Selectivity of wolf predation on red deer in the Bieszczady Mountains, Poland

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A pattern of wolf *Canis lupus* Linnaeus, 1758 predation on red deer *Cervus elaphus* Linnaeus, 1758 was studied in Bieszczady Mountains in 1991–2002. In total 324 remains of red deer > 4 months old, killed by wolves throughout the year, were found. The sex, age and bone marrow fat content of wolf kills were compared with the same characteristics within the free living red deer population. The overall contribution of calves killed by wolves (24%) in October–May was higher than in the population (17%), and decreased from autumn to spring. Adult males were more vulnerable to wolf predation than adult females: stags constituted 62% and hinds 38% of adult red deer killed by wolves, whereas in the population, the percentages were 37 and 63%, respectively. Stags killed by wolves were younger ($\bar{x}$ = 4.1 years old) than hinds ($\bar{x}$ = 8.9 years old). Wolves killed more > 8 years old hinds and < 5 years old stags than available in the population. In wolf kills, the average fat content in femur marrow was higher among hinds (84.9%) than stags (69.3%) and calves (66.1%). Only 8% of hinds had < 70% femur marrow fat content, whereas 40% of calves and 38% of stags had marrow fat values below that level. Marrow fat content showed seasonal variation and was the lowest in March among all sex-age classes. The monthly share of stags in all kills, and hinds in hind-calf part of the sample was negatively correlated with their monthly average bone marrow fat content, and monthly share of calves was positively correlated with monthly average bone marrow fat content of adults. The segregation of social units (hind-calf and stag groups), except during the rutting season, and the low fat reserves of males from midwinter until spring contribute to the high overall incidence of calves and adult males and the relatively low incidence of adult females among wolf kills.

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Introduction

Wolves *Canis lupus* Linnaeus, 1758 inhabit wide areas of northern hemisphere where they coexist with many different species of ungulates (Mech 1970, Bibikov 1985, Okarma 1995). Selectivity of wolf predation on moose *Alces alces*, caribou *Rangifer tarandus caribou*, white-tailed deer *Odocoileus virginianus*, elk *Cervus elaphus canadensis* and Dall sheep *Ovis dalli* during winter has been frequently studied in North America (eg Murie 1944, Mech 1966, Mech and Frenzel 1971, Peterson 1977, Fritts and Mech 1981, Carbyn 1983, Ballard *et al.* 1987, Huggard 1993, Mech *et al.* 1995, Hayes *et al.* 2000, Smith *et al.* 2004). In contrast, only a few

studies have focused on the selectivity of wolf predation within a given ungulate species in Europe (Okarma 1984, Okarma 1991, Bobek *et al*. 1992a, Okarma *et al*. 1995, Gula 2004).

In central Europe the main prey species of wolves is red deer *Cervus elaphus* Linnaeus, 1758 (Leśniewicz and Perzanowski 1989, Śmietana and Klimek 1993, Jędrzejewski *et al*. 1992, 2000, 2002). In the Carpathian Mountains, research on wolf predation on red deer describes age, sex and bone marrow fat content of kills found only during winter (Okarma 1984, Okarma 1991, Bobek *et al*. 1992a, Gula 2004). Moreover no comparison of these characteristics was made with the free living population, which is necessary for the determination of predator selectivity.

The aim of this study was to determine selectivity of wolf predation on red deer (> 4 months old) in respect to age, sex and body condition in different seasons in the Carpathian Mountains. I attempted to explain the mechanisms of seasonally varying predation pattern in relation to the body condition of prey and social structure of the red deer population.

Study area

The study was conducted in the Bieszczady Mountains (a range within the Carpathians) within Bieszczady National Park and adjacent three hunting districts; 49°00'–18'N 22°25'–54'E. The total study area amounted to about 600 km^2. Bieszczady National Park (ca 300 km^2) lies in the highest parts of the Bieszczady Mountains, with the highest peak – 1346 m a.s.l. The lowest point of the study area lies at 420 m a.s.l. in the San River valley northwest of the National Park. Long, parallel mountain ridges build up of Carpathian flysch (Zarzycki and Głowaciński 1986) are a characteristic feature of the area.

About 80% of the study area is covered by forest. According to Michalik (1993) 75% of the tree stand is natural. Within this area botanists distinguish 9 forest plant associations, with Carpathian beech forest *Dentario glandulose-fagetum* as the most common (Michalik 1993). Beech *Fagus silvatica* and in some areas fir *Abies alba* are the dominant tree species. Other important trees are grey alder *Alnus incana*, sycamore *Acer pseudoplatanus* and spruce *Picea abies* mainly introduced by man (Zarzycki 1963). Meadows with blue berries *Vaccinium myrtillus*, grass and sedge associations and, in some places, green alder *Alnus viridis* and mountain-ash *Sorbus aucuparia* scrub (Zarzycki and Głowaciński 1986) cover the zone above 1150 m a.s.l. The average annual air temperature is 4.9°C and during especially severe winters can drop below – 30°C. Annual precipitation is 800–1200 mm. Snow cover persists for 90–120 days in the valleys and for 140–150 days on the mountain tops. Snow depth might exceed 1.5 m, although usually reaches 40–80 cm (Michna and Paczos 1972). The relatively low human density (6 persons/km^2), dominance of forested areas, and geographical location makes the Bieszczady Mountains and its surroundings one of the most valuable ranges for large mammal and avian predators in Poland. Apart from wolves, there are also other large carnivores, such as the lynx *Lynx* and the brown bear *Ursus arctos*. There are five ungulate species in the Bieszczady Mountains: red deer, roe deer *Capreolus capreolus*, wild boar *Sus scrofa*, European bison *Bison bonasus* and moose *Alces alces*. During the winter, most of the red deer migrate from higher mountain elevations to the wintering ranges, lying northwest from the National Park (Śmietana and Wajda 1995).

During the study, red deer, which were the most numerous ungulates, were exploited within the hunting districts every year and inside the National Park they were controlled by yearly culling until 1995. The area was occupied by 3 to 5 wolf packs (10–33 individuals) every year (Śmietana and Wajda 1997, W. Śmietana, unpubl.). Until 1998 wolves were hunted outside the National Park, with a closed season from 1 April to 31 July. Since April 1998, wolves have been fully protected throughout the study area although they are poached frequently.

Material and methods

Examination of red deer killed by wolves

The study area was regularly searched for carcasses of ungulates throughout the year by the author (150–200 days/year), 6–8 park guards and foresters during their routine inspections, and volunteers (100–200 person-day/year) from September 1991 until April 2002. Kills were mostly found by observing raven *Corvus corax* activity and during snow tracking of wolves. *In situ* cause of death, sex, age class (juvenile or > 1 year old) and accurate or approximate date of death was determined. Kills, for which the cause of death was identified as a wolf predation, by obvious evidence of tracks and chase and/or struggle or canine slash marks on the killed animal, were used in this analysis. The mandibles and femurs were removed from the bodies for further examinations in the laboratory. The mandible was used for age determination on the basis of tooth eruption pattern (only individuals up to second year of life) (Lochman 1987), cementum annuli (Mitchell 1967, Godawa 1989), and tooth--wear (Lochman 1987). To determine bone marrow fat content, which may reflect physical condition, a 5–20 g sample from mandible and femur was extracted. Fat content was determined by Neiland's method (1970).

Age-sex structure and physical condition of red deer population

Sex and age structure of the free living red deer was determined by direct observations and by analysis of individuals killed by hunters. Observed red deer were classified as: calves (individuals < 1 year old), hinds (females > 1 year old) or stags (males > 1 year old). Moreover, on the basis of size and shape of the body and by the look of the antlers (Lochman 1987) observed stags were classified to four groups 1) yearlings, 2) stags from third to fifth year of life, 3) stags from sixth to tenth year of life and 4) stags above ten years old. In practice, hunters killed hinds randomly. Therefore, in order to determine the age structure of the free living hinds, 94 mandibles of harvested individuals were collected. Their age was determined using the same method as for red deer killed by wolves. Age and bone marrow fat content of hunted stags could not be used for comparisons because of non random harvest of them. To assess the selection of particular age classes of adult red deer by wolves, Ivlev's selectivity index D (modified by Jacobs 1974) was used according to the formula: $D = (r - p) / (r + p - 2rp)$, where r is the proportion of a given age class in wolf kills and p is its proportion in the free living population. Ivlev's selectivity index ranges from –1 (total avoidance) through 0 (no selection) to +1 (maximum positive selection). The bone marrow fat content of 27 calves and 94 hinds harvested by hunters in the study area was determined. Because sampling of bone marrow from femur decreases trade value of hunted individuals only bone marrow from mandibles was available for analyses.

Results

Age and sex structure

Among 324 red deer > 4 months old killed by wolves, 69 were calves, 96 hinds and 159 were stags. A strong bias against finding dead juvenile red deer prevented evaluation of their share in wolf kills before October; we found only one wolf-killed calf < 4 months old. Due to the usually high consumption of bodies, only 18 calves were sexed: 9 females and 7 males.

The share of a given red deer class in kills varied by months. To test changes of these proportions, I combined consecutive months with similar percentage contributions of red deer classes. From October until May, the overall share of calves in wolf kills (24%) was higher than in the free living population (17%) ($\chi^2 =$ 7.78, df = 1, p = 0.005) (Table 1). The proportion of calves in hind-calf part of the kill sample (0.47) was also higher than their proportion in hind-calf segment of

Table 1. Share of calves in all red deer (calves and adults) killed by wolves and in the hind-calf (calves and hinds) segment of the sample in comparison to the structure of the free living population in the Bieszczady Mountains from 1991 through 2002. [a] Yates' corrected χ^2 was used because of small sample size of calves in the kill sample.

Period	Wolf kills		Population		χ^2	p
	n	Share of calves (%)	n	Share of calves (%)		
Calves and adults						
October–December	98	34	608	20	8.61	0.003
January–February	124	23	551	17	2.27	0.071
March–May	70	10	830	15	1.16[a]	0.281
Calves and hinds						
October–December	67	49	466	27	14.45	< 0.001
January–February	53	55	389	23	23.14	< 0.001
March–May	28	25	583	21	0.08[a]	0.780

the population (0.23) ($\chi^2 = 37.88$, df = 1, $p < 0.001$) (Table 1). Wolves tended to kill more calves than available in the population in October–December and in January–February, but the difference was significant only for October–December sample (Table 1). If only hind-calf part of the samples were compared, differences were significant for both periods (Table 1). In March–May the share of calves in kills was not significantly different from their share in the population neither for total samples nor for their hind-calf segments (Table 1).

In general, adult males were more vulnerable to wolf predation than adult females. Stags and hinds constituted 62 and 38% of adult red deer killed by wolves, respectively, whereas the share of stags and hinds in the adult segment of the free living population was 37 and 63%, respectively ($\chi^2 = 64.61$, df = 1, $p <$

Table 2. Share of females and males in adult red deer killed by wolves in comparison to the structure of the free living population in the Bieszczady Mountains from 1991 through 2002.

Period	Number of adults of both sexes	Share of stags (%)	Share of hinds (%)	χ^2	p
Wolf kills					
June–September	32	47	53	1.35	0.245
October–December	65	48	52	3.18	0.074
January–February	95	75	25	56.12	< 0.001
March–May	63	67	33	23.37	< 0.001
Population					
January–December	3319	37	63		

0.001) (Table 2). Wolves tended to kill more stags than available in adult segment of the population year round but the differences were significant only for January–February and March–May samples (Table 2).

The age distribution of adult red deer killed by wolves differed apparently between sexes (Kolmogorov-Smirnov test: $D = -0.556$, $p < 0.001$) (Fig. 1). On average, stags killed by wolves were younger ($n = 66$, $\bar{x} = 4.1$) than hinds ($n = 61$, $\bar{x} = 8.9$). Among hinds killed by wolves, individuals older than 8 years prevailed (62%) and among stags most individuals were below 5 years old (76%). The age structure of hinds killed by wolves and by hunters also differed significantly ($D = 0.378$, $p < 0.001$) (Fig. 1). The age of 94 hinds killed by hunters averaged 6.0 years
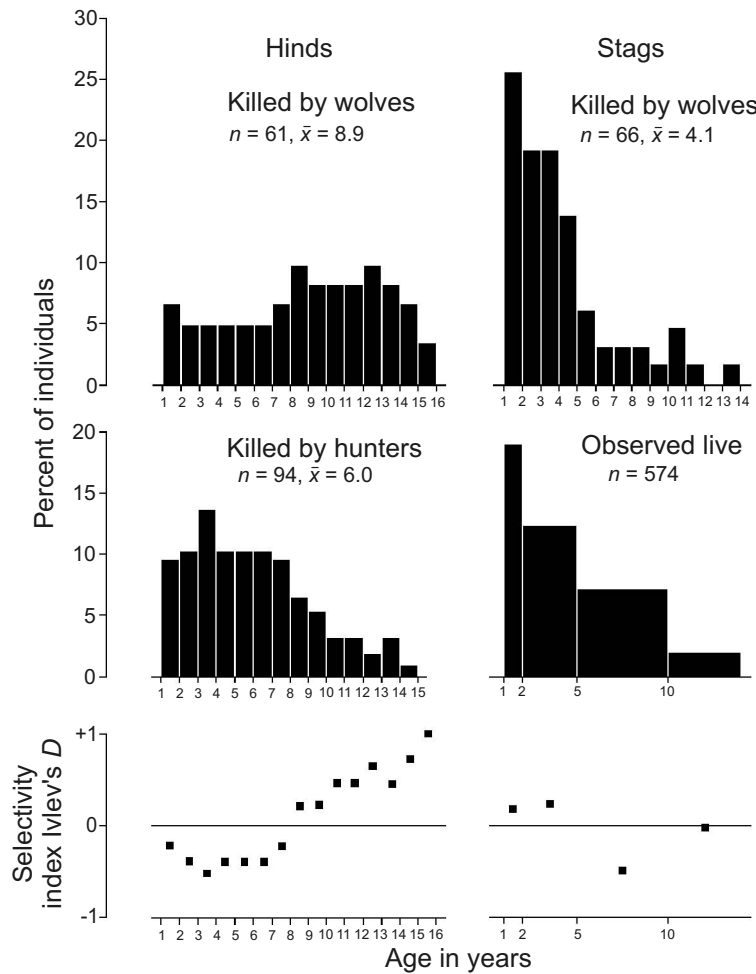

Fig. 1. Age structure of adult (> 1 year old) female and male red deer killed by wolves, killed by hunters and observed live, in the Bieszczady Mountains from 1991 through 2002, and Ivlev's selectivity index for wolf predation on each age class of red deer.

and individuals below 8 years old dominated (75%). Calculated Ivlev's selectivity index was negative for hinds below 8 years old and varied from –0.20 to –0.51 (Fig. 1). Among older hinds Ivlev's index was positive, varying from 0.22 to 1.00 and was increasing with their age. Generally, hinds below 8 years old were less vulnerable to wolf predation than older ones. The age structure of stags killed by wolves also contrasted with the age structure of the free living males (D = –0.191, $p < 0.05$) (Fig. 1). Selectivity index was the lowest for 5–10 years old stags (D = –0.47) and the highest for 2–5 years old ones (D = 0.23). Generally, stags below 5 years old were more vulnerable to wolf predation than older ones.

Condition of red deer killed by wolves and hunters

The average fat content in femur marrow of red deer killed by wolves was the highest in hinds (n = 48, $\bar{x}$ = 84.9%) followed by stags (n = 53, $\bar{x}$ = 69.3%) and calves (n = 35, $\bar{x}$ = 66.1%) (Fig. 2). A significant difference in femur marrow fat content was found between calves and hinds (Mann-Whitney U-test: U = 536, p = 0.005) and between hinds and stags (U = 828, p = 0.003) but not between stags and calves (U = 919, p = 0.942). Only 8% of hinds had femur marrow fat content below 70%, whereas 40% of calves and 38% of stags had marrow fat values below that level (Fig. 2). Femur marrow fat content was similar between young (< 8 years) (n = 19) and old (> 8 years) (n = 28) hinds (U = 236, p = 0.515) and between young (< 5 years) (n = 25) and old (> 5 years) (n = 10) stags (U = 119, p = 0.827), averaging 87.0, 83.2, 67.5, and 64.4%, respectively.

Mandible marrow fat content in calves killed by wolves between November and February (n = 26, $\bar{x}$ = 50.8%) was significantly lower than in calves killed by hunters during the same period (n = 27, $\bar{x}$ = 62.4%) (Mann-Whitney U-test: U =
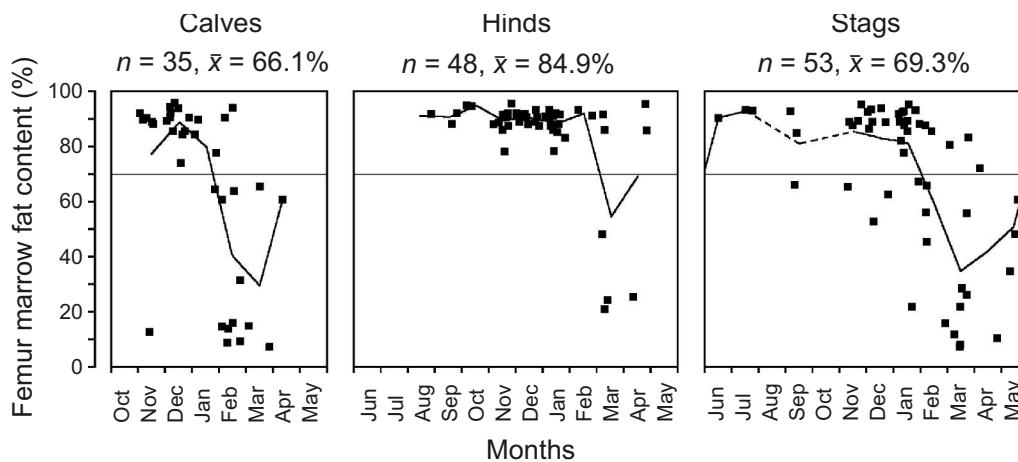

Fig. 2. Femur marrow fat content of red deer killed by wolves in the Bieszczady Mountains from 1991 through 2002. Each point represents one individual plotted against the date when killed. Line shows monthly changes of average femur marrow fat content. Broken line indicates no data for at least one month. Horizontal line indicates critical value (70%) of femur marrow fat content.

195, $p < 0.001$). In November–February, there was no significant difference in bone marrow fat values ($U = 1508$, $p = 0.337$) between hinds killed by wolves ($n = 36$; $\bar{x} = 70.9\%$) and those killed by hunters ($n = 94$, $\bar{x} = 69.6\%$).

The average femur marrow fat content of all age-sex classes of red deer killed by wolves was maintained at high level (77.5–94.6%) during summer, autumn and early winter (Fig. 2). Then, it decreased rapidly among calves and stags in February and among hinds in March. The lowest monthly average fat content in femur marrow for all age-sex classes was recorded in March (Fig. 2). In February–April 86% of calves ($n = 14$), in March–April 50% of hinds ($n = 8$) and in February–May 75% of stags ($n = 20$) had femur marrow fat content below 70%, which contrasts with the remaining part of the year when only 10% of calves ($n = 21$) (Fisher exact test: $p < 0.001$), no hind ($n = 40$) ($p < 0.001$) and 18% of stags ($n = 33$) ($p < 0.001$) had such a low level of the fat content.

From October until May, the monthly share of stags in kills tended to decrease with their growing average fat content in femur marrow ($n = 7$, $r_s = -0.750$, $p = 0.052$). The monthly proportions of hinds in the total number of wolf kills in the same period did not correlate with their average femur marrow fat content ($n = 7$, $r_s = -0.500$, $p = 0.253$), but there was a strong correlation if only hind-calf part of the monthly kill samples were considered ($n = 7$, $r_s = -0.928$, $p = 0.003$). No correlation was found between monthly proportions of calves among kills and their femur marrow fat levels neither for the whole samples ($n = 6$, $r_s = 0.486$, $p = 0329$) nor for hind-calf sub-samples ($n = 6$, $r_s = 0.257$, $p = 0.623$), but there was a strong correlation between monthly proportions of calves in kills and femur marrow fat levels of adults ($n = 8$, $r_s = 0.833$, $p = 0.010$).

Discussion

This study documents that vulnerability of red deer to wolf predation in the Bieszczady Mountains depends on age, sex and body condition and varies according to the time of year. Calves were important prey from October until February. The high vulnerability of red deer calves to wolf predation during winter was described also in earlier studies from the same mountain range by Okarma (1991) and Bobek *et al*. (1992a). In Białowieża Primeval Forest, Okarma *et al*. (1995) found slightly higher share of calves in kills than in the free living population. Gula (2004) claimed that winter wolf predation on red deer in the Bieszczady Mountains is not selective for calves, although in his study calves composed 29% of wolf-killed deer or 42% if only hind-calf part of the sample is considered (which is similar to my results). The researcher compared the kill sample with the data provided by the State Forest Administration. According to this data there were 72 calves per 100 hinds in winter red deer population, which seems to be an unusually high ratio (see Bobek *et al*. 1992b), and is 2.4 times higher than my estimations. In my study the contribution of calves among red deer killed by wolves was decreasing from autumn to spring. This phenomenon was a result of an increase in the contribution

of adults among kills. The lack of correlation between average bone fat levels and monthly proportions of calves in kills suggests that body condition was not a primarily factor predisposing them to wolf predation. Juvenile ungulates being generally slower, weaker (less dangerous to attack) and less experienced with predators than adults, are expected to be usually more vulnerable prey (Mech 1970). My study suggests that such situation persists until the body condition of adults decrease substantially in late winter and in spring. The overall disproportionately higher occurrence of juveniles among wolf kills in my study well corresponds with the most of North American studies on wolf predation on white--tailed deer, elk and moose (eg Mech 1966, Peterson 1977, Fritts and Mech 1981, Huggard 1993, Mech *et al*. 1995 , Hayes *et al*. 2000, Smith *et al*. 2004).

Higher natural mortality of males than females resulting in shorter life span should be expected in highly sex dimorphic species like red deer (Clutton-Brock *et al*. 1982). Contrary to my study, earlier studies conducted in the Carpathians (Okarma 1984, 1991) and in Białowieża Primeval Forest (Okarma *et al*. 1995) reported that hinds are more vulnerable to wolf predation than stags. Gula (2004) found no selection neither for hinds nor for stags, and Bobek *et al*. (1992a) reported slight selection towards stags. However, the sex proportion in the sample of adult red deer killed by wolves could depend on the area from where the material was collected, as female and male groups of red deer occupy separate large ranges most of the year (except the rutting season). Sex ratio among kills could also vary between years and depends on winter severity. In my study area both female and male groups were present, material was collected over a long time (11 years) and, in contrast to the study of Okarma (1984, 1991), Bobek *et al*. (1992a) and Gula (2004), red deer killed by wolves were found year round and sex proportion of the local population was well documented. In my opinion, sex segregation of red deer, except the rutting season (September–October), and the difference in body condition between sexes explains the high contribution of stags and low contribution of hinds to the total number of adults killed by wolves. Hinds living mostly in female groups are obviously less vulnerable (except during March–May) than calves accompanying them, which is not the case in stags living mostly in male groups. Moreover, stags killed by wolves had, in general, lower bone marrow fat content than hinds. This difference was especially clear from mid-winter until spring, when the share of stags in kills was the highest. Monthly proportions of stags among kills tended to increase with decreasing their bone fat levels, which suggests that body condition was a very important factor predisposing them to wolf predation. Mech and Peterson (2003) generalized that adult males of ungulates are most vulnerable immediately before, during and after the rut, but such selection pattern was not found in my study. During the rut, adult males are less alert and, in some systems could become more vulnerable prey class, but on the other hand, during this period, they are in relatively good condition, equipped with weapons (antlers) and aggressive. My results support the opinion of Clutton-Brock (1985) that because of larger size, fast and prolonged growth and lower fat reserves, stags are more likely to die than hinds during periods of food shortage and harsh weather. Higher vulnerability

to wolf predation of elk males than females, during winter were reported by Huggard (1993) and Smith *et al*. (2004). Also in areas where wolves were absent, adult males of *Cervus elaphus* occurred proportionally more frequently than adult females among dead individuals found during winter (Houston 1978, Clutton-Brock *et al*. 1982). I found that hinds are the most vulnerable to wolf predation in the end of winter and in spring, but taken by wolves only proportionally to their availability in the population. The strong correlation between the share of hinds in hind-calf sub-sample of kills and their bone fat levels indicate that their body condition was a very important factor causing they vulnerability to wolf predation.

In cervids, marrow fat makes up only 2–3% of total body fat reserves (McCullough and Ullrey 1983) and fat level in femur marrow, at more than 70–85%, depending on species and age, indicate only that the total body fat of a given individual is above 5% (Adamczewski *et al*. 1987, Torbit et al. 1988, Holand 1992). Fat content in femur marrow below this threshold indicates not only very low total fat stores, but also substantial loss of protein and total body mass (Torbit *et al*. 1985, Delguidice *et al*. 1990). Thus, as remarked by Mech *et al*. (1995), any level below the threshold of bone marrow fat content indicates not only very low fat reserves but also considerable loss of skeletal muscle mass and vigour of the animal. Considering this, I believe that in my study at least 38% (percent of individuals with femur marrow fat content below 70%) of total number of stags, 40% of calves, and 8% of hinds killed by wolves were in poor condition. Positive selection of calves with low bone marrow fat content was found in my study, but unfortunately I was not able to compare bone marrow fat levels of stags killed by wolves with the same characteristic of stags from the free living population. However, this does not disprove my assertion that large number of stags killed by wolves was in poor condition.

Wolf selectivity for old animals has been recorded in numerous studies (eg Murie 1944, Mech 1966, Fritts and Mech 1981, Mech *et al*. 1995, Hayes *et al*. 2000). In my study such a selectivity is true only in case of hinds. Among stags wolves killed mostly 1–5 year old individuals. Such stags are usually the youngest members of male groups or (mostly yearlings) still members of female groups, and normally do not take part in reproduction (Clutton-Brock *et al*. 1982). Red deer males less than 5 years old grow intensively, and, as such, they do not deposit large fat reserves (Dzięciołowski *et al*. 1996). As members of male groups, these individuals have the lowest rank in the hierarchy and graze on the edge of the herd (Appleby 1980, 1982). Probably this reduces their body condition (poor food) and exposes them to wolf attacks. Stags between 5 and 10 years of age are at their optimum, they are the most active males during rut and they copulate with a number of hinds (Clluton-Brock 1985). Although during the rutting season their fat stores substantially decline (Bobek *et al*. 1990, Dzięciołowski *et al*. 1996), this age group stags were less vulnerable to wolf predation than younger males in my study. It must be considered, however, that the age structure of stags killed by wolves and those in the free living population were obtained by different methods. Although in reality, selective pressure on young and fully matured stags might

differ slightly from my results, it is clear that young males dominated among stags killed by wolves. In contrast to my results, North American studies on natural mortality of elk report dominance of >5 year old males both among individuals killed by wolves (Huggard 1993) and dead due to other natural mortality factors (Houston 1978, Smith 1998). The results obtained by Mysterud *et al.* (2003) suggest that, when prime-aged males of reindeer *Rangifer tarandus* are absent or rare, immature ones are more active during rut and as a consequence lose more body mass. Therefore, it might be possible, that high vulnerability of immature, 1–5-year-old males to wolf predation during winter and spring could be an outcome of the heavy harvest of males for trophies, which took part outside the National Park during my study (W. Śmietana unpubl.).

In summary, my study shows that wolves attacking female groups of red deer usually killed calves and old hinds, while attacking male groups they usually killed their youngest members. Wolves killed proportionally more calves from fall until midwinter, and hinds proportionally to their availability in hind-calf groups in the end of winter and in spring. In case of male groups, wolves were more likely to find vulnerable individuals from midwinter until spring and, in consequence killed more stags during this period. High vulnerability of adults from midwinter until spring was caused by their poor body condition. Segregation of social units (hind-calf and stag groups), except the rutting season, and low fat reserves of males from midwinter until spring contribute to the high overall incidence of calves and adult males and the relatively low incidence of adult females among wolf kills.

References

Adamczewski J. Z., Gates C. C. and Hudson R. J. 1987. Fat distribution and indices of carcass composition in Coast Island caribou (*Rangifer tarandus groenlandicus*). Canadian Journal of Zoology 65: 1149–1157.

Appleby M. C. 1980. Social rank and food access in red deer stags. Behaviour 74: 294–309.

Appleby M. C. 1982. The consequences and causes of high social rank in red deer stags. Behaviour 80: 259–273.

Ballard W. B., Whitman J. S. and Gardner C. L. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs 98: 1–54.

Bibikov D. (ed) 1985. [The wolf]. Izdatelstwo Nauka, Moskva: 1–606. [In Russian]

Bobek B., Perzanowski K. and Weiner J. 1990. Energy expenditure for reproduction in male red deer. Journal of Mammalogy 71: 230–232.

Bobek B., Perzanowski K. and Śmietana W. 1992a. The influence of snow cover on the patterns of selection within red deer population by wolves in Bieszczady Mountains, Poland. [In: Global

trends in wildlife management. B. Bobek, K. Perzanowski and W. Regelin, eds]. Świat Press, Kraków–Warszawa, Volume 2: 341–348.

Bobek B., Morow K., Perzanowski K. and Kosobucka M. 1992b. [The red deer (*Cervus elaphus*) – its ecology and management]. Wydawnictwo Świat, Warszawa: 1–200. [In Polish]

Carbyn L. N. 1983. Wolf predation on elk in Riding Mountain National Park, Manitoba. Journal of Wildlife Management 47: 963–976.

Clutton-Brock T. H. 1985. Reproductive success in red deer. Scientific American 252: 86–92.

Clutton-Brock T. H., Guinness F. E. and Albon S. D. 1982. Red deer, behaviour and ecology of two sexes. University Chicago Press. Chicago: 1–378.

Dzięciołowski R., Babińska-Werka J., Wasilewski M. and Goszczyński J. 1996. Physical condition of red deer in a high density population. Acta Theriologica 41: 93–105.

Delguidice G. D., Mech L. D. and Seal U. S. 1990. Effects of winter undernutrition on body composition and physiological profiles of white-tailed deer. The Journal of Wildlife Management 54: 539–550.

Fritts S. H. and Mech L. D. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildlife Monographs 80: 1–79.

Godawa J. 1989. Age determination in red deer, *Cervus elaphus*. Acta Theriologica 34: 381–384.

Gula R. 2004. Influence of snow cover on wolf *Canis lupus* predation patterns in Bieszczady Mountains, Poland. Wildlife Biology 10: 17–23.

Hayes R. D., Baer A. M., Wotschikowsky U. and Harestad A. S. 2000. Kill rate by wolves on moose in the Yukon. Canadian Journal of Zoology 78: 49–59.

Holand O. 1992. Fat indices versus ingesta-free body fat in European roe deer. The Journal of Wildlife Management 56: 241–245.

Houston D. B. 1978. Elk as winter-spring food for carnivores in northern Yellowstone National Park. Journal of Applied Ecology 15: 653–661.

Huggard D. J. 1993. Prey selectivity of wolves in Banff National Park. II. Age, sex, and condition of elk. Canadian Journal of Zoology 71: 140–147.

Jacobs J. 1974. Quantitative measurements of food selection; a modification of the forage ratio and Ivlev's selectivity index. Oecologia 14: 413–417.

Jędrzejewski W., Jędrzejewska B., Okarma H. and Ruprecht A. L. 1992. Wolf predation and snow cover as mortality factors in the ungulate community of the Białowieża National Park, Poland. Oecologia 90: 27–36.

Jędrzejewski W., Jędrzejewska B., Okarma H., Schmidt K., Zub K. and Musiani M. 2000. Prey selection and predation by wolves in Białowieża Primeval Forest, Poland. Journal of Mammalogy 81: 186–2002.

Jędrzejewski W., Schmidt K., Theuerkauf J., Jędrzejewska B., Selva N., Zub K. and Szymura L. 2002. Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). Ecology 83: 1341–1356.

Leśniewicz K. and Perzanowski K. 1989. The winter diet of wolves in Bieszczady Mountains. Acta Theriologica 34: 373–380.

Lochman J. (ed) 1987. [Determining age of game animals]. Państwowe Wydawnictwo Rolnicze i Leśne, Warszawa: 1–255. [In Polish]

McCullough D. R. and Ullrey D. E. 1983. Proximate mineral and gross energy composition of white-tailed deer. Journal of Wildlife Management 47: 430–441.

Mech L. D. 1966. The wolves of Isle Royale. U.S. National Park Service, Fauna Series 7: 1–210.

Mech L. D. 1970. The wolf: the ecology and behavior of an endangered species. University of Minnesota Press, Minneapolis: 1–384.

Mech L. D. and Frenzel L. D. (eds) 1971. Ecological studies of the timber wolf in northeastern Minnesota. USDA Forest Service Research Paper NC-52: 1–67.

Mech L. D. and Peterson R.O. 2003. Wolf prey-relations. [In: Wolves: behavior, ecology, and conservation. L. D. Mech and L. Boitani, eds]. The University of Chicago Press, Chicago: 131–161.

Mech L. D., Meier T. J., Burch J. W. and Adams L. G. 1995. Patterns of prey selection by wolves in Denali National Park, Alaska. [In: Ecology and Conservation of Wolves in a Changing World. L. N. Carbyn, S. H. Fritts and D. R. Seip, eds]. University of Alberta, Edmonton: 293–302.

Michalik S. 1993. [Forest associations of the Bieszczady National Park, their evaluation and protection problems]. Roczniki Bieszczadzkie Tom 2: 51–62. [In Polish with English abstract]

Michna E. and Paczos S. 1972. [Climate of the Bieszczady Mountains]. Ossolineum, Wrocław: 1–72. [In Polish]

Mitchell 1967. Growth layers in dental cement for determining the age of red deer (*Cervus elaphus* L.). Journal of Animal Ecology 36: 279–293.

Murie A. 1944. The wolves of Mount McKinley. Fauna of the National Parks of the United States. Fauna Series 5: 1–238.

Mysterud A., Holand O., Roed K. H., Gjostein H., Kumpula J. and Nieminen M. 2003. Effects of age, density and sex ratio on reproductive effort in male reindeer (*Rangifer tarandus*). Journal of Zoology, London 261: 341–344.

Neiland K. A. 1970. Weight of dried marrow as indicator of fat in caribou femurs. The Journal of Wildlife Management 36: 357–369.

Okarma H. 1984. The physical condition of red deer falling prey to the wolf and lynx and harvested in the Carpathian Mountains. Acta Teriologica 29: 283–290.

Okarma H. 1991. Marrow fat content, sex and age of red deer killed by wolves in winter in the Carpathian Mountains. Holarctic Ecology 14: 169–172.

Okarma H. 1995. The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. Acta Theriologica 40: 335–386.

Okarma H., Jędrzejewska B., Jędrzejewski W., Krasiński Z. A. and Miłkowski L. 1995. The roles of predation, snow cover, acorn crop, and man related factors on ungulate mortality in Białowieża Primeval Forest, Poland. Acta Theriologica 40: 197–217.

Peterson R. O. 1977. Wolf ecology and prey relationships on Isle Royale. United States National Parks Service Scientific Monographs Series 11: 1–210.

Smith B. L. 1998. Antler size and winter mortality of elk: effects of environment, birth year, and parasites. Journal of Mammalogy 79: 1038–1044.

Smith D. W., Drummer T. D., Murphy K. M., Guernsey D. S. and Evans S. B. 2004. Winter predation and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. The Journal of Wildlife Management 68: 153–166.

Śmietana W. and Klimek A. 1993. Diet of wolves in the Bieszczady Mountains, Poland. Acta Teriologica 38: 245–251.

Śmietana W. and Wajda J. 1995. [Present situation and prospects of protection of large carnivores (wolf and lynx) and ungulates in the Bieszczady National Park and its surroundings]. Roczniki Bieszczadzkie 4: 274–277. [In Polish]

Śmietana W. and Wajda J. 1997. Wolf number changes in Bieszczady National Park, Poland. Acta Theriologica 42: 241–252.

Torbit S. C., Carpenter L. H., Swift D. M. and Alldredge A. W. 1985. Differential loss of fat and protein by mule deer during winter. The Journal of Wildlife Management 49: 80–85.

Torbit S. C., Carpenter L. H., Bartmann R. M., Alldredge A. W. and White G. C. 1988. Calibration of carcass fat indices in wintering mule deer. The Journal of Wildlife Management 52: 582–588.

Zarzycki K. 1963. [Forests of the Bieszczady Mountains]. Acta Agraria et Silvestria. Seria Leśna 2: 19–24. [In Polish]

Zarzycki K. and Głowaciński Z. 1986. [The Bieszczady Mountains]. Wiedza Powszechna, Warszawa: 1–182. [In Polish]