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Spring-autumn diet of wolves (*Canis lupus*) in Slovakia and a review of wolf prey selection

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Abstract. The diet of a recovered wolf (*Canis lupus*) population in the Western Carpathian Mountains, Slovakia, was studied by scat analysis in March-November 2001-04 to assess the significance of livestock as a food item. As scat contents often do not reflect the proportions of items ingested, mean percentage volume in scats (m%V) was converted into estimates of biomass consumed using experimentally derived regression equations. Wild ungulates accounted for 92.8% of biomass consumed (mean volume of scats=91.1 %). Cervids clearly dominated wolf diet, found in 75.6 % of all scats (*n*=78) and comprising an estimated 79.3 % of biomass consumed. Macroscopic examination of bone/hoof material was used to classify cervid remains as adult (>1 year old) or juvenile (<1 year old). Of 24 scats in which remains could be classified, 20 contained juveniles and four adults; the ratio of juvenile:adult cervids was highest in summer (10:1). Juveniles were estimated to account for 74.4 % of cervid biomass consumed. The second most important item, wild boar (*Sus scrofa*), was found in 20.5% of scats. It comprised an estimated 13.5 % of biomass consumed. Remains of cattle and sheep were found in one scat each and totalled 4.8 % of biomass consumed, suggesting that livestock was not a major component of wolf diet. Factors influencing prey selection, including wild versus domestic ungulates, are reviewed.

Key words: Canis lupus, cervids, chamois, diet, food habits, predation, prey selection, *Sus scrofa*, wolves

Introduction

The diets of carnivores, in conjunction with their predatory habits, frequently bring them into conflict with humans. This has resulted in persecution by humans with an intensity sufficient to cause population decline, range contraction and, in some cases, extinction (Reynolds and Tapper 1996, Woodroffe 2001, Woodroffe *et al*. 2002). Persecution and excessive hunting eliminated the grey wolf (*Canis lupus*) as well as the brown bear (*Ursus arctos*) and Eurasian lynx (*Lynx lynx*) from most of Europe, including the majority of Slovakia, by the early 20th century (Breitenmoser 1998). Subsequent legal protection allowed relict large carnivore populations to recover in the Slovak Carpathians, but with their recovery came a resurgence of carnivore-human conflicts. For example when, in the mid 1990s, numbers of wild ungulates fell sharply across Slovakia, many hunters and wildlife managers blamed the decline on wolves, although excessive hunting and poaching as well as intensified agriculture seem to have been causes (Hell *et al*. 1997, Finďo 1998). It has been argued frequently that "over-populated" wolves, having devastated commercially valuable game stocks, turned to domestic animals as alternative prey. Likewise, the decline of the Tatra chamois (*Rupicapra rupicapa tatrica*) has been blamed on predation by the recovered wolf population and its inter-specific competition with lynx (see Janiga and Švajda 2002).

Wolves are at low densities in the Slovak Carpathians (Okarma *et al*. 2000) and hunting pressure is high (Rigg and Finďo 2000). Management policy has a major influence on carnivore populations (Linnell *et al*. 2001). As history has shown, hunting and persecution can have devastating consequences. In Slovakia, protected areas are not large enough to support viable populations of large carnivores in isolation and so most if not all wolves live in multi-use landscapes in which conflicts with human interests have commonly led to lethal control, even within National Parks (NPs) that the majority of the public believes should be havens for wildlife (Wechselberger *et al*. in prep.).

Management decisions in general and hunting regulations in particular should be based on results of sound scientific research (Strickland *et al*. 1996). According to Litvaitis *et al*. (1996), it is essential to have a thorough understanding of a species' feeding ecology before management actions are implemented. It follows that if they do not have a major impact on livestock or populations of conservation concern, such as the Tatra chamois, then predators that have been identified as requiring legal protection and/or are within protected areas should not be persecuted on the basis of the premise that they do. Conversely, if it were found to be correct, that large carnivores have become reliant on domestic animals as a major prey item, as has been alleged in Slovakia, then even benign measures such as improved non-lethal livestock protection could present a threat to their survival that would need to be considered in any conservation management strategy (Breitenmoser *et al*. 2002).

Wildlife management relating to large carnivores in Slovakia has yet to complete the transition described by Ratti and Garton (1996), from natural history observations to rigorous scientific investigations using robust research design to test specific hypotheses. Discussions of predator-prey relations tend to be based on anecdotal evidence and coloured by the strong traditions of hunting and game management. Few scientific studies have been done on the diets of live, free-ranging large carnivores in Slovakia and virtually none using modern methods. There is therefore considerable need for more rigorous quantitative study. The aims of the present research were to describe and quantify the diet of wolves in northern Slovakia during the livestock grazing season and hence assess the significance of livestock as a food item for wolves.

Direct observations are rather difficult in the Carpathians, where large carnivores are typically active at night or crepuscular periods and use forested areas less accessible to humans for cover during the day. As the primary goal of the present research was to determine the degree of feeding on livestock typically grazed on pastures from April to November, the collection and analysis of a sample of scats was selected as the most convenient and unobtrusive method available (Litvaitis 2000). In order to quantify carnivore diet by scat analysis, Murie (1944) and numerous workers after him (including the authors of previous quantitative studies of wolf diet in Slovakia) calculated the frequency of occurrence of each food item expressed as a percentage of the total number of scats or of separate food items summed across all scats. However, frequency of occurrence has been shown to be a poor method for establishing the relative importance of different kinds of food (Lockie 1959) because the identifiable faecal residues may not be in the same proportions as the biomasses of foods consumed (Floyd *et al*. 1978, Hewitt and Robbins 1996). The contents of scats vary with the digestibility, size and frequency of meals (reviewed in Litvaitis et al. 1996, Peterson and Ciucci 2003). There are also a number of methodological difficulties associated with identifying scat contents and from them deducing diet (Reynolds and Aebischer 1991). Ciucci *et al*. (1996) compared results from four methods of wolf diet analysis: percentage occurrence, percentage of total dry weight, percentage of total volume and estimated biomass consumed. The latter measure was derived by using correction factors for differential digestibility based on feeding trials with captive animals (Floyd *et al*. 1978, Weaver 1993). The most common inconsistencies among the methods concerned smaller food items. However, the "biomass consumed" method produced a higher estimate for the proportion of domestic ungulates in the diet of wolves. It was therefore selected for the present study.

Material and Methods

Study area

Fieldwork was conducted in north central Slovakia (48˚05' – 49˚12'N, 19˚00' – 20˚00'E) in three areas close to each other and each encompassing a portion of a National Park (Tatranský NP, Nízke Tatry NP and Veľká Fatra NP) together with adjoining agricultural regions, a total study area of c.1,300 km^2. These localities were chosen due to the known presence of wolves in close proximity to pastures used for grazing livestock, with relatively high levels of reported losses to predation. At the time of the study, large carnivores in each of the three NPs were not regarded as belonging to separate sub-populations. However, habitat considered suitable for large carnivores in Slovakia is quite fragmented (Salvatori 2003) and is likely to become more so in the future as transport corridors and urban areas expand. In particular, construction of the four-lane west-east highway D1, when completed, threatens to form a major barrier to the movements of large mammals between Tatranský NP and Nízke Tatry NP unless effective mitigation measures are implemented (see Blanco and Cortes 2003, Callaghan *et al*. 2003).

Elevation in the study area varied from 400m a.s.l. to 2,248 m a.s.l. The Liptov basin between the Západné Tatry (Tatranský NP) and Nízke Tatry was relatively flat agricultural land, made up of a mosaic of pastures for cattle and sheep, arable fields and small patches of coniferous forest. Abrupt breaks of

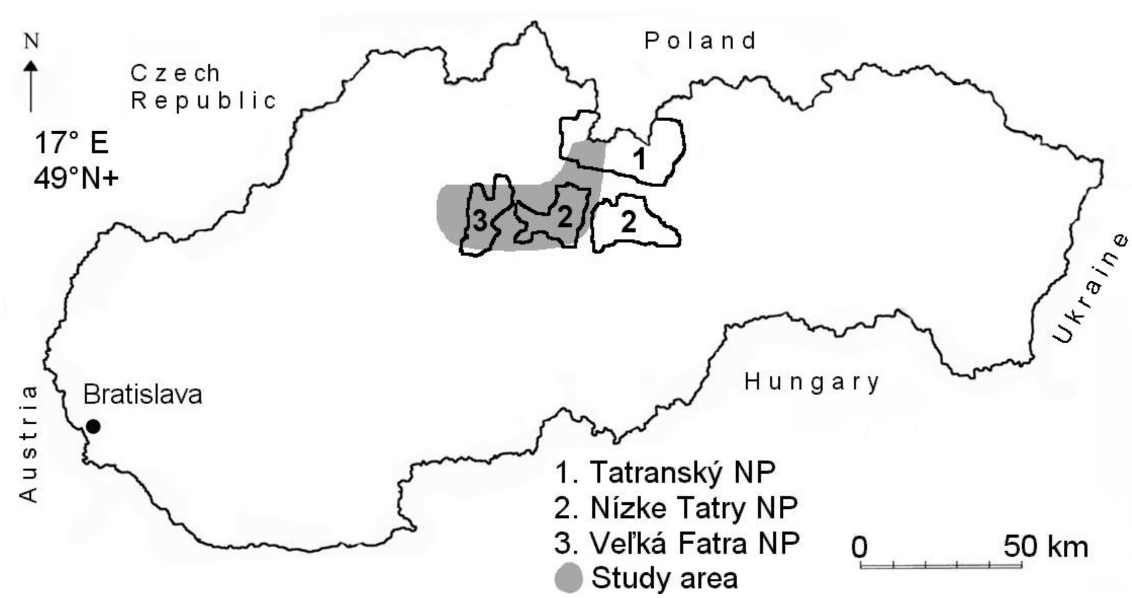

Fig. 1. Location of the study area.

slope, where typically continuous forest cover began, usually marked the boundary of the NPs. Forested slopes in the Západné Tatry and to the north of the main ridge in the Nízke Tatry were dominated by spruce (*Picea abies*), with larch (*Larix decidua*) and rowan (*Sorbus aucuparia*) also common. On the south side of the Nízke Tatry main ridge as well as in Veľká Fatra and Starohorské vrchy, mixed forests predominated. The main tree species there were beech (*Fagus sylvatica*), spruce, fir (*Abies alba*) and maple (*Acer pseudoplanatus*). The height of the upper timberline varied considerably across the study area depending upon slope, aspect, climate, hydrology and soil conditions, and in some areas had been considerably lowered in the past by shepherds and their livestock enlarging alpine meadows. In the sub-alpine zone from c. 1,450-1,550 m up to c.1,800 m a.s.l. were dense stands of dwarf pine (Pinus mugo) interspersed with open meadows. Above c.1,800 m a.s.l. was alpine tundra with some rocky cliffs. Mean annual temperatures ranged from 5.9˚C in the Váh River valley north of the Nízke Tatry up to 0˚C on the main ridge, where annual precipitation reached 1,400-1,500 mm. Snow cover persisted for around 80 days at lower elevations and 180-220 days at higher elevations and in north-facing basins (Vološčuk 1999). The following ungulates were present: red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*) and chamois (native Tatra chamois in the Západné and Nízke Tatry, introduced Alpine chamois *R. r. rupicapra* in Veľká Fatra) as well as domestic cattle (*Bos taurus*) and sheep (*Ovis aries*) grazed on pastures from spring to autumn. Wolves recolonised the study area in the 1970-80s following previous extermination by hunting, trapping and poisoning (Voskár 1976, 1993, Kováč 1984, Mráz 1996, Šimo 1996). During the study, they persisted at relatively low densities of c.1 ind./100 km^2 (Okarma *et al*. 2000, Lehocký 2002).

All the major valleys in the NPs had asphalt roads or gravel tracks, most of them with marked tourist routes that could be quite busy during daylight hours in summer; some were used for cross-country skiing in winter. Main ridges and some lateral ridges also had hiking trails, although in Tatranský NP these were typically closed from 1st November to 15th June. Permanent human settlement tended to be outside the core areas of the NPs, in discrete villages and towns below 800 m a.s.l., surrounded by agricultural or forest land. There was a large ski centre with several hotels in Demänovská dolina, one of the busiest areas for tourism in Nízke Tatry NP both in winter and summer. At the edges of the NPs were several other conglomerations of recreational cottages and holiday homes, mountain hotels and small ski slopes. Ridges without marked paths as well as forested valley slopes received very few visitors. Hunting and game management, including supplementary feeding, were common throughout the area. Forested areas typically had extensive networks of logging roads and hunting paths. Some forests were commercially managed for timber extraction. Grazing above the timberline was gradually excluded from the Západné and Nízke Tatry following the establishment of NPs (Tatranský NP in 1948-49, Nízke Tatry NP in 1978), but was still permitted in Veľká Fatra NP (declared in 2002). Cattle and sheep were also grazed in flood plains, foothills, valleys and on pastures cleared within forests across much of the study area.

Collection and storage of scats

Beginning in March 2001 the study area was investigated for signs of wolf activity. Initial trial surveys were made in localities that, based on topography and vegetation, seemed likely to support large carnivores. Areas where faeces, tracks or other indications of wolf presence were found were re-visited regularly until November 2004. Systematic surveying, for scats and signs, at fixed intervals was not possible due to unequal funding levels and study emphasis during the course of the project. Mountainous terrain and uneven accessibility made a random sampling design unfeasible (Mace and Jonkel 1986) and in any case scats were rarely found away from paths unless carnivore signs could be followed. Therefore scats were usually collected individually as encountered whilst walking along roads, tracks, paths and ridges.

An attempt was made to collect a substantial number of scats from a variety of habitats across a wide geographic area in spring, summer and autumn of four different years (Table 1). Collection was greatly facilitated by the opportunity to work off marked tourist routes in the National Parks, permission for which was obtained from September 2001 until May 2003. Most effort in searching for scats was concentrated in months when livestock were grazed on pastures and were therefore most vulnerable to predation (April-November), although the few scats found in March 2002 and 2003 were included. Home ranges of c.100-300 km^2 (up to 500-

	2001 n = 11			**2002** n = 27			**2003** n = 32			**2004** n = 8			
Season	**ZT**	**NT**	**VF-SV**	**ZT**	**NT**	**VF-SV**	**ZT**	**NT**	**VF-SV**	**ZT**	**NT**	**VF-SV**	**Combined**
Spring	2	1	-	6	5	3	4	2	-	-	-		23
Summer	-	-	1[a]	-	11	-	13	2	-	1	3		31
Autumn	1	6	-	2	-	-	3	5	3	1	3		24
Total	3	7	1	8	16	3	20	9	3	2	6		78

Table 1. Samples of scats included in the analysis of wolf diet according to year, season and area collected. (ZT = Západné Tatry; NT = Nízke Tatry; VF-SV = Veľká Fatra, Starohorské vrchy). ([a] Collected in nearby Malá Fatra NP).

600 km^2 if occasional extra-territorial excursions are included, W. Śmietana pers. comm.) and mean daily movements of c. 22-28 km have been reported for European wolves (e.g. Bloch 1995, Ciucci *et al*. 1997, Kusak and Huber 2000, Okarma *et al*. 1998, Jedrzejewski *et al*. 2001, Promberger *et al*. in lit., Find'o and Chovancová 2004; see review in Mech and Boitani 2003). All scats were collected < 15km and most of them < 8km from livestock, which was therefore considered to have been potentially available to all individuals that contributed scats to the sample.

Scats were identified to species on the basis of their size, shape, content and odour (Litvaitis *et al*. 1996) using personal observations and field guides (Kaczensky *et al*. 1999, Bang and Dahlström 2001); any of uncertain origin were excluded from the analysis. When a wolf scat was identified, all that could be easily picked off the substrate was placed in a plastic bag and labelled with the location and date of collection. Location and elevation were determined by reference to topographic maps (1:50,000 or 1:25,000) and a handheld Global Positioning System (Garmin GPS 12, accuracy ±5-25 m). Scats that were clearly breaking up due to weathering or insect attack were not collected (Reynolds and Aebischer 1991), nor were those for which the month of defecation could not be judged with confidence. Scats were stored by freezing at between -15 and -20˚C as soon as possible after collection, which was usually on the same day but for a small number of scats found during fieldwork in remoter locations this was not possible until up to four days after collection.

Analysis of scats

Scats were removed from the freezer 12-48 hours prior to analysis and, once thawed, were investigated for dietary content following standard techniques (reviewed in Korschgen 1969, 1980, Litvaitis *et al*. 1996, Litvaitis 2000). Each scat was broken open manually in a bucket of water with detergent added (Śmietana and Klimek 1993). It was then washed with tap water for several minutes through a sieve with 1.0 mm mesh. The material remaining on the sieve was spread out in a light-coloured plastic tray and dispersed with forceps to ensure that the whole scat was examined (Spaulding *et al*. 2000). Mammalian hair was identified by examination of the medulla and cuticular surface structure under a 10 x 20 power stereoscopic microscope (Olympus BX 40) enhanced using MicroImage software version 4.0 in comparison with a reference collection and the keys and atlases of Dziurdzik (1973) and Teerink (1991). The presence of bones and hooves/claws in many scats aided identification by comparison to reference material. The percentage volume of each item in a scat was estimated by eye to ±10%.

Analysis of diet

Only scats examined in the laboratory were included in quantitative analyses of diet. They were categorised by month of defecation, aided by field observations of the appearance of scats of known ages (e.g. those found within various periods of time after particular locations had been cleared of scats) and their rates of decomposition, taking recent weather into account. Scats were then divided into three seasons based on typical plant phenology across the study area, although there was considerable variation among localities due to altitude, aspect and landscape features: spring (March-May), summer (June-August) and autumn (September-November).

Several different sets of calculations were made to refine the analysis and, due to the lack of a standardised methodology for analysing diet based on the contents of scats (Sato *et al*. 2000), to allow comparison with various other studies. Firstly, the frequency of occurrence (% F) was calculated by dividing the number of scats in which a particular item occurred (Murie 1944, 1985) by the total number of scats in the sample and multiplying by 100, giving a simple measure of presence/absence.

$$\%F = \frac{\text{No. of scats in which item occurs}}{\text{No. of scats in the sample}} \times 100$$

The relative frequency of occurrence (rel.% F) was calculated by dividing the number of scats in which an item occurred by the number of occurrences of all items in all scats in the sample and multiplying by 100 (Murie 1944). This method is a crude estimate of the relative frequency with which different items are consumed. It does not make allowance for variability in the size of food items, their digestibility or quantities consumed and therefore tends to over-estimate the significance of uncommon food items (Weaver and Hoffman 1979, Śmietana and Klimek 1993).

$$\text{rel.}\%F = \frac{\text{No. of scats in which the item occurs}}{\text{No. of item occurrences in all scats}} \times 100$$

The mean percentage volume (m%V) was calculated by first visually estimating the relative volumes of food items in scats containing >1 item excluding grass/sedge (6.4% of scats) expressed as fractions to ±0.1, the sum of which was always 1.0 for each scat. The numbers of whole scats and fractions of scats in which an item occurred were then summed, the total divided by the number of scats in the sample and multiplied by 100 (Murie 1944, 1985, Weaver and Hoffman 1979, Śmietana and Klimek 1993). This "aggregate percentage" (Litvaitis *et al*. 1996) gives equal importance to each scat regardless of its size.

$$m\%V = \frac{\sum(\text{visually estimated fraction of scat})}{\text{No. of scats in the sample}} \times 100$$

As the relative proportions of items in scats often do not reflect those of the items consumed (Lockie 1959, Floyd *et al*. 1978, Putman 1984, Litvaitis *et al*. 1996, Litvaitis 2000, Peterson and Ciucci 2003), m%V was converted into an estimate of biomass consumed (% B) using the experimentally derived regression equations of Floyd *et al*. (1978) and procedures described by Śmietana and Klimek (1993). Macroscopic examination of bone and hoof material in wolf scats was used to classify cervid remains as either adult (> 1 year old) or juvenile (< 1 year old). It was assumed that the ratio of juveniles to adults was the same for remains that could not be classified (59.3 % of scats with cervids) as for those that could. Mean body masses of food items were taken from Śmietana and Klimek (1993), except for wild boar, cattle and carnivores. Strnádová (2000) reported that wild boar preyed on by wolves in eastern Slovakia in the 1990s were typically 30-50 kg; 40 kg was therefore used as a mean body mass. The respective figure for the fox (*Vulpes vulpes*; 6 kg) was taken from the lower end of the range for adults given by Hell and Garaj (2002). The mean body mass used for the badger (*Meles meles*; 12 kg) was that given by MacDonald and Barrett (1993) for autumn. An arbitrary mean body mass of 6kg was used for other Carnivora not identified to species. Cattle reported killed by wolves in Slovakia during the study were usually yearling heifers or calves (Rigg 2004); 250 kg was therefore used for mean body mass. As hairs of red deer and roe deer could not be differentiated in most cases (Dziurdzik 1973), the remains of these two species were assumed to have been in the ratio of 3.2:1 as found in wolf scats from south-east Poland (Śmietana and Klimek 1993). The ratio of male:female red deer (0.7:1.3) was taken from the same source. Previous studies in Slovakia have suggested that red deer is preyed on considerably more frequently than roe deer in the Tatra Mountains (Voskár 1993, Rigg and Fint'o 2000, Strnádová 2000, 2002). Refuse, grass/ sedge and unidentified items were excluded from this calculation.

$$\%B = m\%V(0.02x + 0.38)$$

where x *is the mean body mass of the prey item in kg.*

Both the microscopic fraction of scats and anynon-food components (grass/sedge) were excludedfrom the analysis of biomass ingested whereas non-food items were included in the frequency of occurrence data (see Reynolds and Aebischer 1991).

Limitations of data and assumptions

McLellan and Hovey (1995) described four types of error associated with the quantitative assessment of diet based on scat analysis: 1) scats from the wrong species may be collected; 2) each scat deposited by the target species may not have an equal chance of being collected; 3) the volume of faecal residue produced after consumption of agiven amount of food varies among different food items; and 4) scats vary in size. In relation to consumption of vertebrate material, a major limitation of scat analysis is that it does not distinguish between items obtained by predation and by scavenging. Results describe food use, which does not necessarily imply selection (Litvaitis *et al*. 1996, Litvaitis 2000).

There was only one species of large wild canid in the study area and so identification of scats in the field was relatively simple. However, as reported by Ciucci *et al*. (1996), there may have been some confusion of wolf scats with those of domestic dogs (*Canis lupus familiaris*). Stray and feral dogs were not common in the study area, so this would most likely concern pets, sheepdogs or hunting dogs, that were usually restricted in their movements. Fresh wolf scats had a characteristic odour that aided identification. Scats of uncertain origin were excluded from the analysis. It was assumed on the basis of these observations and precautions that few if any scats from the wrong species were included in the analysis, although some smaller wolf scats resembling those of the fox or lynx may have been excluded. The results may have been influenced by seasonal variation in weather, vegetation growth, leaf litter, degree of insect activity (Reynolds and Aebischer 1991, Giannakos 1997) as well as site of defecation (e.g. width of track or path, type of substrate) making some scats more visible than others. The number of individual carnivores contributing scats to the sample was unknown. Traditions of prey selection have been reported to differ among wolf packs (e.g. Bibikov 1982). The bias in diet analysis so caused would be expected to increase as individual variation increases but decrease as the proportion of the population contributing scats to the sample increases. In this study it was assumed that collecting scats over a wide area in four different years would limit any individual bias by including scats from different individuals and packs.

Potential error due to the discrepancy between proportions of different items in scat content versus food consumed was compensated for using regression equations (Floyd *et al*. 1978). In the present study it was assumed, as is usual in scat analyses, that material washed through a 1.0 mm sieve and discarded, or that was retained on the sieve but was unidentifiable, derived proportionately from all identified items. Reynolds and Aebischer (1991) found that this was not so for foxes. These authors described a number of other methodological problems rarely considered in studies of large carnivore diet. They recommended pilot studies, computer modelling, detailed examination of each scat's microscopic fraction followed by extensive statistical manipulations. Other authors have considered the differences in results too minor to be of serious concern, or else the time necessary for such procedures excessive or unjustifiable given other errors and uncertainties in, for example, the collection of scats (see Litvaitis *et al*. 1996). The point-frame method, originally developed for diet studies of ungulates, has recently been tested for bears (Sato *et al*. 2000) and wolves (Ciucci *et al*. 2004). Variability in scat size was not considered to have been an important source of bias in the present study; the volume of wolf scats analysed (mean = 76.8 ml, st. dev. = 60.8) was less variable than that of bear scats collected from the same area during the same period.

Results

Diet analyses are presented for the whole sample of scats combined (n=78) in Table 2. Cervids were clearly the most important food item, found in 75.6% of all scats with a mean percentage volume of 73.7 % and comprising an estimated 79.3 % of biomass consumed (Fig. 2). Of 24 scats in which the remains of cervids could be distinguished as either adult (>1 year old) or juvenile (<1 year old), 20 contained remains of juveniles and four of adults. The ratio of juvenile:adult cervids identified in wolf scats was higher in summer (10:1) than in spring (4:1) or autumn (6:2). Juveniles were estimated to account for 74.4 % of cervid biomass consumed.

The second most important item was wild boar, found in 20.5 % of all scats with a mean percentage volume of 17.4 %. It comprised an estimated 13.5 % of the total biomass consumed. An almost significant difference was found in the number of occurrences of cervid or wild boar remains among the three seasons considered ($X^2 = 4.697$, d.f. = 2, $P = 0.095$; Table 3) with wild boar being consumed most often in spring, but not between the two years in which most scats were collected (Fisher's Exact Test, $P = 1$). Remains of wild boar were found significantly more often in scats from the Západné Tatry than in those from the Nízke Tatry (Fisher's Exact Test, $P = 0.043$; Table 4).

	n = 78			
Food item	**%F**	**rel.%F**	***m*%V**	**%B**
Ovis aries	1.3	1.0	0.5	0.3
Bos taurus	1.3	1.0	1.3	4.5
Cervidae	75.6	58.4	73.7	79.3
Sus scrofa	20.5	15.8	17.4	13.5
Rupicapra rupicapra	0	0	0	0
Meles meles	1.3	1.0	1.3	0.5
Vulpes vulpes	2.6	2.0	2.6	0.8
Other Carnivora	2.6	2.0	2.6	0.8
Grass/sedge	26.9	20.8	-	-
Refuse	2.6	2.0	0.7	-

Table 2. Frequency of occurrence (%F), percentage of occurrence in total number of food items (rel.%F), mean percentage volume (m%V) and estimated percentage of biomass consumed (%B) of items identified in wolf scats collected from the Western Carpathian Mountains of north central Slovakia, spring-autumn 2001-04.

The median elevation above sea level at which scats were collected differed significantly among months (Kruskal-Wallis test, d.f.= 8, H= 22.00, P= 0.005). There appeared to be a tendency for wolves to make more use of higher localities in June-July (Fig. 3). Wolves were presumably following vertical migrations of ungulates, especially cervids, and searching for neonates. Occasional opportunistic sightings of wolves made during daylight hours were in accordance with this conclusion. In March, two wolves were observed on each of two occasions at 950 m and 1,200 m a.s.l. in the Západné Tatry. By contrast, on three different occasions in June a single wolf was seen between 1,600 m and 1,900 m a.s.l. in Nízke Tatry NP, either crossing or moving along the main ridge. For example, at 08:30 h on 24.6.2002 a wolf was seen apparently tracking a roe deer that had passed 20 minutes earlier.

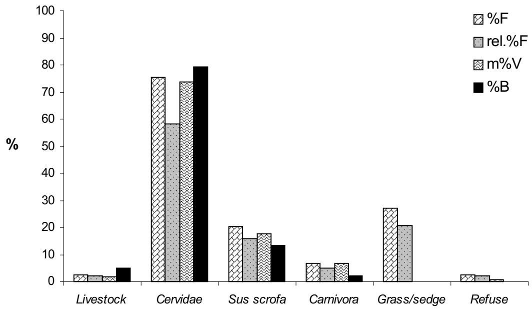

Fig. 2. Comparison of results using four methods to assess wolf diet from scat contents. See Table 2 for abbreviations.

Sightings of wolves in June were all above timberline and within areas used by Tatra chamois, but no evidence of any attempts to catch chamois was recorded and no remains of chamois were found in the faecal material analysed. Scats collected from directly within chamois range in Nízke Tatry NP (n = 9) contained remains of cervids (80 % of all food items) and/or wild boar (20 %). Red deer individuals, females with fawns and mixed or single sex groups, as well as roe deer (individuals and small groups) and groups of wild boar with piglets were seen on many occasions above timberline, within or very near chamois range, from May onwards. Direct observations and snow-tracking indicated that these species tended to over-winter at lower elevations.

Several other items were identified in wolf scats. Badger and fox remains were found in one scat and two scats respectively, all from August-September.

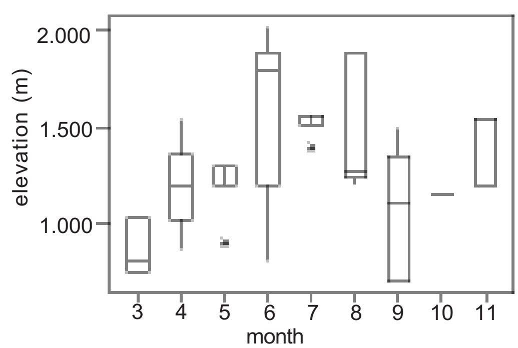

Fig. 3. Box-plot of elevation at which wolf scats (n=55) were found according to month, showing inter-quartile range and outliers.

	actual number of occurrences in scats		
		spring	summer
autumn			
Food item	(n=23)	(n=31)	(n=24)
Cervidae	15	25	19
Sus scrofa	8	3	4

Table 3. Occurrence of main food items in wolf scats according to season.

	actual number of occurrences in scats	
	Nízke Tatry	
Západné Tatry		
Food item	(n=38)	(n=33)
Cervidae	30	22
Sus scrofa	4	11

Table 4. Occurrence of main food items in wolf scats from two mountain ranges.

The two scats containing fox were collected on the same day from the same locality (Poludnica, Nízke Tatry). Refuse (plastic food wrapping) was estimated to comprise 10-30% of the volume of two scats in which it was found (from June and September, both in the Nízke Tatry), whereas the remains of badger and fox comprised 100% of the respective scats in which they occurred. Remains of two other carnivore species were found in one scat each (from July in Západné Tatry and September in Nízke Tatry). Carnivora together comprised an estimated 2.1 % of biomass consumed. Remains of cattle (%B= 4.5 %) and sheep (%B= 0.3 %) were each identified in one summer scat from Západné Tatry and Nízke Tatry respectively. Grass/sedge was found in 26.9 % of scats.

Discussion

Major food items

The findings of the present study indicate that, even in regions with some of the highest levels of reported losses and during the period when flocks are grazed on pastures, livestock is not a major food item for wolves in Slovakia. The results are in accordance with those of other recent work on wolf diet in the Western Carpathians of Slovakia, that cervids are most frequently consumed (Kolenka 1997, Rigg and Finďo 2000, Strnádová 2000, Finďo 2002). The ratio of cervids to wild boar was very similar to that found by Strnádová (2000) in a much larger sample of scats from a wider geographic area. Brtek and Voskár's older study (1985, 1987) placed wild boar ahead of cervids. However, it was conducted during a period when wolves were most numerous in eastern Slovakia and included scats from early spring, autumn and winter so the results probably reflect temporal and/or geographic variations. Okarma (1995) and Strnádová (2000) concluded that wild boar could be locally more important in wolf diet than cervids. In the Carpathians, wild boar are more vulnerable to wolf predation in deep snow (Śmietana and Klimek 1993, Strnádová 2000). Śmietana and Klimek (1993) found no significant differences in the relative proportions of main food items in spring, summer and autumn, but wild boar were consumed more in winter, as Strnádová (2000) also found.

Red deer is the preferred prey of wolves in much of Europe (Cuesta *et al.* 1991, Śmietana and Klimek 1993, Jędrzejewska *et al.* 1994, Jędrzejewski *et al.*2003, Okarma 1995, Okarma *et al.* 1995, Adamic 2000, Rigg and Finďo 2000, Śmietana 2002, Nowak 2003, Mattioli *et al.* 2003, Carrasco 2003, Gazzola 2003). Wolf predation can contribute substantially to total natural mortality of cervids, especially red deer. Predation is usually a less important factor for wild boar, whose body structure, active defence behaviour and large groups maintained year round make them a difficult and dangerous prey that most predators avoid (Jędrzejewski *et al.* 1994, Okarma 1995, Okarma *et al.* 1995). Where they are taken, juveniles are selected (Brtek and Voskár 1985, 1987, Śmietana and Klimek 1993, Voskár 1993, Strnádová 2000). According to Kováč (1996) wolves caused up to 57.3 % of total known red deer mortality in Tatranský NP during the period 1981-94 and 39.3 % of known wild boar mortality in 1984-87. The higher frequency of wild boar in wolf scats from Tatranský NP versus Nízke Tatry NP found in the present study might have been due to a difference in local availability or vulnerability of prey or of hunting traditions among wolf packs.

The finding that a high proportion of ungulates are consumed as juveniles has been reported by previous studies in the Carpathians (Śmietana and Klimek 1993, Voskár 1993, Brtek 1997, Strnádová 2000) and other regions of Europe (see Okarma 1995). Young animals, often fawns, are typically the most prevalent age class killed by wolves in North America and elsewhere (reviewed in Mech 1970, Mech and Peterson 2003). The proportion of cervids consumed as juveniles estimated in the present study was much higher than that found in south-east Poland in summer by Śmietana and Klimek (1993) using a different method to classify cervid remains. The methodology of the present study would overestimate the proportion of cervids consumed as juveniles if juvenile bones and hooves in scats tended to be more recognisable than those of adults. Mech (1970: 176-177) discussed other possible sources of bias in drawing conclusions from the apparent proportion of fawns in scats.

Wolf diet may be more varied during periods without snow cover (e.g. Bibikov 1982, Finďo 2002, Hĺkan *et al.* 2003). Minor food items documented in previous studies in the Slovak and Polish Carpathians have included European hare (*Lepus europus*), mole (*Talpa europea*), rodents, birds, frogs and insects (Śmietana and Klimek 1993, Strnádová 2000, Finďo 2002). Small sample size probably partly explains the apparently narrow diet breadth found in the present study. Wolf scats containing bilberries (*Vaccinium myrtillus*) and beech leaves were seen in summer-autumn of 2003 and 2004 (R. Rigg pers. obs.). The grass/sedge found in many scats might have been consumed to rid the intestine of parasites or the gut of long guard hairs, or as a source of vitamins (Murie 1944, Peterson and Ciucci 2003). Although they usually rely on large ungulates for food, wolves have been described as flexible and opportunistic predators and scavengers (see reviews in Mech 1970, Okarma 1995, Peterson and Ciucci 2003). By exploiting alternative food sources including livestock, carrion, fruit and refuse they have persisted, sometimes at high densities, in parts of Europe and Asia where humans have fragmented, altered or destroyed habitat and reduced or extirpated native prey species (Bibikov 1982, Boitani 1982, Cuesta *et al.* 1991, Papageorgiou *et al.* 1994, Meriggi and Lovari 1996, Álvares and Petrucci-Fonseca 2000, Blanco and Cortés 2000, Jhala 2000, Vos 2000, Barja and Bárcena 2003, Soria *et al.* 2003). The present study confirms that in the Western Carpathian Mountains of Slovakia wolves remain almost entirely independent of anthropogenic food sources.

Prey selection: wild versus domestic ungulates

The overall relative dietary importance to wolves of wild versus domestic prey appears to depend upon the abundance/vulnerability of wild prey and the availability/accessibility of livestock (Blanco *et al.*

1992, Meriggi and Lovari 1996). Where wild ungulates are scarce, wolves prey mostly on domesticated animals (e.g. Papageorgiou *et al.* 1994, F. Álvares pers. comm.). Rapid reduction of wild ungulate populations by human hunters can apparently result in increased predation by wolves on domesticated animals (Śmietana 2002, Tsingarska-Sedefcheva and Dutsov 2003). Conversely, wolves have often been found to prey less on livestock where wild prey populations have remained healthy or have been restored (Fritts *et al.* 2003). However, wolves have a tendency to try to attack any large ungulates they encounter (Mech 1970: 298-299) and so untended, unprotected livestock may still be selected even where wild ungulate densities are high (Blanco *et al.* 1992, Kazcensky 1996, Linnell *et al.* 1996).

Linnell *et al.* (1999) hypothesised that most individuals of large carnivore species will at least occasionally kill accessible livestock whereas Mech (1995 citing Fritts and Mech 1981) stated that most wolves did not. Several recent studies in areas with livestock losses to wolves have reported that, where wild prey was available, only a minority of packs killed livestock (Treves *et al.* 2001, 2003, Jedrzejewski *et al.* 2003, Muhly *et al.* 2003). There is evidence of traditions among wolf packs and lineages (Haber 2003), including of prey preference (Bibikov 1982). It has often been assumed that intense persecution disrupts wolf population demographic structure, particularly by the removal of socially dominant "alpha" individuals, thereby impairing hunting ability and leading to increased predation on livestock (e.g. Voskár 1976, 1993, Klescht 1983). Results of recent research in North America, however, have called into question this implied reliance of wolves on cooperative hunting (Mech and Peterson 2003, Peterson and Ciucci 2003, MacNulty and Smith 2003 but cf. Haber 2003), the significance to a wolf pack of losing "alpha" animals (Brainerd et al. 2003) and the applicability of the linear dominance hierarchy concept to most wild wolf packs (Mech and Boitani 2003, Packard 2003 but cf. Haber 2003). Early observers (Olson 1938, Murie 1944) recognised that wolf packs are essentially extended family groups.

Seasonal and other factors affect the relative availability and vulnerability of wild versus domestic prey, hence influencing predation rates. In general, losses of livestock in Europe, as elsewhere, increase during the grazing season, especially where livestock is grazed in or near forests or on alpine pastures (Kaczensky 1996, 1999, Weber 2003, Rigg 2004). Predation on livestock has been observed to decrease during wild ungulate calving seasons (Śmietana 2002, Rigg 2004). During winter, livestock closed in barns is far less accessible to wolves whereas winter conditions tend to increase wolf hunting success on wild ungulates (Śmietana and Klimek 1993, reviewed in Okarma 1995, Peterson and Ciucci 2003). Many researchers in Europe have concluded that local conditions, livestock husbandry and guarding techniques affect the degree of depredation (Okarma 1995, Kaczensky 1996, 1999, Rigg 2004). In the present study domestic animals were found to form a small portion of the diet of wolves in livestock grazing areas of Slovakia, despite their abundance, presumably due to a combination of medium to high wild ungulate densities (Slovak Wildlife Society unpub. data from pellet counts in 2003) and persistence of traditional husbandry systems in which flocks are attended by shepherds, reducing their availability/accessibility. Low frequency of livestock in wolf diet was reported from all previous quantitative studies in Slovakia (Brtek and Voskár 1985, 1987, Voskár 1993, Kolenka 1997, Rigg and Finďo 2000, Strnádová 2000, Hell *et al.* 2001, Finďo 2002, Janiga and Hrkľová 2002).

Brtek and Voskár (1985, 1987) found remains of dogs and foxes more often than those of sheep in wolf scats. Hell *et al.* (2001) and Finďo (2002) questioned their data, but it may represent local variation. Loss of dogs to wolves has been reported recently by shepherds in eastern Slovakia (Rigg 2004), is common in neighbouring Ukraine (Dyky and Delehan in prep.) and increased in neighbouring southern Poland following reduction of ungulate numbers (W. Śmietana pers. comm.). Predation by wolves on pet, guardian, stray/feral and hunting dogs has also been reported from Romania (H. Schneider pers. comm.), European Russia (Bologov and Miltner 2003, Casulli 2003), Italy (Boitani 1982), Fennoscandinavia (Kojola and Kuittinen 2000 for Finland, Karlsson 2003 for Sweden) and North America (Jurewicz and Thiel 2000, Bangs *et al.* 2002, 2003, Jurewicz 2003, Treves *et al.* 2003). Occasional killing and consumption of foxes (Murie 1944, Mech 1970, Ballard *et al.* 2003) and badgers (Ballard *et al.* 2003, Hĺkan *et al.* 2003) has been documented previously. Small and medium sized mammals including fox, badger, marten (*Martes* spp.) and raccoon dog (*Nyctereutes procyonoides*) constituted c.2-3 % of biomass consumed by wolves in the western part of the Polish Carpathian Mountains (S. Nowak pers. comm.). In Bulgaria, Tsingarska-Sedefcheva and Dutsov (2003) considered a varied diet, including badger and marten, as largely due to reduced availability of wild ungulates.

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