Okarma, H. (1993). Status and management of the wolf in Poland. *Biol. Conserv.*, 66, 153–158.
- Okarma, H. & Kotera, P. (1987). Basal metabolic rate in the gray wolf in Poland. *J. Wildl. Manage.*, 51, 800–801.
- Peters, G. (1993). *Canis lupus Linnaeus, 1758—Wolf*. In *Handbuch der Säugetiere Europas*, 5/1, ed. J. Niethammer & F. Krapp. Aula, Wiesbaden, pp. 47–106.
- Pielowski, Z. (1993). Raport o zwierzętach łownych w Polsce (Report about game animals in Poland). *Bibl. Monit. Środowiska*. Warszawa (in Polish with English summary).
- Pucek, Z., Bobek, B., Łabudzki, L., Milkowski, L., Morow, K. & Tomek, A. (1975). Estimates of density and number of ungulates. *Pol. Ecol. Stud.*, 1, 121–136.
- Profus, P. & Tomek, Z. (1994). Fauna Roztoczańskiego Parku Narodowego. Ssaki. (Fauna of the Roztocze National Park. Mammals). In *Roztoczański Park Narodowy*, ed. T. Wilgat. Wyd. RPN-Oficyna Wyd. Ostoja. Zwierzyniec-Kraków, pp. 195–205 (in Polish).
- Ryszkowski, L. (1982). Structure and function of the mammal community in an agricultural landscape. *Acta Zool. Fennica*, 169, 45–59.
- Śmiertana, W. & Klimek, A. (1993). Diet of wolves in the Bieszczady Mountains Poland. *Acta theriol.*, 38, 245–251.
- Sumiński, P. & Filipiak, W. (1977). Beitrag zur Nahrungsuntersuchung des Wolfes (*Canis lupus* L.). *Z. Jagdwiss.*, 23, 1–5.
- Tomek, A. (1994). Zagadnienia łowieckie w rejonie Roztoczańskiego Parku Narodowego (Game management in the environs of the Roztocze National Park). In *Roztoczański Park Narodowy*, ed. T. Wilgat. Wyd. RPN-Oficyna Wyd. Ostoja. Zwierzyniec-Kraków, pp. 230–236 (in Polish).
- Voskár, J. (1993). The ecology of wolf (*Canis lupus*) and its share on the formalization and stability of the Carpathian ecosystems in Slovakia (in Slovak). *Ochrana Prírody*, 12, 241–276.
- Vyrypayev, V. A. (1979). Trofičeskiye svyazi volka v lesnych biocenozach Tyan-Shanya. In *Biocenotičeskiye issledovaniya elovych lesov Priüssykkulya*. Ilim, Frunze (in Russian).
- Weiner, J. (1973). Dressing percentage gross body consumption and caloric value of the roe-deer. *Acta theriol.*, 18, 209–222.
- Weiner, J. (1987). Budżety energetyczne: metabolizm zwierząt (Energetical budgets: metabolism of animals). In *Ćwiczenia z ekologii*, ed. A. Górecki, J. Kozłowski & M. Gębczyński. Warsaw Univ.-Białystok branch. Kraków-Białystok, pp. 116–139 (in Polish).
- Weiner, J. (1989). Metabolic constraints to mammalian energy budgets. *Acta theriol.*, 34, 3–35.
- World Conservation Monitoring Centre (1993). *World checklist of threatened mammals*. Joint Nature Conservation Committee, Peterborough.