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RESEARCH

Dog in sheep's clothing: livestock depredation by free-ranging dogs may pose new challenges to wolf conservation

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Abstract
Livestock depredation is a common cause of human-carnivore conflicts. In Portugal, free-ranging dogs are increasingly abundant and overlap endangered Iberian wolf territories, with reports of livestock depredation. However, the lack of awareness about dogs' possible role as predators leads to bias against wolves in cases of damages. Our goal was to assess and compare wolf and free-ranging dog's diet composition at southern wolf range in Portugal, to offer insights on dogs' predatory role on livestock and its implications for the conservation of an endangered wolf subpopulation. We assessed diet composition from 107 to 95 genetically confirmed wolf and dog scats, respectively, and complemented the analysis with data from 40 attacks on livestock with successful genetic predator assignment. Scat analysis highlighted goats as the most consumed dog prey in all analysed regions, with lagomorphs, small mammals, and wild boars as second most consumed in each region, respectively. Wolves mainly relied on goats and wild boars in the west, whereas in the central region they mostly fed on birds. The dietary overlap between both canids was very high (Pianka's index $O = 0.93$), showing potential for competition. Additionally, we found that dogs were the sole predators detected in most attacks (62%). Our findings highlight dogs' role as predators of livestock, and possibly also wild species, posing a further challenge to wolf conservation. Alongside adequate husbandry practices, we emphasise the need for a stronger enforcement of the legislation on dog ownership and an effective management of the stray population to reduce human-wolf conflict.

Keywords Iberian wolf · Free-ranging dogs · Diet composition · Livestock depredation · Human-wolf conflict

Introduction

Livestock depredation by large carnivores is one of the main causes of human-wildlife conflicts (Lozano et al. 2019). This is a matter of socio-economic concern for local communities and a major issue for conservationists, as conflicts increase hostility towards carnivore species and reduce the effectiveness of conservation programs (Stahl et al. 2001; Woodroffe and Frank 2005; Liberg et al. 2012). The problem is further aggravated when other animals, which can also be responsible for livestock losses, are not regarded as potential predators (Home et al. 2017). In a

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wide range of socio-environmental contexts, domestic mammals - such as dogs and cats - with different levels of dependency on humans, roam freely in humanised and natural landscapes and may prey on wildlife (Young et al. 2011; Maeda et al. 2019). This is particularly relevant in rural areas, where wildlife is more abundant and accessible. Free-ranging dogs can capture wild species, such as brown hares *Lepus europaeus*, roe deer *Capreolus capreolus*, and wild boars *Sus scrofa* (Krauze-Gryz and Gryz 2014; Duarte et al. 2016; Wierzbowska et al. 2016), increasing the predatory pressure on these prey. They may also pose a direct threat to other carnivores through the spread of diseases, and potential hybridisation with wolves (Vanak and Gompper 2009; Lescureux and Linnell 2014). Dogs are described as generalist and opportunistic predators, their diet mostly consisting of vegetation, human-derived items (e.g. scavenged garbage, food directly provided by people, livestock), and wild mammals (Vanak and Gompper 2009; Young et al. 2011). Their depredation on livestock species, such as domestic sheep (*Ovis aries*), has been reported throughout European landscapes from the northern regions such as Sweden (Sundqvist et al. 2008), Estonia (Plumer et al. 2018), and Poland (Wierzbowska et al. 2016), to the southern like Spain (Echegaray and Vilà 2010) and Italy (Mattiello et al. 2012; Magrini 2014; Fabbri et al. 2018). Due to livestock depredation events, dogs can contribute to escalate the conflict between wolves and humans, as losses can be wrongly attributed to wolves (Echegaray and Vilà 2010; Duarte et al. 2016), increasing the hostility towards the species and jeopardising the effectiveness of conservation programs (Boitani et al. 2015).

In Portugal, the Iberian wolf (*Canis lupus signatus*) abundance drastically decreased during the twentieth century, mainly due to human persecution and habitat loss (Álvares 2011). Currently occurring at 20% of their original range, the wolf is protected by law since 1988, and listed as "Endangered" in the Portuguese Red Data List of Mammals (Pimenta et al. 2023). Whilst most attacks on livestock are attributed to wolves, there is a large population of free-ranging dogs, hereafter referred to as dogs, overlapping wolf territories (Álvares et al. 2015). In 2016, official animal collection centres retrieved around 4000 dogs in central Portugal (DGAL 2017); however, the exact size of the dog population remains unknown. Many of these animals are abandoned hunting dogs and pets (Álvares et al. 2015), but others are owned dogs that due to their role in human activities (*e.g.* guarding livestock) are allowed to roam freely (Espírito-Santo 2007). Despite the high number of dogs in areas of wolf presence (Álvares et al. 2015), no published information on their patterns of prey consumption is currently available for Portugal. To fill this gap, this study aims to assess and compare the diet composition of wolves and dogs at wolf range south of the Douro river, in central Portugal. By using data from genetically confirmed wolf and dog scats, and genetic evidence on potential predators retrieved from livestock depredation events in the study area, we summarise and describe patterns of prey consumption by wolves and dogs, to assess the role of dogs on depredation events. This is a relevant topic for Iberian wolf conservation as not only is the Iberian wolf an endangered species, but the packs inhabiting the study area also show great instability and are at risk of local extinction (Torres and Fonseca 2016). We intend to raise awareness about this topic to foster an effective dog management in the area, to reduce their potentially negative impact and the human-wolf conflict associated with livestock damages.

Methodology

Study area

The study area comprises the whole wolf distribution south of the Douro river in Portugal (Fig. 1). The western region of the study area encompasses two Special Areas of Conservation (SAC) defined in the Natura 2000 Sectorial Plan, namely "Serras da Freita e Arada" (PTCON0047) and "Montemuro" (PTCON00025). This mountainous region, with altitudes up to 1381 m, covers the range of three wolf packs *(i.e.* Arada, Cinfães, and Montemuro). The climate is Mediterranean, with strong oceanic influence, and the area is composed by a mix of native oak *Quercus* spp., birch *Betula pubescens*, and *Castanea sativa* forests, with stands of maritime pine *Pinus pinaster*, the introduced exotic eucalyptus *Eucalyptus globulus*, shrublands (*e.g.* broom *Cytisus* spp., *Pterospartum tridentatum*, gorse *Ulex* spp., heather *Erica* spp.), pastures, agricultural lands, and urban areas (Torres et al 2015a, b). Here, sheep flocks usually graze near settlements, in poorly fenced or unfenced areas, whilst goat (*Capra aegagrus hircus*) flocks tend to scatter across the mountains, sometimes unsupervised. Mixed flocks of sheep and goats are also common, but usually graze in the mountains, under supervision. Cattle (*Bos taurus*) herds usually graze unsupervised in unfenced areas. All species are usually confined during the night (Torres et al. 2015b). Livestock abundance in the studied region includes approximately 12,300 sheep, 2180 goats, and 8650 cattle, which accounts for an average number of 250, 45, and 180 of these animals per parish. There is also intensive production of pigs, rabbits, and poultry in the region (INE 2019).

The central region of the study area houses three wolf packs (*i.e.* Leomil, Lapa, and Trancoso). It is a mountainous area of Mediterranean climate, with average altitudes of 700–800 m, and is dominated by shrublands of broom and heather, stands of maritime pine, and oak woodlands (*i.e. Q. robur*, *Q. pyrenaica*). Here, cattle and goats graze

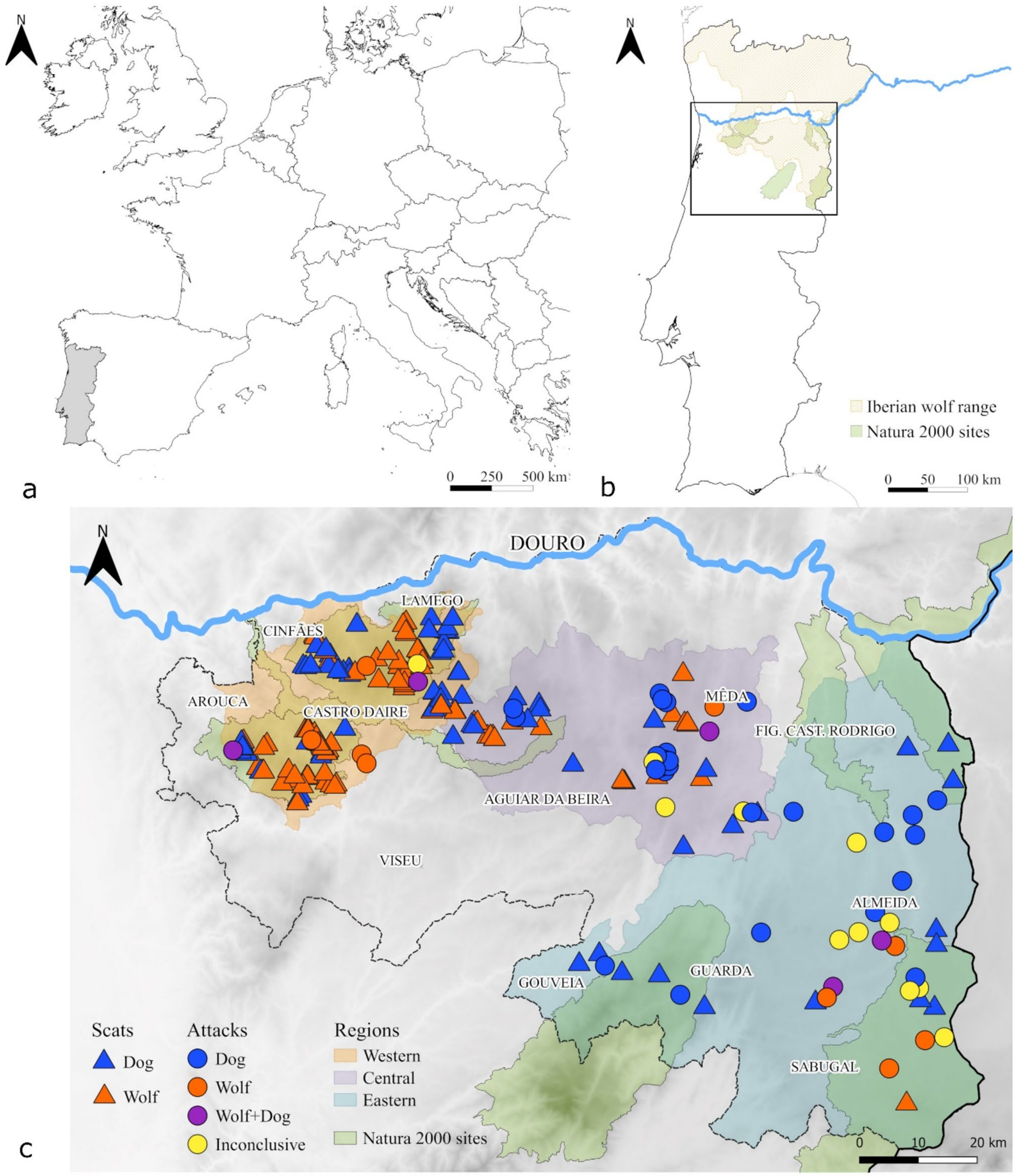

Fig. 1 **a** Portugal's location (shaded) in western Europe. **b** Limits of the study area south of the Douro river, encompassing southern wolf range (dataset adapted from Chapron et al. (2015)) and main Natura 2000 sites. **c** Location of all sampled attacks ($N=51$, circles), and analysed dog ($N=95$, blue triangles) and wolf scats ($N=107$, orange triangles), with delimitation of the three study regions and Natura 2000 sites

unsupervised in poorly fenced areas and, in the case of goats, also scattered through the mountains. Sheep are more abundant, its numbers hovering around 40,437, whilst goats and cattle numbers are approximately 4300 and 8000, respectively (averages of 530 sheep, 60 goats, and 100 cattle heads per parish) (INE 2019). As in the western region, intensive production of pigs, rabbits, and poultry is common. The SAC "Rio Paiva" (PTCON0059), encompassed by both regions, might be an important area of connectivity for wolf packs.

The eastern region encompasses one Special Protection Area (SPA) "Vale do Côa" (PTZPE0039), and sections of three SACs, namely "Serra da Estrela" (PTCON0014), "Douro Internacional" (PTCON0022), and "Malcata" (PTCON0004) (Fig. 1). This is an area of irregular wolf presence. The region is characterised by plateaus ranging from 300 to 950 m, mainly under Mediterranean influence. The vegetation is mainly composed of oak woodlands (*i.e. Q. rotundifolia*, *Q. suber*, *Q. robur*), shrublands, and mosaics of agricultural lands and pastures (Cadete et al. 2015; Pimenta et al. 2017). Here, most farms are dedicated to cattle, mostly grazing in rotational, extensive regimes, unconfined and unsupervised (INE 2019). Livestock abundance stands at an estimated 111,590 sheep, 5890 goats, and 44,080 cattle, averaging 750 sheep, 40 goats, and 300 cattle heads per parish.

Such variety in husbandry practices translates into distinct levels of prey availability and feeding strategies. Wild boar is the only abundant and widespread wild ungulate, whilst roe deer abundance steadily increases towards the south and east. Red deer *Cervus elaphus* is confined to the southeastern region near Sabugal (Torres et al. 2015b; Bencatel et al. 2019).

Data collection

We used data from two sources: (1) wolf and dog scats collected from 2014 to 2022, and (2) attacks on livestock occurring between 2019 and 2021.

Scats were systematically collected year-round in the scope of two on-going monitoring and conservation projects: Wolf Monitoring Plan south of the Douro river – west area (coordinated by ACHLI, Iberian Wolf Habitat Conservation Association), and LIFE WolFlux project (LIFE17 NAT/PT/000554). Scats were collected along transects in areas of suitable wolf habitat, stored in 95% ethanol immediately after collection, and kept at – 20 °C after arrival to the laboratory.

We also compiled information from 51 attacks on livestock reported by the official conservation agency (ICNF, Institute for Nature Conservation and Forests) in collaboration with the LIFE WolFlux project (Fig. 1). ICNF's field technicians received training to standardise sample collection, collecting saliva samples from the fur, skin, or bone around visible bite wounds using cotton swabs, in a total of 288 samples (average of 5.6 samples per attack). They also compiled key information, such as spatial coordinates, type and number of animals killed/injured, and signs of scavengers. Samples were refrigerated until delivered to the laboratory, where they were investigated by molecular identification of the DNA to assess which predator(s) have consumed the carcasses.

Laboratory analysis

In scat and swab samples, DNA from the target species is expected to be low in quantity and quality, as they include DNA from prey, parasites, and microbiome. Thus, precautions must be taken to avoid cross-contamination between samples and the environment (Taberlet et al. 1999). Samples were handled in a laboratory exclusively for DNA extractions from non-invasive samples; disposable protective wear was used to reduce contamination by human DNA, as well as sterile and disposable consumables, reagents, and equipment used exclusively for the treatment of these samples (see Online Resource for full list of measures). DNA was extracted from scats 1 to 2 weeks after collection, using the QIAGEN® QiAamp DNAStool kit, according to the manufacturer's instructions. In each extraction, a maximum of ten scat samples were treated, including a negative control. Similarly, DNA isolation from saliva samples was conducted using the DNeasy® Blood and Tissue Kit (in 76% of samples) or the InnuPREP Forensic Kit, Analytic Jena® (in 24% of the samples). Only up to 6 swabs were processed at a time and different attacks were handled separately. For mitochondrial lineage determination and wolf/dog diagnose, we amplified a DNA fragment corresponding to the d-loop of the mitochondrial DNA using the universal primers Thr-L 15926 and DL-H 16340 (Vilà et al. 1999). As expected, target predator DNA was often degraded and in lower amounts and thus we used a pair of more specific primers: dogDL1 and dogDL3 (Leonard et al. 2002), with an annealing temperature of 50 °C, over 40 cycles. Sequences were generated in an Applied Biosystems™ ABIPRISM® 3730-XL DNA Analyzer, compared with sequences available on Genbank using BLAST, and with haplotypes previously described for wolves and dogs (Vilà et al. 1997). As a wolf-dog hybrid was previously detected in the study area (Torres et al. 2017), we followed the same methodology for species diagnose and wolf/dog discrimination for scat and swab samples. We amplified a panel of 24 microsatellite markers (Torres et al. 2017) which includes the most polymorphic markers known for the wolf populations in the region (Godinho et al. 2011) (see Online Resource for details), using the Qiagen Multiplex

Kit™ following the manufacturer's instructions. We genotyped samples through fragment analysis using capillary electrophoresis on the Applied Biosystems™ ABI PRISM® 3730-XL DNA Sequencer. We employed Bayesian methods to identify clusters and search for hybrids, using STRUCTURE and NEWHYBRIDS software, and ran principal coordinate analyses to validate our findings (see Online Resource). Results were consistent with those from mtDNA and did not suggest the presence of wolf-dog hybrids in the study area.

Data analysis

Scat analysis

We morphologically identified hairs present in scats to determine prey composition. We divided the analyses in two steps: scat washing and hair identification. In the first step, we washed and separated hairs from scats. We noted the occurrence of any material besides hair, such as bones, feathers, plants, mineral matter, or garbage. In the second step, we prepared slides for microscopic evaluation of hair structure following standard procedures (Teerink 1991; De Marinis and Asprea 2006). Hair was identified through both macroscopic evaluation and microscopic analyses of the medulla, cortex, and cuticle characteristics, by comparison with reference materials of southern European wild and domestic ungulates and wild Iberian mammals (De Marinis and Asprea 2006; Valente et al. 2015). Ungulates were categorised at the specific level (*i.e.* donkey *Equus asinus*; cattle, sheep, goat, wild boar, roe deer), whilst other prey were considered by the following categories: mustelids (*i.e.* *Martes* sp., European badger *Meles meles*), small mammals (*e.g.* rodents, shrews), lagomorphs (*i.e.* Iberian hare *Lepus granatensis*, rabbit *Oryctolagus cuniculus*), and birds (identified by the presence of feathers in the scat).

To assess the diet composition of both canids and understand the dietary overlap between wolves and dogs, we estimated, for each prey category, the absolute (AO) and relative (RO) frequencies of occurrence in wolf and dog scats (Lucherini and Crema 1995). They were calculated as follows:

$$AO = \frac{ni}{N} \times 100 \qquad RO = \frac{ni}{Nt} \times 100$$

where

ni number of occurrences of a particular prey category
N total number of scats
Nt total number of occurrences of all prey categories

We used the RO of each prey category to determine the degree of dietary overlap between wolves and dogs in the study area, by using the symmetric niche overlap coefficient O (Pianka 1973), which ranges from zero (no overlap of resources) to one (complete overlap of resources):

$$O_{jk} = \frac{\sum_i^n p_{ij} \cdot p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \cdot \sum_i^n p_{ik}^2}}$$

where

O_{jk} coefficient of niche overlap between species j and k
i food resource (*i.e.* each prey category)
p_{ij} proportion of resource i of the total resources used by species j
p_{ik} proportion of resource i of the total resources used by species k
n total number of food resources

We also estimated the relative volume (RV) of each prey category (*i.e.* the volume of a specific prey category as a percentage of the total volume of all prey categories), considering the volumetric classes proposed by Kruuk and Parish (1981). This metric is commonly used as an estimate of the importance of the different prey in the canids' diets (Balestrieri et al. 2010). Furthermore, we estimated the volume when present (%, *VolPres*) as the relative volume of each prey category across the number of scats in which they were detected. We plotted the AO against the RV and *VolPres* of each category to visualise the contribution of each prey to the total scat volume and assess its importance in overall diet. Analyses were performed in R Studio version 4.0.3 (RStudio Team 2022) and maps were produced with QGIS version 3.16.14-Hannover (QGIS Development Team 2023).

Attacks on livestock

From the 51 sampled attacks, predator DNA identification failed in eight, whereas other two presented sequencing and/or genotyping ambiguities (*i.e.* distinction between dog and wolf was not possible). Information on the prey was not provided in one attack. These eleven attacks are represented as "Inconclusive" in Fig. 1 and were excluded from the analysis. We included attacks in which genetic predator assignment was successful and information on the prey was available ($N=40$ attacks). Each attack was assigned to either dogs or wolves, depending on if only confirmed dog or wolf haplotypes were found, respectively. Whenever an attack showed evidence of both haplotypes ($N=6$ attacks), it was assigned to both species (Fig. 1).

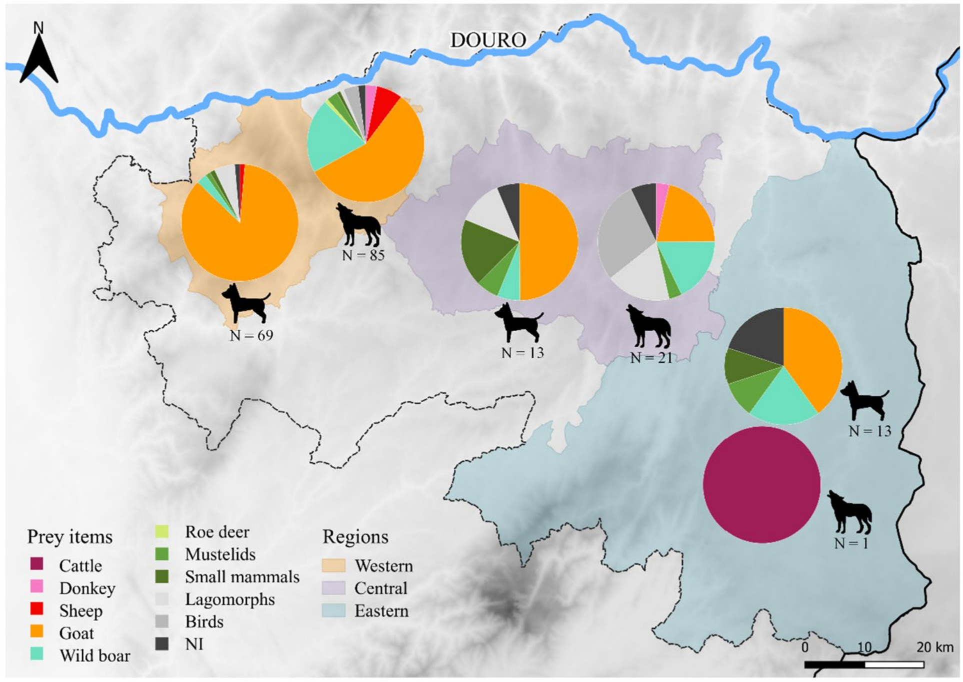

Fig. 2 Overview of dog and wolf's diet composition in the study area, with number of scats analysed

Results

Scat analysis

From 2014 to 2022, a total of 202 scats (107 wolves and 95 dogs) were collected in the study area, their numbers per region are depicted in Fig. 2.

Regarding dogs' diet, we found six different prey items, namely sheep, goats, wild boar, mustelids, small mammals, and lagomorphs. Goats were the most frequently consumed prey in all regions (*RO* = 85.7% in the western, 50% in the central, and 40% in the eastern; Online Resource, Table 1). They constitute over 80% and 50% of volume in total diet in the western and central regions, respectively, but only account for around 30% in the eastern region (Fig. 3). In the western region, the second most consumed prey category was lagomorphs (*RO* = 5.7%), followed by wild boar (*RO* = 2.9%) (Fig. 2). Nevertheless, they contributed to less than 5% of volume in dogs' diet in the region (Fig. 3). Sheep and small mammals represent a large volume when present in dog scats (98%, Fig. 3), but constitute around 1% of volume in overall diet. In the central region, the second most consumed prey were small mammals (*RO* = 18.8%), followed by lagomorphs (*RO* = 12.5%) (Fig. 2). Wild boars and mustelids presented

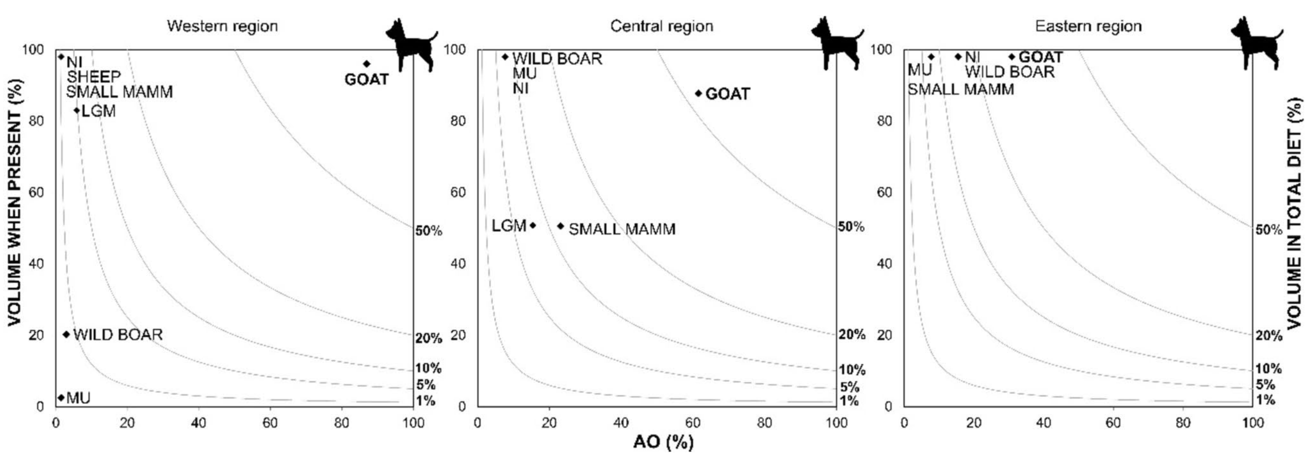

Fig. 3 Estimated volume of prey items (%) versus their absolute frequency of occurrence (*AO* %) in dog diet, for the western, central, and eastern regions. Isopleths connect points of equal relative volume in total diet. LGM, lagomorphs; MU, mustelids; NI, nonidentified

similar frequencies of occurrence (*RO* = 6.3%). As for the eastern region, wild boars were the second most consumed dog prey (*RO* = 20%), followed by mustelids and small mammals (*RO* = 10% for each) (Fig. 2). We also found a large proportion of unknown hairs compared to other regions (Fig. 2).

We identified ten different prey items in wolf scats, namely cattle, donkey, sheep, goats, wild boar, roe deer, mustelids, lagomorphs, small mammals, and birds (Fig. 2). Goats were the most consumed prey item in the western region (*RO* = 56.7%) and constitute much of the total volume in wolf's diet (Fig. 4). Wild boar was the second most consumed prey (*RO* = 20.6%), followed by sheep (*RO* = 7.2%), birds (*RO* = 4.1%), donkey and mustelids (*RO* = 3.1% for each) (Online Resource, Table 1). We found low frequencies of occurrence for roe deer, small mammals, and lagomorphs (*RO* = 1%). In terms of volume in diet, donkey, sheep, and lagomorphs showed a remarkable volume when present in scats (> 80%, Fig. 4), but constitute less than 10% of the overall diet. We found a distinct pattern in the central region, where birds were wolves' most consumed prey (*RO* = 28.6%), followed by goats (*RO* = 21.4%), and wild boar and lagomorphs (*RO* = 17.9% for each) (Fig. 2). Similarly to the western region, the occurrence of donkey and mustelids in wolf scats was very low (*RO* = 3.6%). The one scat analysed from the eastern region solely contained cattle remains (*RO* = 100%) (Online Resource, Table 1).

The overall dietary overlap between the two species, measured by the Pianka index, was very high (*O* = 0.93). When calculated for each region, the overlap was *O* = 0.94 for the western region and *O* = 0.77 for the central region. We did not calculate dietary overlap for the eastern region due to the low number of samples.

Attacks on livestock

From the 40 analysed attacks on livestock, only six occurred in the western region, whilst the central and eastern regions accounted for 17 attacks each (Fig. 5). Attacked species were sheep (80%), cattle (15%), and goats (5%). The number of animals killed per attack varied between one and seventeen for sheep, and one and two for cattle and goats. In some attacks on sheep there were no casualties, but animals were injured. Injured sheep per attacked varied between 0 and 24.

Dogs were the only predator detected in most of the analysed attacks (*N* = 25, 62%), mostly targeting sheep (76%) and cattle (20%), whilst goats were an underrepresented prey (4%). All dog-assigned attacks occurred in the central and eastern regions (14 and 11 attacks, respectively). Conversely, we found that only 23% of attacks (*N* = 9) were attributed to wolves, and all of these were on sheep. Most wolf-assigned attacks occurred in the western and eastern regions (four attacks in each), with only one attack occurring in the central part of the study area. Evidence of both canids was found in 15% of the attacks, evenly distributed throughout the study area (two attacks per region). These mostly focused on sheep (66%), but had some representation of cattle and goats (17%, respectively).

Discussion

The mitigation of human–wolf conflicts is key to ensure the long-term stability of wolf populations, particularly in areas where persecution is high, and wolves are at risk of local extinction (Boitani et al. 2015). This is the case of the wolf

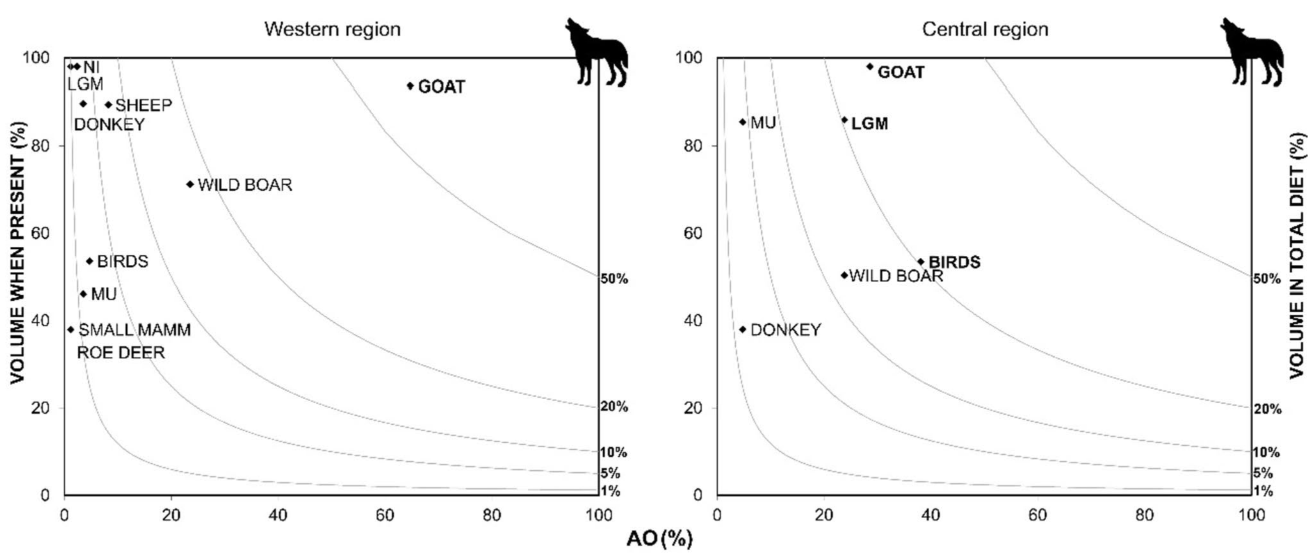

Fig. 4 Estimated volume of prey items (%) versus their absolute frequency of occurrence (AO %) in wolf diet, for the western and central regions. Isopleths connect points of equal relative volume in total diet. LGM, lagomorphs; MU, mustelids; NI, nonidentified

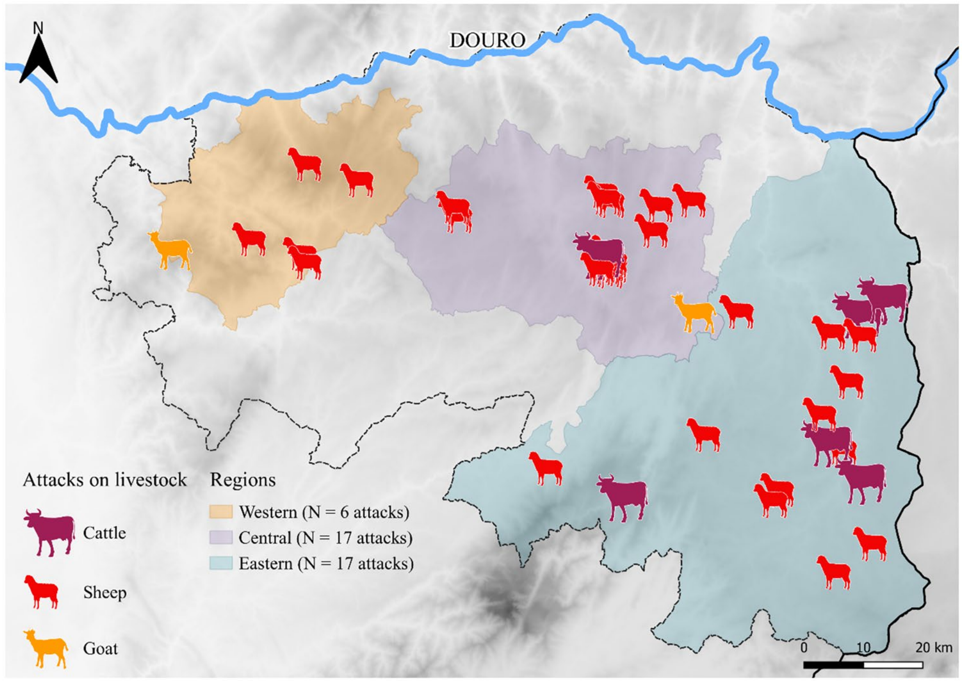

Fig. 5 Distribution of attacked livestock species in the study area, with number of attacks per region

population inhabiting our study area, although attitudes and tolerance levels differ between regions (Espírito-Santo and Petrucci-Fonseca 2017). Some local populations in our study area already recognise the role of dogs as predators of livestock, as many livestock owners have personally witnessed it. Whereas in other regions (e.g. eastern region), livestock owners seldom admit it in the absence of a direct observation (Espírito-Santo 2007), as there is a misconception that dog attacks never go unnoticed by people and are easily distinguishable from wolves. This, coupled with the general lack of knowledge on the current number of wolves and free-ranging dogs in the area, leads to bias against wolves even if dogs are responsible for livestock damages. In the long-term, mitigating human-wolf conflicts involves improving public attitudes towards wolves, and one way to achieve it would be shedding light on dogs' role as potential predators of livestock species. Here, we described the main patterns of prey consumption by wolves and free-ranging dogs, whilst providing evidence of a high dietary overlap between both canids in rural areas in central Portugal.

Our results from scat analyses showed that goats were the most consumed wolf prey in the western range of its distribution south of the Douro river. This is in accordance with previous studies for the same area (Vos 2000; Torres et al. 2015b). Nonetheless, our study provides additional insights regarding wolf diet diversity. We found ten different prey items in wolf scats, in contrast to the five previously described by Torres et al. (2015b). We found that wild boar, formerly reported as the fourth most consumed wolf prey, now ranked as second. We also found evidence of consumption of birds, donkey, mustelids, small mammals, and roe deer, although in lower frequencies of occurrence. The presence of roe deer in scats reflects the success of several reintroduction programs in the last decades and the natural expansion of this ungulate (Torres et al. 2015a). Contrary to other studies, we did not find cattle remains in wolf scats from the western region. This could be due to improvements in husbandry practices (e.g. widespread use of livestock guarding dogs, and livestock confinement at night) (Cortés et al. 2020) or to the decreasing number of cattle heads over the last decade (INE 2019). Overall, our results seem to point to a slight shift in the western packs' diet over the last few years (Torres et al. 2015b), with similar frequencies of consumption of goats, but a great decrease in the frequencies of sheep and cattle, and an increased consumption of wild prey. This shift seems to result from a combined effect of some, if not all, of the above-stated factors: the decreased consumption of livestock could stem from both the decline in cattle numbers and enhanced husbandry practices, which in turn would drive wolves to prey on wild animals. A different trend might be occurring in the central region, where birds and lagomorphs were the first and third most consumed wolf prey, probably because of opportunistic feeding on carcasses from the intensive poultry and rabbit farming. Still, since we could not distinguish between domestic and wild rabbit and did identify Iberian hare in some samples, part of these occurrences might also result from wild prey depredation. Since we only analysed one wolf scat from the eastern region (identifying cattle consumption), our diet composition results for this region are biased.

Regarding dogs, we found that goats were the most consumed dog prey in the whole study area, representing over than 80% and 50% of the total volume in diet in the western and the central regions, respectively. Lagomorphs were also a frequent occurrence in dog scats collected from the western and central regions, which might denote a similar pattern to wolves, as dogs also hunt for hares and wild rabbits (especially hunter breeds). Small mammals and wild boars were the second most frequent prey in the central and eastern regions, respectively. We found low frequencies of sheep and mustelids, and no evidence of birds despite the great availability of poultry farming in some regions. Overall, our results are in line with previous studies where dogs were found to predate on both larger and smaller prey, such as wild boars and brown hares (Krauze-Gryz and Gryz 2014; Duarte et al. 2016; Wierzbowska et al. 2016). This seems to point to a great ability in surviving in both domestic and non-domestic conditions, making dogs resilient competitors. In fact, we found that wolves and dogs share a similar diet composition in the western and central regions, with a high dietary overlap indicating potential for food competition. Naturally, our limited scat sample constrains the robustness of results. Despite this limitation, given the scant information available on this topic, our findings remain an important contribution, shedding light on potential ecological interactions in the area.

We also recognise the degree of uncertainty associated with scat analyses, as they do not allow for differentiation between killed and scavenged prey. Regarding the presence of domestic species in scats, the uncertainty concerning scavenging highlights inadequate practices (i.e. removal of carcasses). Carrion availability, either from intensive farms or abandoned livestock carcasses in pastures, might sustain wolf populations in human-dominated areas, but it also alters their depredatory behaviour creating an habituation to feeding closer to settlements, which in turn increases the chance of negative interactions with humans (Mohammadi et al. 2019; Ciucci et al. 2020). The uncertainty associated with scats can also lead to the misinterpretation of results, as for example the high frequency of goat in dog scats. More than an outcome of active killing, this high frequency could be explained by shepherds feeding livestock remains to their dogs, a common practice in the western area (Dário Hipólito, *pers. comm.*) and a pattern impossible to untangle from true depredation events. Thus, we used a complementary approach to minimise uncertainty and confounding factors regarding livestock consumption. We compared results from each species scat analyses with those from attacks. Similarly to other European regions, most of the reported attacks concerned sheep (Linnell and Cretois 2018), followed by cattle and, to a lesser extent, goats. Most attacks on livestock were assigned to dogs and have all occurred in the central and eastern regions, although dog presence was also detected in two depredation events in the western region. Dog-assigned attacks follow the general pattern, focusing mostly on sheep and cattle. All wolf-assigned attacks were on sheep, but we found evidence of wolf presence in a goat depredation event in the western region, and in a cattle depredation event in the eastern. The fact that only one attack was assigned to wolves in the central region might be related to carrion availability, whose consumption was supported by scat analysis.

The most striking outcome of our analysis is the apparent discrepancy between attacked livestock type and their frequencies of occurrence in scats (both wolfs and dogs'). For example, although no dog scats indicated cattle consumption, most attacks on cattle were assigned to them. Similarly, we have found evidence of donkey consumption by wolves, but there were no sampled attacks on donkeys during our study period. The discrepancy is most remarkable for goats and sheep, which showed opposite trends in our results, and which might be due to several concordant reasons. We hypothesise that most attacks on goats are going undetected or unreported to the official authorities due to current husbandry practices where goats mostly graze in large flocks, scattered throughout the mountains, often unattended, which makes finding the remnants of an attack a challenging task (Vos 2000). In turn, sheep remains are more easily found because of their proximity to villages and higher surveillance from shepherds or guarding dogs (Vos 2000). This proximity may also contribute to disrupt ongoing attacks, thus, although sheep are targeted, the predator may fail to feed on them. In fact, shepherds and livestock owners often report their sheep being wounded, or even killed, with few or even no traces of having been consumed. As previously mentioned, shepherds feeding goat remains to their dogs could also explain the great discrepancy between goat occurrence in scats and attacks from the western region. Nevertheless, the fact that dogs were the sole predators found in most attacks supports the idea that they can be predators of livestock species, which is in line with previous findings for Italy and Poland (Cozza et al. 1996; Wierzbowska et al. 2016). The main threats to European wolf populations are poaching and low public acceptance on account of livestock depredation (Hindrikson et al. 2017). In the central region, for example, most attacks on livestock were assigned to dogs, and only one was assigned to wolves. If dogs' role as predators remains underestimated by local populations, and wolves keep being blamed for dog attacks on livestock, the negative views towards them can be aggravated, jeopardising conservation efforts (Echegaray and Vilà, 2010; Lescureux and Linnell 2014). Informing local authorities and communities on the role of free-ranging dogs as predators is an important step towards a better management of their populations (Young et al. 2011) and, alongside the implementation of adequate husbandry practices, should be prioritized to help reduce human-wolf conflict in the area.

Conclusion

Overall, our study provides new insights on wolf diet diversity and on the predatory role of free-ranging dogs in central Portugal, an area inhabited by an endangered wolf subpopulation at risk of local extinction (Boitani et al. 2015; Torres and Fonseca 2016). We found that wolf diet composition is more diverse than previously described for the western area, with wild boar and roe deer consumption as worth noting cases. This reflects not only the increased availability of these wild ungulates, but also effective husbandry practices which seem to be driving wolves to prey on their natural prey. This is a promising sign from a conservation perspective. We also found that dogs may play an important role as predators of livestock species, being the sole predator found in most of the reported attacks on livestock. At the same time, scat analyses point to a possible depredatory behaviour over wildlife. Thus, the dietary overlap between wolves and dogs was found to be very high at the same spatial level in the western and central regions. However, this pattern should be considered with some caution due to the small sample size. We also showed that livestock consumption patterns retrieved from scat analyses does not reflect the level of conflict in terms of economic losses (Newsome et al. 2016). The opposite is also true, as inferring diet composition from livestock damages data alone gives a too simplistic view, which may affect future management and conservation measures. Thus, both approaches are crucial to better elucidate on patterns of livestock depredation in relation to local husbandry practices. Based on our findings, there are clear avenues for future research. The seeming shift in wolf diet in the western region needs continued monitoring to confirm it as a sustainable trend. Additionally, confirming free-ranging dogs' depredation of wildlife will require further multi-approach studies to fully distinguish between depredation and scavenging. Also, validating the observed dietary overlap between wolves and dogs at the temporal level, and studying dogs' spatiotemporal use of resources and competition with other carnivores are additional research steps that should provide important insights to this subject (but see Teixeira et al. (2023)). We hope our findings raise awareness about dogs' role as predators of livestock and possibly also wild species, and its implications for wolf conservation south of the Douro. There is an urgent need for a stronger enforcement of the legislation on dog ownership by authorities to reduce the number of free-ranging owned dogs, as well as alternative approaches to collect, rehouse and, ultimately, control the stray dog population.

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Availability of data and materials Part of the data collection was performed under a service contract as a part of the Iberian wolf monitoring program run by ACHLI, whilst other was collected by the LIFE WolFlux Consortium. Restrictions apply to the availability of these data, which were used with permission for the current study, and are not publicly available. Data may be available from the authors upon reasonable request and permission from ACHLI and the LIFE WolFlux Consortium.

Declarations

Competing interests The authors declare no competing interests.

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