Review

HORSES AS PREY OF WOLVES: WORLDWIDE PATTERNS AND MANAGEMENT IMPLICATIONS

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1. Introduction

The long-standing nature of the relationship between horses and wolves is evidenced by the fossil record from Eurasia and North America, in which ancient wild horses co-occur with wolf-like canids since the early Pleistocene, 0.8–2.6 million years ago (Flower and Schreve, 2014; Warmuth et al., 2012). Wolves *(Canis lupus)* mainly hunt large herbivores, and horses have similar body size and anti-predatory behaviour as other prey species that they positively select, such as red deer *(Cervus elaphus)* (Llaneza and López-Bao, 2015; Mech and Peterson, 2003). Thus, wolves may have developed a trophic specialisation on horses as a result coexistence over millennia.

Horse domestication began approximately 4,000 years BC in the Eurasian steppes (Outram et al., 2009) in a process that seemingly allowed the persistence of local stocks of wild horses. In the Iberian Peninsula, for example, evidence of the genetic contribution of wild horses to local domestic horses (Warmuth et al., 2011) suggests the survival of wild horse populations until a few thousand years ago and, therefore, the ancient predator-prey relationship presumably endured until recently. Most wild horse populations subsequently became extinct and domesticated horses, usually larger in size and well protected as valuable livestock (Warmuth et al., 2012), are less available to wolves as prey even where their ranges overlap.

Currently, as domestic horses are frequently kept close to human settlements and protected from predators, few populations of feral or free-ranging horses have been documented to suffer predation. Based on 95 bibliographic references published in 1976–2021 and reporting horse consumption, compiled using the online search engine Google Scholar, horses were killed or consumed by a total of 11 carnivore species in 132 study sites worldwide (Fig. 1).

The most frequent predator of horses in Eurasia and North America appeared to be the wolf. Although wolf predation on horses is generally low, it can be significant where horses are grazed extensively and there are low densities of wild prey, such as in central Asia (Balajeid Lyngdoh et al., 2020; Hovens et al., 2000; Hovens and Tungalaktuja, 2005) and southern Europe (Fico et al., 1993b; Lagos and Bárcena, 2018; Vos, 2000). In these areas, horse depredation raises management implications since it frequently involves important economic losses to people dependant on horse husbandry for their livelihoods and who there-

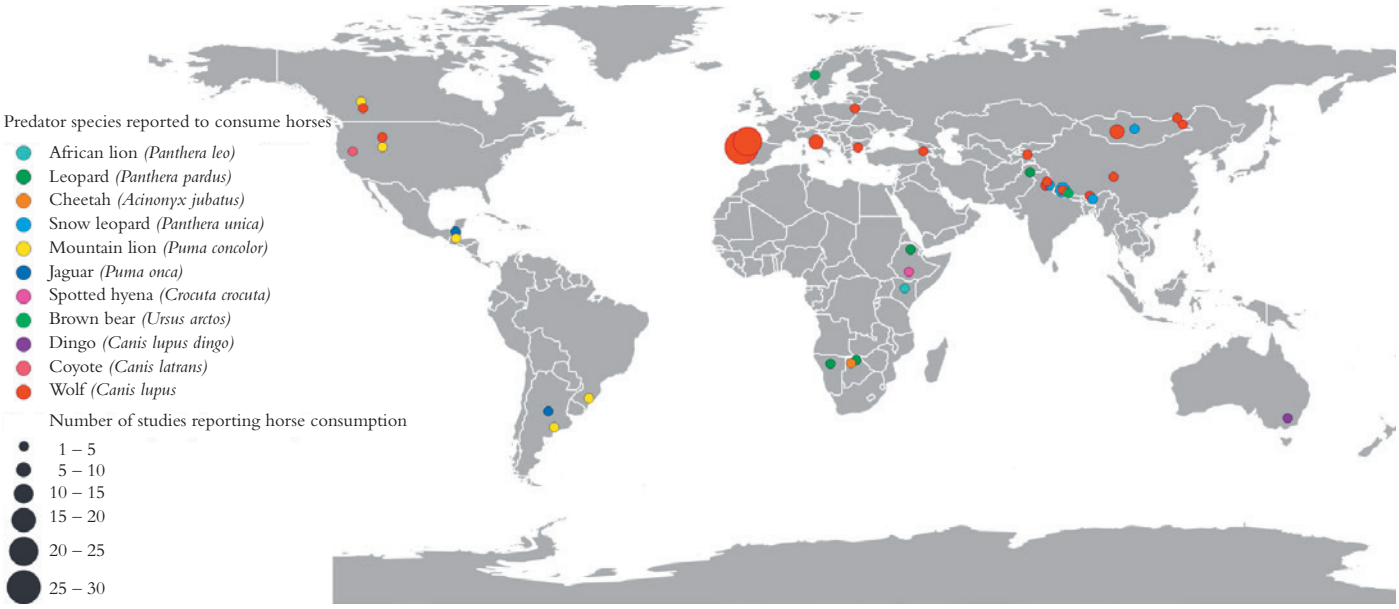

Fig. 1 Locations of 132 study sites[1] (circles) with reported horse consumption by various carnivore species worldwide.

fore become antagonistic towards wolves (Álvares, 2011; Hovens et al., 2000). In Europe, damage to horses is less widespread and of a much lower intensity than that to other livestock species such as sheep, cattle and goats, although there is regional variation (Linnell and Cretois, 2018). Although damage to horses by wolves is fully compensated in most European countries, it is only reported in some southern and Baltic countries, with higher relevance in Portugal and Italy (Fig. 2).

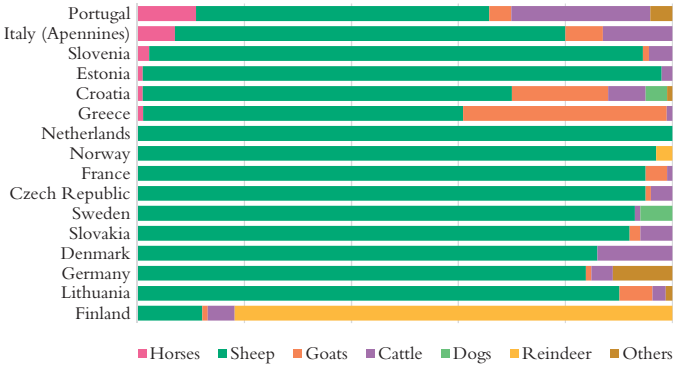

Fig. 2 Relative proportion (%) of livestock species for which compensation was paid due to wolf damage in Europe by country. *Source: adapted from Linnell and Cretois (2018)*

Wolf dietary studies also document the low prevalence of horses as a prey item. A recent review of wolf diet worldwide found that horses were only an occasional prey, particularly in North America, where livestock species, including horses, comprised 8% of wolf diet. In Eurasia, horses comprised approximately 17% of wolf diet (Newsome et al., 2016). However, studies of wolf diet often disregard occasional prey items such as horses, categorising them as "other prey", which are poorly described and quantified. Therefore, overall patterns of intensity and geographic occurrence of horses as wolf prey are still largely unclear, despite their potential management implications.

Besides domestic horses, endangered wild equids are also preyed on by wolves, which has important conservation implications since it might hinder population growth and recovery (van Duyne et al., 2009). This is the case of Przewalski horses and Mongolian Kulans in central Asia (Fig. 3), where wolf attacks are reported to limit population size and induce behavioural responses such as changes in group size and structure (van Duyne et al., 2009; Feh et al., 1994). Efforts to reintroduce Przewalski horses in Hustai National Park, central Mongolia, were greatly impacted by the presence of wolves, with 40% of foals born each year being killed, despite Przewalski horses comprising only a small portion of wolf diet in the area (van Duyne et al., 2009). It has been hypothesised that the social organisation of Kulans, including the establishment of bonds between males and females forming family groups and increased group size in winter, is an adaptation to wolf predation risk that allows better defence of offspring (Feh et al., 1994).

[1] Study sites were in Portugal (27), Spain (22), Mongolia (12), Nepal (11), Italy (8), USA (7), China (7), Ethiopia (6), Canada (5), Botswana (4), India (4), Argentina (2), Australia (2), Guatemala (2), Kenya (2), Poland (2), Bhutan (1), Brazil (1) Bulgaria (1), Pakistan (1), Namibia (1), northern Europe (1), Russia (1), Tajikistan (1) and Turkey (1).

Fig. 3 Wild equids reported as being regular prey for wolves in central Asia. Left: Kulan *(Equus hemionus kulan)*. Right: Przewalski Horse *(Equus ferus przewalskii)* *(Photos: Petra Kaczensky for Kulan; Patricia Moehlman for Przewalski horse)*

Although poorly studied, wolf predation on domestic horses could induce similar population effects or explain social and behavioural traits as for wild equids. In Galicia, northwest Spain, free-ranging mountain ponies, particularly foals, can locally comprise almost 95% of wolf diet (López-Bao et al., 2013), with 59% of foals born each year consumed by wolves (Lagos, 2013). The same pattern is also found in northern Portugal, where free-ranging mountain ponies reportedly comprise over 80% of wolf diet (Casimiro, 2017; Freitas, 2019). Lagos (2013) observed higher vulnerability of foals from mares with less stable social bonds, in small sized bands (< 9 individuals), born at the end of the reproductive period and with variable coat colour. Apart from these studies, there is little information on patterns and determinants related to ecological interactions between wolves and domestic horses.

In order to contribute to research supporting management actions, particularly in areas with high levels of predation, this article aims to:

1. conduct a worldwide review on where and how intensively horses are consumed by wolves;
2. determine the main geographical areas and socio-ecological conditions where horses are most prevalent as wolf prey;
3. discuss general patterns and ecological aspects of wolf predation on free-ranging horses; and
4. provide management recommendations to mitigate damage.

2. Consumption of horses by wolves worldwide

We conducted a literature review and compiled wolf dietary studies published in 1976–2021. We used Google Scholar with the following keywords: "wolf diet", "wolf feeding habits", "horse predation", "horse consumption", "wolf prey selection". Spatial patterns at a global level were represented based on the number of studies per country with reported consumption[2] of domestic, feral or wild horses, including those without proper quantification of horses as a wolf prey item, such as data based on interviews with horse owners, percentage of consumed biomass and percentage of occurrence.

The intensity of horse consumption by wolves was quantified using reported frequency of occurrence (FO) and, if more than one value was presented for the same study area, we estimated the average value. We considered seven colour-coded classes of consumption based on reported values of FO: 0–10%; 10–20%; 20–30%; 30–40%; 40–50%; 50–60%; > 60%. We also considered studies reporting values of prey selection for horses based on Ivlev's electivity index, D (Ivlev, 1961). Geographical coordinates for each study were retrieved from the article or, if specific coordinates were not available, were estimated from study area location.

Horses were reported as a wolf prey item in 70 (55%) of 128 wolf dietary studies worldwide, representing 89 study sites in 15 countries (Fig. 4A). FO values were reported from 63 (71%) of these sites,

[2] It is important to note that many studies do not distinguish between predation and scavenging.

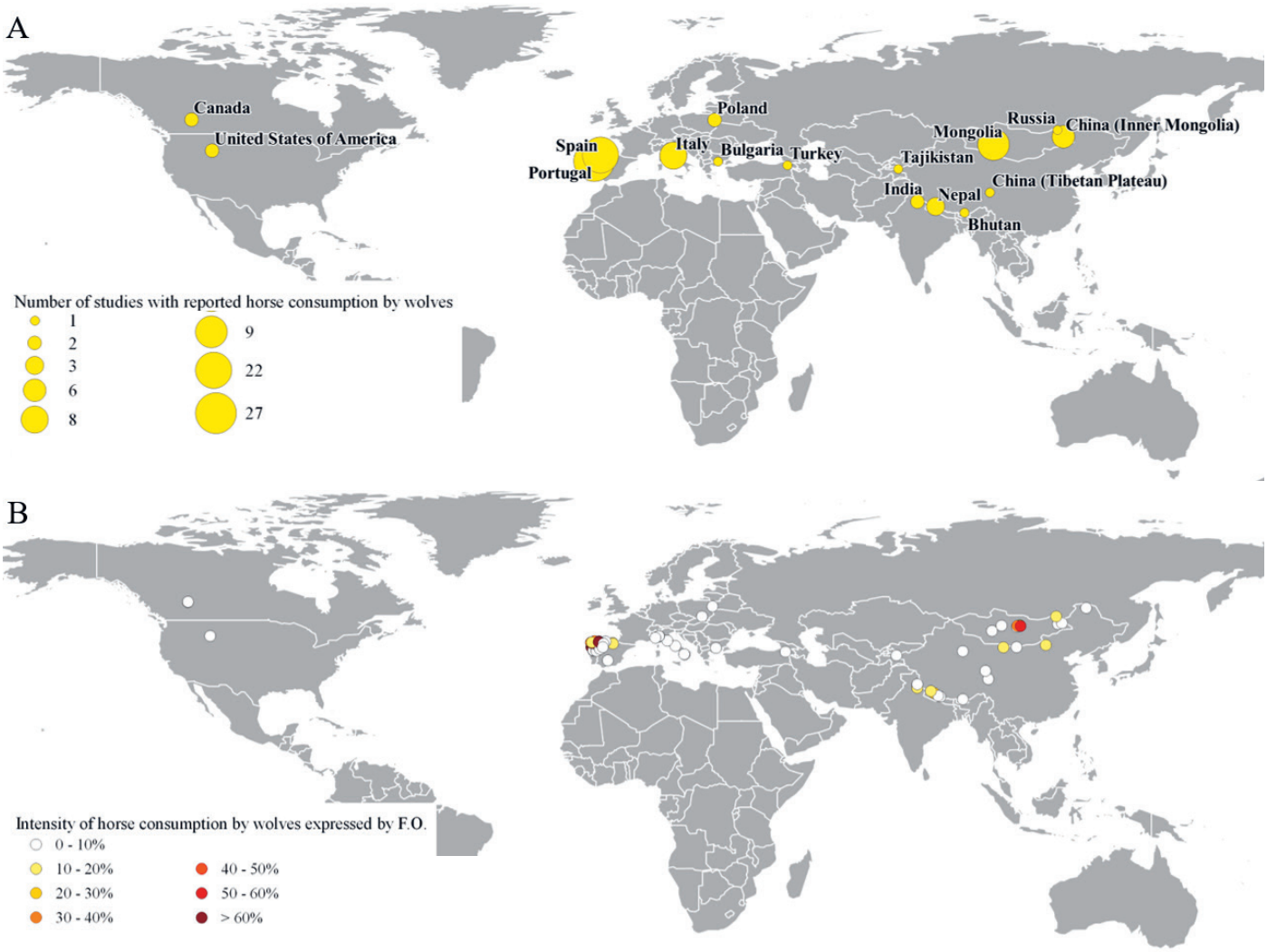

Fig. 4 Locations of 89 study sites with reported horse consumption by wolves worldwide, indicating the number of study sites per country[3] (A) and the reported frequency of occurrence (FO) of horses in wolf diet (B).

allowing quantification of the intensity of horse consumption (Fig. 4B), although prey selection was quantified in only seven (8%) of them. Horse consumption in eastern European countries such as Poland and Bulgaria, in Turkey and in the Himalayan region of India, Nepal and Bhutan was mostly documented as occasional and with low intensity (<20% of wolf diet). In these areas, horses are extensively grazed during the day and corralled or kept near houses at night. Similarly, only two studies in Canada and one in the USA mentioned horses in wolf diet with low frequency (1% and 5%, respectively), which is possibly attributable to higher availability of wild prey, large size of local horse breeds, strict husbandry practices and absence of feral horses within wolf range. In North America, domestic horses are usually well guarded and confined at night, reducing the risk of wolf attacks (Musiani et al., 2003). There are very few populations of feral horses in the current wolf range in the USA (Boitani et al., 2018; Bureau of Land Management, 2014) and, even where wolf and feral horse ranges overlap, predation has not been reported.

Horses reportedly comprised >30% of wolf diet only in Central Asia, Italy and the Iberian Peninsula, where small-sized horses (≈300 kg) are raised under free-roaming systems and thus accessible to wolves through predation or scavenging. In some studies, horses comprised >70% of wolf diet and were positively selected in relation to other wild and domestic prey, meaning that wolves consumed horses in a higher proportion than their local availability. All studies that documented prey selection reported high positive values reflecting strong selection of horses, such as in Portugal (D=0.62 to 0.99; Álvares, 2011; Casimiro, 2017), northern Spain (D=0.87 to 1.00; Lagos and Bárcena, 2018) and Mongolia (D=0.12 to 0.86; Balajeid Lyngdoh et al., 2020; van Duyne et al., 2009). This positive selection seemingly relates to sev-

[3] Study sites were located in Portugal (27), Spain (22), Mongolia (9), Italy (8), China – Inner Mongolia (6), Nepal (3), Canada (2), India (2), Poland (2), USA (2), Bhutan (1), Bulgaria (1), China – Tibetan Plateau (1), Russia (1), Tajikistan (1) and Turkey (1).

Fig. 5 Horse attacked by wolves in Mongolia, showing a bite wound to the hind leg. *(Photo: Hovens and Tungalaktuja, 2005)*

eral factors that can increase the vulnerability of free-ranging horses to wolf predation: the small body size and anti-predatory behaviour of local horse breeds; specialisation on prey that wolves have coexisted with for millennia; and herd management practices (Freitas, 2019; Hovens and Tungalaktuja, 2005; Lagos, 2013; Mech and Peterson, 2003).

In the grasslands of Central Asia, including northern China and Mongolia, several studies document high prevalence of domestic horses among wolf prey (Balajeid Lyngdoh et al., 2020; Hovens and Tungalaktuja, 2005). In Mongolia, domestic horses are an important food resource for wolves (> 40 % of wolf diet), particularly at the end of winter, when horse mortality by starvation peaks and wolves scavenge on the carcasses (Hovens and Tungalaktuja, 2005). Nomadic herdsmen in Mongolia maintain domestic mares and foals close to camps from June to October to collect milk, therefore decreasing horse consumption by wolves during this period (Hovens and Tungalaktuja, 2005). Yet almost every family reports wolf attacks on domestic horses, namely in Hustai National Park, where families own 30–75 horses with an annual depredation rate of 5 % which, due to the high value of domestic horses, represents 70–95 % of their yearly economic losses to wolf predation (van Duyne et al., 2009; Fig. 5). Mongolian pastoralists fully rely on their livestock, raising a strong need to reduce and compensate losses to predation (Hovens et al., 2000; van Duyne et al., 2009; see also Lieb and Elfström, 2021 in CDPnews issue 22).

Locally high wolf predation on horses is also reported in parts of southern Europe. In Italy, wolf attacks on free-ranging horses are mostly limited to some areas (e.g. Apennine mountain range), where horses can locally reach 40 % of wolf diet (Fico et al., 1993). Here, conflicts arise between horse owners and local authorities responsible for managing wolf damage to livestock, since horse owners are often unsatisfied with the implemented policies (Fico et al., 1993). Such conflicts may reach even higher levels in the Iberian Peninsula where damage is greater due to lower availability of alternative prey, lack of effective prevention measures limited compensation, resulting in illegal wolf persecution, especially in Portugal (Álvares, 2011). Wolf predation on horses is common in mountainous areas of northern Spain and Portugal, where a scarcity of wild prey forces wolves to prey almost exclusively on free-roaming horses and livestock under extensive grazing such as cattle, goats and sheep (Lagos and Bárcena, 2018; Pimenta et al., 2018; Fig. 6). Losses of livestock, including horses, represent

Fig. 6 Foals attacked by wolves in Galicia, Centro de la Dorsal Galega (left) and Serra do Xistral (right), showing bite wounds to their hind legs. *(Photos: Laura Lagos)*

significant economic costs (Milheiras and Hodge, 2011) which are not fully compensated, since current compensation schemes only cover confirmed kills and require the use of preventive measures such as livestock guarding dogs and fences that are difficult to apply in free-ranging husbandry systems (Pimenta et al., 2018; see articles by Freitas and Álvares, Lagos and Bárcena, and Lagos and Blanco in this issue).

3. Analysis of the situation in Iberia

We found a larger number of studies reporting horse consumption by wolves in the Iberian Peninsula than in any other region worldwide. Based on 35 publications on wolf diet mentioning horses as prey in a total of 49 study sites[4], there is geographical variation in intensity of horse consumption across the region (Fig. 7). Several studies focused on the agricultural landscapes of León, Spain, and northeast and central Portugal report low levels of horse consumption (<10% of wolf diet), mostly attributed to scavenging from dead horses in dumps, as in the case of the wolf subpopulation south of the River Douro, Portugal (Casimiro, 2017). In some parts of the region, it used to be common to leave carcasses of horses and other livestock in dumps, to be consumed by scavengers. Due to the EU Sanitary Regulation on Livestock Disposal, this practice was considered illegal in Portugal from 2002 and in Spain from 2003 (Lagos and Bárcena, 2015), although disposal of free-roaming horses was later considered an exception and allowed in Portugal from 2011 and Galicia from 2016. The occurrence of domestic horses in wolf diet in many parts of Iberia is therefore likely a result of scavenging rather than predation (Casimiro, 2017; Llaneza and López-Bao, 2015). However, high levels of horse consumption, comprising >40% of wolf diet and involving active wolf predation, are reported in several studies conducted in Peneda-Gerês National Park, northwest Portugal, and the Spanish Autonomous Communities of Galicia and Asturias (Casimiro 2017; López-Bao et al., 2013).

In northern Iberia, wolf predation is widely reported to affect native ponies weighing between 250 and 350 kg, which are traditionally raised under a free-ranging regime year-round in the mountains (e.g. Lagos, 2013; Pereira, 2018) and are strongly selected by wolves (Álvares, 2011; Casimiro, 2017; Lagos and Bárcena 2018). In many of these areas, horses are more abundant than wild ungulates, which are locally scarce (Vingada et al., 2010). Free-ranging horses are more accessible than other livestock which are confined at night, although a high trophic selection of ponies by wolves has been observed even in areas with extensively raised cattle and calves that are also available at night (Álvares, 2011; Lagos and Bárcena 2018), suggesting an evolutionary adaptation of wolves. Iberian mountain ponies seem to have co-evolved with wolves in a predator-prey relationship, as suggested by rock paintings from approximately

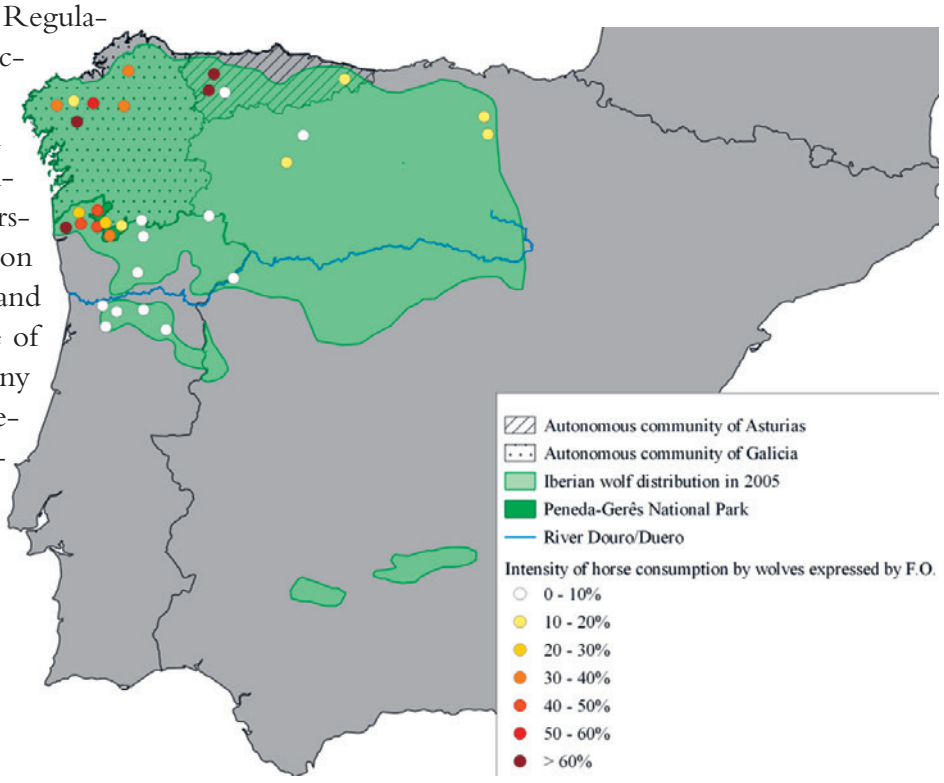

Fig. 7 Locations of study sites (circles) with reported horse consumption by wolves in the Iberian Peninsula in relation to wolf distribution estimated in 2005 (Álvares et al., 2005). Colours indicate the intensity of horse consumption based on reported frequency of occurrence (FO) in wolf diet.

[4] Portugal: 27 study sites in Arga, Paredes de Coura, Peneda-Gerês National Park, Vez/Soajo, Gerês, Pitões das Júnias, Larouco, Leiranco, Alvão Natural Park, Arada, Trancoso, Montemuro, Lapa and Leomil. Spain: 22 study sites in Galicia, Basque Country, northern Spain, northwestern and southwestern Asturias and León.

40,000 years ago which depict wild equids morphologically similar to modern ponies of the area (Pereira, 2018).

Free-ranging horses are frequently preyed on by Iberian wolves *(C. l. signatus)* whenever they are available and can locally or seasonally comprise the majority of wolf diet (e.g. Álvares 2011; Lagos and Bárcena, 2018). In many parts of the Iberian Peninsula, wolf diet has been shifting from a broader diet based on medium-sized domestic species (e.g. goats and sheep) in the 1970s to a narrower diet based mostly on large domestic ungulates under extensive grazing, such as cattle and horses (Llaneza and López-Bao, 2015). This trend seemingly resulted from changes in livestock numbers and husbandry practices together with sanitary regulations on livestock disposal, which affected the availability of different food resources (Llaneza and López-Bao, 2015). Increased predation on horses in recent decades has strong management implications, especially when wolves attack endangered autochthonous local breeds such as the Asturcón in Asturias, Losino in Burgos, Pottoka in the Basque Country, Cabalo de Pura Raza Galega or Faco Galego in Galicia and Garrana in Portugal (Caetano, 2011; Royo et al., 2005; Fig. 8, photos 1–5).

4. General patterns and ecological aspects

The main factor predisposing horses to wolf predation worldwide is the free-ranging management system. However, several other intrinsic and extrinsic factors seem to influence the level of predation, as documented particularly in the Iberian Peninsula. Foals are especially vulnerable during the first months of life, despite the protection of the band, which is linked to higher predation rates in summer (Lagos, 2013). Adult horses are also reported to be regularly consumed by wolves, especially in winter when horses are in poorer body condition as a consequence of lower food availability and harsh weather conditions, leading to increased mortality and subsequent scav-

Fig. 8 Autochthonous breeds of mountain ponies in the Iberian Peninsula preyed on by wolves: (photos 1–3) Garrana, Losino, Asturcón, (photos 4–5) Pottoka and Cabalo de Pura Raza Galega.

(Photos: Joana Freitas for Garrana; Ricardo de Juana for Losino; Gema Sanchéz for Asturcón; Dave Walsh for Pottoka; Laura Lagos for Cabalo de Pura Raza Galega)

enging and/or predation on weak animals (Hovens and Tungalaktuja, 2005; Llaneza and López-Bao, 2015). In this context, natural mortality of free-ranging horses due to disease or environmental conditions can provide large amounts of biomass for wolves to consume during periods of reduced prey availability (Lagos and Bárcena, 2015).

Wolf predation may affect the sexes differently, as males have higher energetic and nutritional costs resulting from high metabolic and growth rates, along with higher exposure to injuries during the mating season and when defending the band, increasing the risk of wolf predation (Garrott, 1991; Lagos, 2013). On the other hand, gestating and lactating females tend to be in poorer condition during winter due to low quality and availability of food, contributing to increased mortality rates (Garrott, 1991).

The ongoing abandonment of rural areas and agricultural land worldwide may contribute to a decline in traditional horse management systems based on extensive grazing, leading to important ecological implications as already reported, particularly in the Iberian Peninsula (López-Bao et al., 2013). Free-ranging horses are pivotal for Iberian ecosystems since they:

1. strongly impact the landscape by controlling plant biomass and shrub cover by grazing, thus reducing the risk of fires;
2. maintain open heathlands including protected habitats; and
3. increase floristic composition, seed dispersal and diversity of arthropod communities in heathlands (López-Bao et al., 2013).

Free-ranging horses also provide a stable food resource for wolves, reducing wolf attacks on more economically valuable livestock species as cattle and goats (Lagos and Bárcena, 2018; López-Bao et al., 2013). In this ecological context, wolf-horse interactions have essential roles in trophic webs and ecosystem functioning. Wolf predation controls horse abundance, promoting habitat heterogeneity and preserving plant and animal diversity, as documented for other carnivore-prey systems (Ripple et al., 2014). Additionally, free-ranging horses are also essential in the form of carrion for several species of scavengers during winter, when there is high horse mortality due to environmental conditions and low food availability (Llaneza and López-Bao, 2015).

5. Management recommendations to mitigate damage

Wolf predation on domestic horses always involves economic losses for their owners, who are often financially disadvantaged (Hovens et al., 2000; Milheiras and Hodge, 2011). Therefore, to reduce its impact on free-ranging horses and mitigate losses to their owners, effective management measures should be implemented, such as: i) increasing the abundance and diversity of wild ungulates to reduce wolf predation pressure, particularly on foals; ii) preventing the removal of horses that die of natural causes to allow wolves to scavenge on their carcasses; iii) applying damage prevention measures compatible with free-ranging horse husbandry systems; and iv) adjusting economic compensation policies to traditional free-ranging horse husbandry systems to decrease the socioeconomic costs related to wolf predation. Hopefully, these measures will mitigate the impact of wolf predation on free-ranging horses, encouraging horse owners to maintain this traditional husbandry practice which has important cultural and ecological roles.

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Table 1 Review of published literature reporting horse consumption by carnivores

Country	Region	Predator species	References
Portugal	Arga	*C. lupus*	Freitas, 2019
		C. lupus	Ringhofer et al., 2017
	Paredes de Coura (Boulhosa and Cruz Vermelha)	*C. lupus*	Álvares et al., 2019
	Peneda-Gerês National Park	*C. lupus*	Álvares, 1995
		C. lupus	Petrucci-Fonseca, 1990
		C. lupus	Álvares et al., 2000
	Vez/Soajo	*C. lupus*	Álvares, 2011
		C. lupus	Casimiro, 2017
		C. lupus	Ferrão da Costa, 2000 Guerra, 2004
		C. lupus	Guerra, 2004
	Gerês	*C. lupus*	Lançós, 1998
		C. lupus	Vos, 2000
	Pitões das Júnias	*C. lupus*	Álvares, 2011
	Larouco	*C. lupus*	Roque et al., 2001
		C. lupus	Álvares, 2011
	Leiranco	*C. lupus*	Álvares, 2011
	Alvão Natural Park	*C. lupus*	Carreira and Petrucci-Fonseca, 2000
		C. lupus	Carreira, 2010
		C. lupus	Passinha, 2018
	South Douro river (Arada)	*C. lupus*	Quaresma, 2002
	South Douro river (Montemuro, Leomil, Lapa, Trancoso)	*C. lupus*	Quaresma, 2002
	Montesinho Natural Park	*C. lupus*	Pimenta, 1998
Spain	Galicia	*C. lupus*	Bárcena, 1976
		C. lupus	Guitián et al., 1979
		C. lupus	Lagos, 2013
		C. lupus	Llaneza and López-Bao, 2015
		C. lupus	Lagos and Bárcena, 2015
		C. lupus	Lagos and Bárcena, 2018
		C. lupus	Llaneza et al., 2012
		C. lupus	López-Bao et al., 2013
	Basque Country	*C. lupus*	Echegaray et al., 2007
		C. lupus	Echegaray and Vilà, 2010
	Northern Spain (Asturias and Galicia, West Galicia, Cantabrian Mountains, Douro Meseta)	*C. lupus*	Cuesta et al., 1991
		C. lupus	Blanco et al., 1992
	NW Asturias	*C. lupus*	Llaneza et al., 1996
	SW Asturias	*C. lupus*	Llaneza et al., 1996
	Asturias	*C. lupus*	Nores et al., 2008
	León	*C. lupus*	Salvador and Abad, 1987
Iberian Peninsula (Portugal and Spain)	unspecified location	*C. lupus*	Ransom et al., 2016
Italy	Abruzzo	*C. lupus*	Fico et al., 1993
	Northern Apennines	*C. lupus*	Ciucci and Boitani, 1998
		C. lupus	Meriggi et al., 1996
		C. lupus	Milanesi et al., 2012
		C. lupus	Meriggi et al., 2015
	Liguria	*C. lupus*	Imbert et al., 2016
	Pollino National Park	*C. lupus*	Ciucci et al., 2018
		C. lupus	Ciucci et al., 2004
Poland	Białowieza Primeval Forest	*C. lupus*	Jędrzejewski et al., 2000
	Carpathian Mountains	*C. lupus*	Gula, 2008
Bulgaria	Rhodope Mountains (West and East)	*C. lupus*	Genov et al., 2008
Northern Europe	unspecified location	*U. arctos*	Ransom et al., 2016
Russia	Daursky State Nature Biosphere	*C. lupus*	Kirilyuk and Ke, 2020
Turkey	Kars	*C. lupus*	Capitani et al., 2016
Pakistan	Machiara National Park	*P. pardus*	Chattha et al., 2013
Tajikistan	Pamir (Alai valley)	*C. lupus*	Watanabe et al., 2010

Country	Region	Predator species	References
India	Kibber Wildlife Sanctuary	*C. lupus; P. uncia*	Mishra, 1997
	Gya-Miru Wildlife Sanctuary (GMWS)	*C. lupus; P. uncia*	Namgail et al., 2007
China (Inner Mongolia)	Dalai Lake National Nature Reserve	*C. lupus*	Zhang et al., 2009
		C. lupus	Huashan et al., 2014
	western Daxing'anling Mountains	*C. lupus*	Wakabayashi et al., 2007
	Xinbacrbuvou Banner	*C. lupus*	Honghai et al., 1998
	Qinghai Province	*C. lupus*	Dai et al., 2020
	Bhijer and Dho Valley	*C. lupus*	Subba, 2012
China (Tibetan Plateau)	Sanjiangyuan region	*C. lupus*	Li et al., 2013
Mongolia	Hustai National Park	*C. lupus*	Hovens and Tungalaktuja, 2005
		C. lupus	van Duyne et al., 2009
	Bogdkhan Mountain Strictly PA	*C. lupus*	Nakazawa et al., 2008
	Mongolian region	*C. lupus*	Balajeid Lyngdoh et al., 2020
		C. lupus	Bandi et al., 2012
	Tsagaan Shuvuut and Turgen Special Protected Areas	*P. uncia*	Sumiya and Buyantsog, 2002
	South Gobi desert	*C. lupus; P. uncia*	Mijiddorj et al., 2018
	unspecified location	*C. lupus; P. uncia*	Ransom et al., 2016
Nepal	Annapurna-Manaslu Conservation Area	*C. lupus; P. uncia*	Chetri et al., 2017
	Annapurna Conservation Area	*C. lupus*	Pahari et al., 2021
		P. uncia	Jackson et al., 1996
		P. uncia	Aryal et al., 2014
		P. uncia	Gurung and Thapa, 2004
	Shey Phoksundo National Park	*P. uncia*	Devkota and Dhoubhadel, 2010
		P. uncia	Devkota et al., 2013
	Humla district (Limi valley)	*C. lupus*	Kunwar, 2015
	Samagaun	*U. arctos*	Chetri, 2013
	Narphu valley	*P. uncia*	Tiwari et al., 2020
Bhutan	Wangchuck Centennial National Park (WCNP)	*C. lupus*	Jamtsho, 2017
Canada	Alberta	*C. lupus*	Musiani et al., 2003
		C. lupus; P. concolor	Salter and Hudson, 1978
		P. concolor	Ransom et al., 2016
	British Columbia	*P. concolor*	Hornocker and Negri, 2009
United States of America	Idaho, Montana and Wyoming	*C. lupus*	Musiani et al., 2003
	Montana	*C. lupus*	Haney et al., 2007
	Montgomery Pass Wild Horse Territory (MPWHT)	*P. concolor*	Turner et al., 1992
	Nevada, Wyoming, Montana	*P. concolor*	Ransom et al., 2016
	Nevada	*P. concolor*	Gray et al., 2008
		C. latrans	Berger and Rudman, 1985
	California	*P. concolor*	Weaver and Sitton, 1978
	Florida	*P. concolor*	Hornocker and Negri, 2009
Guatemala	Petén district	*P. concolor; P. onca*	Soto-Shoender and Giuliano, 2011
Brazil	Rio Grande do Sul (Protected Areas)	*P. concolor*	Schulz et al., 2014
Argentina	Ernesto Tornquist Provincial Park	*P. concolor*	Mills and McDonnell, 2005
South America	unspecified location	*P. onca*	Ransom et al., 2016
Ethiopia	Bale Mountains (Addis Ababa)	*C. crocuta*	Atickem et al., 2010
	Hugumburda	*C. crocuta; P. pardus*	Yirga et al., 2014
	Enderta district (Debri)	*C. crocuta*	Abay et al., 2011
	Enderta district (Aynalem	*C. crocuta*	Abay et al., 2011
Kenya	Melako Conservancy (Laisamis sub-county)	*P. leo*	Narisha, 2015
Namibia	Northern region	*P. pardus*	Rust and Marker, 2014
Botswana	Shorobe village	*A. jubatus; P. pardus*	Kgathi et al., 2012
Africa	unspecified location	*A. jubatus; P. leo; C. crocuta; P. pardus*	Ransom et al., 2016
Australia	Kosciusko mountain	*C. l. dingo*	Newsome et al., 1983a
	Gippsland	*C. l. dingo*	Newsome et al., 1983b