BioOne COMPLETE

Prey and Prey-Age Preference by the Iberian Wolf Canis Lupus Signatus in a Multiple-Prey Ecosystem

Author: Barja, Isabel

Source: Wildlife Biology, 15(2) : 147-154

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/07-096

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Wildl. Biol. 15: 147-154 (2009)
DOI: 10.2981/07-096
© Wildlife Biology, NKV
www.wildlifebiology.com

Original article

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

Isabel Barja

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

Isabel Barja, Unidad de Zoología, Departamento de Biología, Universidad Autónoma de Madrid, E-28049 Madrid, Spain - e-mail: isabel.barja@uam.es

Received 4 December 2007, accepted 3 July 2008

Associate Editor: John W. Laundré

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-

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

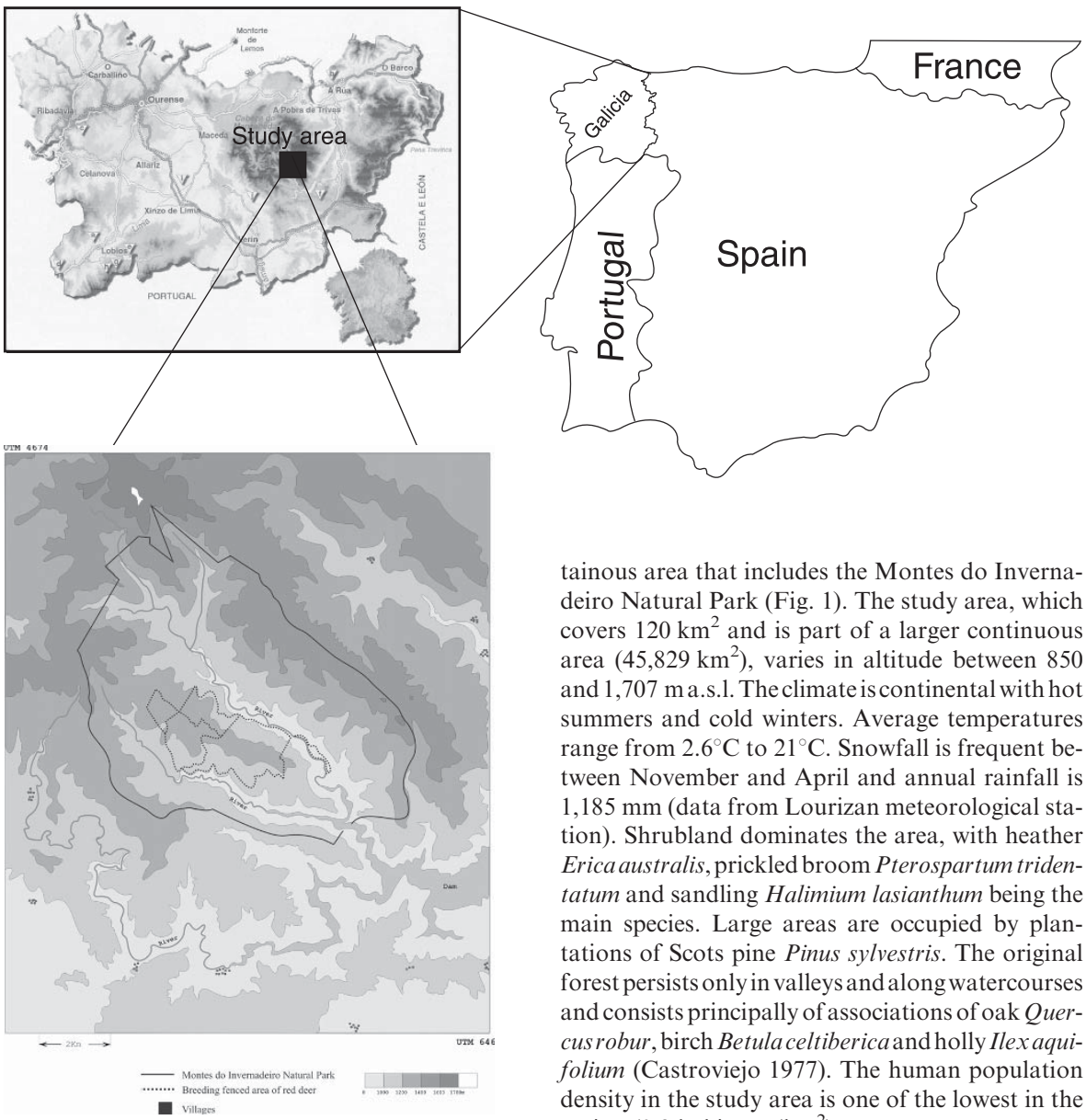


Figure 1. Location of the study area in the Iberian Peninsula.

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

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

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	-	-	-	-	-

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

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

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

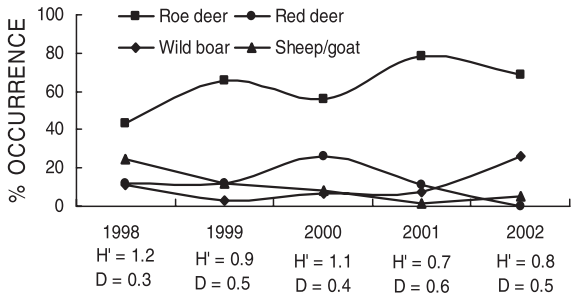


Figure 2. Percentage (frequency of occurrence) of two domestic and three wild ungulate species in the Iberian wolf diet per year. The Shannon diversity index (H') and dominance index (D) are calculated per year. In 1998: N = 74, in 1999: N = 146, in 2000: N = 96, 2001: N = 78 and in 2002: N = 94.

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, $P < 0.001$).

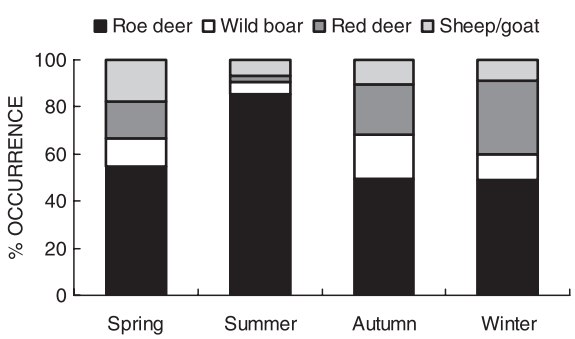


Figure 3. Percentage (frequency of occurrence) of two domestic and three wild ungulate species consumed per season. The percentage of occurrence for each prey species is based on the total number of scats found per season.

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,

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

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

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

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.

Acknowledgements - I would like to thank Xunta de Galicia for the facilities provided during my fieldwork in the Montes do Invernadeiro Natural Park. I am especially grateful to the gamekeepers Basilio Barrio and Tomás Pérez for their collaboration. I would like to thank Antonio Gago for his help with the fieldwork and the paleontologist Eduardo Corona for his help in the analysis of bone remains. The manuscript was improved by helpful comments from Dr. Ferdinand Ruehe, Dr. Marco Apollonio and an anonymous reviewer. Thanks also to A. Burton and N. Selva for revising the English.

References

Andersone-Lilley, Z. & Ozolins, J. 2004: Foods habits of wolves *Canis lupus* in Latvia. - Acta Theriologica 49(3): 357-367.

Ansorge, H., Gesa Kluth, G. & Hahne, S. 2006: Feeding ecology of wolves *Canis lupus* returning to Germany. - Acta Theriologica 51(1): 99-106.

Ballard, W.B., Whitman, J.S. & Gardner, C.L. 1987: Ecology of an exploited wolf population in South-Central Alaska. - Wildlife Monograph 98: 1-54.

Barja, I., Miguel, F.J. & Bárcena, F. 2004: Importance of the crossroads in faecal marking behaviour of the wolves (*Canis lupus*). - Naturwissenschaften 91(10): 489-492.

Barja, I., Miguel, F.J. & Bárcena, F. 2005: Faecal marking behaviour of Iberian wolf in different zones of their territory. - Folia Zoologica 54(1-2): 21-29.

Blanco, J.C. 1998: Mamíferos de España. - Editorial Planeta, Barcelona, 370 pp. (In Spanish).

Carbyn, L.N. 1988: Gray wolf and red wolf. - Journal of Wildlife Management 52: 20-31.

Castroviejo, S. 1977: Estudio sobre la vegetación de la Sierra del Invernadeiro (Orense). - Instituto Nacional para la Conservación de la Naturaleza, Madrid, 97 pp. (In Spanish).

Cuesta, L., Bárcena, F., Palacios, F. & Reig, S. 1991: The trophic ecology of the Iberian Wolf (*Canis lupus signatus* Cabrera, 1907). A new analysis of stomach's data. - Mammalia 55: 239-254.

Dale, B.W., Adams, L.G. & Bowyer, R.T. 1994: Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. - Journal Animal Ecology 63: 644-652.

Dale, B.W., Adams, L.G. & Bowyer, R.T. 1995: Winter wolf predation in a multiple ungulate prey system: Gates of the Arctic National Park, Alaska. - In: Carbyn, L.N., Fritts, S.H. & Seip, D.R. (Eds.); Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Alberta, pp. 223-230.

Faliu, L., Lignereux, Y. & Barrat, J. 1980: Identification des poils de mammifères pyrèneès. (In French with a Spanish summary: Identificación de los pelos de los mamíferos pirenaicos). - Doñana Acta Vertebrata 7: 125-212.

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

Fuller, T.K. & Keith, L.B. 1980: Wolf population dynamics and prey relationships in northeastern Alberta. - Journal of Wildlife Management 44(3): 583-602.

Gazzola, A., Bertelli, I., Avanzinelli, E., Tolosano, A., Bertotto, P. & Apollonio, M. 2005: Predation by wolves (*Canis lupus*) on wild and domestic ungulates of the western Alps, Italy. - Journal of Zoology (London) 266: 205-216.

Glasser, J.W. 1982: A theory of trophic strategies: the evolution of facultative specialists. - Ecology 63: 250-262.

Guitián, J., De Castro, A., Bas, S. & Canals, J.L. 1979: Nota sobre la dieta del lobo en Galicia. - Trabajos Compostelanos de Biología 8: 95-104. (In Spanish).

Holleman, D.F. & Stephenson, R.O. 1981: Prey selection and consumption by Alaskan wolves in winter. - Journal of Wildlife Management 45(3): 620-628.

Hoskinson, R.L. & Mech, L.D. 1976: White-tailed deer migration and its role in wolf predation. - Journal of Wildlife Management 40(3): 429-441.

Jacobs, J. 1974: Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's electivity index. - Oecologia 14: 413-417.

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

Llaneza, L., Fernández, A. & Nores, C. 1996: Dieta del lobo en dos zonas de Asturias (España) que difieren en carga ganadera. (In Spanish with an English summary: The diet of the wolf in two areas from Asturias (Spain) with different livestock occurrence). - Doñana Acta Vertebrata 23(2): 201-214.

Lockie, J.D. 1959: The estimation of the food of the foxes. - Journal of Wildlife Management 23: 224-227.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Mateos-Quesada, P. 2002: Biología y comportamiento del corzo ibérico. - Universidad de Extremadura, Cáceres, 263 pp. (In Spanish).

Mattioli, L., Apollonio, M., Mazzarone, V. & Centofanti, E. 1995: Wolf food habits and wild ungulates availability in the Foreste Casentinesi National Park, Italy. - Acta Theriologica 40: 387-402.

Mattioli, L., Capitani, C., Avanzinelli, E., Bertelli, I., Gazzola, A. & Apollonio, M. 2004: Predation by wolves (*Canis lupus*) on roe deer (*Capreolus capreolus*) in northeastern Apennine, Italy. - Journal of Zoology (London) 264: 249-258.

Mech, L.D. 1970: The wolf. The ecology and behavior of an endangered species. - University of Minnesota Press, Minnesota, 375 pp.

Meriggi, A., Brangi, A., Matteucci, C. & Sacchi, O. 1996: The feeding habits of wolves in relation to large prey availability in northern Italy. - Ecography 19: 287-295.

Meriggi, A. & Lovari, S. 1996: A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? - Journal of Applied Ecology 33: 1561-1571.

Nowak, S., Myslajek, R.W. & Jędrzejewska, B. 2005: Patterns of wolf *Canis lupus* predation on wild and domestic ungulates in the Estern Carpathian Mountains (S Poland). - Acta Theriologica 50(2): 263-276.

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

Roque, S., Alvares, F. & Petrucci-Fonseca, F. 2001: Utilización espacio-temporal y hábitos alimenticios de un grupo reproductor de lobos en el noroeste de Portugal. (In Spanish with an English summary: Spatio-temporal use and food habits of one wolf pack in the Northwest Portugal). - Galemys 13: 179-198.

Ruehe, F., Buschmann, I. & Wameling, A. 2003: Two models for assesing the prey mass of European ungulates from wolf scats. - Acta Theriologica 48(4): 527-537.

Salvador, A. & Abad, P.L. 1987: Food habits of a wolf population (*Canis lupus*) in Leon Province, Spain. - Mammalia 51: 45-52.

Schmidt, P.A. & Mech, L.D. 1997: Wolf pack size and food acquisition. - American Naturalist 150(4): 513-517.

Sidorovich, V.E., Tikhomirova, L.L. & Jędrzejewska, B. 2003: Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990-2000. - Wildlife Biology 9(2): 103-111.

Smietana, W. 2005: Selectivity of wolf predation on the red deer in the Bieszczady Mountains, Poland. - Acta Theriologica 50(2): 277-288.

Smietana, W. & Klimek, A. 1993: Diet of wolves in the Bieszczady Mountains, Poland. - Acta Theriologica 38: 245-251.

Teerink, B.J. 1991: Atlas and identification key hair of West-European mammals. - Cambridge University Press, Cambridge, 223 pp.

Tomé, C. & Vigne, J. 2003: Roe deer (*Capreolus capreolus*) age at death estimates: New methods and modern reference data for tooth eruption and wear, and for epiphyseal fusion. - Achaeofauna 12: 157-173.

Urios, V. 1995: Eto-ecología de la depredación del lobo *Canis lupus signatus* en el NO de la Península Ibérica. - M.Sc. thesis, Universidad de Barcelona, Barcelona, 546 pp. (In Spanish).

Urios, V., Vilà, C. & Castroviejo, J. 2000: Estudio de la incidencia real de la depredación del lobo en la ganadería comparando dos métodos distintos. (In Spanish with an English summary: Real incidence study of wolf depredation on herd comparing two different methods). - Galemys 12: 241-248.

Valdmann, H., Andersone-Lilley, Z., Copa, O., Ozolins, J. & Bagrade, G. 2005: Winter diets of wolf *Canis lupus* and lynx *Lynx lynx* in Estonia and Latvia. - Acta Theriologica 50(4): 521-527.

Vilà, C., Urios, V. & Castroviejo, J. 1990: Ecología del lobo en la Cabrera (León) y la Carballeda (Zamora). - In: Blanco, J.C., Cuesta, L. & Reig, S. (Eds.); El lobo (*Canis lupus*) en España. Situación, problemática y apuntes sobre su ecología. Colección Técnica ICONA, Madrid, pp. 95-106. (In Spanish).

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use