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Grey wolf feeding habits and their geographical variation in Northwest Spain

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ABSTRACT

This study investigates wolf (*Canis lupus*) dietary preferences and their geographical variation by calculating frequency of occurrence and biomass consumption in three areas in the north-western Iberian Peninsula that differ in terms of the type and abundance of potential prey. Wolf dietary preferences were expected to be related to the availability of a species of free-roaming horses (*Equus ferus atlanticus*) and much less to traditional livestock in each habitat.

The diet of wolves was found to comprise mostly Galician feral horses when available, with a low proportion of livestock. The next most consumed species were wild boar (*Sus scrofa*) and cattle (*Bos taurus taurus*). A much higher consumption of traditional livestock (84% biomass) was observed in the one study area where there were no feral horses.

The fact that access to feral horses may help decrease wolf predation on other species of livestock which are more economically important and the environmental benefits of horses in protecting against forest fires suggest that conservation and expansion of this endangered species of horses should be encouraged. Strengthening existing populations and possibly re-introducing native wild species within the wolf's range may be the most environmentally friendly way to reduce economic losses for farmers and cattle breeders.

1. Introduction

Grey wolves (*Canis lupus*) are one of the most widely distributed large carnivores. In the past few decades they have returned to areas of their former range after centuries of being hunted. This will increase contact between grey wolves, humans and livestock (Ansorge et al., 2006; Lanszki et al., 2012; Wagner et al., 2012), thus also increasing conflict with humans because of wolves preying on livestock (Graham et al., 2005; Sillero-Zubiri and Laurenson, 2001).

The complex ecological and social issues arising from human–carnivore conflicts often hinder the formulation of effective conflict resolution and conservation management strategies. In the Iberian Peninsula, the most critical period for was from the 1960s to the early 1970s, when they were subjected to strong pressure and pursued fiercely (Arija, 2010; Valverde, 1971). Since then several laws have been passed to protect their populations and minimize poaching (López-Bao et al., 2015).

In some areas, such as Sierra Morena in southern Spain, wolves are on the verge of extinction as a consequence of illegal hunting (López-Bao et al., 2015), a clear indicator that conservation efforts and changes in legislation might not be enough to protect them. Wolf conservation has been jeopardized by both hunting pressure as a result of the low acceptance of the species by rural people and culling by regional administrations in the Iberian Peninsula (Echegaray and Vilà, 2010; Fernández-Gil et al., 2016). Neither measure has proved effective in reducing livestock depredation (Harper et al., 2008; Treves et al., 2009).

One of the four isolated wolf populations that currently thrive in Western Europe lives in the northwestern quadrant of the Iberian Peninsula, an area covering eight autonomous regions in Spain and Portugal, including Galicia (Linnell and Boitani, 2012). In Galicia, wolf distribution remained steady between 1850 and 2003 (Núñez-Quirós et al., 2007), which is proof of the importance of this area as a refuge for wolves over the last 200 years. At the beginning of the 2000s, Galicia's wolf population density was approx. 2.25 packs per 1000 km2, with 68

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wolf packs identified in the whole 3 Mio ha of Galicia (Llaneza et al., 2012). In 2010, wolves in the northwest of the Iberian Peninsula were categorized as Near Threatened Species by the IUCN (Arija, 2010). The resulting improved protection led to a population increase between 2012 and 2014 to a total of 84 packs (Ministerio para la Transición Ecológica y el Reto Demográfico, 2014), or 2.8 packs per 1000 km2.

In Galicia, livestock breeding is one of the main agricultural activities: There are 1 million cows and 280,000 sheep and goats (López-Bao et al., 2013), accounting for 7% of the region's GDP (Instituto Galego de Estatística, 2018). 2614 wolf attacks were reported between 2005 and 2015 that affected cattle, sheep, goats, and horses (i.e. an average of 240 per year: Gutiérrez et al., 2017). Given the low economic margins in the livestock sector, wolf attacks may represent significant losses for individual farmers. To offset financial losses, the regional administration has established a system of financial aid (Wolf Management Plan or WMP) for those affected. The purpose of the WMP in Galicia is to guarantee the viability of wolves species in the territory, maintaining a stable population there by making them compatible with extensive livestock farming. It establishes lines of aid to alleviate damage caused by wolves and to give them value and turn them into an element that encourages rural and tourist development in the areas where they are found (Xunta de Galicia, 2009).

In western Galicia and northwestern Portugal wolves coexist not only with livestock and wild ungulates but also with populations of the endangered Galician feral horse *Equus ferus atlanticus* (Centro de Estudios y de Investigación sobre la Economía y la Organización de las Producciones Animales, CEREOPA, 1994; Lagos Abarzuza, 2013). This endemic subspecies is a free-roaming animal considered to be a remnant of the feral horses that have lived in the Iberian Peninsula since the Pleistocene (Bárcena, 2012). It is responsible for essential ecological processes such as the conservation of Atlantic heath (*Erica* spp.) priority habitats and the reduction of forest biomass (and thus of forest fires). It is also a common prey of the Iberian wolf and, consequently, a natural protection against depredation of traditional livestock.

Galician feral horses are considered semi-feral from a management point of view but are left unattended to roam free. The legal situation is complex because the administration (Xunta de Galicia, 2012) has made it compulsory to register all types of horses, and all animals must be microchipped and must undergo health controls. Their official "owners" argue that these are wild animals. What little human intervention they experience is limited to one or two days a year when the traditional festivities known as "Curros" or "Rapa das Bestas" are held: this is when the horses' manes are marked and cut and the youngest specimens are sold (Nuñez et al., 2016). Their commercial and economical interest is much lower than that of more traditional livestock species such as cows or sheep. Nowadays, the only use that is made of these horses aside from their role as part of a cultural tradition, is the sale of foals to the meat market. Under current regulations (Spaniush Official Gazette issue 89 of 13 April 2004), it is mandatory to identift, register and manage the livestock population, but Galician feral horses are excluded from this obligation.

Many diet studies have been conducted across the whole habitat range of grey wolves (Ansorge et al., 2006; Bangs and Shivik, 2001; Ciucci and Boitani, 1998) and many of them have investigated grey wolf food habits in relation to wild prey availability (e.g. Okarma, 1995; Meriggi and Lovari, 1996; reviewed by Janeiro-Otero et al., 2020). This has provided an ideal opportunity to analyze the extent to which they are opportunistic predators, and whether wild prey availability is linked to livestock depredation rates. To learn more about their use of food resources in human-populated areas, we studied the diet of grey wolves in three areas in Northwestern Spain. In this region wolves live mainly in highly populated areas with a high level of availability of anthropogenic food sources and traditional agricultural activities such as extensive livestock farming.

The aim of this study is to determine whether wolf diet varies in relation to the availability of wild prey and free-roaming feral horses. We collected and analyzed wolf scat from three different packs located in areas with different prey species and densities. Our initial hypothesis was that consumption of traditional livestock by wolves would be lower in the study areas where Galician feral horses were present, as the presence of free-roaming species is a dominant driver of wolf dietary preferences. The small variety of potential prey, the almost total absence of competition from other predators and the presence of a unique wild ungulate species in the Galician feral horse makes Galicia a particularly interesting conservation setting in which to test our hypothesis.

2. Material and methods

2.1. Study areas

We collected data on wolf diet composition in Galicia, a region in the north-west of Spain (Fig. 1).

2.1.1. Serra do Cando

This is a 5458 ha Site of Community Importance and Special Conservation Area under the European Union's Habitats Directive (92/43/EEC) located at the border between Pontevedra and Orense provinces. It is partly occupied by a wind farm and is bordered to the north by the Serra do Candán and the mountains of Costoia.

Its average altitude is 712 m a.s.l., with a maximum of 1000 m a.s.l. It has an Atlantic climate with low temperature fluctuations (annual average temperature 13 °C, monthly min = 3 °C, max = 23 °C) and abundant rainfall.

Most of the area is covered by gorse (*Ulex europeaus)*, carqueja (*Genista tridentate)* and heather bushes (*Calluna vulgaris)*. Forests are limited to oak (*Quercus robur)* groves and riverside forests formed mainly by ash (*Fraxinus)* and birch (*Betula)* trees in the lower areas and groups of red pine (*Pinus resinosa)* in the higher areas. There are commercial plots of eucalyptus (*Eucalyptus globules)* and pine (*Pinus sylvestris)* on the sloping areas.

Potential prey species for wolf at this site include the wild boar (*Sus scrofa)*, feral horse (*Equus ferus atlanticus)*, roe deer (*Capreolus capreolus)*, Iberian hare (*Lepus granatensis)*, squirrel (*Sciurus vulgaris)*, rabbit (*Oryctolagus cuniculus)*, hedgehog (*Erinaceus europaeus)* and small rodents.

The hunting bag in 2017 was 0.07 heads/km2 for roe deer and 0.64 heads/km2 for wild boar (Xunta de Galicia, 2017).

The livestock density on agricultural land outside the forest is medium in comparison to the other two study areas: 17 cattle/km2 (Instituto Galego de Estatística, 2018), 0.2 sheep/km2, 0.02 goats/km2 and 2 pigs/km2 (INE, 2009). A total of 498 feral horses were surveyed during the scat collection (Abilleria González et al., 2017).

2.1.2. Serra do Candán

This is another Site of Community Importance and Special Conservation Area under the European Union's Habitats Directive (92/43/EEC) that comprises 10,683 ha, located on the border between Pontevedra and Orense provinces. It is also partly occupied by a wind farm, and borders to the south with the Serra do Cando via the mountains of Costoia.

Its average altitude is 750 m a.s.l., with a maximum of 1017 m a.s.l. The Atlantic climate makes for moderate temperature fluctuations and abundant rainfall.

Fauna and flora are similar to Serra do Cando, with the main difference being the absence of feral horse populations.

The hunting bag in 2017 was 0.04 heads/km2 for roe deer and 0.49 heads/km2 for wild boar (Xunta de Galicia, 2017).

The livestock density on agricultural land outside the forest is high: 52.8 cattle/km2 (Instituto Galego de Estatística, 2018), 0.7 sheep/km2, 0.1 goats/km2 and 28.7 pigs/km2 (IGE, 2009).

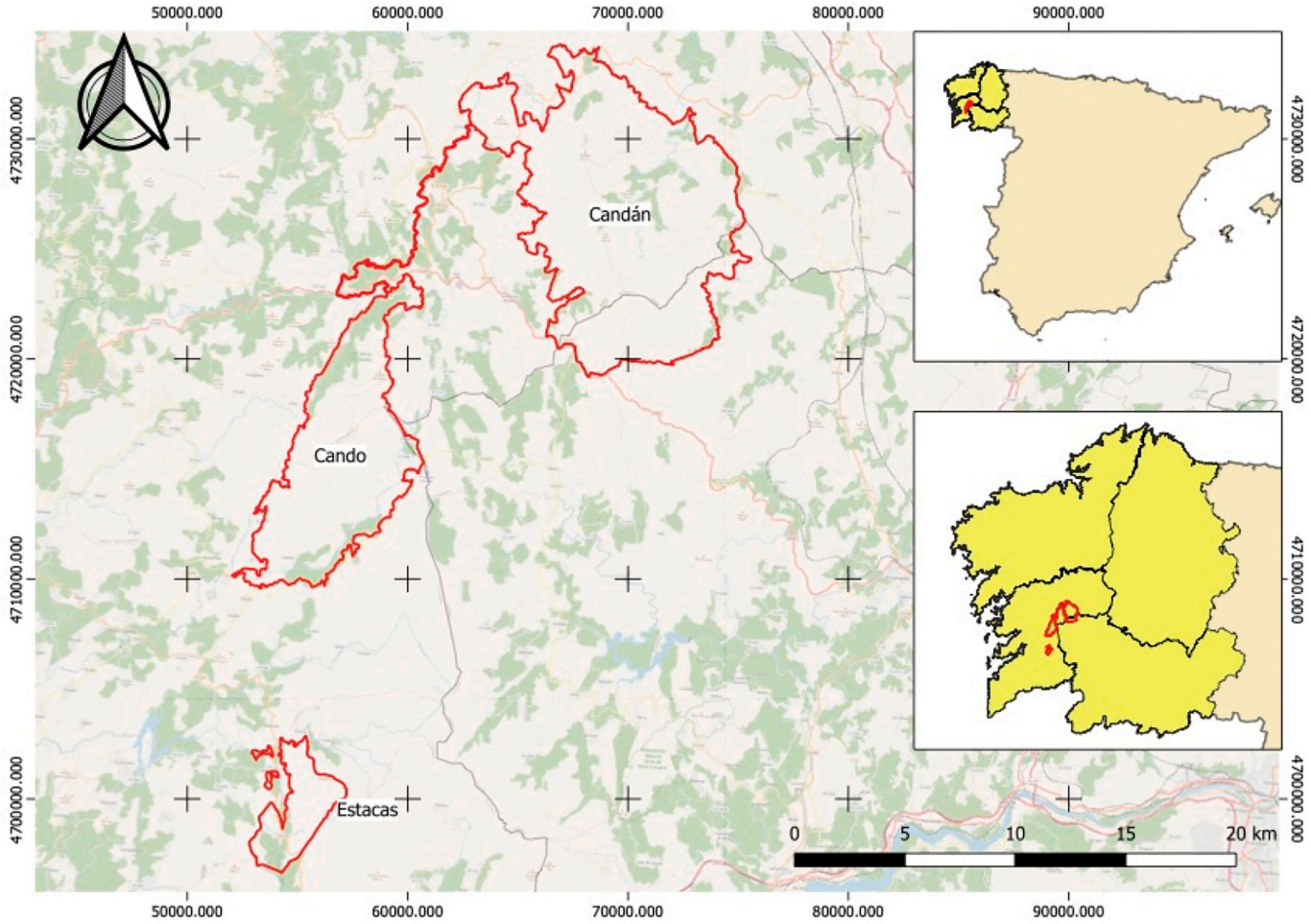

Fig. 1. Map of the study areas.

2.1.3. Estacas

This is an area of commonly-owned mountain land measuring 1405 ha, located in the southern part of Pontevedra province.

Its average altitude is 712 m a.s.l., with a maximum of 1061 m a.s.l. The Atlantic climate makes for moderate temperature fluctuations and abundant rainfall.

The vegetation varies from gorse, carqueja, heather and black broom scrubs, as in Cando and Candán, to oak groves and riparian forests. There are also find commercial plots of eucalyptus and pine.

Potential prey species are the same as in Serra do Cando: wild boar, feral horse, roe deer, Iberian hare, squirrel, rabbit, hedgehog, and small rodents.

The hunting bag in 2017 was 0.05 heads/km2 for roe deer and 0.64 heads/km2 for wild boar (Xunta de Galicia, 2017).

The livestock density on agricultural land outside the forest is low: 8 cattle/km2 (Instituto Galego de Estatística, 2018), 0.4 sheep/km2, 0.1 goats/km2 and 0.2 pigs/km2 (IGE, 2009). There were around 25 Galician feral horses this study area in 2017, and 11 more were relocated here from another area in June 2018 (according to a personal conversation with the common owners of the Estacas mountain land).

2.2. Scat transects

Each study area was subdivided into 2 × 2 km^2 cells using QGIS (QGIS Development Team, 2005). We designed transects of 2 km in each grid cell to ensure that the entire study area was covered homogeneously.

A total distance of 90 km (38 km at Cando, 46 km at Candán and 6 km at Estacas) was toured by Jeep, while crossroads were checked on foot since wolves mark their territories and the probability of defecation is higher there (Barja et al., 2004).

We collected samples between December 2017 and March 2019. The three study areas were visited at least once per season for a total of 29 days. We collected a total of 129 samples: 49 in Cando, 29 in Estacas and 52 in Candán. Scat was identified based on appearance, size, characteristic smell, presence of hair and/or large pieces of bones, absence of dry dog food or other artificial food and presence of other wolf traces in the immediate area (footprints, scratches). The type of habitat, site characteristics, and location of the deposition were recorded in situ at the time of collection.

To distinguish between wolf scat and scat from free-roaming dogs, only scat over 2.5 cm in diameter was collected (Barja, 2009). The presence of wolves was also confirmed via direct methods, using camera trapping in those areas where wolf scat was detected (Image 1), and by direct surveillance and acoustic detection (howling). A wolf expert from the regional government double checked samples of uncertain origin. Scat was conserved in 96% alcohol and stored for subsequent analysis.

2.3. Laboratory analysis

Only scats examined in the laboratory (n = 120) were included in quantitative analyses of diet. Each fecal sample was transferred entirely to a nylon stocking and soaked in water for 24–48 h, completely fragmented and then thoroughly filtered (0.7–0.5 mesh size) in running water several times to remove digestible material until only bone and hair remained in the stocking. The scats were rewashed and wrung to remove any remaining digestible material if necessary. The undigested

Image 1. Young wolf recorded in Serra do Candán, September 2018.

remains were placed on blotting paper, air-dried for 24 h and then weighed.

After washing and drying, the remaining material was spread out in a light-colored plastic tray and dispersed with forceps to ensure that the whole scat was examined (Spaulding et al., 2000). The point-frame method was used to select the hairs that would be identified in each scat (Chamrad and Box, 1964; Ciucci et al., 2004). A grid the same size as the plate was pre-marked with 25 points and placed over each scat. One fiber was randomly selected, pulled from each point and identified.

Fibers were classified into eight different prey categories including roe deer, wild boar, feral horse, cattle, sheep, hare, small mammals, and vegetation.

We identified mammalian hair by examining the medulla and cuticular surface structure under a 10 × 20 stereoscopic microscope (Zuzi 122–7) and comparing with a reference collection, keys and atlases (De Marinis and Asprea, 2006; Lagos Abarzuza, 2013; Lungu et al., 2007; Teerink, 2003). The presence of bones and hooves/claws in many scats helped in identification through comparison to reference material. The percentage volume of each item in a scat was estimated by eye to ±10%.

2.4. Diet estimation

We calculated the percentage of occurrence, i.e. the proportion of samples containing a given food item for each type of prey per scat. The percentage of occurrence method enables relative comparisons to be made of predator diet changes in time and space, but does not reflect the actual intake of particular prey (Klare et al., 2011; Trites and Joy, 2005). We therefore estimated biomass consumption in kg using the linear relationship established by Floyd et al. (1978) for wolves, with modifications by Weaver (1993). This method connects the presence of particular prey in scats with species body weight:

$$Y = 0.439 + 0.008^{*} X$$

where X is the average live mass of a prey species and Y is the prey mass per scat. We considered the average weights of adults in Galicia for feral horses (300 kg), cattle (600 kg), sheep and domestic goats (28,5 kg), roe deer (24 kg), wild boar (67 kg), domestic pigs (250 kg), hare (2 kg), and small mammals (0.02 kg).

We then multiplied the values obtained in the above equation by the number of scats per prey to calculate the relative biomass per prey species:

$$\text{Relative biomass (kg)} = \text{Scats per prey}^{*} (0.439 + 0.008^{*} X)$$

We then divided this figure by the total relative biomass consumed at each study site to obtain the percentage of biomass per prey species:

$$\%\text{biomass} = \sum \text{Relative biomass} / \text{Total relative biomass}^{*} 100$$

Levins' index of niche breadth (Levins, 1968) was calculated according to the following formula:

$$B = \frac{1}{\sum p_j^2}$$

Where B is the Levins measure of niche breadth and p_j the proportion of prey items from food category j.

The Levins measure was then standardized on a scale of 0 (specialist predator–strong specialization in one group of prey) to 1 (generalist predator–opportunistic preying on all groups of prey), according to Hurlbert's (1978) formula:

$$B_A = \frac{B - 1}{n - 1}$$

Where B_A is Levins' standardized Food Niche Breadth, B is Levins' Food Niche Breadth and n is the number of prey items found in the diet.

Finally, we calculated Ivlev's (1961) electivity index (D), as modified by Jacobs (1974), to measure wolf prey preference from −1 (total avoidance of a species) through 0 (no selection)to +1 (maximum positive selection):

$$D = \frac{(r_i - p_i)}{(r_i - p_i - 2r_i p_i)}$$

where r is the proportion of a given prey species in the wolf diet and p is the proportion in the free-living population.

3. Results

A total of 129 scats were collected in the three study areas, but nine were not included in the dietary analysis because they were composed of 100% organic matter, which was discarded after washing.

Samples were mostly found in areas surrounded by forest and scrubland or only scrub, usually gorse. Scats were mostly (>70%) placed on vegetation at a greater height than grass. Only in the samples from Estacas were they evenly distributed on both vegetation and bedrock surfaces (Fig. 2).

The standardized Levin's Food Niche Breath was higher in Candan (BA = 0.49), indicating a tendency towards more generalist feeding habits. Estacas (BA = 0.28) and Cando (BA = 0.05) were closer to 0, showing a tendency towards more specialized feeding habits.

3.1. Serra do Cando

Ivlev's electivity index calculated for this study (Fig. 3) shows a greater selection of wild boar (D = 0.80) and wild horse (D = 0.43) in Cando. Cattle were negatively selected, taking into account their availability in the study area, i.e. they were consumed less than expected from their availability (D = −0.94). Considering sheep, cattle and domestic pig availability and densities in the study area and given that these species were not identified in any of the samples analyzed, Ivelv's index showed that wolves never select any of these species (D = −1).

Feral horses were found to be the most widely consumed species (84% biomass) and also the most frequent prey species (81% FO). They are followed by wild boar (7.7% biomass), due to its smaller relative biomass (9.75 kg) despite the relative high FO (21.28%). Small mammals were also quite common (13% FO), but accounted for a much lower total biomass percentage (2.1%) due to their low relative biomass (2.6 kg). The only traditional livestock species found in the scats was cattle with 2.1% FO and 4.2% of the total biomass consumed. Hare appeared with an FO of just 2.1%, accounting for only 0.36% of the total biomass. Vegetation appeared in 6.4% of the samples in Cando (Table 1, Fig. 4).

3.2. Serra do Candán

Ivlev's electivity index in Candan (Fig. 3) shows an extremely high selection towards roe deer (D = 0.99), domestic goat (D = 0.96), wild boar (D = 0.96) and domestic sheep (D = 0.79). Cattle (D = −0.23), and

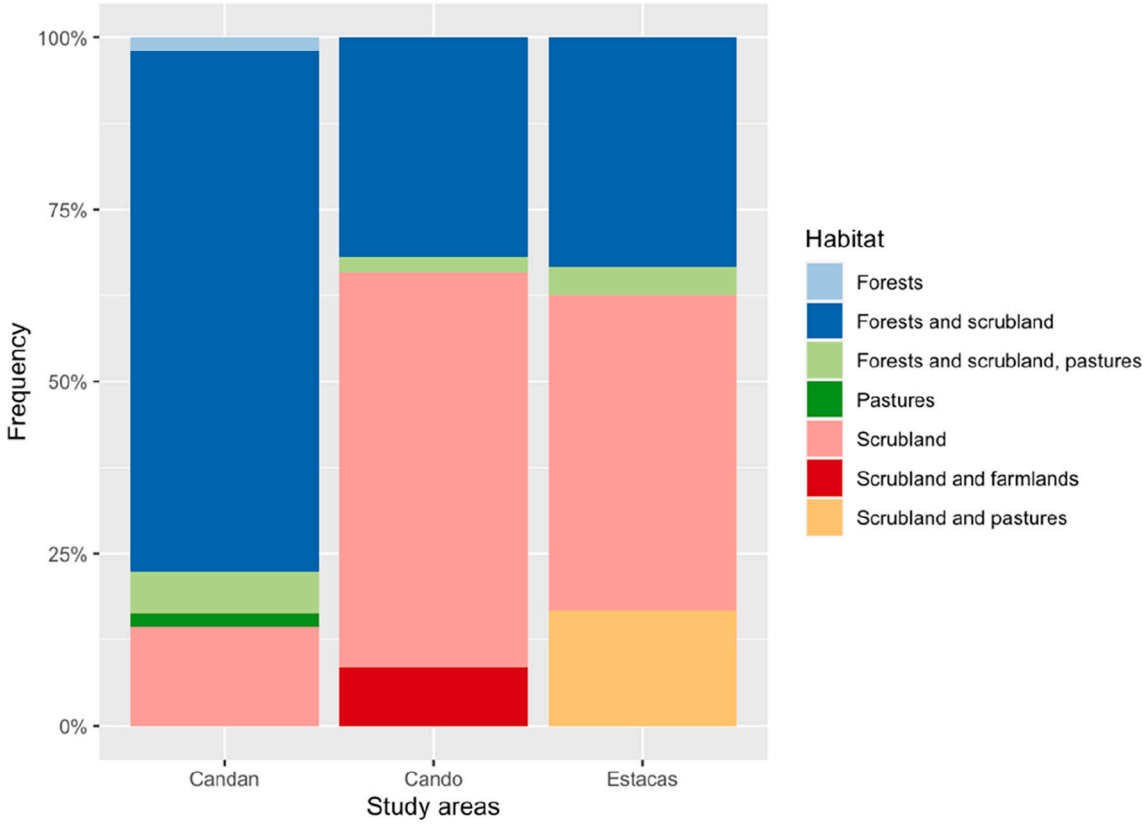

Fig. 2. Characteristics, habitat type (a) and location of scats on the ground (b), where scat was found at all three study sites. The relative frequency was calculated for each study site: Serra do Candán (n = 49), Serra do Cando (n = 47), and Estacas (n = 24).

domestic pigs (D = −0.79) were negatively selected.

In the Serra do Candán, livestock was the primary food source, with cattle the most heavily consumed species (7.7% biomass and 39% FO). Other domestic species were also present in lower percentages (domestic goat with 1.5% of biomass, sheep with 2.1% of biomass and pigs with 3.8% of biomass). Wild boar was the second most preyed species (9.77% of biomass and 26.53% FO). Roe deer and small mammals had similar occurrence levels (14.29% FO) but, as expected, very different percentages of biomass (3.41% for roe deer and 2.56% for small mammals). In this particular study area, there was a relatively high percentage of vegetation present (20.41% FO) (Table 1, Fig. 4).

3.3. *Estacas*

In Estacas, Ivlev's electivity index (Fig. 3) results in a high selection towards domestic goat (D = 0.84), wild boar (D = 0.56), and wild horses (D = 0.51). As in Cando, cattle were negatively selected (D = −0.87). Roe deer, sheep and domestic pigs were not found in the samples analyzed, so Ivelv's index shows that wolves never select any of these species (D = −1) despite their availability.

Similarly to Serra do Cando, the most common species found in the scat is once again the feral horse (77.12% of biomass and 58.33% FO). Wild boar is the second most frequent species (16.67% FO), but its biomass percentage (7.57%) is lower than that of cattle (10.17%), accounting for the lowest percentage (4.17% FO). Small mammals have a considerable presence in the samples (12.50% FO), but a very low biomass percentage (2.37%). Besides cattle, domestic goats were estimated as accounting for 2.59% of the total biomass. They appeared in 8.33% of the samples analyzed (Table 1, Fig. 4).

4. Discussion

There is global interest in restoring large carnivores not only for their conservation but also for the ecosystem services that they provide (Terborgh and Estes, 2010; Ripple et al., 2014). But the conservation and restoration of large carnivores in general, and wolf populations in particular, requires an understanding of the factors that cause them to depredate livestock and thus induce human-carnivore conflict. Conserving both suitable habitats and prey species is key in restoring large carnivores to their natural ranges.

The wolf is historically considered an opportunist species (Carbyn, 1988; Salvador and Abad, 1987). A trophic opportunist consumes whatever food is most abundant, changing its diet depending on food availability. It is believed that when the abundance of one prey type diminishes, opportunist predators begin to prey on a more abundant species (Glasser, 1982).

Wolves are forced to prey on livestock in areas with low-to-zero wild prey availability, as is the case in some regions of the Iberian Peninsula (Cuesta et al., 1991; Torres et al., 2015) and Portugal (Vos, 2000), in Greece (Migli et al., 2005), in the north of Italy (Meriggi and Lovari, 1996), and in the northeast of Belarus (Sidorovich et al., 2003). However, new studies have shown a predisposition towards wild species, even when they are present in lower densities than livestock (Meriggi and Lovari, 1996; Urios et al., 2000; Sidorovich et al., 2003; Janeiro-Otero et al., 2020). This preference could be explained by wolves' ability to size up the cost-benefit ratio of each hunt.

Domestic species can be more energy-demanding than wildlife. Preventive measures such as guard dogs, fences, and barns, and the fact that wolves are more exposed to human persecution due to their proximity to populated areas increase their energy investment.

Our results are aligned with other studies that show that local conditions, rather than wolf numbers, play a key role in determining the

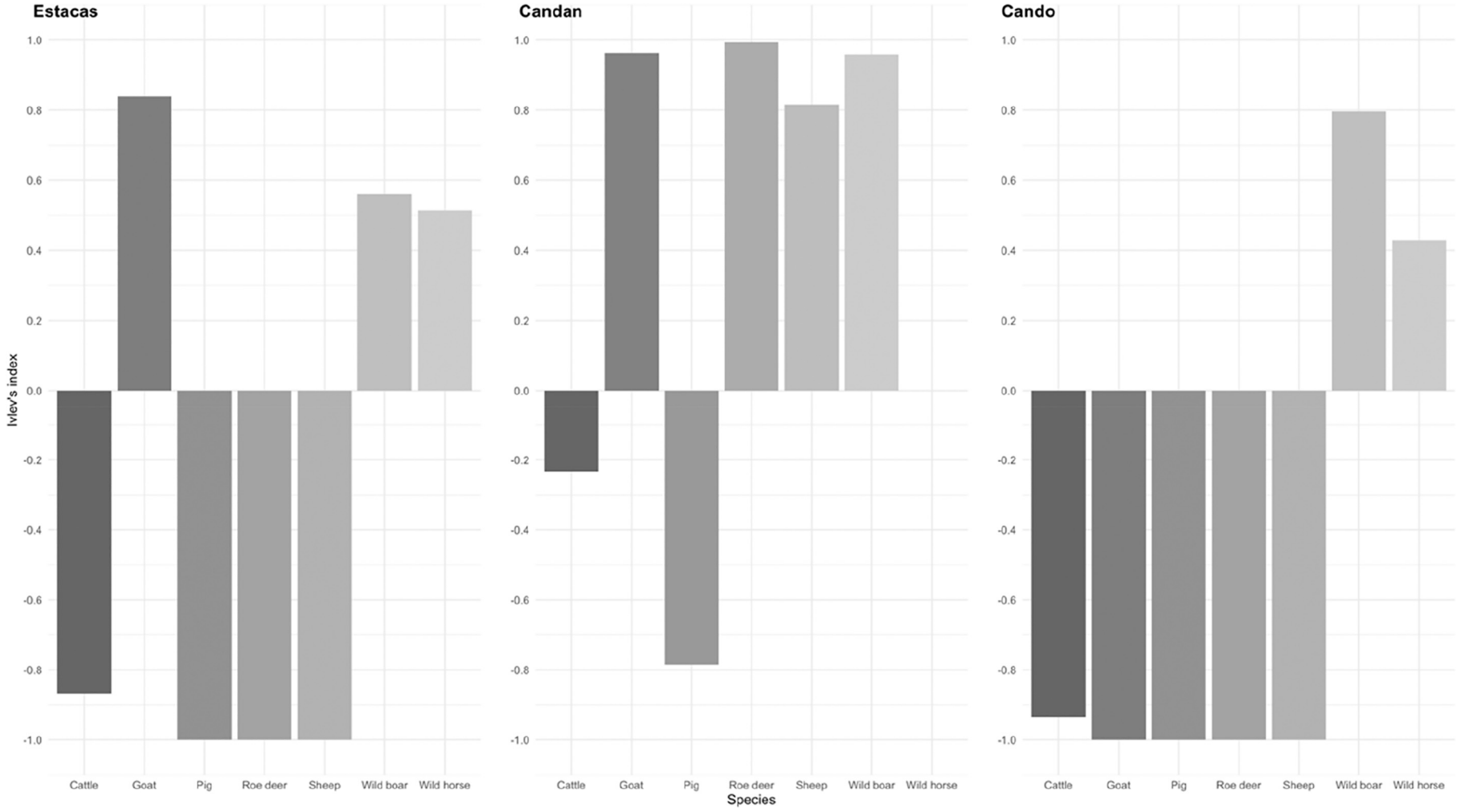

Fig. 3. Prey selectivity (Ivlev's D index) calculated for roe deer (*Capreolus capreolus)*, wild boar (*Sus scrofa)*, Galician wild horse (*Equus ferus atlanticus),* domestic goat (*Capra hircus)*, sheep (*Ovis aries)*, cattle (*Bos Taurus)* and domestic pig (*Sus scrofa domesticus)* based on Iberian wolf scat analysis ($n = 129$) in three areas in Galicia, in north-west Spain. Wolves select species with positive index values, while species with a negative index are negatively selected.

Table 1
Number of occurrences per scat (n), frequency of occurrence (%), and relative biomass (% and kg) of food categories in the three study areas – Serra do Cando, Estacas and Serra do Candán – collected in December 2017–March 2019, based on 120 scats.

Study area	Species	n	FO %	Biomass %	Relative Biomass kg
Serra do Cando	Roe deer (*Capreoulus capreolus)*	0	0.00	0.00	0.00
n = 47	Wild boar (*Sus scrofa)*	10	21.28	7.74	9.75
	Galician wild horse (*Equus ferus atlanticus)*	38	85.65	84.22	107.88
	Domestic goat (*Capra hircus)*	0	0.00	0.00	0.00
	Cattle (*Bos taurus)*	1	2.13	4.16	5.24
	Sheep (*Ovis aries)*	0	0.00	0.00	0.00
	Domestic pig (*Sus domestica)*	0	0.00	0.00	0.00
	Hare (*Lepus granatensis)*	1	2.13	0.36	0.46
	Small mammals	6	12.77	2.09	2.63
	Vegetation	3	6.38	–	–
	Domestic species	1	2.13	4.16	5.239
	Wild species	46	117.02	95.84	120.72
Estacas	Roe deer (*Capreoulus capreolus)*	0	0.00	0.00	0.00
n = 24	Wild boar (*Sus scrofa)*	4	16.67	7.57	3.90
	Galician wild horse (*Equus ferus atlanticus)*	14	58.33	77.12	39.75
	Domestic goat (*Capra hircus)*	2	8.33	2.59	1.33
	Cattle (*Bos taurus)*	1	4.17	10.17	5.24
	Sheep (*Ovis aries)*	0	0.00	0.00	0.00
	Domestic pig (*Sus domestica)*	0	0.00	0.00	0.00
	Hare (*Lepus granatensis)*	0	0.00	0.00	0.00
	Small mammals	3	12.50	2.37	1.32
	Vegetation	0	0.00	–	–
	Domestic species	3	12.50	12.75	6.57
	Wild species	21	87.50	87.25	44.96
Serra do Candan	Roe deer (*Capreoulus capreolus)*	7	14.29	3.41	4.42
n = 49	Wild boar (*Sus scrofa)*	13	26.53	9.77	12.68
	Galician wild horse (*Equus ferus atlanticus)*	0	0.00	0.00	0.00
	Domestic goat (*Capra hircus)*	3	6.12	1.54	2.00
	Cattle (*Bos taurus)*	19	38.78	76.74	99.54
	Sheep (*Ovis aries)*	4	8.16	2.06	2.67
	Domestic pig (*Sus domestica)*	2	4.08	3.76	4.88
	Hare (*Lepus granatensis)*	1	2.04	0.35	0.46
	Small mammals	7	14.29	2.56	3.07
	Vegetation	0	0.00	–	–
	Domestic species	28	57.14	84.10	109.09
	Wild species	21	57.14	15.90	20.62

extent of attacks (Kaczensky, 1996; Gutiérrez et al., 2017). Factors associated with increased risk of predation include habitat type (Jędrzejewski et al., 2005; Treves et al., 2004), calving in forested or brushy pastures (Paul, 2000), limited availability of wild prey (Sidorovich et al., 2003), lack of human surveillance, guard animals or other preventive measures (Kaczensky, 1996), and inadequate disposal of livestock carcasses (Mech et al., 2000).

We have tested the hypothesis that depredation on traditional livestock by grey wolves in Galicia may be lower under circumstances where wild prey and free-roaming horses are abundant at a local scale, in a very specific scenario. Our results suggest that grey wolves feed on feral horses when they are available, and that this drastically reduces depredation of more economically important species of livestock in those areas. Levin's and Ivlex's index values seem to support this hypothesis.

Feral horses not only take the edge off livestock attacks but also bring other environmental benefits. Their presence increases the richness and diversity of plant species (Fagúndez et al., 2017) and limits the growth of gorse (Aldezabal et al., 2013), thus reducing the risk of forest fires because gorse generates large quantities of highly flammable biomass (Madrigal et al., 2012). Feral horses are also a representative feature of Galician tradition and heritage (Nuñez et al., 2016). Predatory selection of feral horses has been observed before elsewhere in the north of the Iberian Peninsula, specifically is in an area in the west of Asturias (Llaneza et al., 1996), and in northern Portugal (Vos, 2000). In Mongolia there are examples of wolves preying on free-roaming horses (Hovens and Tungalaktuja, 2005; Hovens et al., 2000) and on the recently reintroduced population of Przewalski horses (*Equus przewaslki)* (Bandi et al., 2012).

Serra do Candán, the only study area without Galician feral horses, is also the area where most domestic species other than cattle and goats (sheep and pigs) were found in the wolf diet. As expected, wolf depredation on traditional livestock was found to be greater there than in Estacas and Serra do Cando, suggesting that the absence of feral horses may be a reasonable predictor of the extent of livestock depredation by wolves. This is also the area with the highest livestock consumption despite being the only one where roe deer was consumed. This could be due to the generally significantly lower densities of roe deer in comparison to Galician feral horses in the whole of Galicia. Even in this case, roe deer were actively consumed, despite being rare.

Serra do Cando and Estacas show very similar diet compositions. The feral horse population is much greater in Serra do Cando (498 individuals versus 36 in Estacas) but this is offset by the size difference between the two areas. The dispersal capacity of the wolf must be considered. Wolf packs usually hunt within a territory and it is not uncommon for territories to be as large as 130 km2 or even more where prey is scarce. Wolves often cover large areas to hunt, traveling as far as 50 km a day (Harrington and Mech, 1979). Therefore, the wolf pack in Estacas most probably not only feeds on feral horses there but also on those in neighboring areas.

The high consumption of cattle in comparison to other domestic species may be due to their greater numbers (up to 53 heads/km2 in the Candán area) to their heavy weight, and to the fact that they are left unattended to graze freely for long periods of time where they are most vulnerable to grey wolf attacks. Goats and sheep are usually kept in barns overnight, which makes them less vulnerable than cattle. In Galicia, 99% of pigs are housed in sties, which are inaccessible to wolves; grey wolves may scavenge on dead animals at the open carcass dumps of farms (Chavez and Gese, 2005), which would explain why pig was found in the scat samples collected in Serra do Candán.

Like other studies carried out in the Iberian Peninsula (Llaneza et al., 1996), we find that the contribution of small mammals to wolf diet is largely irrelevant. Small mammals are not worth hunting in energy terms as they provide few calories; only when larger prey is scarce may rodents be found in wolf scat. Elsewhere in Spain, the consumption of this type of prey by wolves is greater (Salvador and Abad, 1987; Urios et al., 2000), but their low biomass makes them an unimportant part of the wolf's diet. The site characteristics and the location of scats seems not to have any influence on the type of prey consumed.

4.1. *Conservation implications*

To conclude, this case study illustrates that damage to livestock is moderate in Cando and Estacas despite their high predator densities than in Candán. Our findings suggest that measures should be taken to encourage the conservation of Galician feral horses, not just because they are essential as alternative prey targets to the domestic livestock

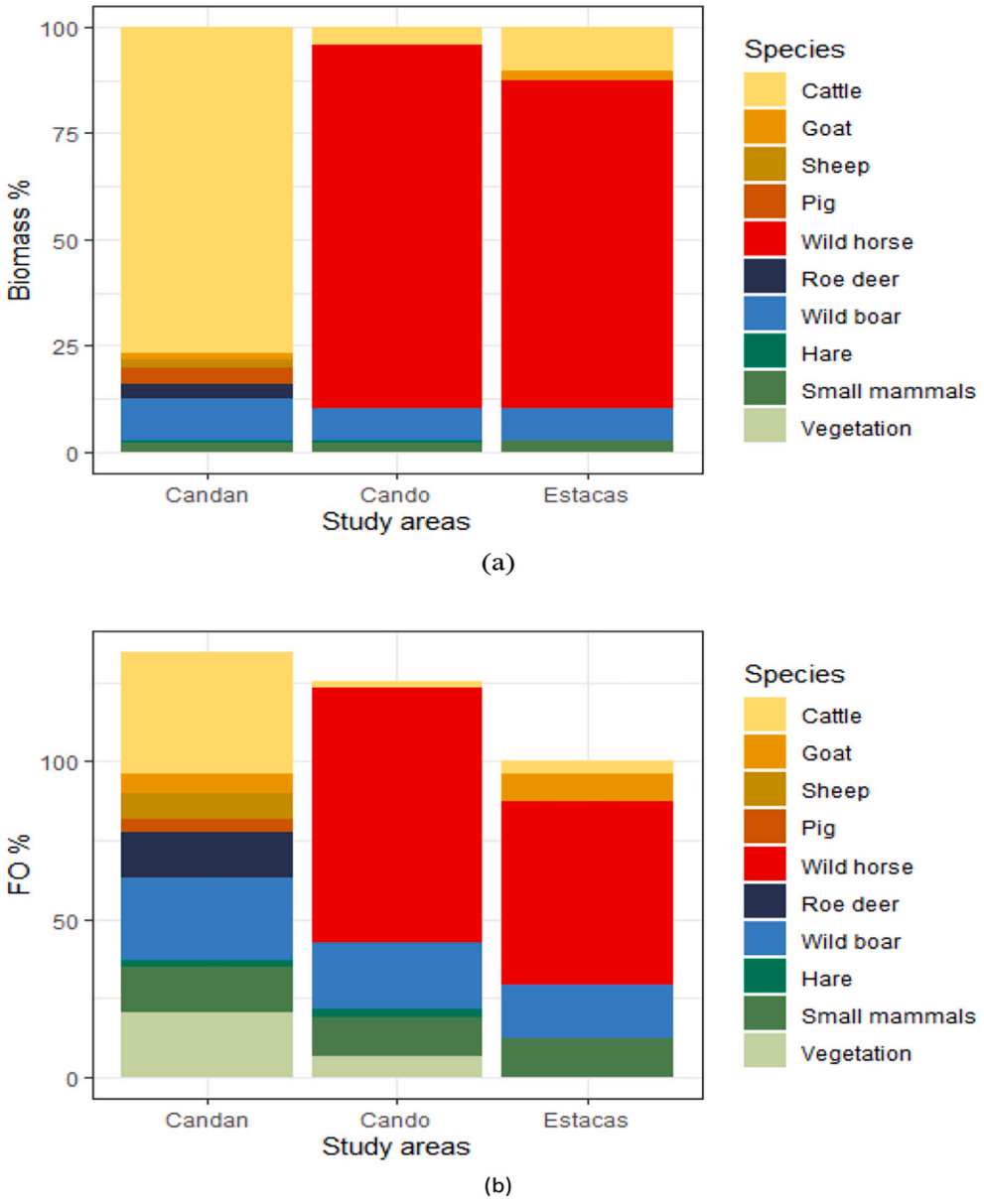

Fig. 4. Comparison by biomass % (a) and FO % (b) of domestic and wild prey species present in grey wolf scat in the three study areas. Biomass consumption is estimated by linking the presence of prey in scats with species body weight. The sum of prey occurrence can exceed 100% because some scat contained more than one species type.

that comprise the main source of income for local farmers and cattle breeders, but also because of their role in reducing the forest biomass that causes forest fires.

The only economic benefit from Galician feral horses is the sale of meat for an average of €1.5/kg (Fernández and Rodríguez, 2010), a very small amount in comparison to the average of €4.6/kg for cattle. Nor do feral horses provide farmers with the additional income that they can obtain from other products derived from traditional livestock species such as wool or milk. Ensuring a stable population of feral horses in the study areas could drastically reduce the number of attacks on more economically important livestock, and therefore the financial losses of farmers, and result in a greater acceptance of and tolerance towards the wolf, thus also reducing the social conflict between farmers and wolves.

On the other hand, the complexity of the financial aid provided by the Galician Administration to farmers after a wolf attack must be mentioned. First, the carcass must be reported not later than 24 h after the attack and a forest ranger must be able to certify (by checking for wolf signs and examining the type of wounds suffered by the animal) that the attack was by a wolf. Secondly, the resulting financial aid can take more than a year to come through, which means a major economic impact for the farmer.

But encouraging the conservation and development of wild species and feral horse populations is not be the only action that should be taken to mitigate human-wolf conflict in the study areas. Unattended livestock may be subject to repeated attacks in the same area because grey wolves may return to the kill site to keep on feeding, finding new vulnerable prey in the process (Karlsson and Johansson, 2010). Measures to remedy this should include prevention methods such as electric fences or guard dogs, which are one of the best ways to prevent substantial losses and are particularly appropriate where there are wolves in proximity to unfenced pastures. Greater flexibility and assistance from the administration is also needed. Funds could be created under which part of the money from animal insurance can be used to create a guarantee fund to pay compensation for attacks on livestock.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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