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Patterns of wolf *Canis lupus* predation on wild and domestic ungulates in the Western Carpathian Mountains (S Poland)

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We studied the predator-prey relationships among wolves *Canis lupus* Linnaeus, 1758, wild ungulates, and livestock in the managed mountain forests of the Western Carpathians (S Poland). Though roe deer *Capreolus capreolus* dominated in the community of wild ungulates and livestock was abundant within the study area, the three wolf packs preyed mainly on red deer *Cervus elaphus* (42% of food biomass), and next on the roe deer (33%). In both species of deer, wolves preferred killing females and juveniles more frequently than expected from their respective shares in the populations. Wild boar *Sus scrofa* made up 4% of the food biomass, in accordance with its low share in the ungulates community. Despite the easy access of wolves to numerous unprotected sheep flocks pastured on meadows among woods, livestock constituted only 3% of the wolf food biomass. Wolves preyed mostly on sheep (88%), killing on average 34 per year. Most cases of livestock depredation occurred in August––September, on pastures located most often >50 m apart from buildings. Usually, lack of proper guarding was conducive to wolf attacks.

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Introduction

In many regions of Europe, wild ungulates prevail in the wolf *Canis lupus* Linnaeus, 1758 diet, with the red deer *Cervus elaphus* being the most preferred prey in regions where it is numerous (review in: Okarma 1995). Wolf preference for red deer was reported from the Białowieża Forest, E Poland (Jędrzejewski *et al*. 1992, 2000, 2002a), Bieszczady Mts, SE Poland (Śmietana and Klimek 1993, Śmietana 2000), the Ukrainian Carpathians (Jakiwczuk 1996), and several localities in the European part of Russia (review in: Filonov 1989). Most of the studies on wolves in Central and Eastern Europe have been conducted in large forest tracts sparsely inhabited by humans and with a significant contribution of protected areas. Red deer often dominate in the ungulate communities within such woodlands (Okarma 1995).

In Poland, the largest proportion of the wolf population inhabits managed forests (Jędrzejewski *et al.* 2002b), which are largely covered with coniferous plantations (mostly pine *Pinus silvestris* in lowlands and spruce *Picea abies* in mountains). The roe deer *Capreolus capreolus* is the main animal of the ungulate community (60–80%) in most of exploited forests (Budna and Grzybowska 2000). Furthermore, in many regions wolves have access to sheep, goats, and cows grazing on adjacent pastures. In such conditions, if wolves are opportunistic predators, we would expect significant shares of roe deer and livestock in their diet. However, Jędrzejewski *et al.* (2000) proposed that wherever red deer occur in the ungulate community, it shapes the food composition of wolves. Red deer is always taken more often than expected from its share in the community, and the contributions of other species to wolf diet are negatively correlated to red deer abundance (Jędrzejewski *et al.* 2000).

In this paper, we report on the study conducted in the Western Carpathian Mountains (Southern Poland), with mountain ridges covered by spruce forests, and valleys densely populated by people. Wolves co-exist there with three species of wild ungulates: roe deer, red deer, and wild boar *Sus scrofa*. Sheep dominate among the domestic animals. The goal of our study was to find out: (1) the wolf diet composition and prey selection patterns in the wild ungulate community, and (2) the contribution of livestock to wolf kills and the impact of wolf predation on the local livestock.

Study area

The study was conducted in 1997–2001 in the western-most range of the Polish Carpathian Mountains (49°23'–49°53' N, 18°45'–19°48' E), located near the Polish-Slovakian and the Polish–Czech border. The region includes two mountain ranges: Silesian Beskidy Mts and Żywiecki Beskidy Mts (total area 745 km^2), separated by the Soła River valley. The altitude ranges from 300 to 1557 m a.s.l. Most of the area is covered by spruce forest (55–90%) with the addition of beech *Fagus silvatica* and fir *Abies alba*. Forests have their continuity into both, the Slovakian and Czech side of the border line. The average temperature in July varies from 12°C (mountains) to 16°C (basins). The respective temperatures in January are between –3°C and –6°C. Snow cover remains on the ground 80 days per year in basins to 160 days on northern slopes and summits (Atlas of the Bielsko Province 1981).

The region is densely inhabited by humans (on average, 150 person/km^2). Numerous towns and villages are located mostly in river valleys and on lower, deforested slopes (up to 600 m a.s.l.). There are some agriculture and livestock farms, where small sheep and goat flocks are an important source of income. Most of the forests are exploited, only 1% is protected in a few nature reserves. Among the forests, large meadows are located; some of them are still used as pastures for livestock grazing, and the rest have been unused for a long time, so subsequently these areas have been naturally recolonized by young spruce, beech, and birch *Betula* sp. trees. There are a large number of weekend cabins and recreation centers along forest peripheries as well as many ski lifts, ski routes, and tourist paths in the forest. Human penetration into the forest is intense during weekends and holidays.

Ungulate community is dominated by the roe deer (74%), followed by the red deer (21%), and the wild boar (5%). The guild of large predators includes the wolf, the lynx *Lynx lynx*, and the brown bear *Ursus arctos*. All these predators are protected in Poland, but the wolf is a game species in Slovakia, with a 2-month hunting season in winter. In 1997–2001, the study area was occupied by four wolf packs, one in the Silesian Beskidy Mts and three in the Żywiecki Beskidy Mts (Pierużek-Nowak 2002).

Material and methods

Analysis of diet composition and wild prey of wolves

We studied the wolf diet on the basis of 390 scats and 93 kill remains of wild prey collected from three wolf packs during 1997–2001. We distinguished the packs using long-distance snow tracking (Śmietana and Wajda 1997) and howling stimulation (Harrington and Mech 1982). Kills and scats were searched by snow tracking wolves in winter, walking along forest roads and paths, and visiting abandoned pup-rearing and rendezvous sites in summer. Among prey remains found we were able to recognize a gender and an age class (adult or juvenile) for 28 red deer, 23 roe deer and 4 wild boar.

Analysis of scats followed the standard method of drying and washing through a 0.5-mm mesh sieve (Lockie 1959, Goszczyński 1974). Prey were identified by hair, bone, hooves, claws, and feather remains according to the taxonomic keys of Dziurdzik (1973), Pucek (1981), Debrot *et al.* (1982), and Teerink (1991) as well as by comparison to the collection of the Mammal Research Institute Polish Academy of Sciences in Białowieża. In the case of roe deer, red deer, and wild boar, wherever possible, age classes (juvenile <6 months or adult >6 months) were determined by comparison to reference material (hair and bones of ungulate species of known age) (Jędrzejewski *et al*. 1992).

The composition of food was expressed as: (1) the percentage of scats, which contained different prey species relative to the total number of faecal samples (frequency of occurrence) and (2) the percentage of biomass of a particular food component relative to the total biomass consumed by wolves. The biomass of food components was obtained by multiplying the weight of prey remains found in scats by coefficients of digestibility (after Lockie 1961, Goszczyński 1974, Lode 1990, Roger *et al.* 1991, Jędrzejewski and Jędrzejewska 1992). The following coefficients of digestibility were used: rodents and insectivores – 23, medium-sized mammals – 50, ungulates – 118, insects – 5, plant material – 4. We analyzed the food composition in two seasons: autumn-winter season (1 October – 15 April) and spring-summer season (16 April – 30 September).

The breadth of the food niche was calculated according to Levins' (1968) formula: $B = 1/\Sigma p_i^2$, where p_i is a contribution of every group of wolf prey in the total biomass of food consumed by wolves. We brought wolf food components into 5 groups: (1) insectivores; (2) rodents; (3) medium-sized mammals (hare, badger, and fox); (4) wild ungulates; (5) livestock. Thus, index B could achieve value from 1 (strong specialization in the one group of prey) to 5 (opportunistic preying on all available groups of prey). We calculated the similarity of diet composition between seasons following the formula of Pianka (1973):

$$\alpha_{sw} = (\Sigma p_{sa} \cdot p_{wa}) \cdot [(\Sigma p_{sa}^2) \cdot (\Sigma p_{wa}^2)]^{-1/2},$$

where α_{sw} is a degree of similarity of food composition in the spring-summer season (s) and autumn-winter season (w), p_{sa} is a contribution of a prey a in the total biomass of preys consumed by wolves in the spring-summer season, p_{wa} – contribution of prey a in the total prey biomass consumed by wolves in the autumn-winter season.

The species structure of the ungulate community in the study area was estimated on the basis of hunters' inventories, conducted every winter by snow-tracking on regular transects and supported with whole year observations. We took into account only the data from those hunting divisions, which were located within wolf territories. Due to the possibility of underestimation of ungulate numbers by hunters (comp. Pucek *et al.* 1975, Jędrzejewska *et al.* 1997) the densities of ungulates were not taken into consideration in this work. To estimate the percentage contribution of particular ungulate species in the total biomass of ungulates in the study area, we used body mass of deer and wild boar (of different age and sex) taken by hunters in the Żywiecki Beskidy Mts in 1997–2001, and the sex and age structure of roe deer and red deer from the hunters inventories. The mean estimated body masses were: 100 kg in red deer, 19 kg in roe deer, and 40 kg in wild boar.

Wolf preference for ungulate species was calculated on the basis of selectivity index D of Jacobs (1974): $D = (r - p)/(r + p - 2rp)$, where r means contribution (fraction) of a given prey species in the total number of ungulates killed by wolves, and p – contribution of this species in the ungulate community in the study area. Similarly, selectivity index was calculated for sex and age classes of prey (red and roe deer). D varies from –1 (total avoidance of a given species), to 0 (random choice) to 1 (the strongest positive selection).

Data on wolf predation on livestock

To quantify damage caused by wolves to livestock, we used several sources of information: official reports from the commissions assessing damage, interviews with local farmers, and inspections of the damage places. In 1997–2001, we collected data on 172 domestic animals killed by wolves in 35 attacks, of which we verified in the field 23 places of damage. In each inspected place, we counted the number of killed animals and estimated the percentage of carcass consumed. For one of the studied packs (Grapa), we were able to obtain the complete information on livestock depredation caused by those wolves. Furthermore, for Grapa pack, we estimated the role of livestock in the wolf diet and the total impact of wolves on the local livestock populations, based on the average daily food intake of wolves (5.58 kg; Jędrzejewski *et al.* 2002a), total number of livestock accessible in the pack's home range (the Silesian Beskidy Mts), the number of attacks and killed domestic animals, and the percentage of carcass consumption.

Results

Wolf diet composition

Analyses of scats revealed that red deer and roe deer were the most important prey of wolves (Table 1). Red deer occurred in 30% of all collected faecal samples,

Table 1. Diet composition of wolves in the Western Carpathian Mountains in 1997–2001. %Occ – percentage of occurrence in scats, %Bio – percentage of the total biomass consumed. + denotes contribution to diet < 0.05%. Seasons: spring-summer = 16 April – 30 September, autumn-winter = 1 October – 15 April. Categories to estimate the breadth of food niche (after Levins 1968): (1) insectivores; (2) rodents; (3) medium-size mammals (hare, badger, fox); (4) wild ungulates; (5) livestock. [a] pieces of fabric, glass, and paper.

Item	Spring-summer		Autumn-winter		Whole year	
	%Occ	%Bio	%Occ	%Bio	%Occ	%Bio
Red deer *Cervus elaphus*	31.0	39.6	29.6	46.7	30.5	42.2
Roe deer *Capreolus capreolus*	32.9	34.4	32.6	29.4	32.8	32.6
Undetermined Cervidae	24.3	15.2	30.4	18.3	26.4	16.4
Wild boar *Sus scrofa*	9.0	5.4	7.4	2.3	8.5	4.2
Wild ungulates total	92.5	94.6	94.1	96.7	93.1	95.4
Sheep	4.7	3.2	1.5	1.5	3.6	2.6
Cow	0.4	0.1	0.7	0.1	0.5	0.1
Dog	0.4	0.2	–	–	0.3	0.1
Livestock total	5.5	3.5	2.2	1.6	4.4	2.8
Brown hare *Lepus europaeus*	3.5	1.6	7.4	1.7	4.9	1.6
Fox *Vulpes vulpes*	0.4	0.1	–	–	0.3	0.1
Badger *Meles meles*	0.8	0.2	–	–	0.5	0.1
Undetermined carnivores	0.4	+	–	–	0.3	+
Undetermined vole *Microtus* sp.	0.4	+	1.5	+	0.8	+
Undetermined mouse *Apodemus* sp.	0.4	+	–	–	0.3	+
Mole *Talpa europaea*	–	–	1.5	+	0.5	+
Undetermined Insectivora	0.4	+	–	–	0.3	+
Birds	0.4	+	–	–	0.3	+
Insects	3.1	+	1.5	+	2.6	+
Plant material	59.2	+	53.3	+	57.2	+
Mineral material	5.9	+	5.9	+	5.9	+
Anthropogenic material[a]	0.8	+	1.5	+	1.0	+
Number of scats or biomass of food consumed (kg)	255	356.6	135	212.9	390	569.5
Breadth of food niche *B*		1.11		1.07		1.10

and its contribution to the total biomass of consumed food reached 42%. Roe deer was found in 33% of scats and comprised 33% of total biomass. In total, cervids (together with undetermined remains of Cervidae) made up 91% of biomass of the food eaten by wolves. Wild boar constituted 4% of the total biomass. Among the medium-sized mammals, only the brown hare *Lepus europeus* was more important as wolf prey, occurring in 5% of scats and consisting 2% of total biomass. Livestock (sheep, goats, cows, and dogs) were found in 4% of faeces and made up only 3% of biomass of the wolf food. During the cold season, red deer were more important prey for wolves than in the spring-summer season, whereas the contributions of roe deer, wild boar and livestock were slightly higher in spring-summer (Table 1). However, the differences were not significant ($G = 1.188$, df = 2, $p > 0.5$, G – test for heterogeneity of percentages, calculated for percentage of biomass). Pianka's index ($\alpha = 0.99$) confirmed the similarity of the wolf diet during both seasons.

There were significant differences in the contributions of red deer, roe deer, and livestock to the diet of the three packs ($G = 72.07$, df = 4, $p < 0.001$; Table 2). In the diet of the Grapa and Groń packs, the ratio of red deer and roe deer biomass was close to 1:1, whereas the Halny pack killed significantly more red deer. The most intense predation on domestic animals was found in the Groń pack (nearly 8% of total biomass). Furthermore, the Grapa pack from the Silesian Beskidy Mts consumed more wild boars (6% of biomass) than the packs occupying the Żywiecki Beskidy Mts (Table 2). Pianka's index α showed a big similarity of the diet of Grapa and Groń packs (0.93), and considerably smaller overlap between Halny

Table 2. Comparison of diet composition of wolves in two parts of Western Carpathians, the Silesian Beskidy Mts (Grapa pack) and the Żywiecki Beskidy Mts (Groń and Halny packs) in 1997–2001. Symbols and further explanations as in Table 1.

Item	Grapa		Groń		Halny	
	%Occ	%Bio	%Occ	%Bio	%Occ	%Bio
Red deer *Cervus elaphus*	30.1	39.5	24.1	31.7	51.6	80.5
Roe deer *Capreolus capreolus*	35.3	37.7	32.2	29.1	12.9	4.6
Undetermined Cervidae	24.3	13.1	32.2	29.2	29.0	13.6
Wild boar *Sus scrofa*	10.7	5.7	3.4	1.3	3.2	+
Wild ungulates total	93.8	96.0	90.8	91.3	93.5	98.7
Sheep	2.2	1.5	8.0	7.2	3.2	0.7
Cow	0.4	0.1	1.1	0.4	–	–
Dog	0.4	0.2	–	–	–	–
Domestic animals total	3.0	1.8	9.2	7.6	3.2	0.7
Other food items	62.9	2.2	73.6	1.1	58.1	0.5
Number of scats or biomass of food consumed (kg)	272	397.4	87	113.2	31	58.9
Breadth of the food niche B		1.08		1.19		1.03

and Grapa (0.76) and between Halny and Groń packs (0.72). The mean index of similarity of food niche between all packs amounted 0.80. Food niches of wolves from the study area were very narrow (*B* from 1 to 1.2; Tables 1 and 2), indicating a strong specialization of the wolves in one group of prey – wild ungulates.

Selection of prey from wild ungulate community

On wolf trails, we found the remains of 46 roe deer (50% of discovered kills), 43 red deer (46%), and 4 wild boar (4%). Comparison to the ungulate structure indicated that red deer were taken more often, and roe deer more rarely than expected from their respective contributions to the ungulate community (G = 14.344, df = 2, $p < 0.001$; Fig. 1). Wild boar were killed according to their share in the ungulate community. The similar result was obtained when the biomass of wolf prey species and the biomass of ungulate community were compared (G =

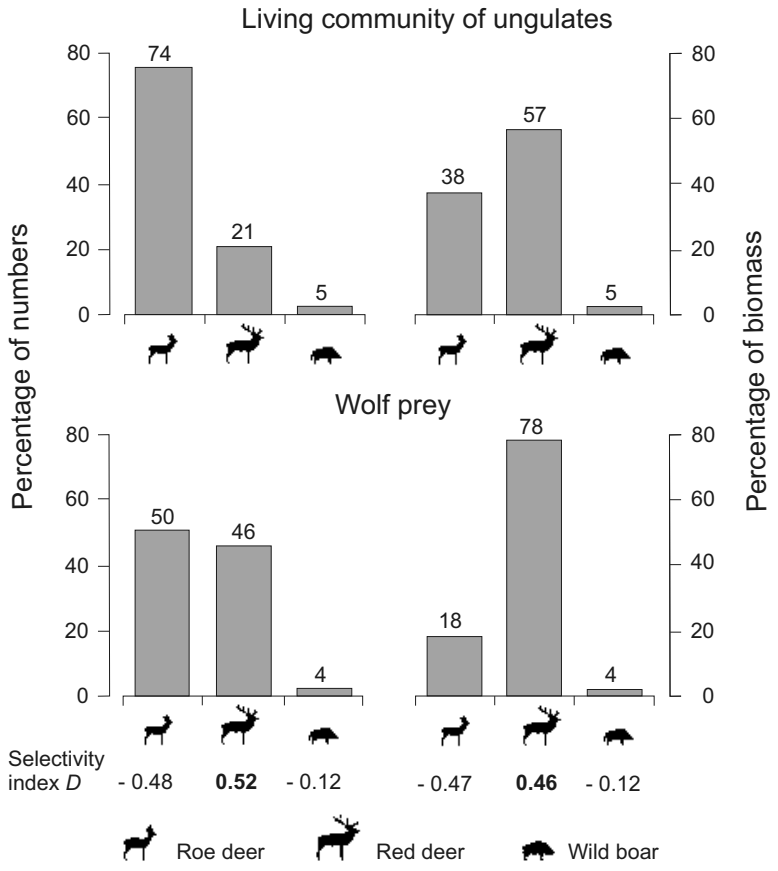

Fig. 1. Prey selection by wolves from the wild ungulate community in the Western Carpathian Mountains in 1997–2001. *D* – index of selectivity after Jacobs (1974).

Table 3. Comparison of sex and age structure of red deer and roe deer killed by wolves with the species structure of ungulate community (Western Carpathian Mts).

Wild ungulate community or wolf prey	Sex class/age class (%)			
	Adult females	Adult males	Adults of both sexes	Juveniles
Red deer *Cervus elaphus*				
Ungulate community	41	39	80	20
Wolf kill remains (n = 28)	54	14	–	32
Selectivity index D	0.26	−0.59	–	0.31
Wolf prey in scats (n = 90)	–	–	26	74
Selectivity index D	–	–	−0.83	0.84
Roe deer *Capreolus capreolus*				
Ungulate community	44	37	81	19
Wolf kill remains (n = 23)	65	13	–	22
Selectivity index D	0.41	–0.59	–	0.09
Wolf prey in scats (n = 90)	–	–	61	39
Selectivity index D	–	–	−0.41	0.46

10.694, df = 2, $p < 0.005$). In the total biomass of prey, the red deer strongly dominated (78%). Comparison with the sex and age structure of both species in the living populations showed that wolves avoided adult male red deer, and preferred females and calves (G = 16.853, df = 2, $p < 0.001$), and positively selected female roe deer (G = 16.301, df = 2, $p < 0.001$; Table 3). Among prey remains recovered from wolf scats, juveniles strongly predominated (red deer: G = 61.847, df = 1, $p < 0.001$, roe deer: G = 9.866, df = 1, $p < 0.005$; Table 3).

Damage to livestock

In 1997–2001, 35 attacks in 28 farms occurred (Table 4). Sheep were the most common prey of wolves (88%). On average, 5 domestic animals were killed during one attack (SD = 4.7, range 1–22). Annually, from 15 to 48 livestock were killed, on average 34.4 animals (SD = 12.1). More damage occurred in the Silesian Beskidy Mts, although attacks in that region started later, in 1998 (Table 4). Every year the mean number of livestock killed there was 25.5 (SD = 9.4, range 16–37), while in the Żywiecki Beskidy Mts it varied from 1 to 28, on average 14 (SD = 10.2). Wolf attacks occurred from May to November (Fig. 2), with the biggest intensity recorded in August (44% of attacks) and September (26%).

The number of wolf attacks (for 24 well-documented cases) on bigger flocks (≥ 40 sheep) and smaller ones (1–15 sheep) were similar (13 and 11 attacks). In larger flocks wolves killed, on average, 6.5 animals during one attack (range 2–22, SD = 5.4). In smaller flocks 3.6 animals per attack were seized (range 1–7, SD = 2.5). While 68% of killed animals derived from bigger flocks, the total damage

Table 4. Comparison of species and number of livestock killed by wolves in the Silesian and the Żywiecki Beskidy Mts. [a] Mean (± SD) number of damage per 100 km^2.

Year	Livestock killed by wolves					
	Sheep	Goats	Calves	Dogs	Total	*N* animals/100 km^2
			Silesian Beskidy Mountains			
1997	–	–	–	–	–	0
1998	16	–	–	–	16	4.2
1999	37	–	–	–	37	9.6
2000	18	9	2	–	29	7.7
2001	17	3	–	–	20	5.2
All years	88	12	2	0	102	5.3 (± 2.6)[a]
Percent	86	12	2	0	100	–
			Żywiecki Beskidy Mountains			
1997	12	3	–	–	15	4.2
1998	18	–	–	–	18	5.0
1999	1	–	–	–	1	0.3
2000	8	–	–	–	8	2.2
2001	25	–	–	3	28	7.8
All years	64	3	0	3	70	3.9 (± 2.8)[a]
Percent	92	4	0	4	100	–
			Whole area			
1997	12	3	–	–	15	2.0
1998	34	–	–	–	34	4.6
1999	38	–	–	–	38	5.1
2000	26	9	2	–	37	5.0
2001	42	3	–	3	48	6.4
All years	152	15	2	3	172	4.6 (± 1.6)[a]
Percent	88	9	1	2	100	–

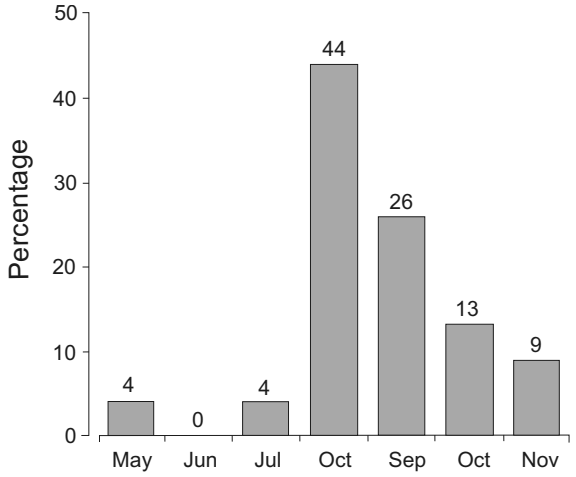

Fig. 2. Seasonal distribution of wolf depredation on livestock (n = 23 attacks).

Table 5. Contribution of domestic animals to the diet of Grapa pack in the Silesian Beskidy Mts, 1998–2001. Pack size estimated during the year round tracking in 1998–2001 (Pierużek-Nowak 2002). Food requirement in a spring-summer season: daily food intake of the wolf (5.58 kg, after Jędrzejewski *et al.* 2002a) multiplied by number of days in the season (168 days). The annual food requirement obtained after adding the autumn-winter season (197 days). The number of livestock killed by the pack from Table 4. Consumption of domestic animal carcasses was estimated by multiplying the mean weight of the kill of a given species by the average percent of consumption of the kill by wolves (based on data from 35 domestic animals killed by wolves from the Grapa pack).

Parameter	Grazing seasons				Mean (SD)
	1998	1999	2000	2001	
Number of wolves in the pack (summer/winter)	3/3	5/5	8/6	9/7	4.7 (2.5)
Food requirement of the pack in spring-summer (kg)	2812	4687	7500	8437	5859 (2582)
Annual food requirement of the pack (kg)	6110	10183	14096	16132	11630 (4431)
Number of livestock killed by the pack during the grazing season	16	37	29	20	25.5 (9.4)
Domestic animals eaten by wolves (kg)	275	525	351	305	364 (111.8)
Contribution of livestock to the total food consumption in spring-summer (%)	9.8	11.2	4.7	3.6	7.7 (3.9)
Estimated contribution of livestock to the annual wolf diet (%)	4.5	5.2	2.5	1.9	3.5 (1.6)
Contribution of livestock to the annual wolf diet based on the analysis of faeces (mean for all years)	–	–	–	–	1.8

amounted 10% of their number. In smaller flocks depredation reached 35% of heads in flocks. Most of attacks (67%) took place on pastures adjacent to, or within forest. In 71% of cases, the animals stayed at least 50 m apart from buildings. Mostly livestock were kept in a wooden pen (1.2 m high) or stayed within low wire fences (79% of all cases). Dogs (usually mongrels) were present in 75% of cases, but most of them were tethered nearby. None of the farms, which suffered wolf attacks, was protected by livestock guarding dogs.

For one pack (Grapa) we recorded and examined all cases of damage and assessed its pressure on livestock (Table 5). Based on the number of killed animals, we estimated the total share of livestock in the wolf diet and compared it to the results of scats analysis. The total contribution of domestic animals to wolf diet varied from 3.6 to 11.2% of food biomass (on average 7.7) during the grazing seasons, and from 1.9 to 5.2% (on average 3.5) during the whole year. This estimate is similar to the result obtained by scat analysis (mean 1.8% of food biomass; see Table 2). Based on data from farmers and local communities, we estimated the number of livestock that were pastured within the home range of the Grapa pack on about 360 individuals (range 320–420). During the grazing season, that pack killed on average 25.5 domestic animals, which made up 7.1% of total number.

Discussion

Wolf diet in the Western Carpathian Mts comparedto other European populations

Our study revealed that red deer, despite of its secondary share in the ungulate community, was the most important prey for wolves in the Western Beskidy Mts. Earlier studies conducted in the Białowieża Primeval Forest (NE Poland) and the Bieszczady Mts (SE Poland) showed that red deer made up about 40–50% of all ungulates killed by these predators and 70–80% of their food biomass (Jędrzejewski *et al.* 1992, 2000, Śmietana and Klimek 1993). This foraging pattern of wolves in the Beskidy Mountains well corresponds to a model of functional response of wolves to changes in red deer abundance (Jędrzejewska and Jędrzejewski 1998, Jędrzejewski *et al.* 2000). The second most important prey of wolves in our study area (in terms of food biomass) was the roe deer. Its contribution to wolf food was much bigger than in other, not so intensively managed forests (Śmietana and Klimek 1993, Śmietana 2000, Jędrzejewski *et al.* 2002a). Similarly, remains of roe deer were found in 33% of wolf stomachs in the Slovakian Carpathians (Hell 1990), and in 52% of stomachs in Romania (Ionescu 1992).

Wild boar was rarely hunted by Beskidian wolves, which reflected its small share in the ungulate community. However, in some regions of Europe, the wild boar made up a significant part of the wolf diet, but this resulted from the bigger contribution of that species to the local ungulate community (Brtek and Voskár 1987, Jędrzejewski *et al.* 2000, Finďo 2002) or increasing susceptibility to wolf predation in winter seasons (Śmietana and Klimek 1993).

Deep (usually 70–80 centimeters) and long-lasting (to 160 days) snow cover helped wolves in their hunting. We observed that roe deer became an easy prey for wolves during and after heavy snow falls. Then they gathered near feeders, numerous in that area, or at forest edges and stayed trapped in the deep snow for many days. Wolves regularly inspected such places and thus killed roe deer frequently. Similar hunting behaviour regarding the white-tailed deer *Odocoileus virginianus* was reported from North America (Kunkel and Pletscher 2001).

As was reported in numerous studies from Eastern Europe and North America, wolves preferred to kill juvenile and female deer or moose *Alces alces*, rather than adult males (Peterson *et al.* 1984, Ballard *et al.* 1987, Fuller 1989, Okarma 1991, 1995, Voskár 1994, Jędrzejewska and Jędrzejewski 1998). Wolves in the Western Carpathian Mts showed similar preferences for both red and roe deer. Only the contribution of juvenile roe deer among remains of wolf kills was proportional to their share in the community (contrary to the results of scat analyses, which revealed preference for this age class).We can explain it with a very small body mass of young roe deer, which caused fast and complete consumption by wolves and made finding of such remains very difficult.

Factors influencing wolf damage to livestock

In more transformed areas of Europe, wolves mostly prey on domestic animals, feed on plants or even at dumps (Macdonald *et al.* 1980, Bibikov 1985, Ragini *et al.*

1985, Meriggi *et al.* 1991, Papageorgiu *et al.* 1994, Meriggi and Lovari 1996). Wolves' attacks on domestic animals were often the main reason for the extermination of this predator (Young and Goldman 1944, Pulliainen 1965, Mech 1970). Nowadays, damage is an important problem connected with wolf conservation and recovery in various regions (Mech 1995). Predation on livestock occurs frequently in the densely inhabited Europe, where wolf habitats are fragmented and adjacent to areas of cattle and sheep farming (Boitani 2000, Jędrzejewski *et al.* 2004). In our study area, only 3% of the contribution of domestic animals in the food biomass of wolves proved that livestock had marginal importance as a food source for wolves. A similar share of livestock in the wolf diet was found in other parts of the Carpathians (Brtek and Voskár 1987, Hell 1990, Finďo 2002).

Because of the widespread, traditional sheep farming, wolves first of all killed sheep. The same structure of damage was reported from other parts of the Carpathians (Śmietana 2000, Mertens *et al.* 2001, Finďo 2002), from Bulgaria (Genov and Kostava 1993), Italy, Spain, and Portugal (Meriggi *et al.* 1991, Blanco *et al.* 1992, Meriggi and Lovari 1996, Ciucci and Boitani 1998). However, in the lowlands, where cattle farming is common, calves and cows are frequent or even prevail amongst wolves' kills (Ionescu 1992, Jędrzejewski *et al.* 2002b, 2004).

In the Western Carpathians, the average number of livestock killed during a single attack (5 individuals) was comparable to that reported from Slovakia (4 individuals; Finďo and Hood 2001), and bigger than in Bulgaria (1.5–2.6 individuals; Genov and Kostava 1993) and Italy (3 individuals per attack; Ciucci and Boitani 1998). Probably, in our study area, wolves had enough time for killing more animals during the attack, because they were usually not disturbed by humans or dogs. The observed increase of attacks at the end of summer was also reported from Slovakia (Voskár 1994), Bulgaria (Genov 1992), and Italy (Meriggi *et al.* 1991, Ciucci and Boitani 1998). Most likely, it resulted from a decreasing susceptibility of growing red deer calves for wolf predation, an increasing food demand and mobility of growing wolf pups (Śmietana 2000, Jędrzejewski *et al.* 2001), as well as worsening weather conditions that lessened attentiveness of shepherds and dogs for livestock.

Wolves attacked unprotected flocks regardless of their size. During attacks on bigger flocks they killed more sheep, which was also revealed from Italy (Ciucci and Boitani 1998). The most susceptible to damage were flocks pastured near or within forests, similarly as in North America (Bangs and Shivik 2001).

The total wolf predation on the local population of domestic animals was estimated in Italy (0.4%), but it concerned livestock in the whole region, not only those pastured near or within wolf home ranges (Ciucci and Boitani 1998). According to these authors, the biggest damage occurred in the areas recently recolonized by wolves. The total impact on livestock pastured within the home range by the newly established wolf pack in the Silesian Beskidy Mts (on average 7%) and the contribution of livestock to the food biomass of this pack, were both decreasing in consecutive seasons. It reflected an increasing awareness of local farmers to wolf presence and involvement of preventing methods such as guarding

dogs and mobile cloth fences called "fladry" (Nowak and Mysłajek 2005). Similarly, the total pressure on domestic animals accessible to wolves was also assessed in the Bieszczady Mts, S Poland (Śmietana 2000) and the Romanian Carpathians (Mertens *et al.* 2001). A larger impact by wolves was found in the Bieszczady Mts (6.5%), where flocks were not protected, than in Romania (1%), where flocks were better supervised, with involvement of guarding dogs.

Based on all these findings, we can conclude that in managed forests, where the structure of the ungulate community is disturbed by humans but red deer are still abundant, wolves prey mostly on wild ungulates (with preference for red deer), and the overall depredation of local livestock is not high. Furthermore, the level of damage to domestic animals depends on preventing measures involved in husbandry practices and can be decreased by introducing efficient protection methods.

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