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Original article

Prey and prey-age preference by the Iberian wolf *Canis lupus signatus* in a multiple-prey ecosystem

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In many regions of the Iberian Peninsula, wild ungulates have disappeared and wolves *Canis lupus* often depend on garbage dumps and domestic animals. This paper represents an example of wild ungulate preferences of the Iberian wolf *Canis lupus signatus* in an environment with no human-wildlife conflicts, because wolves rarely predate on livestock. I studied the patterns of prey selection by the Iberian wolf during May 1998-October 2002 in north-western Spain, in an area which supports a diverse community of wild ungulates and in which also domestic ungulates are present. My analysis of 593 wolf scats showed that wild ungulates were consumed preferentially over other prey (i.e. domestic ungulates, carnivores and lagomorphs). Roe deer *Capreolus capreolus* was the most important prey species followed by red deer *Cervus elaphus* and wild boar *Sus scrofa*. Domestic ungulates were poorly represented in the wolf diet. Predation frequencies of domestic and wild ungulates varied seasonally and between years. The consumption of roe deer and wild boar increased during the birthing season, probably because of the higher vulnerability of newly born animals; wolves predate mainly on juvenile roe deer and wild boar.

Key words: Canis lupus signatus, domestic ungulates, faeces, feeding habits, Spain, wild ungulates, wolves

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Most studies on the feeding ecology of the wolf *Canis lupus* have been conducted in North America (Mech 1970, Hoskinson & Mech 1976, Fuller & Keith 1980, Holleman & Stephenson 1981, Ballard et al. 1987, Dale et al. 1994, Schmidt & Mech 1997). In Europe, there have been various studies on wolf diet, some of which showed wild ungulates as the wolf's main prey (Jędrzejewski et al. 1992, Smietana & Klimek 1993, Mattioli et al. 1995, Okarma 1995, Meriggi et al. 1996, Andersone-Lilley & Ozolins 2004, Gazzola et al. 2005, Smietana 2005, Nowak et al. 2005, Valdmann et al. 2005). However, the feeding habits of Iberian wolves *Canis lupus signatus* have received little attention (Guitián et al. 1979, Salvador & Abad 1987, Cuesta et al. 1991, Urios 1995) and the studies performed have shown that the species' food habits are highly variable depending on the areas in which the species occurs. In many regions of the Iberian Peninsula, domestic ungulates are of importance, whereas in other areas, the most relevant prey is wild ungulates (Salvador & Abad 1987, Vilà et al. 1990, Cuesta et al. 1991, Llaneza et al. 1996). However, the former studies were fundamentally descriptive, and usually only included data corresponding to one year. It is not known, therefore, whether and how wolf feeding habits change over time. Furthermore, the information contained data, which did not study the age of the selected prey. The trophic ecology of the Iberian wolf, therefore, remains largely unknown.

The aim of my study was to test the hypothesis that the Iberian wolf is an opportunist species (Carbyn 1988, Salvador & Abad 1987). To test this hypothesis, I predicted that: 1) the wolf consumes the most abundant prey species and also food which is easier to acquire (i.e. domestic ungulates, carrion and garbage), 2) the consumption of prey species varies throughout the year according to prey vul-

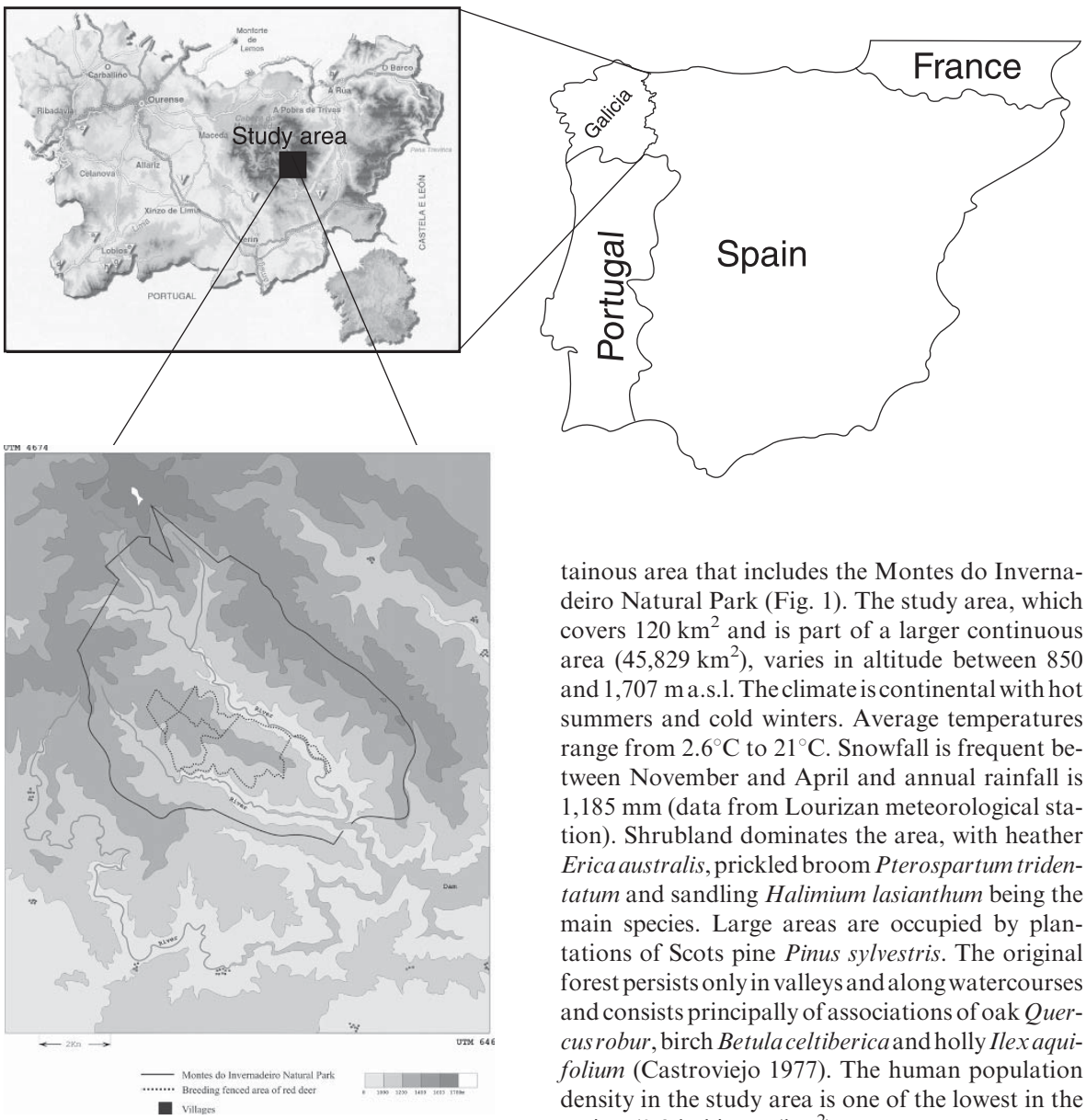

Figure 1. Location of the study area in the Iberian Peninsula.

nerability, so wolves will prey on the individuals and species easier to capture, and 3) for an opportunist species, in a multiple-prey ecosystem and with high food availability, trophic specialisation should not be observed over time.

Material and methods

My study was conducted in the Macizo Central Ourensano in Galicia (northwestern Spain), a mountainous area that includes the Montes do Invernadeiro Natural Park (Fig. 1). The study area, which covers 120 km^2 and is part of a larger continuous area (45,829 km^2), varies in altitude between 850 and 1,707 m a.s.l. The climate is continental with hot summers and cold winters. Average temperatures range from 2.6°C to 21°C. Snowfall is frequent between November and April and annual rainfall is 1,185 mm (data from Lourizan meteorological station). Shrubland dominates the area, with heather *Erica australis*, prickled broom *Pterospartum tridentatum* and sandling *Halimium lasianthum* being the main species. Large areas are occupied by plantations of Scots pine *Pinus sylvestris*. The original forest persists only in valleys and along watercourses and consists principally of associations of oak *Quercus robur*, birch *Betula celtiberica* and holly *Ilex aquifolium* (Castroviejo 1977). The human population density in the study area is one of the lowest in the region (0.8 habitants/km^2).

Scat analysis and collection

Both prey and prey-age preferences of the Iberian wolf were assessed from scats collected systematically every 45 days during May 1998-October 2002. Scats were collected by surveying roads and firebreaks in the study area. Faecal marking sites (mainly crossroads) were also included in the search, because the probability of defecation in these places is greater (Barja et al. 2004, 2005). Hair samples and bone remains collected in each scat were placed individually in bags. Misidentification of wolf scats was minimised because no feral dogs occurred in

the study area, and scats with a diameter of <2.5 cm were excluded from the sample.

The date of collection and age of all scats were registered. Maps with a grid of 1 km^2 cells (Universal Transverse Mercator, UTM) were used to record the scat position. Scat age (fresh (deposition-4 days old), medium (5 days-1 month old) and old (>1 month old); I. Barja, unpubl. data) provided an estimate of the defecation date and allowed analyse of the seasonal variation in the diet. Fresh faeces were characterised by a strong smell, a layer of mucus, and no signs of drying out. Medium-aged faeces had lost their scent and the layer of mucus, but maintained their characteristic shape. Old-aged faeces did not smell and did not preserve their characteristic shape.

Analysis of scats followed standard procedures (Lockie 1959). Guard hairs as well as bone and hoof remains found in the scats were used to identify the wolves' mammalian prey. The cuticle patterns of the hairs were compared with those in reference manuals (Faliu et al. 1980, Teerink 1991) and with reference hairs collected in the study area. Their macroscopic characteristics were also compared with the collection material, the origins of which are well-known. Bone and hoof remains were also analysed to identify the prey species, but mainly to assess their age: juveniles (<1 year of age) or adults (>1 year). The criteria used to assess ungulate age classes were the ossification of sutures, the porosity of joint bones, and the presence of deciduous teeth (Tomé & Vigne 2003). For wild boar *Sus scrofa* remains, I also used the hair colour to differentiate between adults and juveniles, because piglet hairs have stripes until they moult for the first time at four months of age (Blanco 1998). Reference bones collected from prey species in the study area were also used in identification. The same person conducted all species identifications and the age class assessments in order to reduce observer bias.

Prey and biomass estimation

The linear regression model used for ingested prey was $y = 0.0731 + 0.00406x$ ($R^2 = 0.84$, $F = 42.4$, $df = 1,8$, $P = 0.0002$; derived from Table 1 in Ruehe et al. 2003), where y is the biomass ingested (in kg) per collected scat, and x the average consumed mass (in kg) of an individual of each prey type.

To estimate the ingested biomass of domestic and wild ungulates (i.e. roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, wild boar, sheep *Ovis aries* and goat *Capra aegagrus*), the relative proportions of the two age classes (juvenile and adult) were taken into account (Table 1). However, to calculate the ingested biomass of fallow deer *Dama dama* and mouflon *Ovis orientalis*, the average mass for the two age classes was used, because it was impossible to assess the relative age of the consumed individuals. For carnivores and lagomorphs, the ingested biomass was calculated considering only the mass of adults. The mass of adult individuals was estimated by averaging the mean mass of males and females.

Table 1. Composition of Iberian wolf diet during May 1998 - October 2002 based on 508 scats. The ingested biomass ([a] in kg) was calculated using body masses only for adults. The birds ([b]) were not included in the linear regression model, because only mammals were included in the feeding trials. These results were estimated on the basis of the consumed prey mass of an individual prey, which represents x in the biomass equation. The prey mean mass ([c] in kg) was obtained from Urios 1995, Llaneza et al. 1996, Blanco 1998 and Mateos-Quesada 2002.

	Number of scats (N = 508)		Ingested biomass		Prey mean mass[c]		
Type of food	N	%	kg	%	Adult	Juvenile	Mean mass
Wild ungulates							
Roe deer	319	62.8	38.2	42.9	24.5	7	11.5
Red deer	64	12.6	28.1	31.6	90	25	90
Wild boar	51	10.0	10.2	11.5	75	22	31.2
Fallow deer[a]	5	1.0	0.9	1	51.5	5.2	28.4
Mouflon[a]	1	0.2	0.1	0.1	33.8	2.3	18.1
Domestic ungulates							
Sheep	39	7.7	7.4	8.3	28.5	5	28.5
Goat	15	2.9	2.7	3	26.3	5	26.3
Other prey							
Dog[a]	3	0.6	0.4	0.5	15.0	-	-
Badger[a]	3	0.6	0.4	0.5	12.0	-	-
Cat[a]	1	0.2	0.1	0.1	4.3	-	-
Rabbit[a]	6	1.2	0.5	0.5	1.2	-	-
Birds[b]	1	0.2	-	-	-	-	-

To determine the densities of wild ungulates (i.e. roe deer, red deer and wild boar) in the study area, observations of all species were registered along four transects whose total length was 82 km. These paths were inspected on a monthly basis during two days from June 2000 to July 2001 using an off-road vehicle. A total of 1,148 km were surveyed during the study period. The transects chosen for the censuses were overall representative of the whole study area, including the principal habitats. During the wild ungulate censuses, I only counted individuals that were observed within a distance of 100 m in a straight line from the vehicle. For each observation, the following data were registered: date, species, number of observed individuals, presence of young in the group, and the GPS-position of the observed animals. A total of 225 wild ungulates were observed. The method of assessing prey availability assumes that each prey species is equally observable. However, wild boar and other wild ungulates (e.g. roe deer and red deer) are not equally observable. As the wild boar is a species which is very difficult to observe, its availability in the study area is possibly higher than estimated. The community of wild ungulates inhabiting the area had the following structure: roe deer, red deer and wild boar with 59.6, 30.2 and 10.2% of all ungulates, respectively. Goats and sheep are maintained in an intensive system (700 individuals) in the study area, whereas cows *Bos taurus* and horses *Equus caballus* are in an extensive system (86 individuals). All domestic and wild ungulates were potentially available to wolves all year around.

Data analysis

I used a hierarchical log-linear analysis (Backward method) to investigate the effects of season and year simultaneously on the consumption of domestic and wild ungulates.

To analyse the seasonal variation, I pooled the months of the year in the four seasons: spring (April-June), summer (July-September), autumn (October-December) and winter (January-March).

I used the Shannon diversity index (H') to analyse the seasonal and annual diversity of the diet, with roe deer, red deer, wild boar, goats and sheep being the prey species considered, and the dominance index (D) to analyse if some prey species dominated in the seasonal and annual diet. I calculated the Ivlev's electivity index (E; Jacobs 1974) to quantify the wolves' selectiveness towards wild ungulates (roe and red deer, and wild boar) and domestic ungulates (sheep, goats, cows and horses). E varies from 1 (strongest preference) to -1 (strongest negative selection), with 0 indicating a random removal of prey.

Results

General remarks

A total of 593 scats were used for dietary analysis. A fraction (10.9%) of the scats consisted of a combination of soil, plants (e.g. false brome *Brachypodium sylvaticum*) and undetermined matter; 6.2% of the scats contained soil and 9.4% contained *B. sylvaticum*, but none of these items were considered to be food. The majority (98.5%) of the analysed scats contained remains of just one prey species, and only 1.5% contained remains of two prey species. Prey species were identified in 87.3% of the scats collected.

In terms of biomass, the types of food identified in the analysed scats were wild ungulates (87.1% including roe deer, wild boar, red deer, fallow deer and mouflon), domestic ungulates (11.3% including goat and sheep), carnivores (1.1% including dog *Canis familiaris*, cat *Felis catus* and badger *Meles meles*) and lagomorphs (0.5% rabbit *Oryctolagus cuniculus*).

If only the scats in which the prey species could be identified were taken into account (N = 508), the results showed that wild ungulates were more often consumed than other prey (87.1% biomass of all prey consumed). Roe deer was the most important prey in this respect, accounting for 38.2% of the ingested biomass, followed by red deer (28.1%) and wild boar (10.2%; see Table 1). Other wild ungulates (i.e. fallow deer and mouflon) represented only 1.1% of the ingested biomass. Domestic ungulates represented 10.1% in terms of the ingested biomass (sheep 7.4% and goats 2.7%; see Table 1). Occasionally, wolves consumed other prey such as carnivores and lagomorphs, but they represented only 1.6% of the biomass ingested (see Table 1). The differences in the consumption of the different prey species were significant ($\chi^2 = 2{,}313.6$, df = 12, 508, $P < 0.001$).

Ivlev's electivity index (E) showed that the roe deer (E = 0.4) and wild boar (E = 0.3) were positively selected by wolves. Goat/sheep (E = -0.8) and cow/horse (E = -1.0) were negatively selected, being consumed less often than it might be expected from their estimated availability in the study area. Ivlev's electivity index for red deer (E = -0.02) showed values

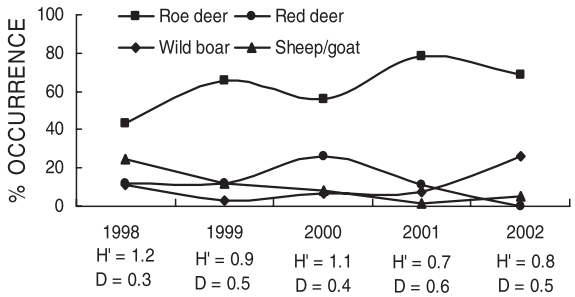

Figure 2. Percentage (frequency of occurrence) of two domestic and three wild ungulate species in the Iberian wolf diet per year. The Shannon diversity index (H') and dominance index (D) are calculated per year. In 1998: N = 74, in 1999: N = 146, in 2000: N = 96, 2001: N = 78 and in 2002: N = 94.

around zero, indicating that there is no selection. The differences in the assessed abundances of the wild ungulates roe deer (59.6%), red deer (30.2%) and wild boar (10.2%) were statistically significant ($\chi^2 = 83{,}1$, df = 2, 225, $P < 0.001$).

Annual and seasonal patterns

Roe deer was the main prey taken in all years (Fig. 2). In 2001, the lowest dietary diversity and the highest dominance were found, taking into account the following prey species: roe deer, red deer, wild boar, goat and sheep. The highest diversity and the lowest dominance values corresponded to 1998 (see Fig. 2).

Roe deer was the prey species that was consumed most often in all seasons (Fig. 3), but especially during summer (52.0%; frequency of occurrence) and spring (26.2%). The consumption of wild boar was greater in spring (37.1%) and autumn (31.0%) than in summer (19.8%) and winter (12.1%). The highest consumption of red deer occurred in spring (37.4%), followed by autumn (28.1%), winter (26.9%) and summer (7.6%). The consumption of domestic ungulates (sheep and goats) also showed seasonal variation, with consumption significantly higher in spring (50.0%) and summer (23.8%) than during autumn and winter. Taking into account both domestic and wild ungulates, the lowest dietary diversity and the highest dominance values were obtained in summer (H' = 0.56, D = 0.74). The highest dietary diversity and lowest dominance values corresponded to autumn (H' = 1.24, D = 0.33), and were followed by spring (H' = 1.18, D = 0.37) and winter (H' = 1.15, D = 0.37).

The hierarchical log-linear analysis showed that there was an interaction between seasons and years in the consumption of domestic and wild ungulates (including the prey species roe deer, red deer, wild boar and sheep/goats; hierarchical log-lineal: $\chi^2 = 104.5$, df = 36, $P < 0.001$).

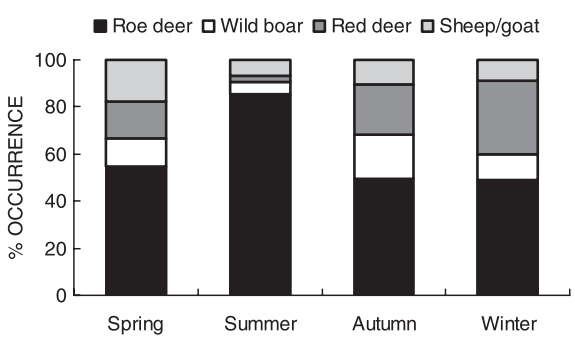

Figure 3. Percentage (frequency of occurrence) of two domestic and three wild ungulate species consumed per season. The percentage of occurrence for each prey species is based on the total number of scats found per season.

Prey-age preferences

Analysis of bone remains allowed the identification of prey species in 85 of the 119 scats in which they were found. Of the scats, 69.4% contained bone remains of roe deer, while 27.0% contained wild boar bones, 2.4% goat/sheep bones and 1.2% red deer bones. Wolves selected juveniles from roe deer and wild boar populations: 74.1% of roe deer and 82.6% of wild boar whose age was determined were juveniles (< 1 year old).

Discussion

The wolf is considered an opportunist species (Carbyn 1988, Salvador & Abad 1987). A trophic opportunist consumes the food which occurs most abundantly, changing its diet depending on food availability. When the abundance of one prey type diminishes, opportunist predators begin to prey on a more abundant species (Glasser 1982). Therefore, significant variations in the diet composition among season and years are expected.

The wolves studied fed mainly on wild ungulates, while domestic ungulates and other preys (carnivores, lagomorphs and birds) were taken occasionally. In my study, the consumption rate of wild and domestic ungulates did not depend on their availability. Wolf preferential consumption of wild ungulates has also been reported from other parts of Europe (Jędrzejewski et al. 1992, Smietana & Klimek 1993, Gazzola et al. 2005, Smietana 2005,

Nowak et al. 2005, Valdmann et al. 2005, Ansorge et al. 2006). The presence of livestock remains in wolf scats implies scavenging behaviour, because no attacks on livestock were reported during my study. Furthermore, in a zone of the study area (Montes do Invernadeiro Natural Park), horses and cows were kept in an extensive system, but there was no indication that wolves preyed on them (neither on adults nor on young). Fritts & Mech (1981) noted that several wolf packs, although living in areas close to farms, continued preying on wild ungulates and did not kill domestic ungulates.

The scarce consumption of livestock species in the study area could be correlated with the high abundance, richness and diversity of wild ungulates, as it was indicated by Meriggi et al. (1996) in a study conducted in northern Italy. Some reseachers (Meriggi & Lovari 1996, Urios et al. 2000, Sidorovich et al. 2003) indicated that attacks on livestock are less frequent in areas where there are several wild prey species. However, predation on domestic ungulates may remain high if livestock is locally abundant and the methods of livestock raising are inappropriate, i.e. the livestock is left unguarded in the countryside (Meriggi & Lovari 1996). In some regions of the Iberian Peninsula with high human population densities and scarce wild preys, wolves take livestock, carrion and even garbage (Salvador & Abad 1987, Vilà et al. 1990, Cuesta et al. 1991, Roque et al. 2001).

My study shows that, among wild ungulates, roe deer was positively selected by wolves, being consumed more often than its availability indicated. Red deer was taken in proportion to its availability. However, despite their abundances, the domestic ungulates were rarely eaten, being negatively selected. The preference for roe deer was high in all seasons and years. Also, in other regions of Europe, the preferred prey of the wolf is roe deer (Meriggi & Lovari 1996, Mattioli et al. 2004, Valdmann et al. 2005, Ansorge et al. 2006). The selection of adult roe deer may be due to its greater vulnerability in comparison with other wild ungulates (e.g. adults of red deer and wild boar), which are larger in size. Dale et al. (1995) also found that wolves predated mainly on caribou *Rangifer tarandus*, although moose *Alces alces* were more abundant. The wolves hardly ever killed red deer in the study area, and most of it could have been consumed as carrion. The presence of red deer remains in wolves' scats coincided in time and space with the presence of dead red deer in the reproduction fences which were located in the study area, and the carcasses were left in the field. During my study, I observed that when red deer carcasses were taken outside the fences by men, wolves would frequently attend to feed on them.

Roe deer were the main prey in all the seasons and years, but the consumption of the species increased mainly in summer, coinciding with fawning when juveniles are especially vulnerable. Roe deer fawns are left alone by their mothers for long periods of time, making them even more vulnerable to wolf predation (Jędrzejewski et al. 1992). Wolves also consumed more wild boars during the birthing seasons (i.e. spring and autumn). Wild boars are born mainly in March, but a second birthing period can occur in autumn if the conditions are favourable (Blanco 1998). Other researchers have also found a higher consumption of juvenile individuals due to their vulnerability (Mech 1970, Ballard et al. 1987, Salvador & Abad 1987, Jędrzejewski et al. 1992, Urios 1995, Mattioli et al. 2004). The positive selection of young roe deer and wild boar may be considered opportunist behaviour, because the individuals of this age class are easier to capture than adults due to their inexperience. The wolves consumed more juvenile wild boars than juvenile roe deer during the birthing season. A single wolf or a few wolves are unlikely to be able to handle adult healthy wild boars, and the capture success rate for adult wild boars should be expected to be lower than for adult roe deer. The high availability of juvenile roe deer and wild boars in spring and summer, however, seems to provide wolves with enough food when their energy needs are high (i.e. during the period when they have cubs).

Conclusions

The trophic position of the wolf in the study area is closer to a facultative specialist than to an opportunist species, because a facultative specialist may change from a key food item when other profitable prey is available (Glasser 1982). Furthermore, it is important to emphasise that the predation upon roe deer in the study area could depend on local feeding specialisation of the studied wolves.

The study of wolf populations inhabiting areas which are only a little altered by men, and with a high availability of wild ungulates and low human population densities, provides very valuable information on the wolf diet under conditions of low human interference. Understanding the factors related to wolf prey preferences in areas where different potential

prey species coexist is of great use in reducing the number of attacks on livestock. In areas with low wild ungulate densities, and where wolves therefore prey on domestic ungulates, reinforcement of wild prey numbers, surveillance of livestock and limitation of the access to carrion would force wolves to specialise in the consumption of wild prey and to transmit this behaviour to their offspring. This would help minimise the conflicts between wolves and humans, which without doubt would help to guarantee the long-term conservation of the species.

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