Influence of snow cover on wolf Canis lupus predation patterns in Bieszczady Mountains, Poland

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Influence of snow cover on wolf *Canis lupus* predation patterns in Bieszczady Mountains, Poland

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Sex, age, bone marrow fat (BMF) content, degree of carcass utilisation and terrain features were analysed for 118 ungulates killed by wolves *Canis lupus* in the Bieszczady Mountains, Poland, during the winters of 1992-1995 to assess the influence of snow depth on the wolves' predation patterns. In Bieszczady, the snow conditions during the study period were milder than average, with an average total annual snow depth of 1,372 cm and an average snow cover lasting for 94 days. Red deer *Cervus elaphus* were the primary wolf prey (81%), whereas wild boar *Sus scrofa* and roe deer *Capreolus capreolus* were killed less often (9% and 10%, respectively). The majority of prey (74%) was killed in creeks and ravines. The carcass exploitation by wolves was high; of the recovered prey, 55% was more than 60% consumed. The average condition of red deer, as based on BMF, was high (83.4%). BMF varied most among red deer stags and calves, and varied with annual snow depth ($N = 29$, $P < 0.0$ 1; $N = 28$, $P = 0.09$) and monthly mean snow depth ($\tau = -0.37$, $P < 0.005$; $\tau = -0.25$, $P = 0.06$). Wolves killed adult red deer in creeks and ravines with the same frequency regardless of snow depth, whereas calves were killed less often in these places than should be expected from their overall proportion in the sample ($N = 95$, $\chi^2 = 24.34$, $P < 0.001$). During periods with thinner snow cover, consumption of red deer carcasses was slightly higher than during periods in which the snow cover was deep ($\tau = -0.42$, $P < 0.045$).

Key words: Canis lupus, Cervus elaphus, predation, red deer, snow, wolf

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Snow cover is a major abiotic factor influencing wolf *Canis lupus**prey relationships. Above-average snowfall increases the ability of wolves to kill prey due to reduced body condition and mobility of the prey. Thus, wolves kill more prey (Nelson & Mech 1986), hunt in larger groups (Fuller 1991) and are more likely to make multiple kills when snow is unusually deep (Mech, Adams, Meier & Burch 1998). Deep snow also reduces the condition of calves born in the previous springs (Mech, McRoberts, Peterson & Page 1987, Mech, Nelson & McRoberts 1991) and increases the physical condition and numbers of wolves (Mech et al. 1998).

The effects of snow may be important not only in areas where winters usually are severe and long lasting, but also in areas where winters are milder with periods of warming, and snow cover does not persist throughout the winter. I analysed the patterns of wolf-caused mortality of ungulates in relation to snow cover in the Bieszczady Mountains in the Polish Carpathian Mountains which is an area with mild alpine climate and frequent mild winters.

Study area

The study was conducted in the Bieszczady Mountains, Poland (49°N, 22°E) during three consecutive winters from 1992/93 through 1994/95. The highest peaks in this mountain range are more than 1,300 m a.s.l., and the average elevation of valleys is about 500 m a.s.l. About 70% of the area is forested with beech *Fagus silvatica*, alder *Alnus incana*, fir *Abies alba*, spruce *Picea abies* and sycamore *Acer pseudoplatanus* as the predominant tree species. The density of humans in the highest part of the range is about 2 people/km^2, and the average for the entire area is 10 people/km^2. The region is inhabited by numerous ungulate species, including red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, bison *Bison bonasus* and wild boars *Sus scrofa*, and the carnivore species include wolf, brown bear *Ursus arctos*, lynx *Lynx lynx*, wild cat *Felis rufus*, red fox *Vulpes vulpes*, badger *Meles meles*, otter *Lutra lutra* and pine marten *Martes martes*. The study area covers 600 km^2 and includes five forests districts of the Bieszczady Mountains (Baligród, Cisna, Komańcza, Stuposiany and Wetlina).

The multi-annual average temperature in July is 16°C, and in January -6°C. The average monthly precipitation is 125 mm and the annual average 800-1,200 mm. At altitudes within 500-800 m a.s.l., the snow cover persists for 90-140 days, appearing in October-December and disappearing in February-April. The maximal snow cover depth usually does not exceed 40-80 cm, but may reach a maximum of 150 cm.

Red deer is the most numerous ungulate species in the region with officially estimated densities ranging within 0.9-3.0 deer/km^2. However, harvest quotas indicate that the actual densities are at least twice as high (Perzanowski & Krzakiewicz 2000). Roe deer and wild boar are less abundant species with average densities of 0.2-4.5 and 4.4 animals/km^2, respectively (Perzanowski 2000, Perzanowski & Kanzaki 2000). The average weights of adult red deer are about 180 kg for stags and 120 kg for hinds, about 20 kg for adult roe deer and about 100 kg for wild boar. The wolf densities recorded in Forestry Administration inventories based on surveys in forest districts are 10.5-13.1/100 km^2. However, the method employed tends to overestimate the number of predators (Śmietana & Wajda 1997). Tracking surveys conducted during 1991-1995 in the Bieszczady National Park and the surrounding forest districts resulted in an estimated density of 4.2 wolves/100 km^2 and estimated home range sizes of three wolf packs ranging within 84-90 km^2. The pack size in this study varied within 3-10 (Śmietana & Wajda 1997). Wolves mostly prey on red deer, whereas roe deer and wild boar are killed less frequently (Leśniewicz & Perzanowski 1989, Śmietana & Klimek 1993).

Methods

Remains of 118 confirmed or probable wolf kills were examined during the three consecutive winters of 1992-1995. Kill remains were found between November and April by either local game managers during their daily routine inspections of the forest districts or the author and volunteers from the Earth Watch Organisation (50-120 people/day/year), who searched along forest roads and paths for wolf tracks and raven activity. Only 30% of the prey was found when following wolf tracks; the remaining 70% was found by observing raven activity. As the smaller sized prey (i.e. roe deer, young wild boars and red deer calves) is likely to be fully consumed more often than larger sized prey, the chances of localising this type of prey based on raven activity is smaller which might bias the results towards larger sized prey. Wolf kills were identified on the basis of tracks, scats and other signs showing that wolves had been present and feeding on the carcasses. If signs of other large predators (e.g. lynx and brown bear) were observed, such carcasses were excluded from analysis despite the fact that wolves had been present. The following data were collected for each kill: date, species, sex, age and condition of the prey. The age of the prey was estimated according to tooth wear or tooth eruption. The condition of the prey was evaluated from samples of femur marrow collected and tested for fat content according to the method described by Neiland (1970). The non-fat residuals in the femur samples were neglected as they constituted

Table 1. Snow cover characteristics of the winters 1992/93-1994/95, their mean and multi-annual mean of 1972-1986, in the Bieszczady Mountains, Poland. Sum of daily snow cover is an additive value of snow depth measured in consecutive days of a winter.

	Winter			Mean of	Mean of
	1992/93	1993/94	1994/95	1992-1994	1972-1986
Sum of daily snow cover for winter (mm)	2188	784	1143	1372	2484
No. of days with snow on the ground	108	80	95	94	105

Table 2. Prey species and their sex/age selection according to Manly's selectivity index (MSI ± SE; no selection at 0.33), carcass consumption rate, killing site features of ungulates killed by wolves and bone marrow fat (BMF) contents during the consecutive winters of 1992/93-1994/95 in the Bieszczady Mountains, Poland. * indicates insufficient data.

Prey species	N	Expected N	MSI (± SE)	No. of carcasses > 60% consumed	No. of carcasses found in creeks and ravines	% BMF (± SE)
Wild boars	11	7.3	0.48 (± 0.047)	9	7	75.9 (± 5.24)
piglets	11	*	*	9	7	75.9 (± 5.24)
adults	-	*	*	-	-	*
Roe deer	12	20.1	0.19 (± 0.030)	10	3	74.2 (± 7.68)
calves	7	*	*	7	-	74.2 (± 7.68)
adults	5	*	*	3	3	*
Red deer	95	90.6	0.33 (± 0.033)	50	77	83.4 (± 1.75)
calves	28	27.6	0.34 (± 0.029)	15	20	86.0 (± 1.98)
hinds	38	38.0	0.33 (± 0.029)	19	31	86.0 (± 2.36)
stags	29	29.4	0.33 (± 0.028)	16	22	77.4 (± 4.17)
Total	118			69	87	79.9 (± 1.70)

only 2-4% of the total dry weight of the sample (Okarma 1991). The amount consumed by wolves was estimated at 20% intervals. The terrain at kill sites was assigned to one of two categories: creeks and steep ravines and 'other types of terrain'.

Snow depths were recorded daily by the State Institute of Meteorology and Water Resources (IMIGW) at Komańcza and Wetlina situated in the study area. Winter snow indices were calculated by summing daily snow cover depths and counting days with snow cover. Snow depth at each kill site was evaluated by assigning snow depth measurement from the nearest measuring point to the killing event in question.

Differences in consumption rates and proportions of prey recovered were tested using χ^2, and ANOVA was used to examine for differences in bone marrow fat content after having been arcsine transformed to normalise the distribution. The relationships between selected characteristics of prey and snow cover parameters were tested using the Kendall tau correlation coefficient.

Manly's selectivity indices were calculated for three prey species and red deer calves, hinds and stags based on numbers of prey found in each class and estimated proportions in the populations based on Regional Forestry Office (RFO) data (Manly 1974). As the figures of red deer numbers provided by the RFO are considered to be underestimated when compared to the actual harvest rate data (Perzanowski & Krzakiewicz 2000), they were corrected using a coefficient of 2.7 as recommended by Bobek, Perzanowski & Zieliński (1986).

Results

Snow cover

All winters during the study period were milder than the long-term averages for the area. Sums of snow depth for each winter were lower than the multi-annual averages at both measuring sites (Table 1). The duration of snow cover was generally short, although it was about average in the winter of 1992/93 (see Table 1). Based on snow depth and duration, the winter of 1992/93 was the most severe, and the winter of 1993/94 was the mildest.

Species, sex and age structure of prey

A total of 118 wolf kills was found during the three consecutive winters of 1992-1995 and included 95 red deer, 12 roe deer and 11 wild boar (Table 2). Compared to their density, wild boars were overrepresented among the wolf prey, red deer were killed proportionally to their occurrence, and roe deer were underrepresented among the animals killed by wolves (see Table 2).

Among the 95 red deer killed by wolves, most were hinds (38) followed by stags (29) and calves (28; see Table 2). Of 29 hinds of known age, the majority (59%) was older than seven years, whereas most of the stags (64%) were 4-7 years old (Fig. 1). Of the 12 roe deer, seven (58%) were fawns, three (25%) were adult males and only two (17%) were adult females. All wild boars

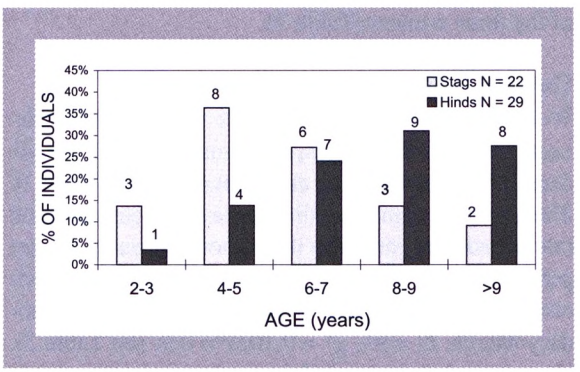

Figure 1. Age composition of adult red deer killed by wolves during the consecutive winters of 1992/93-1994/95 in the Bieszczady Mountains, Poland.

Table 3. Categories and their sex/age selection according to Manly's selectivity index (MSI ± SE; no selection at 0.33), carcass consumption rate, killing site features and bone marrow fat (BMF) contents of red deer killed by wolves during the consecutive winters 1992/93-1994/95 in the Bieszczady Mountains, Poland. Data are given for each of the three winters separately and for early (November-December) and late (January-March) winter. * indicates insufficient data.

	N	MSI (± SE)	No. of carcasses > 60% consumed	No. of carcasses found in creeks and ravines	% BMF (± SE)
1992/93					
calves	5	*	3	4	76.6 (± 6.56)
hinds	7	*	4	6	89.3 (± 1.07)
stags	4	*	2	1	83.2 (± 9.11)
Total	16		9	11	83.8 (± 3.15)
1993/94					
calves	11	0.30 (± 0.042)	6	7	88.6 (± 2.86)
hinds	18	0.35 (± 0.041)	11	15	87.0 (± 2.77)
stags	14	0.35 (± 0.043)	7	12	90.9 (± 2.23)
Total	43		24	34	88.7 (± 1.54)
1994/95					
calves	12	0.38 (± 0.028)	6	10	87.5 (± 2.25)
hinds	13	0.30 (± 0.028)	5	12	83.0 (± 5.80)
stags	11	0.32 (± 0.026)	6	10	58.2 (± 7.03)
Total	36		17	32	74.3 (± 3.68)
Early winter					
calves	12	-	7	10	89.9 (± 1.68)
hinds	17	-	8	15	87.5 (± 2.25)
stags	17	-	10	13	84.1 (± 4.90)
Total	46		25	38	87.6 (± 2.19)
Late winter					
calves	16	-	9	11	83.0 (± 3.09)
hinds	21	-	10	18	83.1 (± 3.75)
stags	12	-	6	10	67.9 (± 6.59)
Total	49		25	39	79.4 (± 2.61)

killed by wolves were either piglets or yearlings, but their sex could not be determined as large proportions of their carcasses had been consumed (see Table 2).

Among red deer, hinds were the most frequently killed during all of the three winters. Stags constituted 25% of wolf-killed red deer during the most severe winter (1992/93) and 33% in the mildest winter (1993/94). Calves were killed in similar proportions in the most severe winter (1992/93) and the medium severe winter (1994/95; 31 and 34%, respectively), but less often in the mildest winter (1993/94; 25%). The selectivity index shows neither an apparent wolf selection for calves, hinds or stags during the entire study, nor for each of the three winters (Table 3).

Carcass exploitation

Wolves consumed more than 60% of the red deer carcasses in 53% of the cases, and in most cases of the roe deer (83%) and wild boar carcasses (82%; see Table 2). There was no significant difference in the consumption rate of red deer carcasses throughout the entire winter periods ($N = 95$, $\chi^2 = 0.68$, $P = 0.9$), the early winter periods (October-December) or the late winter periods (January-March: $N = 95$, $\chi^2 = 0.10$, $P = 0.9$; see Table 3). However, wolves tended to exploit carcasses more completely during periods of low snow depth ($N = 13$, $\tau = -0.42$, $P = 0.045$; Fig. 2).

Killing sites

Except for roe deer fawns, most prey (74%) were recovered in creeks and ravines, and the occurrence of remains in this type of terrain did not vary with winter snow depth ($N = 118$, $\chi^2 = 2.33$, $P = 0.6$; see Table 2) or monthly mean snow depth ($N = 13$, $\tau = -0.21$, $P = 0.3$). Red deer calves were less frequently killed in creeks and ravines than adults of both sexes ($N = 95$, $\chi^2 = 24.34$, $P < 0.001$).

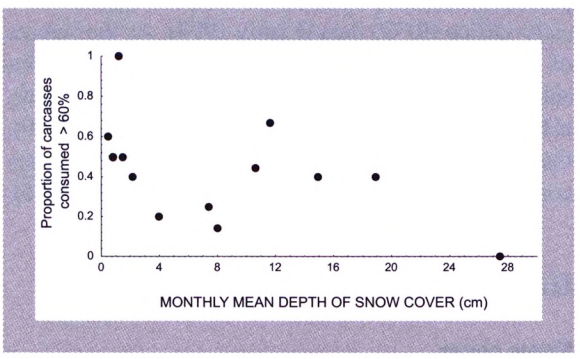

Figure 2. Correlation between proportion of red deer calves consumed (> 60%) by wolves and monthly mean of snow cover depth (N = 13) during the consecutive winters of 1992/93-1994/95 in the Bieszczady Mountains, Poland; ($\tau = -0.42$, $P = 0.045$).

Condition of prey

The average bone marrow fat (BMF) content was high (80.0%) in all recovered preys. However, the sample of wild boar and roe deer was small (N = 7), as most carcasses were almost completely consumed and bone marrow was therefore impossible to obtain.

The average condition of killed red deer was good (BMF = 83.4%); the lowest fat contents (BMF = 74.3%) occurred during the medium severe winter (1994/95) and the highest (BMF = 88.7%) during the mildest winter (1993/94; $N = 95$, $P < 0.01$; see Table 3). The BMF was lower during late winter ($N = 95$, $P < 0.05$; see Table 3) than during early winter, and correlated with the monthly snow cover depth ($\tau = -0.21$, $N = 95$, $P < 0.005$). The condition of red deer stags was the most variable, and was lowest during the medium severe winter (1994/95; $N = 29$, $P < 0.01$; see Table 3). BMF values in stags were significantly lower in late winter ($N = 29$, $P < 0.05$; see Table 3) than during early winter, and were negatively correlated with monthly mean depth of snow cover ($N = 29$, $\tau = -0.37$, $P < 0.005$). The condition of calves was lowest in the most severe winter (1992/93; $N = 28$, $P = 0.09$) and was lower in late winter ($N = 29$, $P = 0.06$) than in early winter (see Table 3). Calves killed in months with low mean snow cover depth had higher BMF than calves killed in months with deeper snow cover ($N = 28$, $\tau = -0.25$, $P = 0.06$). BMF in hinds appeared to be lowest in the severe winter (1992/93), but did neither decline significantly in late winter (see Table 3) nor vary with monthly mean snow cover depth ($N = 38$, $\tau = 0.08$, $P = 0.3$).

Discussion

The characteristics of recovered wolf prey in this study correspond well with those reported from previous studies on diet of wolves in the region. Red deer were the main prey during winter (81% of killed prey) and constituted 94.3% of the biomass consumed. The finding of no apparent wolf selection for red deer contradicts the selection patterns found at other sites. Winter selection for red deer by wolves has been reported from most of Europe (Okarma 1995). However, it is difficult to show a statistical selection for a prey item that is so dominating in the diet due to a resulting low statistical power of the test.

Wild boar constituted an estimated 9.3% of the prey species killed, compared with 11% of winter diet based on stomach contents (Leśniewicz & Perzanowski 1989) and 17% based on scat contents (Śmietana & Klimek 1993), and with exclusion of other food items such as domestic animals and small mammals wild boars constituted 17.2% (Leśniewicz & Perzanowski 1989) and 21.1% (Śmietana & Klimek 1993) of the total biomass consumed by wolves, which is almost twice as much as found in my study. This difference may be related to the reduced possibility of recovering wild boar carcasses (which were often consumed completely), but even then wild boars were underrepresented in my sample. The positive selection for wild boar as prey by wolves is known from several locations in Russia, whereas records from another location in Poland show an opposite trend (Okarma 1995). However, a strong negative correlation between the densities of wolves and wild boars has been reported in Bieszczady which supports the significance of wild boar as prey for wolves (Kanzaki & Perzanowski 1997). Śmietana & Klimek (1993) estimated the amount of roe deer biomass consumed by wolves in winter to be about 3.5% of the total biomass consumed, and the 12 roe deer killed by wolves as found in my study constituted 2.3% of the total biomass. This low percentage of roe deer in the wolf diet is related to the generally low density of roe deer in the Bieszczady Mountains (0.2/km^2; Perzanowski 2000) and bias of finding killed roe deer due to complete consumption, but it might also reflect a low preference for this prey similar to what has been reported from other sites (Okarma 1995).

Bobek, Perzanowski &Śmietana (1992) claimed that wolves tend to select red deer calves and stags. My study did not support this as wolves killed calves, stags and hinds in proportion to their occurrence in the population, but it is possible that I did not find a selection of calves, because of a lower probability to find killed calves which are often completely consumed. Selection for calves has been reported from other studies (Jedrzejewski, Jedrzejewska, Okarma & Ruprecht 1992, Okarma 1995).

As all the three winters in my study were relatively mild, snow cover had no dramatic influence on the wolf*prey relationship. However, in this area with generally low snow cover, terrain features appeared to be important in the wolves' hunting strategy. They killed most of their prey in creeks and ravines, where the animals may be easier to intercept, as they have to slow down and change gait. Bobek et al. (1992) reported that when the snow cover was thinner than 10 cm, all kills occurred in valleys and ravines, but when the snow cover exceeded 40 cm, only 59% were killed in this type of terrain. In my study, I did not find such a clear relationship, probably because the snow cover was relatively thin throughout the study period. The smaller proportion of calves killed in creeks and ravines

indicate that adults are killed most often in such places because they are more vulnerable there. In general, low utilisation of kills occurs when snow is deep and prey is easier to kill. In my study, despite snow conditions, red deer were consumed to a lesser degree than in other places (Fritts & Mech 1981, Fuller 1991). This relatively low consumption rate may reflect 1) small pack size due to human harvest and 2) high human disturbance which often caused wolves to abandon their prey. During the survey, we found some evidence that people often cause wolves to abandon prey. In several cases, freshly killed stags were found without a head, most probably because it had been taken by people searching for antlers (R. Gula, unpubl. data). Despite the overall consumption level, wolves tended to eat more when snow was shallow, which confirms earlier findings from Bieszczady (Bobek et al. 1992) and other areas (Peterson 1977, Carbyn 1983, Potvin, Joliocoeur & Huot 1988).

Severe winter conditions negatively influence the body condition of ungulates due to higher energy costs for locomotion and thermoregulation. Data collected by Okarma (1991) suggest that wolves kill deer that have lower than average BMF values. Despite this selection pattern, the relatively good condition of prey taken by wolves in my study suggests a good condition of prey in this population, which is probably related to low winter severity. However, it is impossible to show whether this reflects the average BMF in the population, or whether the condition of animals killed by wolves was lower than average, i.e. the BMF value in the general population could have been even higher.

Conclusions

Wolves in the Bieszczady Mountains preyed mostly on red deer, however, they tended to select wild boar, avoid roe deer and kill red deer in proportion to their occurrence. However, this conclusion ignores the known bias that smaller prey are less detectable than larger prey due to complete consumption. Also, the dominance of red deer in the diet weakened the statistical power of the selection test. During mild winters with thin snow cover, ungulates killed by wolves had high fat reserves, which probably reflected the good condition of the prey populations. Wolves tended to kill most prey in creeks and deep ravines and exploited carcasses to a relatively high degree. Wolf hunting patterns were affected by even moderate changes in snow cover. During periods with lower snow depth, wolves tended to consume carcasses to a higher degree, killed stags and calves in relatively good condition and more often killed calves in creeks and ravines.

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