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ORIGINAL PAPER

Spatial variability in wolf diet and prey selection in Galicia (NW Spain)

Laura Lagos[1] · Felipe Bárcena[1]

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Abstract

We studied wolf (*Canis lupus*) diet for three different landscapes in the north-western Iberian Peninsula, differing in land uses and availability of food for wolves. We examined 2740 scats, collected over a period of 4 years, in order to describe wolf diet, its geographic variation, and trophic preferences. The most consumed species were wild pony, roe deer and cattle. We observed differences in wolf diet among the three study sites, related to the availability and accessibility of food resources in each habitat. For the two study sites in northern and central Galicia, wolves showed similar diet, with high occurrence of wild pony (37 vs. 34%) and cattle (20 vs. 23%), but differing in the consumption of wild ungulates (16 vs. 8%) and carrion (7 vs. 14%). Wolf diet in eastern Galicia's mountain ranges was entirely different, due to the higher consumption of wild ungulates (70%). Wolves showed clear prey selection patterns. Between wild ponies and livestock, wolves positively selected ponies. Among wild ungulates, wolves positively selected roe deer. Wild pony and roe deer are key species for wolf feeding in Galicia. In the Galician wild pony range, ponies are the main food for wolves. Given that the availability of wild ponies may contribute to the decrease in wolf predation on cattle, it is essential to develop innovative administrative decisions in such areas to preserve this traditional equid population. In the same way, the population of roe deer should be strengthened in the livestock areas outside the range of wild pony.

Keywords *Canis lupus* · Galician wild ponies · Predation on livestock · Prey selection · Roe deer · Scat analysis

Introduction

In Europe, large carnivores such as wolves (*Canis lupus*) coexist with human populations (Chapron et al. 2014). In this context, wolf damage to livestock, as well as wolf depredations on game species, is a constant source of conflict (Graham et al. 2005; Kaczensky 1999; Sillero-Zubiri and Laurenson 2001). The wolf is present today even in highly humanised landscapes across the continent (Linnell et al. 2001). In such areas, conflicts generated by wolves may intensify when wild prey is scarce, due to an increase in the frequency of attacks on livestock (Meriggi et al. 1996; Sidorovich et al. 2003). Conservation of large carnivores in this scenario is challenging and requires precise knowledge of their ecology. An example of this situation can be found in the region of Galicia, in north-western Spain, where wolves live in human-dominated landscapes (Llaneza et al. 2012) and specially in habitats where livestock is a major economic activity.

The food habits of wolves are variable across the distribution area of the species (Newsome et al. 2016; Peterson and Ciucci 2003). However, wolves consume mostly large and medium-sized ungulates in most of their distribution area (Newsome et al. 2016). Wolf diet consists mainly of wild ungulates in North America (Arjo et al. 2002; Ballard et al. 1987; Mech 1966; Potvin et al. 1988; Scott and Shackleton 1980), in the east and centre of Europe (Ansorge et al. 2006; Jędrzejewski et al. 2000; Nowak et al. 2005; Sidorovich et al. 2003; Śmietana and Klimek 1993), in some areas of Italy (Capitani et al. 2004; Gazzola et al. 2005; Mattioli et al. 1995; Mattioli et al. 2004; Meriggi et al. 1996; Pezzo et al. 2003), in the centre and east of Finland (Gade-Jørgensen and Stagegaard 2000), and in some areas of the Iberian Peninsula (Cuesta et al. 1991; Llaneza et al. 1996). In other areas of Europe, wolves feed mainly on livestock, as in some areas of the Iberian Peninsula (Cuesta et al. 1991; Torres et al. 2015; Vos 2000); in Greece (Migli et al. 2005); in the centre of the Apennines, in the north of Italy (Meriggi et al. 1996); or in the northeast of Belarus, when wild prey become scarce (Sidorovich et al. 2003). Variability in the diet can be

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✉ Laura Lagos
laura@astilleroslagos.com

[1] Nutritional Research and Analysis Institute, University of Santiago de Compostela, c/ Constantino Candeira s/n, 15782 Santiago de Compostela, Spain

explained mainly by the availability and vulnerability of the prey community for each region (Marquard-Petersen 1998). Furthermore, several studies have shown wolf preferences for certain prey among the several available in a region (Ansorge et al. 2006; Barja 2009; Gazzola et al. 2005; Mattioli et al. 2004, 2011).

Wolves in the Iberian Peninsula are distributed throughout habitats with varying availability of food resources (Blanco et al. 1990; Cuesta et al. 1991). In the Cantabrian Mountains, in the east of Galicia, in western León and in Zamora, wolves coexist mostly with wild ungulate populations (Cuesta et al. 1991). In the west of Galicia and northwest of Portugal, wolves coexist with the traditional populations of ponies (Nuñez et al. 2016), called wild ponies (Lagos 2013) or garranos (*Equus ferus atlanticus*) (Bárcena 2012). However, in other regions of Spain, the potential wild prey are scarce and the only food resource available to wolves is livestock (Cuesta et al. 1991). This different availability of food is related to several variables, with anthropogenic land uses playing a relevant role for each area.

Even within the same region, ecological conditions may change across different landscapes, meaning wolves face different threats. The legal status of the wolf in north-western Spain is regulated by Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Fauna and Flora (Habitats Directive). The wolf population north of the river Duero is included in Annex V. As a consequence, the Spanish authorities must ensure that the exploitation and taking in the wild of said population is compatible with maintaining it in a favourable conservation status. Understanding prey community, wolf diet and wolf preferences across different habitats within a single region is of the essence, as this would allow the development of management strategies able to ensure a favourable conservation status for the wolf, an obligation that the Spanish authorities are bound to comply with as per the Habitats Directive (Trouwborst 2014).

In the northwest of the Iberian Peninsula, systematic studies about the diet of wolves with a broad spatial approach have been developed more than 30 years ago (Cuesta et al. 1991). More recent studies have been published with a local scope (Barja 2009; Llaneza et al. 1996; Vos 2000). In this time, habitats have changed (Calvo-Iglesias et al. 2009) and, consequently, wolves have changed their diet (Lagos and Bárcena 2015). An in-depth description of the diet of wolves will reveal their different survival strategies in relation with the available prey. Studies on the diet of carnivores are essential in order to acquire knowledge on the ecological interactions that take place, to determine which human-carnivore conflicts may arise with the local population, or even how the environmental policies adopted can affect the preservation of populations and ecological interrelationships (Lagos and Bárcena 2015). Moreover, this kind of studies contributes to the formulation of effective management strategies (Bagchi and Mishra 2006). For example, information on the diet of carnivores provides knowledge on which types of livestock should be protected in order to prevent conflicts and which wild prey populations should be fostered.

This study aims to describe the diet of wolves in Galicia and to analyse its geographical variations in relation to prey availability in three habitats with differential human uses of land, in order to provide insight on how wolves adapt themselves to the humanised landscapes, and the conflicts arising for each area. Our work covers three zones of Galicia, representing different trophic conditions in terms of food availability for wolves (Fig. 1): (1) abundance of livestock, wild ponies and medium density of wild ungulates; (2) abundance of livestock and wild ponies, low density of wild ungulates; and (3) abundance of wild ungulates, lack of wild ponies and scarcity of livestock. This may help develop a knowledge-based management of the habitat for minimization of human-wolf conflicts and wolf conservation.

Materials and methods

Study area

We studied the diet of wolves in three locations of Galicia, in north-western Spain (Fig. 1). The climate is European Atlantic, with Mediterranean influence in the southeast (Carballeira et al. 1983). Annual rainfall nets 1000–2037 mm and average annual temperature 8.7–14.7 °C, and snowfalls can occur from two to five times in a year in the centre-north or more frequently in the southeast (Meteogalicia 2003-2008).

Habitat characteristics in the study sites are largely marked by the different types of human activity present in the areas, which entail diverse land uses. We have considered the surface of the study area as the aggregation of the 1-km^2 Universal Transverse Mercator (UTM) squares that were surveyed. For land use estimation in each study site (Fig. 2), we selected a square comprising the set of 1-km^2 UTM squares that were surveyed (Fig. 1.). To this end, we used the map of land uses and cover for Galicia 2003 (Instituto de Estudios do Territorio 2003), which included 48 categories of land use. We developed a map featuring six classes of land use: (1) mining, industrial and urbanised areas; (2) crops; (3) grasslands, meadows and forage crops; (4) *Pinus* and *Eucalyptus* stands devoted to forestry production; (5) deciduous woodlands and scrubland; and (6) rivers, reservoirs and lakes.

Our study area consisted of three study sites (Fig. 1): (1) valley of the river Eume, (2) centre of the Dorsal Galega and (3) south of the Macizos Centrales of Ourense. These three sites differ with regard to land use, abundance of livestock and wild ponies and density of wild ungulates.

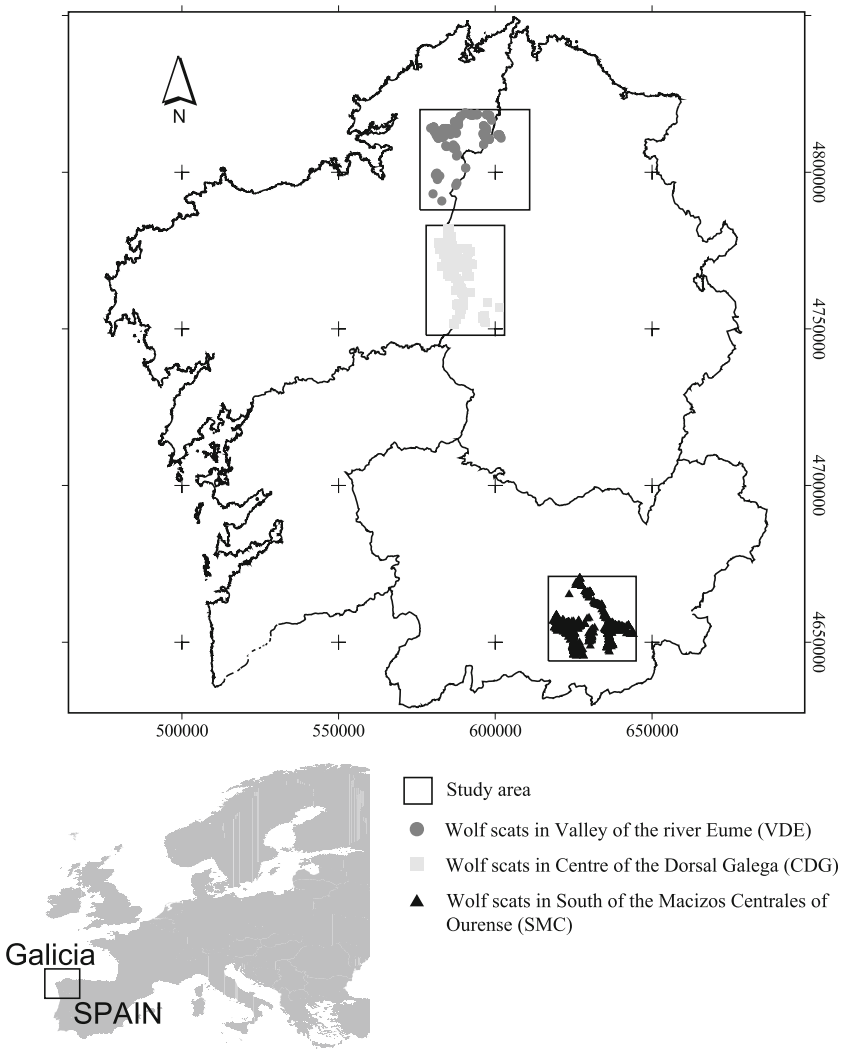

Fig. 1 Location of the three sites that make up the study area in Galicia (northwest Spain): (1) VDE—valley of the river Eume, (2) CDG—centre of the Dorsal Galega, (3) SMC—south of the Macizos Centrales of Ourense; with detail of the position of the wolf scats analysed

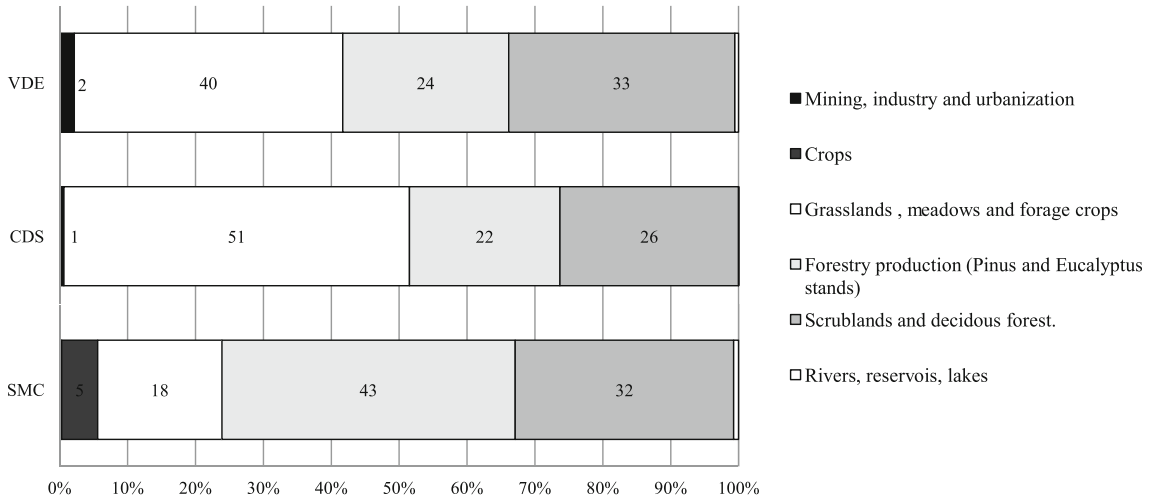

Fig. 2 Land uses and their percentages for the three sites composing the study area. Land uses were obtained from the land uses and cover for Galicia 2003 (Instituto de Estudios do Territorio 2003). We reclassified the 48 categories of land use of this map into 6 classes, useful for the purpose of our study

The valley of the river Eume and the surrounding mountains (VDE) extends for 302 km^2 (UTM 29T 593,500W; 4,840,000N), with altitudes ranging between 200 and 800 m above the sea level (m.a.s.l.). The vegetation in the mountains is composed by heathlands with heather (*Erica* sp. and *Calluna vulgaris*) and gorse (*Ulex minor* and *U. europaeus*), woodlands dominated by oak (*Quercus robur*), forest plantations of pines (*Pinus radiata* and *P. pinaster*) and of eucalyptus (*Eucalyptus globulus* and *E. nitens*) and a mosaic of meadows in the valleys. Human population density is 34.8 inhabitants/km^2 (INE 2004), but most the population is concentrated in the village of As Pontes de García Rodríguez.

The presence of a coal mine, a thermal power plant and several industrial parks means that up to a 2% of the land is dedicated to mining and industrial activity (Fig. 2). This, together with a high percentage of scrubland and deciduous forest (33%) and forestry production areas (24%), indicates a process of abandonment of the traditional lifestyle, based on agrarian and livestock activities, and an opportunity for the establishment of large wild ungulate populations. However, there is still a 40% of land dedicated to grasslands and forage crops, linked to farming activities that remain economically relevant. Roe deer *Capreolus capreolus*, wild boar *Sus scrofa* and red deer *Cervus elaphus* are present in the area. Galician wild ponies are abundant in the mountains. This endemic population of wild ponies, whose vital cycles are adapted to the environment, do not rely on human management and are abundant in the mountains covered by gorse scrub (Bárcena 2012); they are rounded up annually in a traditional way by the villagers, who remove most of the foals, which nowadays are used for meat (Iglesia 1973; Bárcena 2012; Lagos 2013; Nuñez et al. 2016). The livestock present in the area consists mainly of cattle (*Bos taurus*) (Table 1), which remain in the pastures on a permanent basis. Over the period 2003–2006, wolf population oscillated between six wolves in two different packs and seven wolves in one single pack (Lagos 2013).

In the centre of the Dorsal Galega (CDG; 259 km^2; 29T 591,000W; 4,765,500N; 400–900 m.a.s.l.), the vegetation in the mountains consists of scrublands of gorse and heather, pine plantations and pastures. On the gentle slopes and in the valleys, vegetation consists of a mosaic of meadows and crops, alternating with deciduous forests featuring oak and birch (*Betula celtiberica*), and plantations of pine and eucalyptus. The human population (21.3 inhabitants/km^2: INE 2004) lives in small disperse hamlets of only a few houses and is mainly engaged in cattle farming (Table 1). Additionally, 51% of land dedicated to grasslands and forage crops (Fig. 2) indicates the importance of livestock production as the main human activity in the area. Roe deer and wild boar densities are low. Galician wild ponies are present in different densities in the majority of the mountains. Wolf population consisted in two packs, which comprised a minimum of six adult wolves in 2003 and a maximum of 16–17 in 2006 (Lagos 2013).

Table 1 Numbers (*n*) and biomass (*B*), in tons (t), for wild ponies and livestock in the valley of the river Eume (VDE), centre of the Dorsal Galega (CDG) and south of the Macizos Centrales of Ourense (SMC). Wild pony population was estimated through total counts, and numbers for livestock were retrieved from official censuses: number of cows as the average census 2003–2006 (IGE 2003-2006), number of sheep and goat registered in 2006 (Consellería do Medio Rural: F. López, com. pers.), pigs as the average census 2003–2005 (IGE 2003-2005) and poultry (INE 2003)

	VDE		CDG		SMC	
	n	*B* (t)	*n*	*B* (t)	*n*	*B* (t)
Wild ponies	448	134	215	64	0	0
Livestock						
Cattle	28,976	17,386	43,727	26,236	2504	1502
Sheep-goat	7928	357	9761	439	12,328	555
Industrial farms						
Pigs	469	94	11,259	2252	2381	476
Poultry	323	< 1	10,023	20	60,000	120
Rabbit	76	< 1	234	< 1	900	2

In the south of the Macizos Centrales of Ourense (SMC; 247 km^2; 29T 631,000W; 4,657,500N; 400–1400 m.a.s.l.), the landscape is dominated by plantations of pine (*Pinus sylvestris* and *P. pinaster*) and bushlands with *Erica* sp. and *Pterospartium tridentatum*. In the valleys, the landscape consists of crops, mainly of grapes, and riparian forest. Human population density is lower in this area, 17.4 inhabitants/km^2 (INE 2004). Forestry production is the preponderant land use. Pine stands, scrubland and deciduous forest summarise the 75% of the area surface (Fig. 2.). These land uses create a good habitat for the maintenance of large populations of wild ungulates. The higher presence of crops in this area is explained by vineyards. Roe deer and wild boar are widespread, and red deer is present in the north and east. Livestock is scarce and their husbandry makes them scarcely accessible to wolves (Table 1). Wolf population varied between two packs with approximately 14 wolves in 2003 and six packs with around 24 wolves in 2006 (Lagos 2013).

Surveys of wolf scats and prey community

Between 2003 and 2006, we carried out surveys along roads once every 1–2 months to collect wolf scat samples. A total of 251 days and 4394-km-long transects were employed in this task. We drove along forest trails and fire breaks in a four-wheel-drive vehicle at an average speed of 10.34 km/h (933 km in VDE, 1540 km in CDG and 1921 km in SMC). We surveyed on foot 100-m-long transects centred on crossroads, following all the directions of the crossroads, as wolves mark these spots more frequently (Barja et al. 2004; Peters and Mech 1975; Vilà et al. 1994). A total of 710 km were sampled by walking along these 100-m transects, 373 transects in

VDE, 3555 in CDG and 3172 in SMC. Signs of wild ungulate presence (mainly tracks and faeces but also sounds, rooting, wallowing, rubbing and resting sites) were registered along these 100-m transects on the 1-km^2 Universal Transverse Mercator (UTM) grid, and the number of transects walked per grid was used as a measure of the monitoring effort. Observed bands of wild ponies and herds of cattle (extensive free-ranging and extensive in fenced pastures) were also registered during surveys with binoculars (× 42, × 50). For each band of ponies and herd of cattle, we counted the number of individuals and wrote down sex and age composition. Identification of stallions was helpful to identify the different bands of ponies present in the study area. In addition, we developed a specific study about wild pony predation by wolves on three mountainous areas of CDG (Lagos 2013), so the total number of ponies was known there by means of individual identification of every pony, utilising natural markings.

Scat analysis and wolf diet

We found and examined 2740 wolf scats, 293 in VDE, 1063 in CDG and 1384 in SMC. Scats were attributed to wolves based on scat appearance, size, content and presence of other wolf traces in the immediate area (footprints, scratches). In addition, wolf presence was confirmed via direct methods, using camera trapping in those areas where wolf scats had been detected. In a specific project of camera trapping carried out in CDG between 2006 and 2008, we obtained 64 pictures of wolves vs. 1 picture of a domestic dog (*Canis familiaris*) with a survey effort of 204 camera trap nights (Lagos 2013). The carnivores sympatric with wolves, whose faeces could be misidentified as wolf scats in the area, are the dogs and red foxes (*Vulpes vulpes*). We distinguished wolf scats from fox scats using a size criterion, whereas to distinguish wolf scats from dog scats, general differences in appearance, size and content were considered. Dogs encountered in the field were usually small hunting dogs from neighbouring villages; thus, their faeces are small in size. In addition, these scats usually contain traces of dog food. Larger dogs, such as the mastiffs used to protect livestock, whose scats are of similar size to wolf scats, were restricted exclusively to well-known areas of the study sites, and their scats were easily identified as belonging to dogs, since they always include traces of dog food or human food, such as potatoes, etc. For instance, the dog captured by the camera was a mastiff dog from a neighbouring farm. Stray dogs were never encountered, nor trapped on cameras.

We developed a reference collection of hairs of the mammals present in the region. This collection was complemented with the macroscopic description of hairs, including length and thickness measurements, plus microscope pictures of cuticles and medullae for each species.

In the field, we conducted a preliminary visual analysis of the hair present in the scats. Our experience and training in using the reference collection allowed the identification of the species consumed in 1690 scats containing items easily identified by colour patterns and appearance, such as hairs of the pig (*Sus domestica*), wild boar, roe deer (when red deer was not present) and sheep or poultry feathers. Pigs in our study area were predominantly of either the "large-white" breed or the "landrace" breed (Danish) or of a crossbred between the two; therefore, their white or blonde bristles were easily distinguishable from those of the wild boar. It was also possible to identify grapes in the field as the scat content. We collected samples (hair samples and occasionally bone fragments) from 1050 faeces whose content could not be easily identified in the field for further analysis in the laboratory. We did not collect whole faeces due to their important function in territorial marking behaviour for wolves (Peters and Mech 1975, Vilà et al. 1994, Barja et al. 2004, 2005). To prevent analysis of the same scats in consecutive samplings, we marked them with coloured pieces of wire.

Samples were washed and dried in the lab, and the hair of the species consumed was identified. First, identification was conducted through the macroscopic characteristics of the hairs: thickness (measured with a digital calibre with a precision of ± 10 μm), length and colour. These features were compared to the reference collection. The 476 samples that could not be identified through their macroscopic features were prepared and observed through a × 100–600 microscope. Preparations for microscope observations of the cuticle followed the method of Teerink (1991) with modifications; for cuticle slides, we used hair spray without gas as medium, instead of gelatine. For observation of the medulla, we used the procedure of Crocker (1998). The cuticle and medulla characteristics were compared to specific atlas and keys (De Marinis and Asprea 2006; Debrot et al. 1982; Teerink 1991), as well as to microscope pictures of slides of hair from our collection of reference.

Wolf consumption for each species was expressed as its relative frequency of occurrence (F_o), calculated as the number of times an item of a specific prey species was found in the scats, expressed as a percentage of the total amount of prey items. Thus, one scat containing hair of two species counts as two items, and thus, the total number of items was 2929 while the scat samples numbered 2740. We grouped the species consumed in six categories: (1) wild ungulates: roe deer, red deer and wild boar; (2) wild ponies; (3) domestic ungulates: cow, donkey (*Equus asinus*), sheep (*Ovis aries*), goat (*Capra hircus*); (4) carrion: species not accessible as prey, like pig, chicken (*Gallus gallus*), ostrich (*Struthio camelus*) and domestic rabbit (*Oryctolagus cuniculus*), or garbage; (5) other mammals: dog, hare (*Lepus granatensis*), badger (*Meles meles*) or rodents; and (6) fruits. Scats containing items from which the food consumed could not be recognised, such as

soil, grass and undifferentiated material from meat or small pieces of bones, were classified as undetermined. Using a chi-square test (Dytham 2003), we analysed differences in the frequency of occurrence for each group of food in the diet across study sites. A Fisher test generalised for $r \times c$ contingency tables was used when 20% of expected frequencies were ≤ 5 (Pardo and Ruiz 2002). We also compared wolf diet across study sites using the *Morisita-Horn* similarity index ($C_{M\text{-}H}$), as modified by Wolda (Magurran 1988). In addition, we evaluated differences in the diet between areas by a correspondence analysis (Pérez 2004). The correspondence analysis was used as an exploratory of the relationship among the food items and the areas, as well as among all food items present in the diet of wolves. This analysis allows to visually evaluate the feeding strategies of wolves in each area.

Food availability and prey selection

We measured the abundance of wild prey using an index of relative abundance based on signs of animal presence (Gibbs 2000), calculated as the number of signs registered divided by the kilometres of transects surveyed. For this aim, the previously described 100-m-long transects were used. In the case of wild boar, we used only tracks and faeces. Wild pony population was estimated through the counts of different bands observed during successive surveys and from Lagos (2013). Numbers for livestock were retrieved from official censuses (Table 1), although extensive cattle numbers were estimated through total counts of observed herds as well. In order to convert numbers to biomass (B) in tons (t), we considered the average weights of adults, 300 kg for wild ponies, 600 kg for cattle, 45 kg for sheep and goat and 2 kg for poultry. Furthermore, we estimated the density of wild ponies and domestic prey in tons per square kilometre (Table 3).

In order to compare consumption and availability of food for wolves and thus quantify wolf feeding preferences, we calculated Ivlev's selectivity index D as modified by Jacobs (1974):

$$D_i = \frac{r_i - p_i}{r_i + p_i - 2r_i p_i}$$

where r_i is the fraction of the species i of all the prey composing the diet and p_i is the fraction of the same prey in the prey community. Since we used different methods to assess the abundance of wild ungulates vs. wild ponies and domestic prey, we calculated different D indexes. We first assessed wolf preference between roe deer, red deer and wild boar. Secondly, we assessed wolf preference between wild ponies and livestock. For this last analysis, we calculated the index both considering the total census of cattle and just cattle accessible by wolves (extensive cattle observed during surveys).

In addition, we used a rank system based on Johnson (1980) to determine if any prey was disproportionately consumed in comparison to its availability in any study site. If the frequency of occurrence (F_o) of a given species is in the same rank (order) as its abundance (I_a or density) for the three study sites, then consumption agrees with availability.

Results

Wolf diet composition

We identified the food items consumed by wolves in 94.6% of the 2740 scats analysed. The remaining 149 scats contained items that were classified as "indeterminate food" and consisted in digested soft animal tissues, unidentifiable bone fragments or ingested soil. Ninety three percent of the scats contained one single food item, 6.3% contained two items and 0.3% contained three items. We found 16 mammal species, three bird species (poultry, in all cases) and three different types of fruits (Table 2).

Wild ungulates (mean $F_o = 31.57\%$, SE = 19.48, $n = 3$) and wild ponies (mean $F_o = 23.69\%$, SE = 11.68) were the main food occurring in the scats. Domestic ungulates (mean $F_o = 22.89\%$, SE = 8.25) and carrion (mean $F_o = 11.37\%$, SE = 2.16) were the food groups following in frequency of occurrence in scats. Wild ponies and livestock together accounted for 66.66% of mean frequency of occurrence in the diet of the wolves in VDE and CDG (SE = 0.77), while in SMC, 70.28% of the diet consisted in wild ungulates. As for species, wild pony showed the highest occurrence in the scats, representing the main food in VDE and CDG, followed by roe deer (mean $F_o = 22.93\%$, SE = 13.21), which had its maximum prevalence in SMC (Table 2). Cattle were the livestock species most frequently consumed, with a high frequency of occurrence in VDE and CDG (Table 2). Carrion made an important complement of wolf diet in the three study sites, while other mammals showed low frequency of occurrence in the scats (Table 2). Grapes were found in wolf scats in SMC, the only sector with considerable vineyard extension, and accounted for 97% of the fruits consumed.

Geographical differences related to food availability

In the north and centre of Galicia (VDE and CDG), Galician wild ponies accounted for a high frequency of occurrence in scats, with similar consumptions for both areas ($\chi_{cc}^2 = 0.95$, $df = 1$, $p = 0.329$), followed by domestic ungulates, whose frequency of occurrence did not differ between both sites ($\chi_{cc}^2 = 0.24$, $df = 1$, $p = 0.628$) (Table 2). Wild ungulate occurrence was found to be low both in VDE and CDG (Fig. 3, Table 2), but it was significantly higher in VDE ($\chi_{cc}^2 = 14.11$, $df = 1$, $p < 0.001$). Carrion occurrence was significantly higher in

Table 2 Wolf diet composition based on the analysis of 2740 scats for the three sites: VDE (valley of the river Eume), CDG (centre of the Dorsal Galega) and SMC (south of the Macizos Centrales of Ourense). Composition is expressed by the absolute (n) and relative (F_o %) frequency of occurrence of each species. "n" is the number of scats analysed and "N" is the total number of items found ($N = \Sigma n_i$)

Species consumed	VDE $n = 293$		CDG $n = 1063$		SMC $n = 1384$	
	n	F_o (%)	n	F_o (%)	n	F_o (%)
Wild boar *Sus scrofa*	7	2.28	23	2.07	285	18.86
Roe deer *Capreolus capreolus*	41	13.36	71	6.39	741	49.04
Red deer *Cervus elaphus*	1	0.33	–	–	36	2.38
Total wild ungulates	49	15.96	94	8.46	1062	70.28
Pony *Equus ferus*	114	37.13	377	33.93	–	–
Total wild ponies	114	37.13	377	33.93	–	–
Donkey *Equus asinus*	–	–	6	0.54	–	–
Cattle *Bos taurus*	60	19.54	260	23.40	10	0.66
Goat *Capra hircus*	24	7.82	40	3.60	25	1.65
Sheep *Ovis aries*	9	2.93	49	4.41	62	4.10
Total domestic ungulates	93	30.29	355	31.95	97	6.42
Pig *Sus domestica*	9	2.93	145	13.05	67	4.43
Rabit *Oryctolagus cuniculus*	3	0.98	13	1.17	21	1.39
Poultry *Gallus gallus* and others[1]	1	0.33	1	0.09	100	6.62
Garbage/sludge waste	9	2.93	0	0.00	3	0.20
Total carrion	22	7.17	159	14.31	191	12.64
Dog *Canis familiaris*	6	1.95	28	2.52	19	1.26
Badger *Meles meles*	3	0.98	11	0.99	5	0.33
Hare *Lepus granatensis*	0	0.00	13	1.17	7	0.46
Micromammals[2]	3	0.98	4	0.36	5	0.33
Total other mammals	29	9.45	125	11.25	99	6.55
Grapes *Vitis vinifera*	–	–	–	–	61	4.04
Other fruit[3]	0	0.00	1	0.09	1	0.07
Total fruits	0	0.00	1	0.09	62	4.10
Undetermined food	17	5.54	69	6.21	63	4.17
Total items (N)	307	100.00	1111	100.00	1511	100.00

[1] Others include ostrich (*Struthio camelus*) and turkey (*Meleagris gallopavo*)

[2] Micromammals include shrew (*Sorex* sp.,), wood mouse (*Apodemus sylvaticus*), vole (*Microtus* sp.,) and other not identified micromammals

[3] Apple (*Malus domestica*), chestnut (*Castanea sativa*)

CDG in comparison to VDE ($\chi_{cc}^2 = 10.40$, $df = 1$, $p = 0.001$). Wolf diet in SMC was remarkably different in comparison to the other two sites (Table 2, Fig. 3): it showed a higher occurrence of wild ungulates (SMC-VDE $\chi_{cc}^2 = 312.70$, $df = 1$, $p < 0.001$; SMC-CDG $\chi_{cc}^2 = 986.34$, $df = 1$, $p < 0.001$), wild pony was not present, livestock occurrence was scarce (SMC-VDE $\chi_{cc}^2 = 152.850$, df = 1, $P < 0.001$; SMC-CDG $\chi_{cc}^2 = 270.79$, $df = 1$, $p < 0.001$) and the frequency of occurrence of carrion did not differ from its values for CDG and SMC ($\chi_{cc}^2 = 1.29$, $df = 1$, $p = 0.257$), but it was significantly higher than for VDE ($p < 0.05$).

The diet of the wolves in the three areas was differentiated as well in the symmetric plot that represents the major axes of dietary variation identified by correspondence analysis

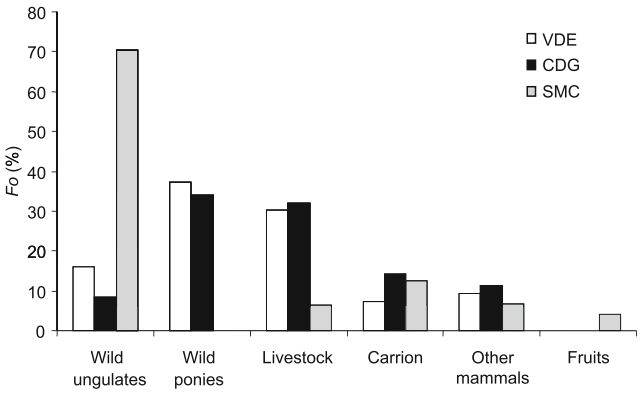

Fig. 3 Frequency of occurrence (%) of the main groups of food in the valley of the river Eume (VDE), centre of the Dorsal Galega (CDG) and south of the Macizos Centrales of Ourense (SMC)

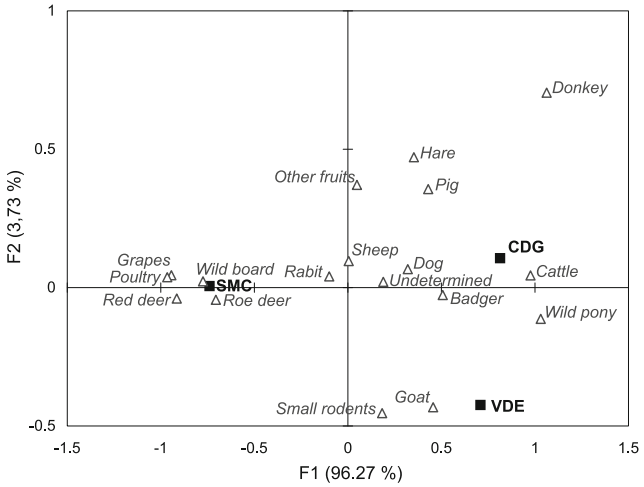

Fig. 4 Symmetric plot. Dimensions 1 and 2 of the correspondence analysis comparing frequency of occurrence of food items by area

(Fig. 4). Consumption of cattle, wild pony and badger by wolves are associated to CDG, consumption of goat and small rodents occurred mainly in VDE and the diet of wolves in SMC is characterised by occurrence of roe deer, wild boar, grapes and poultry.

As for species, roe deer dominated the diet in SMC, accounting for almost 50% of occurrence, while its consumption was significantly lower in the other sites (Table 2; SMC-VDE $\chi_{cc}^2 = 131.11$, $df = 1$, $p < 0.001$; SMC-CDG $\chi_{cc}^2 = 542.77$, $df = 1$, $p < 0.001$). Wild boar frequency of occurrence in the scats in SMC was 8–9 times higher than in VDE and CDG (Table 2; SMC-VDE $\chi_{cc}^2 = 50.28$, $df = 1$, $p < 0.001$; SMC-CDG $\chi_{cc}^2 = 170.755$, $df = 1$, $p < 0.001$). Wild ponies and cattle amounted together to over 50% of diet occurrence in VDE (56.68%) and CDG (57.35%) ($\chi_{cc}^2 = 0.02$, $df = 1$, $p = 0.888$), while these food items did not even reach 1% of occurrence in SMC ($p < 0.001$). The frequency of occurrence of cattle did not differ between VDE and CDG ($\chi_{cc}^2 = 1.83$, $df = 1$; $p = 0.176$; Table 2). Wild pony occurrence in the diet was also similar between VDE and CDG ($\chi_{cc}^2 = 0.95$, $df = 1$; $p = 0.329$; Table 2).

We observed a high Morisita-Horn similarity index for VDE and CDG ($C_{M\text{-}H} = 0.95$), while diet for SMC showed the lowest similarity both when compared to CDG ($C_{M\text{-}H} = 0.19$) and VDE ($C_{M\text{-}H} = 0.31$).

When comparing diet composition to food availability (Table 3), we found that the area ranks of availability and occurrence in the diet coincided for all species, except for sheep and goat in VDE and SMC and except for wild boar between VDE and CDG. Joint availability for sheep and goat was maximum in SMC, but this is the area where these species of livestock were less consumed by wolves. Wild boar was consumed more often in VDE as compared to CDS; however, the abundance index turned out to be higher for this last site. Therefore, the high consumption of wild ponies and cattle in VDE and CDG was consistent with the higher density of said species in these sites, while the higher consumption of roe deer in SMC was also consistent with a higher availability of this species, and the rank for the consumption of pig carrion was in concordance with the pig census for the three study sites.

Selection of prey

The Ivlev selectivity index calculated for wild ponies, cattle and sheep plus goats indicated a strong selection for wild ponies in VDE and CDG, while sheep and goats were also positively selected (Fig. 5a). The same positive trophic selection for wild ponies ($D = 0.87$ in VDE; $D = 0.90$ in CDG) in comparison with cattle ($D = -0.68$ in VDE; $D = -0.42$ in CDG) and sheep+goat ($D = -0.25$ in VDE; $D = -0.62$ in CDG) was observed if we considered only cattle accessible for wolves, i.e. free-ranging cattle and cattle in fenced pastures. In all study sites, roe deer was positively selected by wolves against wild boar (Fig. 5b).

Discussion

Our study shows that wolves in Galicia feed mainly on large and medium-sized ungulates, as in the rest of their distribution range (Mech and Peterson 2003; Newsome et al. 2016). Wild ponies and cattle are the main food in the areas situated in the north and centre, while roe deer and wild boar compose most of the diet in the east. Carrion is also an important food source for wolves, as it was in other areas of the Iberian Peninsula (Cuesta et al. 1991; Reig et al. 1985), Italy (Boitani 1992) or Greece (Migli et al. 2005). However, the effect of the EU regulation regarding the disposal of livestock carcasses, as a consequence of the bovine spongiform encephalopathy (BSE) crisis in Europe, caused a drop in the consumption of carrion by wolves, which was evident in the last years of the period of study (Lagos and Bárcena 2015).

Wolf diet studies have often collected whole scats for analysis. However, we chose to examine scats in the field and only to collect samples of the scats, leaving the rest in their original position. We consider this method to be less invasive, given the role of faeces in scent-marking behaviour, which wolves use for territorial advertisement (Barja et al. 2004; Barja et al. 2005; Peters and Mech 1975; Vilà et al. 1994). The large sample size ($n = 2740$) in our study has allowed for an in-depth description of wolf diet. Even occasional food has been detected, i.e. species occurring with frequencies as low as 0.33%, as in the case of deer in VDE. This large sample has allowed us to understand, for example, that there was a potential conflict in place, owing to wolves feeding on grapes and therefore causing damage to grape farming. The description of wolf diet may be biased depending on where, how and when samples are collected (Steenweg et al. 2015). Concerning

Table 3 Comparison between availability of prey (t/km^2 represents density of biomass calculated from total numbers for wild ponies, livestock and carrion; I_a represents relative abundance index for wild ungulates) and frequency of occurrence (F_o %) for each species present in wolf diet across study sites. Ranks are used to show the comparison: first number indicates the order of the study site concerning availability (density or abundance index), and the second number shows the order concerning frequency of occurrence of the species in the diet. Food items are marked with asterisks if ranks disagree

	VDE			CDG			SMC		
	Density (t/km^2)	F_o (%)	Ranks	Density (t/km^2)	F_o (%)	Ranks	Density (t/km^2)	F_o (%)	Ranks
Wild ponies	0.45	37.13	1–1→	0.25	34.47	2–2→	–	–	–
Livestock									
Cattle	57.57	19.54	2–2→	101.30	23.40	1–1→	6.08	0.66	3–3→
Sheep+goats*	1.18	10.75	3–1→	1.70	8.01	2–2→	2.25	5.76	1–3→
Carrion									
Pig	0.31	2.93	3–3→	8.69	13.05	1–1→	1.93	4.43	2–2→
	I_a	F_o (%)	Ranks	I_a	F_o (%)	Ranks	I_a	F_o (%)	Ranks
Wild ungulates									
Wild boar*	1.04	2.28	3–2→	1.65	2.07	2–3→	5.64	18.86	1–1→
Roe deer	2.23	13.36	2–2→	1.49	6.39	3–3→	5.64	49.04	1–1→

Arrow symbols "→" represent that ranks should be compared between study areas (in horizontal) for each food item

these potential problems associated with estimation of wolf diet through scat collection, our sample design largely prevented bias: we collected scats along roads, survey routes were well distributed across the territory and surveys were evenly balanced throughout the year, over several years. However, scats collected on roads are still bound to be biased in some degree, as they may, for instance, exhibit a greater occurrence of small mammals as compared to scats collected from home sites (Steenweg et al. 2015).

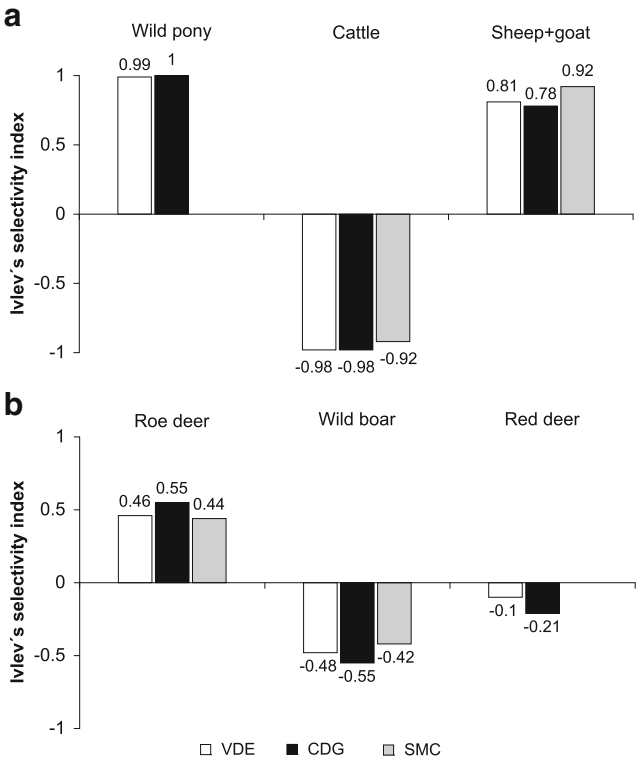

Fig. 5 Ivlev's selectivity index as modified by Jacobs for wild ponies and livestock (**a**) and for the wild ungulate community (**b**) for all three study sites: valley of the river Eume (VDE), centre of the Dorsal Galega (CDG) and south of the Macizos Centrales of Ourense (SMC). *D* value close to 1 implies positive selection and close to − 1 indicates avoidance

Another bias that should be considered is the potential misidentification of predator species by external appearance of scats (Davison et al. 2002, Janečka et al. 2008). In order to correctly assign faeces to the predator under study in the presence of sympatric carnivores, faecal pH, bile acid and even DNA analysis have been used (Litvaitis 2000). All of them are laborious and expensive techniques, so scientists tend to rely on simpler methods. In the case of wolves, a criterion based on size, along with the presence of associated tracks, has been the differentiating characteristic most commonly used for identification (Fritts and Mech 1981, Huggard 1993, Jhala 1993, Gade-Jørgensen and Stagegaard 2000, Arjo et al. 2002, Chavez and Gese 2005). Appearance and composition (Marquard-Petersen 1998), spatial location (Gade-Jørgensen and Stagegaard 2000) or even odour (Vos 2000) are among the other criteria in use. In our work, the scats were identified based on size, appearance and composition, along with the presence of associated tracks. There are only two other carnivores in our study area whose scats could be potentially misclassified as wolf scats: fox and dog. The majority of fox scats are smaller than wolf scats, and domestic dog scats usually have grain appearance, as they include dog food, while stray dogs are not present in the area. Furthermore, our extensive field work in addition to the use of camera trapping has allowed us to confirm the presence of wolves, as well as to

deny the presence of dogs whose scats could be misidentified as wolf scats in the territory.

In order to attribute hair to the correct species, we followed the recommendations of Spaulding et al. (2000), who suggested the appropriate prior training of the observer, the use of a reference collection and the analysis of the whole excrement, in order not to overlook any prey. However, we considered it more appropriate to collect abundant samples of hair instead of removing scats from the field, as explained above.

We have studied wolves inhabiting different habitats in terms of human activities and availability of food both from domestic and wild sources. We observed differences in wolf diet among the three study sites. These divergences seem related to varying availability of food resources in each habitat, since practically for all species, the ranks of frequency of occurrence in the diet agree with the ranks of availability if areas are compared. Both in VDE and CDG, cattle breeding is a relevant activity, entailing 40–51% of land use devoted to pastures and forage crops, whereas scrublands sustaining wild ponies occupy the high lands. In these two areas, wolves mainly feed on wild ponies and cattle, which are the most abundant and accessible prey. However, a strong positive selection of ponies was observed when compared with livestock. Populations of wild ponies are fully accessible to wolves. Accessibility of cattle depends on the husbandry system in practice. The systems that make cattle vulnerable to wolf predation are free-ranging cattle and cattle confined in fenced pastures, since both systems imply the existence of calves in the pastures during the night. The Ivlev index that considered only these vulnerable cattle also showed that wolves feed mainly on wild ponies despite the higher census of accessible cattle in these areas. This fact, together with the observed decrease on wolf damage to cattle in the season when wolves are focused on the consumption of foals (Lagos 2013), means that availability of wild ponies contributes to the decrease of wolves' predation on cattle, which reduces the economic losses of the farmers, since the calves have greater economic value than the foals.

The higher industrialisation of VDE and the higher percentage of scrubland, deciduous forest and forestry production areas indicate both a certain abandonment of the agrarian activities and a proper habitat for the existence of large populations of wild ungulates. In CDG, industrial farms are present and they used to provide a source of carrion for wolves. VDE and CDG differ in the consumption of wild ungulates, which was higher for VDE, and carrion, which was higher in CDG. In VDE, higher densities of wild ungulates, together with less abundant livestock and carrion, explain the higher consumption of wild ungulates. SMC's habitat is markedly different from those of the other two areas. This is a mountainous area, inhabited by a sparse and aged human population, which has for the most part abandoned agricultural and livestock activities. Livestock is scarce there nowadays and it is not accessible to wolves, since it is stabled in closed sheds during the night. Forestry is the main land use (43%), and forestlands together with scrublands and deciduous forests (32%) constitute a suitable habitat for wild ungulates. Thus, wild ungulates are the most consumed food in SMC, since they are present at higher density and the scarce livestock is not accessible to wolves.

Wolf diet variation across areas within the same region has been described before (Capitani et al. 2004; Llaneza et al. 1996; Marquard-Petersen 1998; Mattioli et al. 2004; Meriggi et al. 1996). The abundance of a particular species seems to be the decisive factor for it to become the most frequent prey of the wolf on a certain locality (Marquard-Petersen 1998). Other variables affecting the vulnerability of the prey, as habitat (Mattioli et al. 2004) and anti-predatory strategies of the different species against wolves, or even the size of the pack, the experience of the wolves in the pack and probably cultural factors, may also come into play. For instance, Sand et al. (2006) found that the age of the male wolf leader determined the success of the pack when hunting elk. In the case of livestock, the husbandry system is the main factor affecting prey accessibility or vulnerability (Meriggi and Lovari 1996; Okarma 1995).

In all three study sites, sheep and goats are usually shepherded during the day and stabled in closed sheds during the night. However, in some areas of VDE, from where wolves were absent for some years prior to our study, we observed flocks of sheep and goats grazing unattended that suffered wolf attacks. That might explain the higher consumption of sheep and goat in VDE, where these species census is lower than in the other two areas. Between CDG and SMC, the observed consumption of sheep and goat in SMC, lower than expected according to their abundance in that area, might be related to differences in the disposal system of carcasses (given part of the consumption of these species could be done as carrion), slight differences in the husbandry method or even to the greater availability of wild ungulates in this area. This last explanation could indicate that when wild prey are abundant, wolves mostly feed on them despite the existence of livestock, as it has been observed in other studies (Barja 2009; Capitani et al. 2004; Gazzola et al. 2005; Meriggi et al. 1996; Nowak et al. 2005).

In the eastern mountains of Galicia (SMC), wolf diet consisted of wild ungulates up to 70% and roe deer was the main prey. Roe deer seems to be the main wild prey of wolves in the Iberian Peninsula (Cuesta et al. 1991; Salvador and Abad 1987). Specifically, in the Natural Park of Invernadeiro, close to SMC, a frequency of occurrence of 90% was recorded in the 1970s (Bárcena 1977) and of 62.8% in more recent times (Barja 2009). Additionally, the consumption of roe deer and wild boar has increased all across Galicia over the past 30 years (Lagos and Bárcena 2015, Llaneza and López-Bao 2015). We observed that, among wild ungulates, wolves showed positive selection for roe deer, as in many other areas of Europe (Ansorge et al. 2006; Barja 2009; Capitani et al. 2004; Mattioli et al. 2004). However, wild boar is preferred in part of the Apennine Mountain Range (Capitani et al. 2004; Mattioli

et al. 2004; Meriggi et al. 1996). Other factors may influence predation pattern; snow undoubtedly increases the vulnerability of prey and enables wolves to hunt adults, which would be very difficult to kill in other conditions, for example moose (Mech 1966; Peterson 1977; Post et al. 1999). In the Carpathians, wolf predation on wild boar occurs practically exclusively during winters, at high snow cover period (Śmietana and Klimek 1993).

One of the approaches to wolf-human coexistence in livestock farming areas would be to favour increased densities of wild ungulates. Thus, in theory, wolves would prey on them and attacks on livestock would eventually decrease, as it has been observed in other areas (Sidorovich et al. 2003). The populations of wild ungulates in Galicia have been on the rise in recent years (Lagos and Bárcena 2015). However, wild ungulates generate problems of coexistence with human rural populations as well. They cause damages to crops and forest plantations (Partl et al. 2002; Reimoser and Putman 2011; Schley et al. 2008), as well as traffic accidents (Lagos et al. 2012). Wild ungulate populations in Galicia are subject to a strong level of human pressure through hunting, and in many areas, they cannot attain population densities sufficient for them to acquire the status of predominant prey.

However, a debate about the suitability of restoring wild ungulates to reduce wolf predation on livestock has arisen recently (Newsome et al. 2016). We observed higher consumption of wild ungulates and lower consumption of livestock in the areas of Galicia where wild ungulates are more abundant (SMC, VDE), but in these areas, livestock are likewise less available. Hence, other factors than wild prey densities, including wild pony abundance, and livestock abundance and availability—resulting from the system of husbandry—or even wolf cultural factors may also come into play. It is difficult to assess the relative effect of wild prey abundance and livestock husbandry methods on the level of wolf predation on livestock, but increasing prey numbers alternative to livestock might always be complementary to the implementation of measures to protect livestock from wolf predation.

In the north and centre of Galicia, wild pony is the main food of wolves, while other wild ungulates do not exceed 16% of occurrence in scats. In addition, according to our results, wolves positively selected wild ponies against livestock. This predatory behaviour of wolves had already been observed in the north of Galicia (Bárcena 1976). All other areas in the north of the Iberian Peninsula where wild Atlantic pony (garrano) populations exist, they also represent a substantial part of the diet of the wolf, 67.7% in one locality in the west of Asturias (Llaneza et al. 1996) and 41.3% in Peneda Gerês National Park (Vos 2000). In the rest of Europe, the populations of free-ranging horses do not overlap with the current wolf range. However, wolves in Mongolia prey on domestic horses, which are set to roam freely in certain times of the year (Hovens and Tungalaktuja 2005; Hovens et al. 2000), and on the recently reintroduced population of Przewalski horses *Equus przewaslki* (Bandi et al. 2012). Within wild pony population, wolves focus their predation on foals (Lagos 2013). Foals are one of the largest prey of wolves in Europe (Hermida 2009). This predator-prey system formed by wolves and Galician wild ponies probably has its origin in the Pleistocene (Bárcena 2012; Hermida 2009) and shows interesting strategies of both predator and prey (Bárcena and Lagos, unpublished). It might even explain the larger size of Iberian wolves as compared to what could be expectable as per the latitude of the Iberian Peninsula (Hermida 2009).

In Galicia, the probability of wolf occurrence is related with the density of horses (Llaneza et al. 2012). Equids perform there the ecological role as main wolf prey exerted by roe deer, deer or wild boar in eastern Galicia and in other parts of Europe. The conservation of a large population of wild ponies in the mountainous landscapes of the north and centre of Galicia may act as a way to decrease predation on valuable cattle (Lagos 2013). However, wolf predation on foals can also be the cause of conflict with the locals which traditionally harvest the ponies and take profit from them, although these same locals are usually cattle farmers as well, and they prefer that wolves kill foals rather than calves, which have a considerably higher economic value. It is difficult to design measures to reduce wolf predation on ponies. Nevertheless, certain management decisions, aimed to achieve a medium size of bands and stability of groups, could reduce in some way the impact of wolves on foals (Lagos 2013).

Joint occurrence of domestic ungulates and carrion was over 35% in the north and centre of Galicia. Wolf diet usually includes livestock where wolves and extensive livestock farming coexist, as in the centre of Portugal (Torres et al. 2015), certain areas of the Apennines in Italy (PMV = 19–51%: Meriggi et al. 1996) or in the Italian Alps during the summer, when herds roam freely in the mountains (F_o = 19%, Gazzola et al. 2005). Wolves seldom feed mainly on domestic species, although it is worth highlighting cases of 98% frequency of occurrence for goat in northern Portugal (Vos 2000), 94–96% in central-west Portugal (Torres et al. 2015) and 82% of livestock carrion during winters in Greece (Migli et al. 2005). When wild prey become scarce, predation on livestock increases (Sidorovich et al. 2003). Attacks on livestock farms, especially on beef cattle farms, are common in the study sites of VDE and CDG (Lagos 2013). However, part of the consumption of livestock may be explained by wolves feeding on livestock carrion, despite the decrease in this food resource (Lagos and Bárcena 2015). Cow was the domestic species most frequently consumed, and its occurrence in wolf diet has markedly been on the rise in Galicia over the last decades (Lagos and Bárcena 2015; Llaneza and López-Bao 2015); however, in the 1970s and 1980s, the combined consumption of sheep and goats had higher occurrence (Cuesta et al. 1991). Changes in the cattle farming management, as the appearance of the semi-extensive cattle confined in fenced pastures,

together with the decline of sheep and goat livestock census likely explain that cattle has become the livestock species more consumed (Lagos and Bárcena 2015). Cattle has been managed as free-roaming in some areas, and from the 1980s, a new management system for beef cattle aroused in the centre of Galicia: herds of sucker cows with calves living permanently in fenced pastures, meaning that calves are accessible to wolves during the night (Lagos 2013), while previously, the majority of cattle was confined at night. In other parts of Europe where wolves feed on domestic ungulates, sheep and goats are usually the most consumed species (review in Meriggi et al. 1996). The highest consumption of cattle has been documented in central and southern Spain ($F_o = 57\%$ in summer, Cuesta et al. 1991). In north-eastern Belarus, 35.8% occurrence of cattle was observed during periods of wild ungulate scarcity (Sidorovich et al. 2003). The high consumption of cattle in the habitats of the north and centre of Galicia is due to the greater numbers of this kind of livestock, in addition to the different husbandry systems of the distinct species of livestock. Goats and sheep are usually housed in stables overnight, which makes them less vulnerable than the cattle. A better understanding of the factors that can affect the vulnerability of the cattle to wolf predation is essential, in order to implement measures to improve the protection of livestock and thus decrease human-wolf conflicts.

We observed the importance of grapes as a food resource in SMC, which had also been revealed by Cuesta et al. (1991). This is suggestive of the adaptability of wolves to the feeding resources available in each habitat. Consumption of grapes by wolves may create a potential conflict with grape farming. In the area, other mammals such as fox, wild boar or roe deer consume grapes as well. So far, there are no specific conflicts involving wolves in the area, since other species are blamed by farmers for the damages.

The observed occurrence of dog in wolf diet (< 3%) is very low as compared to the values given by Cuesta et al. (1991) for western Galicia (17.75%) and for the Cantabrian Mountains (15.20%), which showed dogs to be a frequent food for wolves in the 1970s. This decrease in the consumption of dogs has likewise been observed by Llaneza and López-Bao (2015). However, dogs appear to remain a food resource used by wolves in certain areas where other prey are not available. Wolves can kill domestic dogs from the neighbouring villages that occasionally go to the forest; wolves entering villages or farms to kill dogs have been also reported. Hunters claim that wolves kill hunting dogs as well, even during driven hunts. In addition, part of the occurrence of wolf in the diet of wolves could be due to the consumption of carrion.

Conclusion

Our results concerning wolf diet in Galicia confirm the existence of various human-wolf ongoing conflicts across the habitats studied, principally caused by damage to livestock. Conflicts can also arise from wolf predation on wild pony foals and game species and even due to the consumption of grapes in the vineyards. The trophic ecology of wolves in the anthropogenic habitats of Europe depends largely on the natural resource management accomplished. Our recommendation is to ensure a habitat supporting rich and abundant populations of wild prey, so that wolves are not forced to prey on livestock, together with encouraging the adoption of measures to protect and properly handle livestock. In western Galicia, wild ponies are the main and preferred prey of wolves. In these livestock farming areas, the conservation and fostering of the existing population of wild ponies is instrumental, as they attenuate wolf impact on cattle (Lagos 2013). The low economic value of foals in comparison with calves entails that the economic impact of wolf predation on foals is much lower than for calves. Therefore, they are important for keeping wolf population at an acceptable level of conflict. Given the observed wolf positive selection of roe deer, hunting management should aim at increasing the density of roe deer populations, in order to provide alternative prey than livestock.

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