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Consumption of carnivores by wolves: a worldwide analysis of patterns and drivers.

Tese de mestrado em Ecologia, orientada por Doutor Francisco Álvares e Doutor Paulo Gama Mota e apresentada ao Departamento de Ciências da Vida da Faculdade de Ciência e Tecnologia da Universidade de Coimbra

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COVER IMAGE

"*Duel of titans*"

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CONSUMPTION OF CARNIVORES BY WOLVES: A WORLDWIDE ANALYSIS OF PATTERNS AND DRIVERS.

Thesis submitted to the Department of Life Science,
Faculty of Science and Technology of the University of Coimbra
for the degree of Master in Ecology

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To mom and in the loving memory of

Nádia Marques.

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And Mom, this one is for you. I live to make you proud.

ABSTRACT

Interspecific interactions are very important in all ecosystems and several are known among mammalian carnivores. Competition is one of the main interactions among carnivores and is often intense leading to the extreme event of interspecific competitive killing, known as intraguild predation. This happens when a species kills and eats other from the same guild that consumes similar and sometimes scarce resources. Gray wolves (*Canis lupus*) are widespread top predators and one of the species most involved in interspecific killing among carnivores. Despite the potential implications on wildlife management and human welfare, wolf predation on other carnivores, such as domestic dog (*Canis familiaris*), has been overlooked and the presence of carnivore species on wolf diet is poorly studied. Considering this lack of knowledge on one of the most studied carnivores, this study aimed to understand the role of intraguild predation on wolf diet, by determining global patterns of carnivore consumption by wolves and its ecological and human related determinants as well as discuss the ecological, behavioral and management implications of this matter.

A analysis was conducted based on data collected from an extensive literature review on 120 studies addressing wolf diet worldwide. General patterns on carnivore consumption by wolves, were assessed based on the sampling sites reporting consumption of carnivores from compiled studies and analyzed by considering: number and ecological traits of consumed carnivore species and magnitude of carnivore consumption as well as patterns on spatial (continent) and seasonal variation. The potential drivers for carnivore consumption by wolves were access by choosing ecological and human-related variables with potential relevance on wolf trophic ecology and evaluate their effect on the magnitude of the carnivore species consumption and number of carnivore species consumed by wolves.

Results showed that intraguild predation by wolves is not such a rare event, with a total of 143 sampling sites worldwide with reported consumption of carnivore species by wolves (67% of all sampling sites reviewed). From all European sampling sites reviewed, 82% reported carnivore consumption by wolves, from North America 55% and from Asia 45%. A total of 35 carnivore species were reported as prey-species on wolf diet studies, which, in general, involves an occasional consumption (0,1% to 5% of wolf diet). The 5 carnivore species group constituted by medium-sized generalist carnivores with reported scavenging behavior, were the type of carnivores more often consumed by wolves. In general, dogs were the most common carnivore species to be consumed with occurrences in 49% of the sampling sites reporting carnivore consumption by wolves, but absent in the North American sampling sites reviewed. Canidae is the Family most common in all of the three continents and represents 58% of all Family appearances in the sampling sites reporting carnivore consumption. The magnitude and number of carnivore species consumed by wolves showed no significant differences between seasons. GLM analysis revealed: higher consumption of carnivores by wolves are significantly related to nonprotected areas, higher values of human density and lower consumption of: wild ungulates, domestic ungulates and small mammals; also revealed that higher number of carnivore species consumed are significantly related to nonprotected areas, lower consumption of small mammals and to low NDVI (normalized difference vegetation index) values.

This study brought relevance and knowledge about Intraguild predation in one of the most studied species worldwide, the gray wolf. Human presence and activities probably are the greatest key-factor influencing wild prey and mesopredators abundances, potentially driving wolves to intraguild predation. High consumption levels of carnivores by wolves can signalize non-protected ecosystems that are being threatened by human's densities. The increased number of different carnivore species in wolf diet can also signalize loss of biodiversity and instable habitats. However, intraguild predation is a very complex interaction, and more studies on this topic are needed to understand more specific patterns and drivers. Densities of most of the carnivore species consumed by wolves might be released due to human wastes or to the extirpation of larger predators as the wolf. This release in mesopredator species who contact almost as much with wildlife as with humans, such as feral dogs, can bring innumerous issues to both sides. Whenever these mesopredators represent a danger to wildlife and to humans and are not properly controlled, wolf predation on these species can provide an important ecosystem service. More studies on this subject should be performed on other large carnivore species, as they can raise awareness on the positive effects of top predators in human-dominated landscapes and appeal to their conservation.

Key-words: Intraguild predation, *Canis lupus*, Interspecific killing, Competition, Mesopredators.

RESUMO

Em todos os ecossistemas existem vários tipos de interações interespecíficas. A competição é uma das principais interações entre carnívoros e muitas vezes a sua intensidade pode levar ao fenómeno extremo de competição, a predação de outros carnívoros. Este fenómeno ocorre quando uma espécie mata e alimenta-se de outra com um nicho trófico semelhante. O lobo (*Canis lupus*) é uma das espécies mais envolvidas neste tipo de interações. Apesar das suas potenciais implicações na gestão da vida selvagem, a predação do lobo a outros carnívoros, como o cão (*Canis familiaris*), e a presença destes na sua dieta ainda é pouco estudada. Considerando esta falta de conhecimento numa das espécies mais estudadas de carnívoros, o presente estudo teve como objetivo avaliar o papel da predação do lobo a outros carnívoros na sua dieta, explorando os padrões globais do seu consumo pelo lobo e possíveis fatores determinantes, assim como discutir as implicações dos resultados na ecologia e conservação do lobo.

Foi realizada uma análise com base em dados recolhidos de uma extensa revisão bibliográfica mundial a 120 estudos de dieta do lobo. Os padrões gerais do consumo de carnívoros foram avaliados com base nos locais de amostragem com consumo de carnívoros dos estudos compilados, e analisados considerando: o número de espécies de carnívoros consumidas, as características ecológicas das mesmas e a magnitude do seu consumo pelo lobo, assim como os padrões espaciais (continente) e variação sazonal. Os fatores determinantes para o consumo de carnívoros pelo lobo foram analisados selecionando variáveis ecológicas e antropogénicas com potencial importância na ecologia trófica do lobo e avaliando os efeitos das mesmas na magnitude do consumo de carnívoros e no número de espécies de carnívoros consumidas.

Os resultados demonstraram que a predação de carnívoros pelo lobo não é um fenómeno raro, com um total de 143 locais de amostragem com consumo de carnívoros pelo lobo (67% de todos os locais de amostragem revistos). Na Europa, 82% de todos os locais de amostragem revistos apresentaram consumo de carnívoros pelo lobo, na América do Norte e na Ásia, 55% e 45% (respetivamente). Nos estudos revistos foram contabilizadas no total 35 espécies de carnívoros consumidas e no geral representam um tipo de consumo ocasional (0,1% a 5% da dieta do lobo). O tipo de carnívoros mais consumidos pelo lobo incluiu 5 espécies caracterizadas por médio-porte, dieta generalista e necrofagia. No geral, o cão foi a espécie mais consumida, representado em 49% dos locais de amostragem com consumo de carnívoros, no entanto, o seu consumo não foi registado na América do Norte. A Família Canidae foi a mais consumida nos três continentes, representando 58% das presenças de todas as famílias nos locais de amostragem com consumo de carnívoros. Não foram encontradas diferenças na magnitude ou número de espécies de carnívoros consumidas pelo lobo entre estações do ano. A análise estatística revelou que um maior consumo de carnívoros pelo lobo está relacionado com áreas não protegidas, valores altos de densidade humana e baixo consumo de: ungulados selvagens, ungulados domésticos e pequenos mamíferos; também revelou que um maior número de espécies de carnívoros consumida está relacionado com áreas não protegidas, baixo consumo de pequenos mamíferos e baixos valores de NDVI (Índice de Vegetação da Diferença Normalizada).

O presente estudo proporcionou conhecimentos relevantes sobre a predação de carnívoros por uma das espécies mais estudadas mundialmente, o lobo. A presença humana e as suas atividades são provavelmente os maiores fatores-chave a influenciar a abundância de presas selvagens e de mesopredadores, exercendo potencialmente uma grande influência na predação de carnívoros pelo lobo. Níveis elevados de consumo de carnívoros pelo lobo podem sinalizar ecossistemas desprotegidos e afetados pela densidade humana. Números elevados de espécies de carnívoros consumidas pelo lobo podem também sinalizar perda de biodiversidade e habitats instáveis. Porém, o consumo de carnívoros é uma interação complexa, e mais estudos são necessários para uma melhor compreensão dos seus padrões e fatores determinantes. A densidade das espécies de carnívoros mais consumidas pelo lobo pode aumentar devido a recursos antropogénicos e ao extermínio de grandes predadores, como o lobo. Este aumento de mesopredadores, que exploram habitats selvagens e humanizados (como os cães vadios) pode trazer diversos problemas para vida selvagem e para as populações humanas onde estes se inserem. Quando estes mesopredadores representam uma ameaça para a vida selvagem e humana e não são devidamente controlados, a predação do lobo a estas espécies pode ser um importante serviço de ecossistema. Mais estudos deste tipo devem ser realizados noutras espécies de grandes predadores, pois realçam serviços de ecossistema que podem ser prestados por estas em áreas humanizadas e apelar para a sua conservação.

Palavras-chave: Consumo de carnívoros, *Canis lupus*, Interações interespecíficas, Competição, Mesopredadores

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1.Introduction

A food web defines who is eaten by whom in a given ecosystem. Traditional food-webs are typically represented by three trophic levels predators, herbivores and plants (Figure 1). However, real food-webs are much more complex involving a network of direct and indirect trophic interactions (Hairston *et al.*, 1960; Polis and Strong, 1996; Terborgh and Estes, 2010). Thus, interspecific interactions, such us competition, can greatly influence food webs. As an example, the loss of consumers in a certain trophic level, such us top predators, can promote an increase of species located in a lower trophic level - herbivores and mesopredators -, leading to several changes in ecosystems through a cascading effect (Ripple *et al.*, 2014). Therefore, trophic interactions are not only controlled by bottom-up forces - the limitations of resources like plants and prey - but also by top-down forces - the effects mediated by consumers, such as predators and herbivores (Power, 1992; Terborgh and Estes, 2010). Predators exert several effects in food webs as they shape not only prey numbers but also extend their effects to several other species, having important roles in influencing ecosystems' structure and dynamics (Terborgh and Estes, 2010; Estes et.al, 2011). Predators provide scavenger subsides, easing the acquisition of food by scavengers from their kills (Wilmers *et al.*,2003); they influence disease dynamics, since decreases in predators' densities usually lead to higher prey densities that promote more disease transmissions between individuals (Terborgh and Estes, 2010); and, most importantly, they maintain the abundance and richness of species at lower trophic levels, since controlling herbivores' densities and suppressing the occurrence of more generalist and small-sized predators allows the recovery of vegetation and smaller preys' densities, respectively (Winemiller and Polis, 1996; Ritchie *et al.*, 2012; Ripple *et al.*,2014).

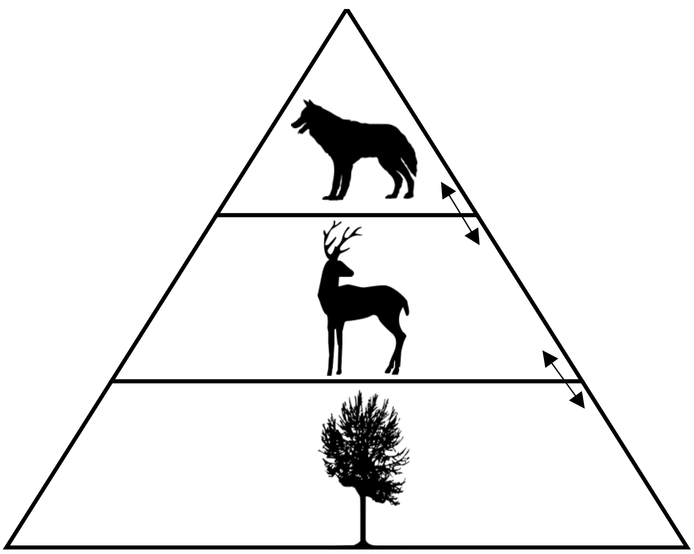


Figure 1 – Three level cascades (e.g. wolf – deer – plants) are typically focused on direct interactions among organisms (image ⓒ web).

1.1 Top predators and mesopredators

Among predators, two main groups can be considered based on their different trophic roles on food webs: top predators and mesopredators (Roemer *et al.*, 2009; Newsome *et al.*, 2017). Top or apex predators are the species located higher in trophic position, typically large-bodied, occurring at lower population densities and normally selecting larger prey (Ritchie and Johnson, 2009). Mesopredators, are the mid-ranking predators in food webs usually generalists and suppressed by the largest or competitively dominant top predators (Levi and Wilmers, 2012; Newsome *et al.*, 2017).

Mesopredators have important effects on ecosystems, such as: i) influence top predators' densities by being reservoirs for pathogens that limit larger predators' populations (Roemer *et al.*,2009); ii) act as important seed dispersers and increase the chances of germination and plants' genes flow, due to their generalist diet (Jordano *et al.*, 2007); iii) fill the role of apex predators whenever they are absent in special ecosystem conditions (Roemer *et al.*,2009); for example, coyotes (*Canis latrans*) act as mesopredators in the presence of the larger gray wolf (*Canis Lupus*, wolf from here on) but in wolves' absence coyotes can (although it is not mandatory) constitute bigger packs and hunt larger prey (Gese and Grothe,1995; Berger and Conner, 2008; Fig.2). However, mesopredators can also have negative ecological effects. Mesopredators can occur at higher densities and are more resilient than apex predators (Prugh *et al.*,2009) consequently, less vulnerable to extinction (Roemer *et al.*,2009). Furthermore, mesopredators have a more generalist diet so they affect a wider range of prey (Ritchie and Johnson, 2009). In this context, when mesopredators populations get over abundant it leads to a higher predation pressure what can lead to decreases or even extinction of prey species (Courchamp *et al.*,1999; Johnson *et al.*,2007; Roemer *et al.*,2009;).

Figure 2 - Wolf watching over two coyotes running away in North America (photo ⓒ Brent R Paull)

In natural conditions, top predators such as large mammalian carnivores, suppress the negative outcomes of mesopredators by killing them, competing for resources and instilling fear (Johnson *et al.*, 2007; Newsome *et al.*, 2017). However large carnivores' numbers have strongly decline worldwide mainly due to habitat loss and human persecution (Ripple at. al, 2014; Prugh *et al.*,2009). As a consequence of large carnivore declines, densities and ranges of mesocarnivores are likely to increase, leading to an ecological process known as "mesopredator release", a term created by Soulé and colleagues in 1988 to describe the process where mid-sized carnivores become more predominant in ecosystems where larger carnivores were missing (Courchamp *et al.*, 1999; Crooks and Soulé, 1999; Ritchie and Johnson, 2009; Roemer *et al.*,2009;). The outcome of this process depends on the species that is released and on its function and role in the ecosystem but often involves negative effects as shown by several evidences found both in terrestrial and marine ecosystems (Roemer *et al.*, 2009; Newsome *et al.*, 2017). For example the decline of the top predator dingo (*Canis lupus dingo*) in Australia allowed populations of feral cats (*Felis catus*) and foxes (*Vulpes vulpes*) to overgrow, triggering marsupials' decline and extinctions (Johnson *et al.*, 2007). In worldwide oceans, the sharp decline of shark populations is expected to result in complex community fluctuations such as trophic cascades and mesopredator release, resulting in decays of some commercial fish (Ferreti *et al.*, 2010).

Mainly due to their capacity to be more resilient and became more abundant, ecological impacts of mesopredators should be expected to exceed those of apex predators, contributing to the same or to new conflict with humans (Prugh *et al.*,2009). Mesopredator release has negatively affected many ecosystems and result from several interspecific interactions between top and mesopredators, which are well illustrated by the mammalian carnivore guild.

1.2 Interactions among carnivores: the role of intraguild predation

Interspecific interactions are very important in any ecosystem and several are known among mammalian carnivores. Mating (hybridization) is known to happen between several species. For example: wolf (*Canis lupus*) as well as wildcats (*Felis silvestris*) can mate with their domestic relatives, domestic dogs (*Canis familiaris*) and cats (*Felis catus*) respectively (Mengel, 1971; Randi, 2008; Fig.3). Also, among several species belonging to genus *Canis*, hybridization seems to be frequent because taxa are so closely related that they can mate and produce fertile descendants (Lehman *et al.*, 1991; Wayne *et al.*, 1997). Hybridization, specially between endangered wild species with exotic species or domestic relatives, rises several conservation issues as it can lead to local extinctions although, natural hybridization also has an important role in the evolution of many species in the past (Allendorf *et al.*, 2001). Besides hybridization, competition is one of the main interactions among carnivores and is often intense, especially among members of the same family (Palomares and Caro, 1999; Donadio and Buskirk, 2006; Lourenço *et al.*, 2013).

Figure 3 - The dark coat color of the North American black wolves was shown to be derived from past hybridization with domestic dogs (Anderson, *et al.* 2009; photo © Bridger Peaks)

Competition happens whenever individuals from the same (intraspecific competition) or different species (interspecific competition) use the same limited resources (e.g. food, refuge) and have to compete to each other in the process to get it (Birch, 1957). When organisms affect directly the other competitors it is called interference competition, while when organisms affect indirectly the other competitors only by reducing resources it is called exploitative competition (Tilman, 2004). Mammalian carnivores are famous competitors with several examples woldwide: in Africa, spotted hyena's (*Crocuta crocuta*) interference competition and kleptoparasitism (when one species takes a prey killed by another species) limit the feeding time of African wild dogs (*Lycaon pictus*) (Creel and Creel, 1996); in India, domestic dogs compete with the Indian wolf (*Canis lupus pallipes*) for blackbuck offsprings (*Antelope cervicapra*) (Jhala, 1993) and, the introduction of dingo (*Canis familiaris dingo*) in Australia might have been the main cause for the extinction of several carnivorous Marsupials, such as the thylacine (*Thylacinus cynocephalus*) and the Tasmanian devil (*Sarcophilus harrisii*) (Corbett, 1995).

Interspecific competition often involves killing, becoming an extreme form of competition (Donadio and Buskirk, 2006) and it happens when the individuals involved kill each other or only one kills the other (Palomares and Caro, 1999; Lourenço *et al.*,2013). Interspecific killing between mammalian carnivores, often involving consumption of the victims, is very common in nature and is responsible for up to 68% of known mortality causes in some species (Palomares and Caro, 1999). Traditionally, predation and competition systems are assessed separately when, in reality, one species or more can act both as predator and competitor with other species belonging to the same or similar trophic level (Polis *et al.*,1989). The extreme phenomenon of interspecific competitive killing, when a species kills and eats other from the same guild that consumes similar and sometimes limited resources, is called intraguild predation (Polis and Holt, 1989; Lourenço *et al.*,2013;). According to theoretical models, intraguild predation can drive to exclusion, coexistence or alternative stable states between species (Polis and Holt, 1992). Intraguild predation results in avoidance behaviors (Polis and Holt, 1992; Newsome *et al.*, 2017) so, it can strongly affect species occurrence and habitat selection. For example, kit foxes (*Vulpes macrotis*) increased their territories to avoid being predated by coyotes (*Canis latrans*) in Mexico (Moehrenschlager *et al.*,2007) and a similar pattern is found between cape foxes (*Vulpes chama)* and bat-eared foxes (*Otocyon megalotis*) in South Africa that are predated by black-backed jackals (*Canis mesomelas*) (Kamler at. al, 2013). The Black-backed jackals can also be predated by the African wild dog (*Lycaon pictus*) and, consequently, their numbers are suppressed (Kamler *et al.*,2007). These interactions are crucial for ecosystem functioning as intraguild predation can be a very important factor in controlling mesocarnivore's species, pests and invasive species, and it also decreases suppression on smaller prey (Polis and Holt, 1992). Intraguild predation is a global and frequently powerful complex interaction shaping many animal communities. However, since is not so well known as other types of interspecific interactions, more studies on the role of intraguild predation would improve our knowledge of population and community ecology (Polis *et al.*,1989; Donadio and Buskirk, 2006; Lourenço *et al.*, 2013). Canids are one of the carnivore families most involved in this type of interactions (Palomares and Caro, 1999) as they are represented by several mesocarnivores as well as top predators, such as the wolf.

1.3 The gray wolf as a case study

Wolves are widespread top predators that occur throughout all northern hemisphere in a wide range of habitats from wilderness and remote areas to highly human-dominated landscapes, as far as there is available food resources (Sillero-Zubiri *et al.*, 2004; Mech and Boitani, 2003). Wolf diet is extremely flexible but large ungulates comprise most of wolf diet, although they can also consume smaller prey items and carrion (Mech and Boitani, 2003; Zlatanova *et al.*, 2014; Mech *et al.*, 2015; Newsome et., al 2016). Therefore, wolf predation on ungulate species is the main ecological direct effect of this large carnivore in food webs webs and therefore it has been widely studied (Mech and Boitani, 2003). Where wild ungulates, such as moose, deer and wild boar, are scarce, wolves often feed in domestic ungulates (Mech and Boitani, 2003), becoming wolf predation on livestock the main reason to human-wolf conflicts and persecution (Meriggi and Lovari, 1996). Wolves can also predate smaller carnivore species (i. e. intraguild predation) both by killing them for competition or by direct consumption as a complementary food resource**.** In fact, wolves are one of the carnivore species most involved in interspecific killing (Palomares and Caro, 1999; Fig.4).

Figure 4 – Brown bear taking over a wolf-killed deer in the Yellowstone National Park, this type of encounters can often turn violent due to competition for carcasses (photo © Stan Tekiela).

Wolf's interspecific killing and intraguild predation have strong and important implications on ecosystems and, sometimes, rises many conservation issues for this species. In Yellowstone National Park (USA), there is a well-known example, wolves began killing coyotes immediately after being reintroduced, leading to a decrease on coyote populations and consequently other mesopredator populations that compete directly with coyotes, like red foxes, increased and also their smaller preys could benefit from this (Smith *et al.*,2003). Wolves are also known to attack and eat domestic dogs, despite the frequent occurrence of interbreeding with them (Mech 1970; Fig.5). Domestic dogs are distributed worldwide and often live in close proximity with humans, who provide them food and refuge, what may consequently lead to high population densities of stray dogs (Vanak and Gompper, 2009). Due to the emotional connection between humans and dogs, wolf predation on their domestic relatives have low public acceptance (Mech, 1995; Naughton-Treves *et al.*,2003;). In fact, valuable dogs such as hunting or sled-dogs, can be attacked and even killed by wolves which is an emotional and economic loss for the owners, as reported in Canada and Scandinavia (McNay, 2002; Backeryd, 2007). However, domestic dogs can become feral and induce negative effects on native wildlife and ecosystems, by filling the role of a medium-sized canid within the carnivore community, e.g. a mesopredator. Feral dogs may also be perceived as predators influencing prey activity and habitat use (Miller *et al.*,2001; Lenth *et al.*,2008). But above all, feral dogs can perform a high predation pressure on wildlife, particularly when occurring at high densities as there are evidences of feral dogs being efficient predators of wild ungulates, such as red deer (Vanak and Gompper, 2009; Duarte *et al.*,2016). Other threat from feral dogs to sympatric wild carnivores are pathogens, since most feral dogs are unvaccinated and are common reservoirs of zoonoses capable of affecting wildlife, such as rabies and canine parvovirus (Sillero-Zubiri *et al.*, 2004; Vanak and Gompper, 2009). As populations of feral dogs became bigger, the probability to contact with wildlife increases, increasing consequently the risk of new infections to affect endangered species (Brickner, 2002). Furthermore, especially in humanized landscapes, livestock damages attributed to wolves can actually be made by feral dogs (Salvador and Abad, 1987; Mech and Boitani, 2003). As an example, a study in north Spain confirmed that feral dogs had overlapped ranges with wolves and were the major responsible for livestock predation (Echegaray and Vilà, 2010). Based on the evidences above, wolf predation on domestic dogs can become an essential ecosystem service for controlling feral dogs and their negative impacts in wildlife and human interests (Mech, 1970).

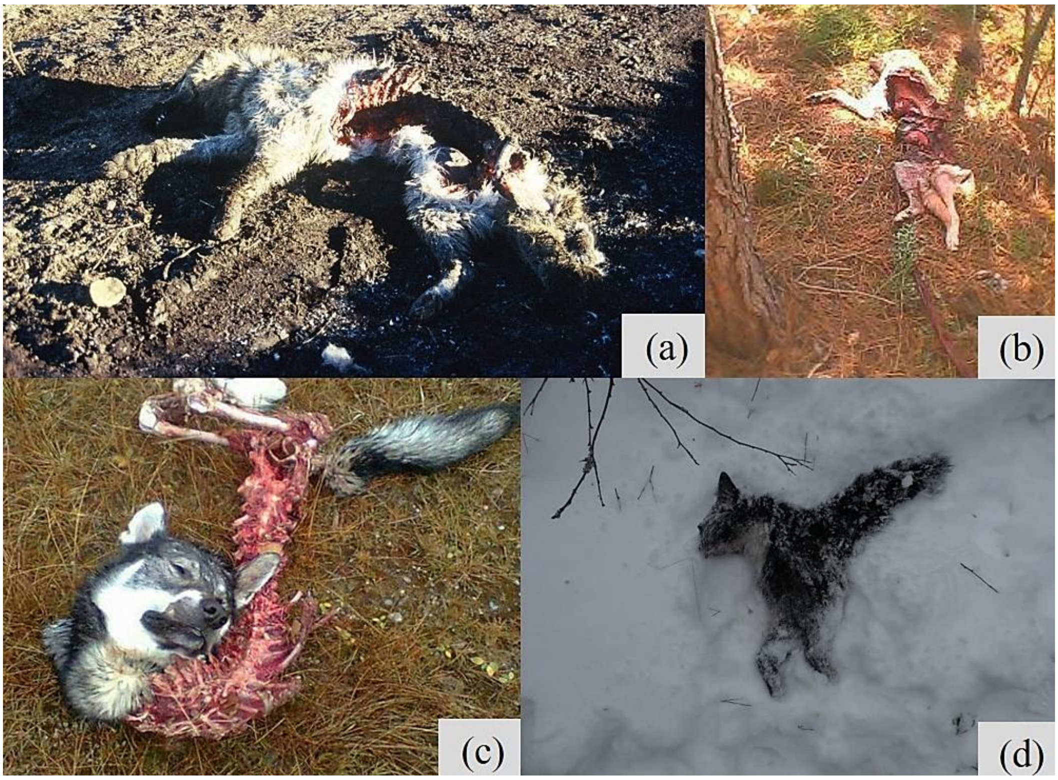


Figure 5 - Domestic dogs consumed by wolves in Iberian Peninsula (a – photo © Francisco Álvares; b - photo © web; c – photo © web); and a domestic cat consumed by wolves in Poland (d – photo © Sabina Novak).

Wolf diet has been extensively studied based on stomach content and scat analysis, documenting the presence of carnivore species as an occasional food item in wolf diet worldwide (Reynolds and Aebischer, 1991; Mech and Boitani, 2003; Klare *et al.*,2011). Palomares and Caro (1999) suggested intraguild predation is common among mammalian carnivores although, the consumption of a kill may depend on the availability of other food items. Yet, for example, black bears (*Ursus americanus*), otters (Lutrinae), martens (*Martes* sp.), mustelids (Mustelidae) and domestic dogs have been reported as prey species in studies focusing wolf diet (Darimont *et al.*, 2004; Lagos, 2013; Marucco, 2003). However, most studies including recent reviews on wolf diet at a continental or global level (e.g. Zlatanova *et al.*, 2014; Newsome et., al 2016) do not present detailed information regarding consumption of carnivores. Despite the potential implications on wildlife management and human welfare, wolf predation on other carnivores has been overlooked and the presence of carnivore species on wolf diet is poorly known. This fact is surprising if we consider that wolves are one of the most studied mammals worldwide and that diet is one of the most studied traits in this large carnivore (Mech and Boitani, 2003). Therefore, to our knowledge, no previous studies addressed the role of intraguild predation on wolf diet and the magnitude, geographical variation or environmental drivers related to carnivores as an alternative food resource, a topic with strong implications in ecosystem processes.

Considering this lack of knowledge on one of the most studied carnivores, this study aims to understand the role of intraguild predation on wolf diet, by determining global patterns of carnivore consumption by wolves and its ecological and human related determinants as well as discuss the ecological, behavioral and management implications of this topic. Based on the available knowledge described above, we hypothesize that: i) Intraguild predation is relevant on wolf trophic ecology with carnivore species being widely consumed by wolves although at low intensity; ii) Wolf predation on carnivores is mostly focused in generalist and medium sized carnivores, e.g mesopredators, and is determined by ecological conditions related to human activity.

To address these hypothesis, it will be conducted a analysis based on data collected from an extensive literature review on wolf diet worldwide in order to evaluate:

- Which and how many carnivore species are reported as prey item on wolf diet studies;
- Which carnivore species and families are more reported as prey item for wolves;
- How relevant are carnivores as a food resource, considering their consumed Frequency and Biomass;
- Which are the main traits (family, body size, trophic niche) of the carnivores consumed by wolves;
- Which are the spatial and temporal patterns on carnivore consumption by wolves;
- Which are the ecological and human-related variables that determine carnivore consumption by wolves;
- If intraguild predation on wolves can provide a potential and beneficial ecosystem service.

The expected results should contribute for wolf conservation and management by enhancing the ecosystem services provided by this top predator in controlling mesopredator populations, particularly feral domestic dogs.

2.Methodology

2.1 Data collection and organization

Data on the wolf's diet was collected from an extensive literature review using Google Scholar, Web of Science, reference lists of obtained publications and grey literature, such as technical reports and PhD thesis. A total of 120 worldwide studies on wolf diet were reviewed for this research (Appendix I), comprising analysis of scat (114) and/or stomach content (8) and/or other type of samples such as kills (3).

Since some of the compiled studies included more than one sampling site, sampling sites were selected as a research unit for this study. The compiled studies included a total of 212 sampling sites worldwide in which 143 reported consumption of carnivore species by wolves. Considering the 143 sampling sites reporting carnivore consumption worldwide, in 53 (37%) results were presented as Frequency of Occurrence (F.O. from here on), in 27 (19%) as percentage of consumed Biomass (Biomass from here on), in 30 (21%) through both approaches (F.O. and Biomass) and in 33 (23%) by other type of approaches that were not considered in our study. These "other approaches" to assess wolf diet in sampling sites included: Percent Frequency of Occurrence (P.F.O.), percent of volume, crude Biomass, only food items identification (from scats, killing or other record) and, also included studies with F.O. and/or Biomass where it was not possible to retrieve the exact values of prey consumption (e.g. represented only in graphics or vague references in the text).

Sampling sites reporting consumption of carnivore species by wolves were used in this study to assess general patterns and drivers of this particular interspecific interaction. Geographic coordinates of each sampling site were retrieved, whenever possible from study area description in the article itself or obtained via *Google Maps,* based on the detailed geographical location of the sampling site mentioned in the article. Coordinates of sampling sites with no specific geographical location were taken approximately from areas known to be close or to include these sampling sites (for example, a wolf pack from a National Park was assigned with the coordinate of the National Park where it occurs). The coordinates were imported to *QSIG 2.18* along with the actual digital map of the gray wolf distribution from *The IUCN Red List of Threatened Species*™ and then, exported as a map image with the geographical distribution of the 143 sampling sites reporting carnivore consumption by wolves (Fig. 1).

2.2 Assessing general patterns of carnivore consumption by wolves

General patterns on carnivore consumption by wolves, were assessed based on sampling sites reporting consumption of carnivores and analyzed by considering: number and ecological traits of consumed carnivore species and the magnitude of carnivore consumption as well as patterns on spatial (continent) and seasonal variation.

Sampling sites reporting carnivore consumption by wolves were sorted by respective continent as well as decade and season of the sampling period. Spatial patterns on carnivore consumption were analyzed per Continent (Europe, North America and Asia) and globally. Seasonal patterns were analyzed considering two periods: Spring/Summer and Fall/Winter.

Carnivore species reported to be consumed by wolves were categorized by taxonomic Family and analyzed considering the number of species per sampling site and the number of sampling sites reporting a certain species

To assess the magnitude of consumption of each carnivore prey species, we considered the percentage of carnivores' consumption in each sampling site measured by F.O. and Biomass and calculated the maximum, minimum and mean values, per continent and globally. Seven classes related to the magnitude of carnivore consumption were considered based on percentage values of reported F.O. and Biomass: **1 -** 0,1 to 0,19%; **2 -** 0,2% to 0,49%; **3 -** 0,5% to 0,99%; **4** – 1% to 4,9%; **5** – 5% to 9,9%; **6** – 10% to 19,9%; **7** – 20% to 29,9%. Posteriorly each class of frequency was quantified geographically per Continents and taxonomically per Families. Since domestic dogs were the most common consumed carnivore species, analysis were conducted specifically for this prey species.

Furthermore, each carnivore species reported to be consumed by wolves was characterized according to several ecological and morphological traits (Appendix II and III), namely: average adult weights, classes of weight, primary diets and reported scavenging behaviors (scavenging from here on). Characteristics of all reported carnivore species were obtained from a single bibliographic reference (Wilson, D. E. and Mittermeier, R. A., 2009) except for domestic dog (Iljin, 1941), domestic cat (Bradshaw, 2006) and wolf (Mech, 1974). Some values for average adult weight were obtained based on the mean between reported maximum and minimum adult weights or between the maximums and minimums of each sex's adult weight, and categorized according to 5 classes: **1 -** ≤1kg; **2** – 1 to 5kg; **3** – 6 to 10kg; **4** – 11 to 35kg; **5 -** ≥35kg. For each of these classes, the belonging species presences in sampling sites were summed. Primary diet of each carnivore species was categorized as carnivorous or omnivorous following each species' main diet preferences (carnivores are the species that rely their diets primarily on meat and omnivores have their diets more diverse and not so dependent on meat) and scavenging behavior was considered if reported in literature (Wilson, D. E. and Mittermeier, R. A., 2009; Iljin, 1941; Bradshaw, 2006 and Mech, 1974). Carnivore species reported as wolf prey were sorted by classes of weight, primary diet and scavenging in order to characterize the main traits of the most important carnivores consumed by wolves.

Since most seasonal studies don't distinguish winter from autumn and summer from spring, we considered only two types of season: cold seasons (1 - Winter and/or Autumn) and warm seasons (2 -Spring and/or Summer). Two one-way ANOVA's were performed to check if there were any significant differences between the percentages of carnivore consumption and number of carnivore species consumed among seasons.

2.3 Assessing factors determining carnivore consumption by wolves

In order to assess the ecological and human-related factors determining carnivore consumption by wolves only studies with F.O. were included since they better represent the actual frequency that each item was consumed and also better reflect evidences regarding rare food items such as carnivore species (Ackerman *et al.*, 1984; Klare *et al.*, 2011). Biomass reflects the size of each prey item and since smaller preys are less likely to comprise a total scat, Biomass values are often overestimated (Mech, 1970; Ackerman *et al.* 1984). Test for Pearson correlation was performed on the FO and Biomass percentages of carnivore consumption, showing that the correlation was very high and significate between these two values (ρ=0,911; p<0,05; Appendix V). In order to simplify our analysis, since F.O. and Biomass values are so highly correlated and measure the same thing (degree of consumption), F.O. values were all selected for the analysis and Biomass values were only selected in cases where F.O. was not available.

Two Generalized Linear Models (GLM) were performed to check if there were any significant explanatory variables (independent variables) and their type of relation with our dependent variables: the percentage of carnivore consumption (classes were not used in this case because for determining the drivers' influence, it is more logic to use the exact values of the dependent variable) and the number of carnivore species consumed in the sampling sites. It was analyzed the distribution of the dependent variables: carnivore percentage of consumption didn't have normal distribution so it was log-transformed for this analysis; and the number of species had Poisson distribution. Ecological and human drivers (considered as independent variables) were chosen according to their potential relevance for wolf trophic ecology and were obtained from global data sets available online or from the compiled studies.

Independent variables retrieved from compiled studies, were the percentage of reported consumption of several food items considered potential drivers for carnivore consumption, such as: domestic ungulates, wild ungulates and small mammals. In order to categorize the importance of the consumption of each of these food items in wolf diet, they were categorized by the following classes: **1-** ≤4,9%**; 2-** 5% to 19,9%; **3-** 20% to 49,9%; **4-** 50% to 79,9%; **5-** ≥80%. These variables reflect possible scenarios for higher competition levels with other carnivores (i.e. small mammals), the availability of wolf main natural prey (i.e. wild ungulates) or the proximity to livestock and human activities (i.e. domestic ungulates). Also, included as an independent variable, the presence or absence of protected areas was registered from compiled studies. The environmental and human related variables obtained from global data sets were thoughtfully selected as possible drivers for Intraguild predation scenarios. As indicators of human pressure, we considered: roads density, human density, cattle density, anthromes (measures the anthropogenic transformation of terrestrial biomes), agricultural area, urban area and forest cover. As indicators of environmental conditions, we considered: mean altitude, temperature seasonality, precipitation seasonality and Normalized Difference Vegetation Index (NDVI - measures ecosystems' productivity). The previous 11 variables values were obtained from digital thematic maps from the data sets using a buffer zone of 10 km which corresponds to the minimum size in wolf home ranges described in literature (Mech and Boitani, 2003). For each respective coordinate of each sampling site was considered the period (decade) of sampling. Some data were directly used for analysis as the number of cells within each buffer zone and others are mean values (Appendix VI). Anthromes were quantified as the degree of human impact during the last century in a scale where: negative values are habitats that became wilder, 0 (zero) values are non-altered habitats and positive values are anthropized habitats. Test for Pearson correlation was performed on the 11 environmental and human related variables (Appendix VII). High correlation values were found between most variables, and for GLM tests small correlation is desired. Therefore, for GLM tests were selected only 2 variables considered to be most representative of environment and human pressure conditions: NDVI and human density, respectively (Table 1).

All statistical analyses were performed in IBM SPSS Statistics (SPSS Statistics 24.0).

Table 1 – List of ecological and human drivers initially considered as possible independent variables for the analysis tests, the respective source from where they were retrieved and the type of indicator. In bold are the independent variables included in the GLM tests.

	Source	Indicator
Small mammals class of consumption	**Compiled studies**	**Food resource**
Wild ungulates class of consumption	**Compiled studies**	**Food resource**
Domestic ungulates class of consumption	**Compiled studies**	**Food resource**
Protected Area	**Compiled studies**	**Human pressure**
Human density	**Online databases**	**Human pressure**
Cattle density	Online databases	Human pressure
Anthromes	Online databases	Human pressure
Agricultural area	Online databases	Human pressure
Urban area	Online databases	Human pressure
Forest Cover	Online databases	Human pressure
Mean altitude	Online databases	Environmental conditions
Temperature seasonality	Online databases	Environmental conditions
Precipitation seasonality	Online databases	Environmental conditions
NDVI (Normalized Difference Vegetation Index)	**Online databases**	**Environmental conditions**

3.Results

Based in an extensive literature review on wolf diet covering all worldwide range of this large carnivore, 120 studies were reviewed and analyzed (Appendix I), corresponding to a total of 212 different sampling sites. From all sampling sites, 143 (67%) reported consumption of carnivore species by wolves (Fig.6). Since some authors do not discriminate the exact values of consumption for occasional food items (such as carnivore species), it was possible to evaluate the magnitude of carnivore consumption by wolves based on F.O. and Biomass values only in 87 sampling sites (61% of all sampling sites reporting consumption of carnivore species by wolves).

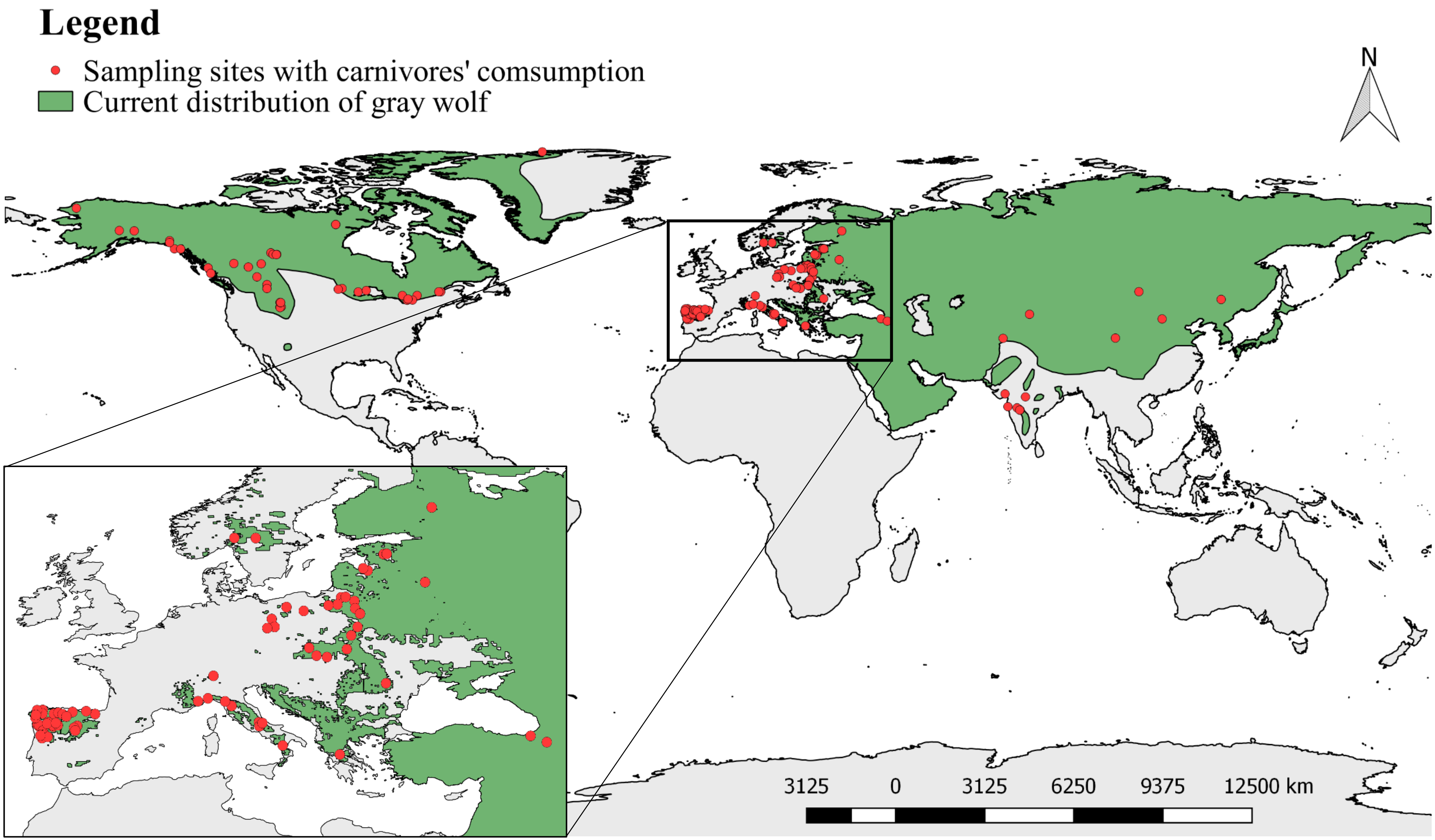


Figure 6 – Geographical distribution of the sampling sites reporting carnivore consumption by wolves (N= 143 sampling sites - red points) based in 120 reviewed studies on wolf diet. Inset map represents Europe, the continent with most sampling sites reporting carnivore consumption by wolves (N=88). Green area corresponds to gray wolf current distribution map according to *The IUCN Red List of Threatened Species™*.

3.1 General patterns of carnivore consumption

All the three continents encompassed by wolf range had sampling sites reporting consumption of carnivore species by wolves (Fig.7 – A). The geographical distribution of the sampling sites reporting carnivore consumption correspond to: 88 sampling sites in Europe (corresponding to 82% of all European sampling sites reviewed), 13 in Asia (45% of all Asian sampling sites) and 42 in North America (55% of all North American sampling sites). Even though Europe is the continent totaling a higher number of sampling sites, when take into proportions it also remains as the continent with more studies reporting carnivore consumption by wolves.

Most (68%) of the 143 sites reporting carnivore consumption were sampled between the 1990's and the 2000's (Fig.7 – B). First compiled references reporting carnivore consumption by wolves date back to 1940's, while only 3% of the sampling sites are in the current decade (2010's).

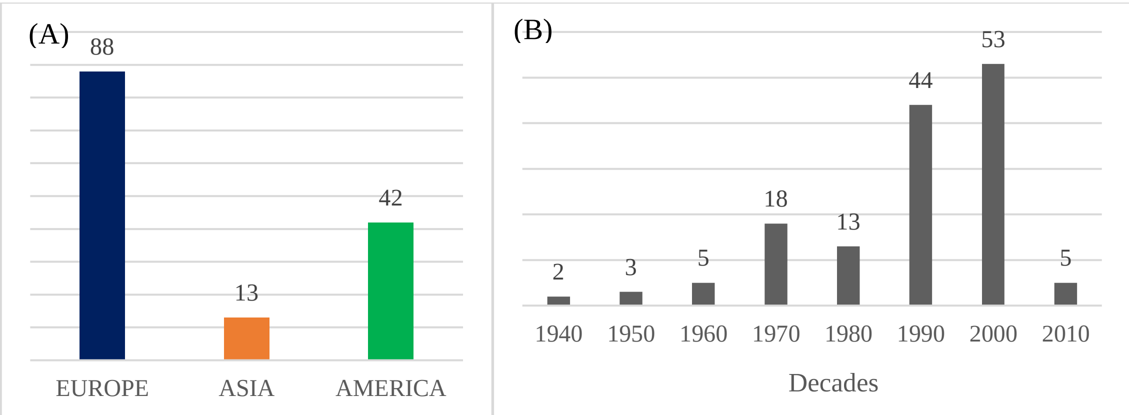


Figure 7 – Number of sampling sites reporting carnivore consumption by wolves per Continent (A) and per decades (B).

Regarding the magnitude of carnivore consumption per sampling site, based in the maximum, minimum and mean values of reported F.O. and Biomass of carnivore species consumed by wolves, is evident that North America has the highest mean values both for Biomass and F.O. (Fig. 8). In general, mean values are much lower than reported maximum values. Minimum values should in fact be lower than represented here since some authors do not discriminate the exact values.

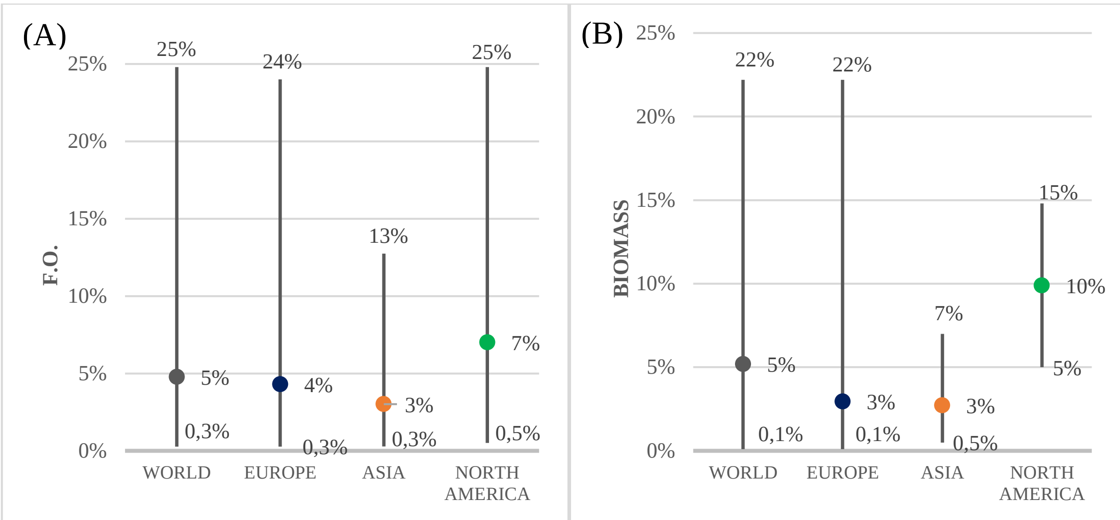


Figure 8 – Maximum, minimum and mean values (colored points) of Frequency of Occurrence (A) and Biomass (B) values from carnivore species consumed by wolves based on 143 sampling sites with reported carnivore consumption.

In total, there are, at least, 35 species of carnivores reported as prey-items in wolf diet studies worldwide, with 12 carnivore species reported for Europe, 14 species for Asia and 24 species for North America (Fig. 9). In general, domestic dogs were the most common carnivore species to be consumed by wolves with occurrences on wolf diet in 70 sampling sites, mostly located in Europe (N=39), only 3 in Asia and none in North America. Considering proportions of all reviewed sampling sties, 88% of the European sites, 23% of the Asian sites and 0% of the North American sites reporting consumption of carnivores (88, 13 and 42 respectively), contained dog remains. Beside dogs, in Europe, red foxes, European badgers and domestic cats were the most common consumed carnivores in general, appearing in 30%, 19% and 18% respectively of the European sampling sites reporting carnivore consumption. The red fox was also the most common consumed carnivore in Asia, represented in 44% of the Asian sampling sites reporting carnivore consumption. North America showed a different tendency than the other two continents with: wolf found in 42%, black bear in 21%, raccoon in 17% and red fox in 14% of all American sampling sites with carnivore consumption (N=42).

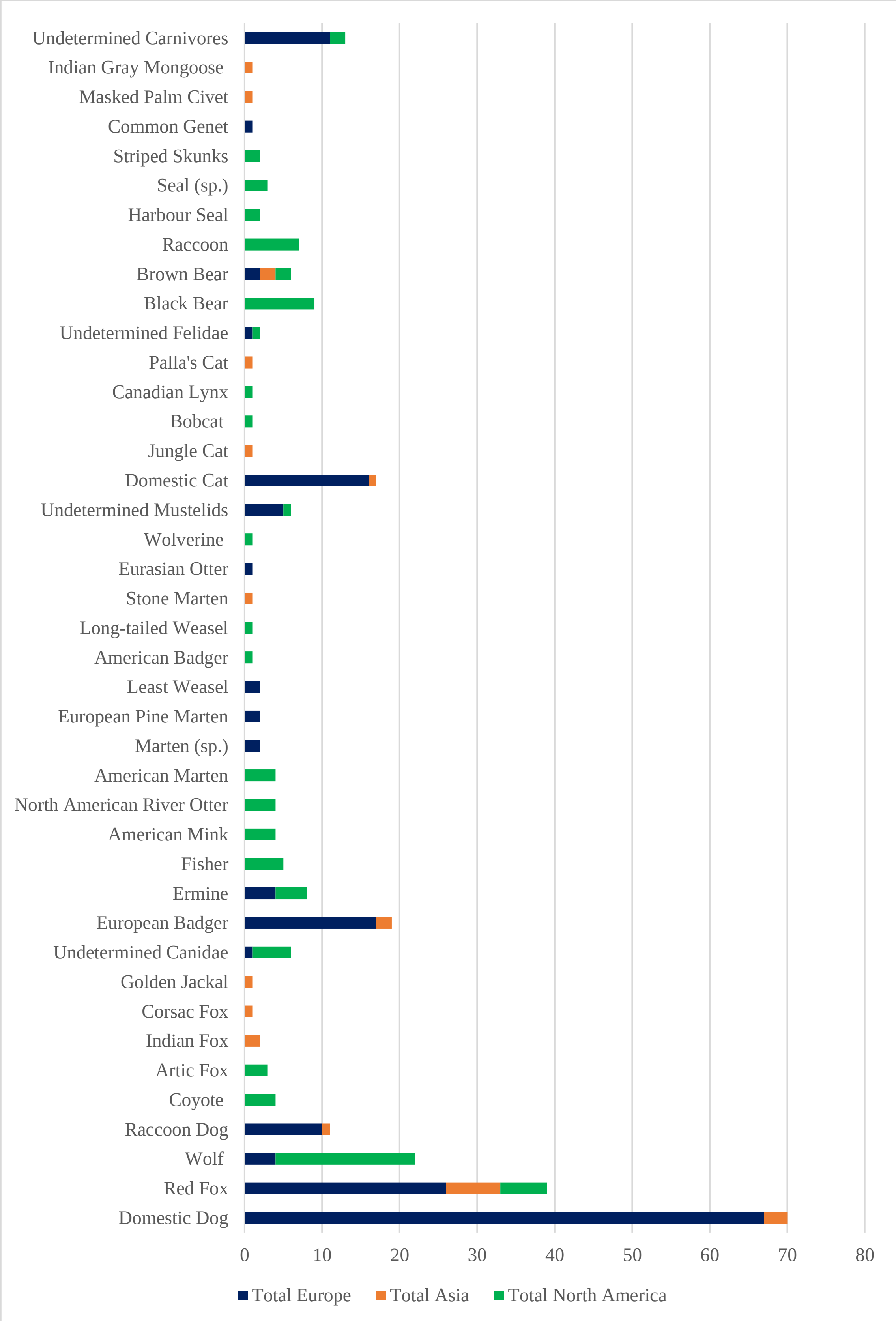


Figure 9 – List of carnivore species reported to be consumed by wolves according to the number of sampling sites in which each species was reported as prey item in the three Continents.

At Family level, in general and by continent, Canidae is the most common being reported 159 times in the sampling sites (Fig. 10) followed by Mustelidae with 61 reports. In Europe, felids (Felidae) are also one of the most common families being reported 17 times in European sampling sites, although this family is only represented by the domestic cat (only in one European sampling site felid species was undetermined). In Asia, canids (*Canidae*) are the most common (reported 15 times in Asian sampling sites) but, apart from that, the other families don't have big differences between each other. In North America, after canids and mustelids (*Mustelidae*), ursids (*Ursidae*) are also very common being reported 11 times in American sampling sites.

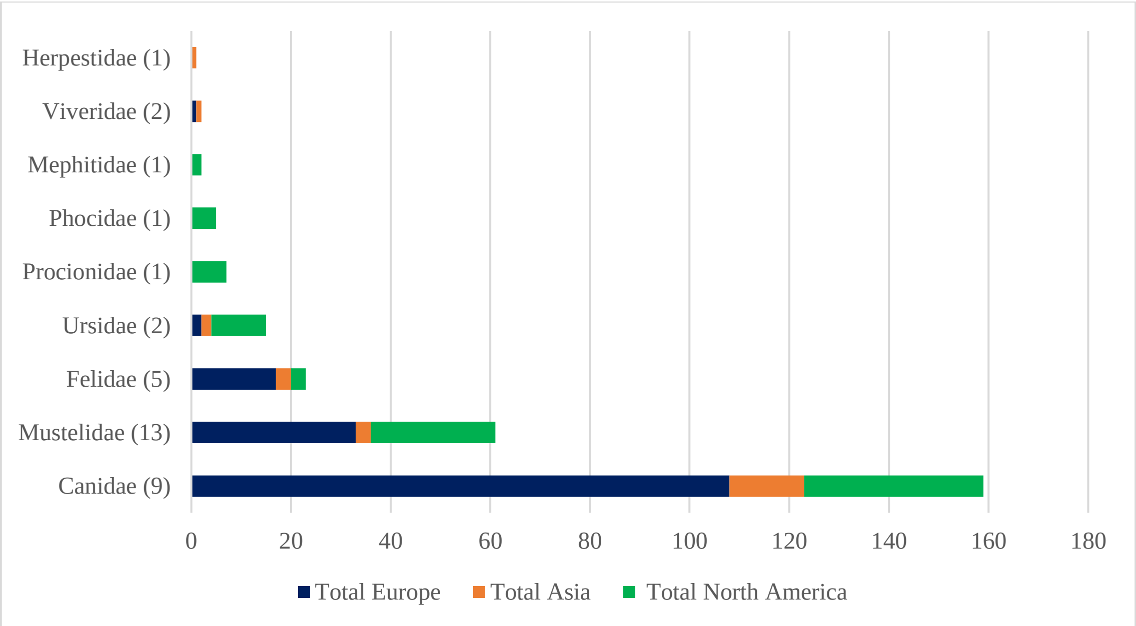
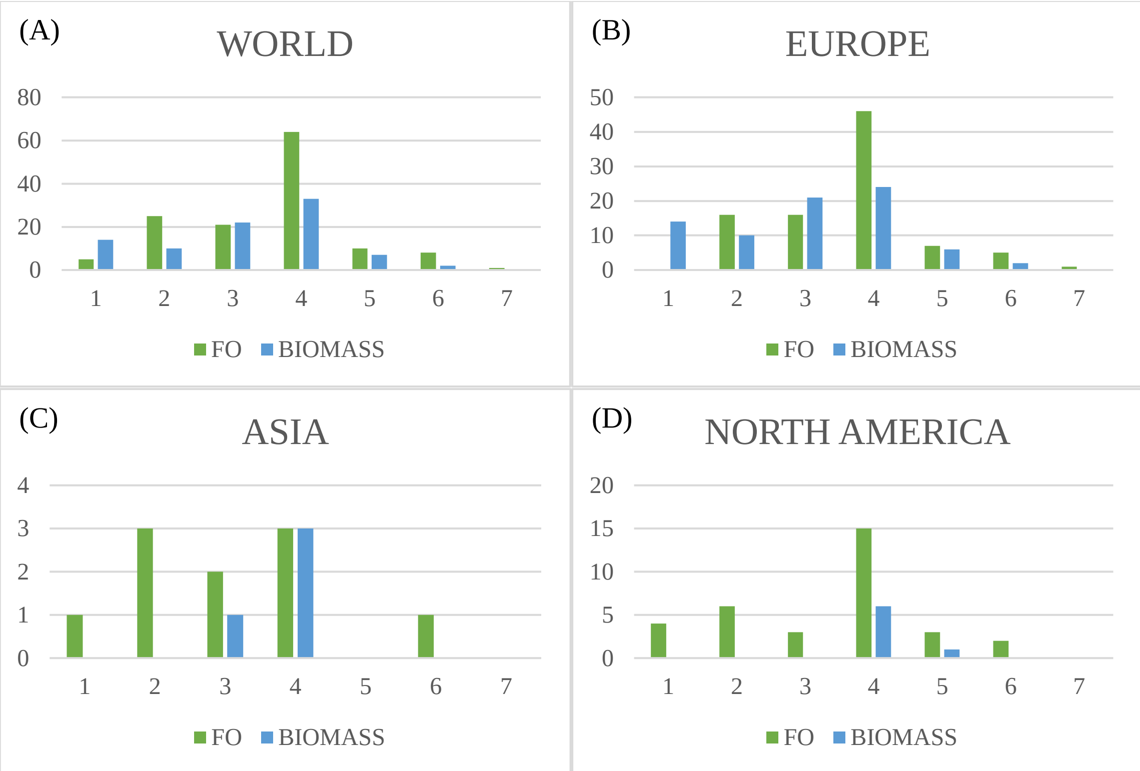


Figure 10 – List of carnivore taxonomic Families reported to be consumed by wolves according to the number of times each family member was reported as prey item in the sampling sites of the three Continents. Between parentheses is the number of consumed species reported for each Family.

The distribution of classes representing the magnitude of carnivore consumption by wolves (based on reported F.O. and Biomass values) show that in general carnivores represent 1 to 5% (Class 1 to 4) of wolf diet, reaching up to 30% only in Europe (Class 7; Fig.11).

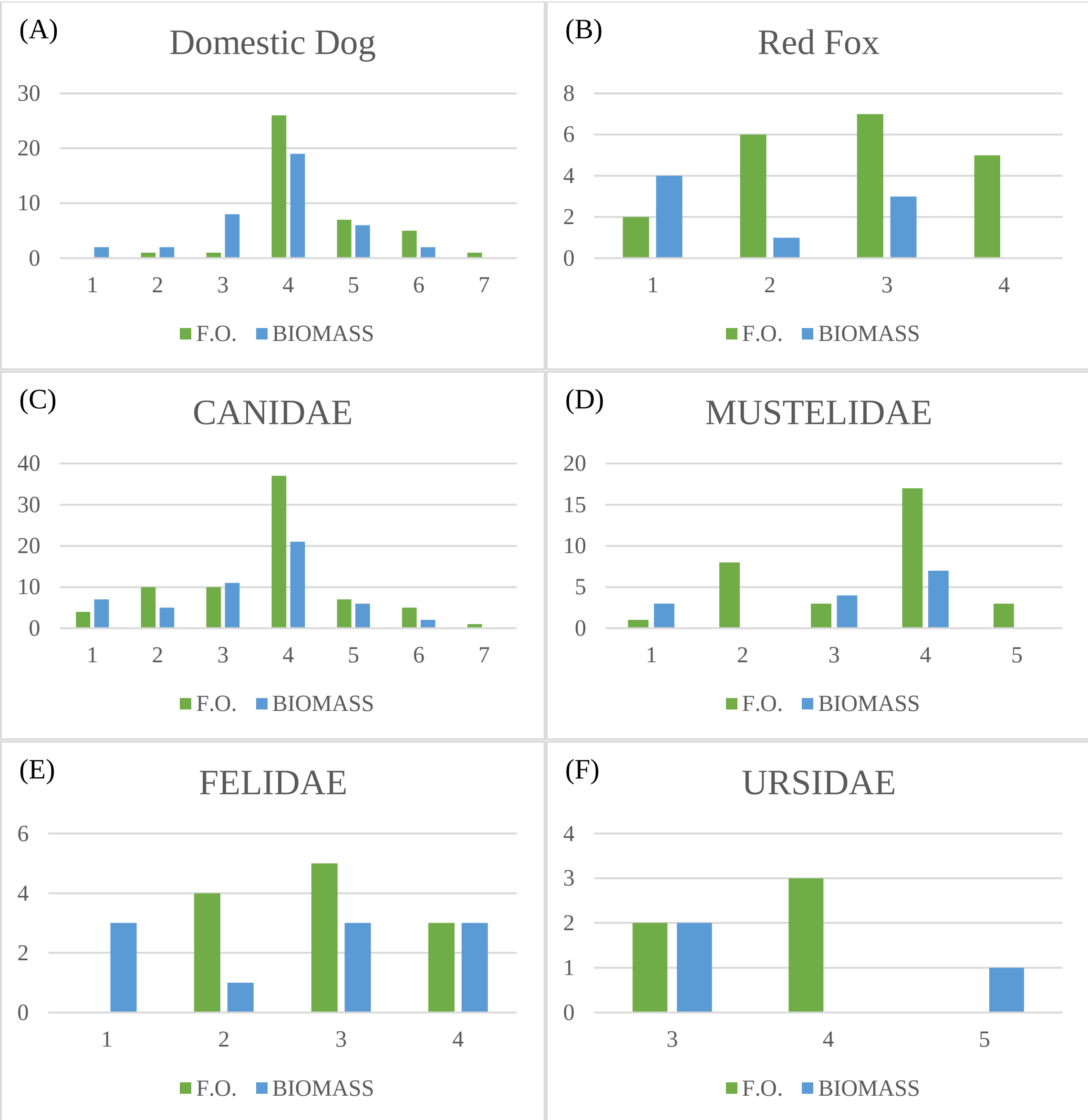


Consumption classes:

1 - 0,1 to 0,19%; **2** - 0,2% to 0,49%; **3** - 0,5% to 0,99%; **4** – 1% to 4,9%; **5** – 5% to 9,9%; **6** – 10% to 19,9%; **7** – 20% to 29,9%.

Figure 11 – Distribution of classes representing the magnitude of carnivore consumption by wolves (based on reported Frequency of Occurrence and Biomass) according to the number of times each category appeared in the sampling sites globally (A) and per continent (B, C, D).

The distribution of classes representing magnitude of carnivore consumption by wolves (based on reported F.O. and Biomass values) for the most represented species (domestic dog and red fox) and taxonomic Families (Canidae, Mustelidae, Felidae and Ursidae) shows that the most consumed species (domestic dog) and Families (Canidae and Mustelidae) have a bigger range of values of consumption than the others (Fig. 12) and usually represent 1 to 5% (Class 4) of wolf diet. The less consumed Families (Mustelidae, Felidae and Ursidae) and species (red fox) don’t reach values of consumption above 10% (Class 6 and 7) Fig.12 – B, E, F).



Consumption classes:
1 - 0,1% to 0,19%; **2** - 0,2% to 0,49%; **3** - 0,5% to 0,99%; **4** – 1% to 4,9%; **5** – 5% to 9,9%; **6** – 10% to 19,9%; **7** – 20% to 29,9%.

Figure 12 – Distribution of classes representing the magnitude of carnivore consumption by wolves (based on reported Frequency of Occurrence and biomass) according to the number of times each category appeared in each species reported to be consumed by wolves and categorized by the respective families most commonly consumed: domestic dog (A), red fox (B), Canidae (C), Mustelidae (D), Felidae (E) and Ursidae (F).

Regarding a main morphological characteristic – body weight – of carnivore species consumed by wolves, results shows that wolves consume more frequently species with average adult weights between 11 to 35kg (class 4), smaller than their own (Fig.13; Appendix II). Yet, is even less common for wolves to consume species with less than 1kg (class 1) than species with the same or bigger weight than wolves (class 5).

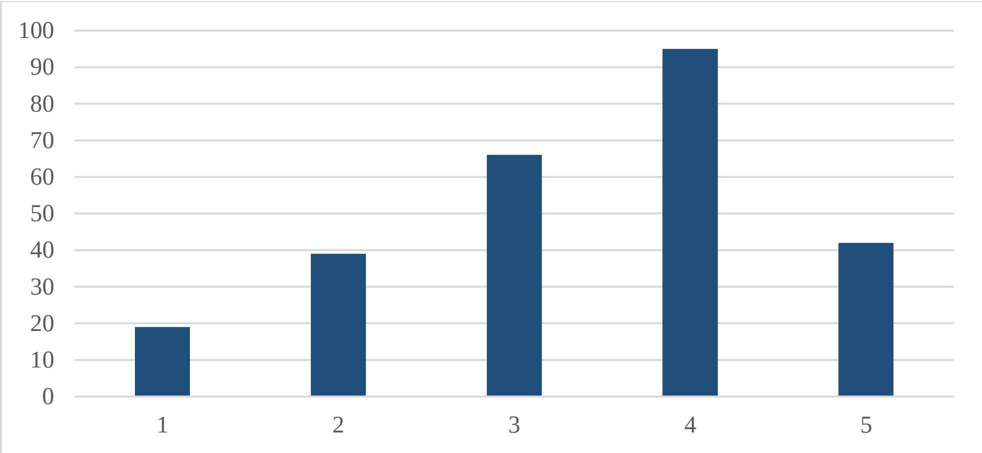


Figure 13 – Distribution of weight classes of carnivore species consumed by wolves according to the number of times a species of each class appears in the sampling sites. Weight Classes: 1 - ≤1kg; 2 – 1 to 5kg; 3 – 6 to 10kg; 4 – 11 to 35kg; 5 - ≥35kg.

Regarding the ecological characteristics, trophic niche and scavenging behavior – of carnivore species consumed by wolves, species with diets depending mainly on meat (carnivore, comprising 67% of all species) were less times consumed than omnivore species (Fig. 14; Appendix II). Species with reported scavenging behavior (scavengers, comprising 56% of all species) were consumed a lot more frequently than non-scavengers' species (Fig.15).

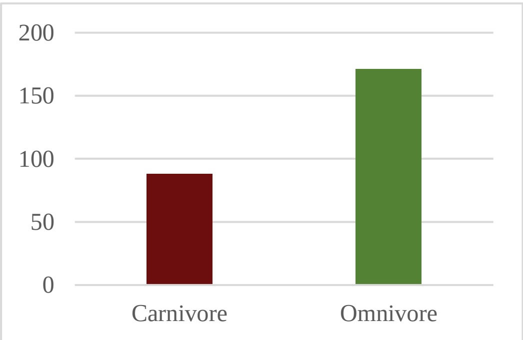


Figure 14 – Trophic niche of carnivore species consumed by wolves based on their primary diet (carnivore and omnivore: see methods for details) according to the number of times a species of each category appears in sampling sites.

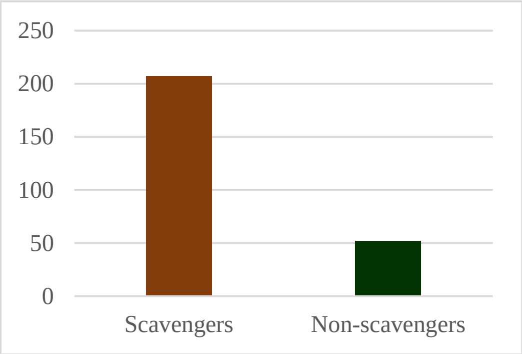


Figure 15 – Scavenging behavior of the carnivore species consumed by wolves according to the number of times a species of each category appears in sampling sites.

When sorting carnivores and omnivores per their scavenging behavior and weight classes (Fig.16) it turns evident that carnivore species that are middle-sized (6 to 35 kg – Class 3 and 4) omnivores and with scavenging behavior are the most common prey of wolves.

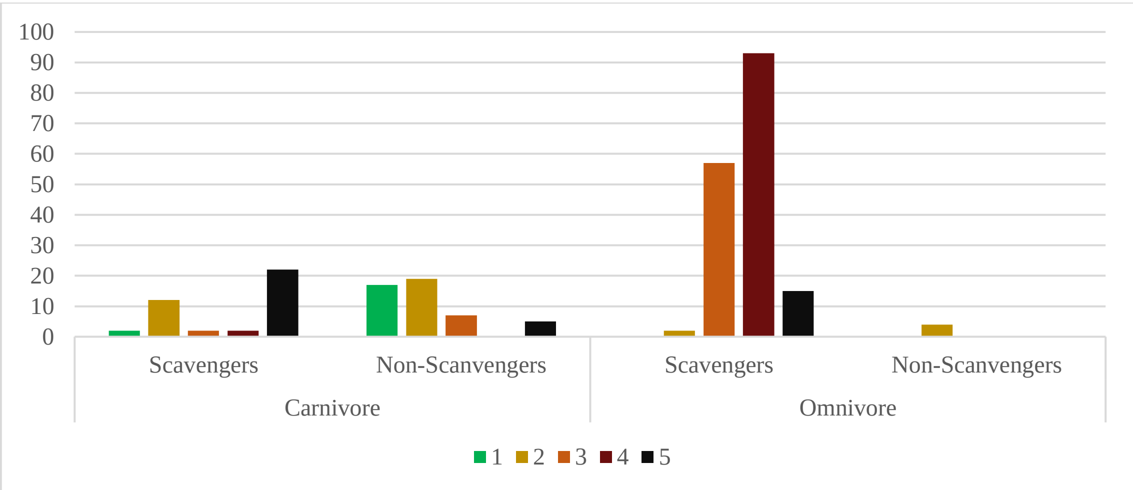


Figure 16 – Weight classes, primary diet and scavenging behavior of the carnivore species consumed by wolves according to the number of times a species of each category appears in sampling sites. Weight Classes: 1 - <1kg; 2 – 1 to 5kg; 3 – 6 to 10kg; 4 – 11 to 35kg; 5 - >35kg.

There were no significant differences between seasons (Winter/Autumn and Summer/Spring) in the percentage of carnivore consumption (ANOVA, Z=0,117; p>0.05) as well as in the number of carnivore species consumed by wolves (ANOVA, Z=1,398; p>0.05) (Appendix IV – Table S4 and S5).

3.2 Drivers for carnivore consumption

The GLM model revealed that five independent variables (protected area, domestic ungulates class of consumption, wild ungulates class of consumption, small mammals class of consumption and human density) showed a significant interaction ($p<0,05$) with the percentage of carnivore consumption by wolves (Appendix VIII – Table S9). Examining the B values of each environmental and human related variables with a significant interaction with the percentage of carnivore consumption by wolves (Table 2), it's possible to evaluate the type of interactions occurring: non-protected areas (N) and human density have positive correlations with the dependent variable (B's with positive values), so higher values of carnivore consumption are correlated to non-protected areas and to higher values of human density. On other side, classes of consumption of domestic ungulates, wild ungulates and small mammals have negative correlations with the dependent variable (B's with negative values), so higher values of carnivore consumption are correlated to lower classes of consumption of domestic ungulates, wild ungulates and small mammals. NDVI has also a negative correlation with the dependent variable although is not significant ($p>0,05$).

Table 2 -Results from the GLM model for the interaction between the percentage of carnivore consumption by wolves and the environmental and human related variables in the 87 sampling sites. Significant results are marked in bold.

Parameter	**B**	**Std. Error**	**95% Wald Confidence Interval**		**Hypothesis Test**		
			Lower	**Upper**	**Wald Chi-Square**	**df**	**Sig.** (p value)
(Intercept)	-0,041	0,4667	-0,956	0,873	0,008	1	0,930
[Protect Area =N]	0,274	0,0870	0,103	0,444	9,912	1	**0,002**
[Protect Area =Y]	0[a]	.	.	.	.	.	.
Domestic ungulates class of consumption	-0,138	0,0567	-0,249	-0,027	5,936	1	**0,015**
Wild ungulates class of consumption	-0,198	0,0602	-0,316	-0,080	10,829	1	**0,001**
Small mammals class of consumption	-0,141	0,0711	-0,281	-0,002	3,958	1	**0,047**
NDVI	-0,005	0,0032	-0,011	0,002	2,050	1	0,152
Human density	0,000	0,0002	-0,001	-6,789E-5	5,338	1	**0,021**
(Scale)	0,184[b]	0,0252	0,141	0,241			

Dependent Variable: Log (Carnivore consumption %)

Model: (Intercept), Protected Area, Domestic ungulates class of consumption, wild ungulates class of consumption, small mammals class of consumption, NDVI, Human density.

a. Set to zero because this parameter is redundant.

b. Positive values – proportional interactions; Negative values – inversely proportional interactions.

The GLM model for the interaction between the number of carnivore species consumed by wolves and the environmental and human related variables in the 143 sampling sites revealed that three independent variables (protected area, small mammals class of consumption and NDVI) showed a significant interaction ($p<0,05$) with the number of carnivore species consumed by wolves (Appendix VIII – Table S10). Examining the B values of each environmental and human related variables (Table 3), it's possible to evaluate the type of interactions occurring with the dependent variable: non-protected areas (N) have a positive correlation with the dependent variable (B's with positive values), so higher number of carnivore species consumed are correlated to non-protected areas; small mammals classes of consumption and NDVI have negative correlations with the dependent variable (B's with negative values), so higher numbers of carnivore species consumed are related to lower consumption of small mammals and lower values of NDVI. Domestic and wild ungulates classes of consumption had also a negative correlation with the dependent variable and human density a positive correlation although, none of these variables were significant ($p>0,05$).

Table 3 - Results from the GLM model for the interaction between number of carnivore species consumed by wolves and the environmental and human related variables in the 143 sampling sites. Significant results are marked in bold.

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test		
			Lower	Upper	Wald Chi-Square	df	Sig. (p value)
(Intercept)	1,883	0,6709	0,568	3,198	7,878	1	**0,005**
[Protect Area =N]	0,354	0,1372	0,085	0,623	6,651	1	**0,010**
[Protect Area =Y]	0[a]	.	.	.	.	.	.
Domestic ungulates class of consumption	-0,144	0,0881	-0,317	0,029	2,671	1	0,102
Wild ungulates class of consumption	-0,005	0,0898	-0,182	0,171	0,004	1	0,952
Small mammals class of consumption	-0,258	0,1022	-0,459	-0,058	6,381	1	**0,012**
NDVI	-0,009	0,0034	-0,015	-0,002	6,527	1	**0,011**
Human density	7,828E-5	0,0003	0,000	0,001	0,095	1	0,758
(Scale)	1[b]						

Dependent Variable: Number of carnivore species consumed

Model: (Intercept), Protected Area, Domestic ungulates class of consumption, wild ungulates class of consumption, small mammals class of consumption, NDVI, Human density.

c. Set to zero because this parameter is redundant.

d. Positive values – proportional interactions; Negative values – inversely proportional interactions.

4.Discussion

This study evaluates for the first time, the patterns and drivers related to the consumption of carnivore species by wolves demonstrating that intraguild predation is common worldwide and reported in all three continents within wolf range: Europe, Asia and North America. The number and composition of the carnivore species most consumed varies across Continents but, overall, consumption has higher incidence in generalist mesocarnivores with reported scavenging behavior, with the Family Canidae being the most commonly consumed globally. Also, this study reveals the significant environmental and human-related factors related to the number of carnivore species consumed by wolves as well as the magnitude of their consumption, providing valuable insights on wolf behavioral ecology and wide implications on wolf management.

4.1 Finding the patterns: which, why and where carnivores are consumed by wolves?

As expected by considering wolf cautiousness and capacity to evaluate the cost-benefit of each hunt, most of the carnivore species consumed are in fact smaller than wolves (Weaver, 1994; Mech *et al.*, 2015). The biggest consumed species (>35kg), such as black bears, are less rare in wolf diet than the smallest species (<1kg). Consumed carnivores with less weight are composed by the smallest mustelids (such as the least weasel), which feed on different prey than wolves and are normally not considered to have scavenging behavior (appendix II). Thus, these smaller prey species rarely compete with wolves for food acquisition. Nevertheless, most carnivore species eaten by wolves are primarily omnivores but, what highlights it's almost all of these have reported scavenging behaviors. Wolves are highly territorial animals and many carnivore species consumed by wolves do scavenge wolf's kills (Mech, 1994). These results suggest that intraguild predation in wolves might be mainly driven, not by direct competition for prey but, by competition for kills.

Canids were the most common Family to appear in wolf diet in all the three Continents. Previous studies have already shown that the Family Canidae was the most involved in interspecific killing, as killers and victims, being wolf the most cited as the killer (Palomares and Caro, 1999). It's interesting to note that wolves consume species which may mate with, like the coyote and the domestic dog. However, mating between these species might only happen in unusual opportune circumstances such as in lone wolves during dispersion (Mech, 1970; Mech and Boitani, 2003). Domestic dogs are more commonly consumed than coyotes. Wolves largely exclude coyotes and kill them typically when they approach to scavenge wolf kills, while domestic dogs are usually related to more humanized areas and the consumption of these might be driven by other causes, such as high dog densities or scarcity of alternative prey (Mech and Boitani, 2003; Ripple *et al.*, 2013).

The domestic dog (further discussed in the management implications section) and the red fox were found to be the most common carnivore species consumed by wolves. Food competition between foxes and wolves is unlikely to happen, particularly in preserved habitats, because their niche overlap is low (Patalano and Lavari, 1993; Sillero-Zubiri *et al.*, 2004; Bassi, 2012). Therefore, competition is rare unless resources are very scarce. Wolves might not be "antagonistic to foxes" due to direct competition unless their eating something wolves also want (Mech, 1970). Red foxes do scavenge and are known to do it commonly upon wolves kills (Mech, 1994; Wilson and Mittermeier, 2009). Murie (1944) also describes how wolves visit foxes den-sites searching for cashed food (kleptoparasitism) and that foxes follow wolf tracks when they carry prey carcasses away with them - in one case the wolf even seemed aware he would be followed and tried to mislead. This type of behaviors can lead to, sometimes, unpredictable violent encounters and consequent consumption of the kill, especially if the fox is young and unexperienced - in fact fox life-history patterns are characterized by "high juvenile and subordinate adult mortality" (Sillero-Zubiri *et al.*, 2004). The selection of adult foxes as prey and consequent predation seem less probable, even because foxes usually are too careful to be predated by wolves and fox adult mortality is normally low (Patalano and Lovari, 1993; Sillero-Zubiri *et al.*, 2004).

Wolves were the most common species to appear on wolf diet in North America. Wolf hairs found in wolf scats or stomachs can be a consequence of grooming, especially in seasons when females take care of pups (Liu, 2003). Many times, wolf hairs are excluded from diet analysis (for example: Arjo, 2002; Muller, 2006; Tourani, 2014). Anyhow, it's possible as well, wolf being included in dietary analysis without cannibalism involved sometimes, especially when in trace amounts it suggests ingestion by grooming (Gade-Jordensen and Stagegaard, 2000). However, cannibalism among wolves cannot be discarded as many authors have reported aggression and cannibalism in wolves. Breeding females kill and may consume other subordinate females and/or their cubs (McLeod, 1990; Wolff and Peterson, 2010), practicing not only cannibalism but also infanticide. Kuyt (1972) also reported skeletal remains of cubs next to dens suggested signs of cannibalism. In North America, intraspecific aggression due to space competition is often the primarily cause of adult wolves' mortality (Cubaynes *et al.*, 2014). Wolves usually have higher risks of fatal encounters in the edges of their territories because in these "buffer zones" the chance to find a member of a neighborhood wolf pack is higher and these situations can lead to lethal competition interactions for territory (Mech 1977; Mech, 1994). When a pack member is injured or killed, even by other causes, fellow members of the pack can eat it (Raush, 1967). Based in these evidences, wolf might not be as common in his own diet as it seems but aggression is, in fact, very common and consequent cannibalism does happen and may not an occasional event.

The European badger in Europe, mustelids in general and the raccoon in North America are as well commonly represented in wolf diet. Most studies do not provide much importance to mustelids and raccoon consumption as an indicator of competition or intraguild predation. Wolves can usurp dens of European badger and use them as their own den sites, since they are very suitable for the purpose (Kowalczy *et al.*, 2002; Theuerkauf *et al.*, 2002; Schmidt *et al.*, 2008). This might create a possibility for lethal physical confrontations between European badgers and wolves for competition over space resources, in which the wolf has expectably more chances to win. Despite the fact some of these species scavenge, such as European badgers and raccoons, their main food resources include invertebrates and fruits, not overlapping with wolf diet (Roper, 1994; Mysłajek *et al.*, 2016). Many studies have already considered some mustelids and raccoon as a prey item for wolves (for example: Messier and Cretê,1985; Marucco, 2003; Darimont *et al.*, 2004; Nowak *et al.*, 2011; Lagos, 2013) and in interspecific lethal interactions mustelids are typically one of the most involved as victims (Palomares and Caro,1999). This evidences lead to the assumption that raccoons and mustelids might be perceived only as an alternative prey and not as a competitor for prey.

The domestic cat appeared regularly on wolf diet in Europe. There seems to be a lack of knowledge about the interaction between these two species, although probably is related simply to food acquisition by wolves. This makes sense because cats are not considered scavengers and hunt small animals (even when not feral) therefore, they seem not to compete with wolves (Coleman *et al.*, 1997). Domestic cats may be perceived as prey by wolves in human-dominated landscapes and due to their characteristics can be more easily killed.

The Ursidae family, one of the most commonly represented in North American wolf diet, included two consumed species that are much larger than wolves: the black bear and the brown bear. When brown bear was consumed, the remains were often identified as cubs and black bear consumption in one case was also thought to be a cub (Fritts, 1981; Capitani, 2016; Corradini, 2016). Bear cubs can be considered an abundant food supply in some areas and smaller species sometimes do kill cubs or juveniles of larger species (Mech, 1970; Palomares and Caro, 1999). Still, wolves and bears scavenge each other's kills so, antagonist interactions between these two large carnivores can happen for food, more precisely carcasses which bears win more often, or to defend young cubs (Mech, 1981; Ballard, 1987; Haber, 1987; Servheen and Knight 1990). Wolves have also been reported to eat bear carcasses that died by other causes, like human hunting (Theberge *et al.*, 1978; Rogers and Mech, 1981). As mentioned before, wolves are usually very careful with their choices related to physical confrontations, even though packs of wolves can actually kill bears as large as adult black bear females, even when there's no scavenging involved. Therefore, despite the good probability of direct competition on kills, situations involving bear consumption by wolves are probably more related to pup predation (Rogers and Mech, 1981; Horejsi *et al.*, 1984). Wolves were reported more times consuming black bears than brown bears, probably because brown bears are larger-bodied and possibly more aggressive than black bears (Herrero, 1985).

No significant differences in the consumption or number of carnivore species consumed by wolves were found between cold and warm seasons. This is surprising once it is known that wild prey abundances are lower in winter than in summer (Mech and Boitani, 2003). Consequently, it would be expected to occur more competition and chances of consuming other type of food items during cold seasons. Additionally, it is known that some mesopredators (e.g. the red fox) scavenge more often during winter, selecting other predators' kills instead of other cause-dead ungulates (Selva *et al.*, 2005). Therefore, it is important to consider that other factors driving carnivore consumption by wolves can be transcending the effects that seasons could have, such as human impacts.

4.2 Finding the drivers: which factors affect carnivore predation by wolves?

Interspecific killing among carnivores is common but the consumption of the victim is considered to be dependent on the availability of other food items (Palomares and Caro, 1999). In fact, this study showed that lower consumption of wild ungulates, the main food resource selected by wolves, is related to a higher magnitude of carnivore consumption. This pattern is particularly evident in Europe, the Continent with a higher proportion of sampling sites reporting carnivore consumption and where several dietary studies reporting consumption of carnivores had also low numbers or negative tendencies of wild ungulates in wolf diet (e.g. Guitián *et al.*, 1979; Boitani, 1982; Sidorovich *et al.*, 2003; Álvares, 2011). Consumption levels of domestic ungulates were as well lower when predation of carnivore species by wolves was higher. Domestic ungulates in human-dominated landscapes where wild ungulates are in low numbers, often become wolf main prey (Meriggi and Lovari, 1996; Mech and Boitani, 2003; Meriggi *et al.*, 2011; Torres *et al.*, 2015). Whenever wild ungulates become scarce and domestic ungulates are less or not available, competition levels are likely to increase between wolves and other predators, increasing the probability of fatal interactions among these predators and posterior consumption of the victims, as suggested by Palomares and Caro (1999) in accordance with our findings. In addition, our model also showed that lower consumption of small mammals by wolves is also related to higher consumption of carnivore species by wolves. Small mammals, such as rodents, seem to be an important alternative food resource for wolves, and may compose most of wolf diet in areas where wild ungulates are scarce and densities of small mammals are high, such as in the Artic or in agricultural areas (Mech and Boitani, 2003). Whenever small mammals are relevant in wolf diet, competition between wolves and mesocarnivores is also likely to increase, increasing the probability of lethal interactions among these predators and posterior consumption of the victims, once again, as suggested by Palomares and Caro (1999) in accordance with our findings.

Higher values in the magnitude of carnivore consumption by wolves were related with higher human densities and to non-protected areas. Obviously, regions located outside protected areas are more likely to have higher levels of human presence and consequent human-related activities. Human-dominated and agricultural landscapes show lower abundances of wild ungulates, where generalist mid-size carnivores (mesopredators) can become common (Prugh *et al.*, 2009; Ripple *et al.* 2015). In this ecological context, wolves tend to feed on other type of food-items besides large ungulates (Zlatanova *et al.*, 2014; Newsome *et al.*, 2016). This may explain higher magnitude of carnivore predation by wolves. Human garbage, rodents and livestock are examples of alternative food resources available to predators in areas with high human densities (Newsome *et al.*, 2014). Large-sized predators, such as wolves can well survive in these areas with high human densities, although having an increased vulnerability to local extirpation (Newmark *et al.* 1994). However, mesopredators benefit from their smaller size and generalist behavior accessing more easily to human wastes and environments for alternative food resources than larger predators (Prugh *et al.*, 2009; Newsome *et al.*, 2014). Enhancing mesopredators densities in areas with high human density, consequently increases competition for food resources among co-occurring species of predators and, therefore, lethal interactions are more likely to happen with larger predators generally winning (Donadio and Buskirk, 2006; Newsome *et al.*, 2014).

In order to discuss what might influence the number of carnivore species consumed by wolves, first, we have to take into account that a higher number of species in diets doesn’t obligatorily means higher levels of consumption. Low consumption of small mammals by wolves, low levels of NDVI and non-protected areas are significantly related to higher numbers of carnivore species consumed by wolves.

Our models revealed that low consumption of small mammals by wolves, low levels of NDVI and non-protected areas are significantly related to higher numbers of carnivore species consumed by wolves. However, higher number of carnivore species in wolf diet do not obligatorily means higher magnitudes of carnivore consumption. As already mentioned before, small mammals are considered an alternative food resource for wolves under conditions of low availability of their main prey, also, some wolves can rely their diets more on small mammals than usual if small mammals’ densities are high (Mech and Boitani, 2003; Newsome *et al.*, 2014; Zlatanova *et al.*, 2014). However, low availability of small mammals affects more directly their main predators, mesocarnivores (Gordon et al, 2015). In such conditions, scavenging can become a supplementary food resource with mesopredators benefiting from scavenging carcasses of prey killed by larger carnivores, such as wolves (De Vault *et al.*, 2003; Wikenros *et al.*, 2014). So once again, this pattern suggested by our results can be related to intraguild predation by wolves while protecting carcasses. Regarding the influence of NDVI on the number of carnivore species consumed by wolves is important to note that NDVI reflects plant productivity as well as vegetation dynamics and distribution, which affects animal population dynamics and, ultimately, all biodiversity (Pettorelli *et al.*, 2005). Low levels of NDVI correspond to scarcity or absence of vegetation cover and subsequently to less productive environments, affecting negatively upper trophic levels (McKinney, 2002). Plants have strong effects on lower trophic levels (herbivores) and indirect effects on higher trophic levels (predators) so, less plant abundance and diversity affects predators by affecting primarily their prey (Scherber *et al.*, 2010). Therefore, low levels of NDVI can lead to scarcity of prey for both apex and mesopredators, leading to higher competition and lethal interactions among more predator species with opportunistic consumption of the victims. This pattern may explain the effect of low NDVI in the increased number of different carnivore species in wolf diet. Protected areas apprehend, almost undoubtedly, a significant component of biodiversity and buffer it from threating processes (Gaston *et al.*, 2008). Thus, outside protected areas is more expectable to occur lower values of NDVI (due to e.g. deforestation and habitat loss) and consequent lower densities of wild prey (Scherber *et al.*, 2010; Ripple *et al.* 2015). Outside protected areas there is also human presence and agricultural landscapes that benefit more mesopredators than large carnivores (Newsome *et al.*, 2014). Subsequently, under these conditions, increased competition among more predator species and higher potential for intraguild predation by wolves is likely to occur.

4.3 Management implications: ecosystem services provided by wolves in controlling feral dogs and other mesopredators

Domestic dogs were the most common carnivore species to be consumed by wolves in Europe and it was also consumed in Asia with less expression. Areas with lower number of wolves and high numbers of dogs can lead to higher competition levels between these two canids, which may lead to fatal encounters (Lescureux and Linnel, 2014). In North America (mainly in Canada and Alaska) and many parts of Asia, populations of wolves are numerous and stable and occupy large wilderness areas where dog occurrence is scarce and localized (Ginberg and MacDonald, 1990; Boitani, 2003). In contrary, European wolf populations occur in human-dominated landscapes where the occurrence of domestic dogs, particularly feral dogs, is widespread within wolf range (Boitani, 2000). This ecological context might lead to higher dog consumption by wolves in Europe compared to other Continents. However, besides ecological factors several sociological and other human-related factors also influence dog predation by wolves. In fact, the way that dogs are used by humans and the human attitude towards them results in different abundances and in a variety of wolf–dog interactions (Veich, 2000; Lescureux and Linell, 2014). Following this, is also important to consider there are different types and categories of dogs. Domestic dogs have a huge variety of different colors, shapes and sizes and they can be categorized as domestic, stray or feral dogs, primarily distinguishable by their dependence and reliance on humans, in a descending order respectively (Green and Gipson, 1994). Domestic dogs can also exercise functions for and with humans that might implicate a stronger interaction with wildlife, such as hunting. These dissimilarities on dog morphology and behavior can lead to different ways of wolves perceiving dogs as competitors or as prey.

In many European countries is illegal to abandon dogs, however, this is hardly enforced and most countries are lacking knowledge on the size and trends of their stray/feral dog populations (Tasker, 2007). In Asia, it is well known India's intense and acute problems with stray dog population size, attacks on people and rabies. In India, stray dogs can be caught but, after sterilized they are released again so, breed control exists but they can keep interacting with people and wildlife in many ways (Lenin *et al.*, 2016). In North America, methods to deal with stray/feral dog's populations are more efficient: in the lower United States, to reduce wildlife damages related to dogs it is allowed to persecute or even kill dogs that chase or harass wildlife (Tischler, 2007); in Alaska, problematic feral dog packs have been killed by aerial shooting (Green and Gipson, 1994) and anyone can shoot dangerous dogs and/or dogs that chase livestock and annoy wildlife (Alaska Statute § 03.55.030, 1949); and in Canada, there is a practice called "dog culling" whereby members of the communities can kill stray dogs to control populations which frequently attack humans (CTV News, May 16, 2017). Regardless the effectiveness and ethics of these methods to control stray/feral dogs, the reported differences across Continents can partially explain the differences detected between their consumption by wolves per Continent. Also, the absence or rarity of dog consumption by wolves in North America and in Asia, might be replaced by predation on ecologically similar canids: the coyote in North America and the golden jackal in Asia. These two species are, as the domestic dog, generalist middle-sized canids that can also occur in urban areas and potentially get over abundant near human settlements (Jhala and Moehlman, 2004; Newsome and Ripple, 2015). Taking in consideration the recent population expansions of coyotes and golden jackals (Newsome *et al.*, 2017), it can be expected that where these mesopredators get overabundant in the future, they might as well become a more common prey species for wolves, such as the domestic dog.

Attacks and depredation on dogs by wolves might be uncommon but aren't absent in North America. In fact, 80 cases of wolf-human encounters were evaluated in Alaska and Canada where 6 of these had dogs present in which several were attacked (McNay, 2002). Fritts and Paul (1989) also investigated wolf attacks on domestic dogs in Minnesota, where most occurred in the backyard of the dogs' owners and some were consumed. These facts confirm that dog consumption by wolves is not absent in North America but, might be so rare and localized that most studies addressing wolf diet are not able to detect it. Also, since these events in North America are associated to dogs with owners, in most situations the owners' attempts to stop the attacks might reduce the probability of their consumption by wolves. However, the reasons leading to dog predation are not fully understood. It's known that wolves can recognize which preys are more profitable to hunt without many injuries or without being killed (Weaver, 1994; Wirsing, 2003; Mech *et al.*, 2015). While some large dogs are able to injure or even kill wolves (Álvares, 2011), others are indeed smaller and/or more naive and exposed (because of dog-human interactions), which might interfere in the way wolves perceive them. In fact, wolf predation is more related to prey vulnerability then density (Bergman *et al.*, 2006). Backeryd (2007) suggested that dogs killed and consumed in American yards were probably perceived as prey, since these incidents happened mostly when prey densities were low, while when dogs are killed and consumed on the outdoors, they should be perceived by wolves as competitors.

Most of the carnivore species consumed by wolves were medium-sized generalist carnivores with scavenging behavior reported, whose abundance might be released due to human wastes or to the extirpation of larger predators as the wolf. This release in mesopredator species who contact almost as much with wildlife as with humans, can bring an innumerous quantity of issues (e.g. disease outbreaks and local extinctions) to both sides (Prugh *et al.*, 2009). Wolf predation on these species can be a valuable ecosystem function to control mesopredator populations and to identify altered ecosystems. Our findings support the theory that attacks and consumption of domestic dogs depend on main prey densities, domestic dog densities and if dogs are perceived as prey or as competitors depending on the circumstances of the encounters. The type of attacks that take place in house yards, or close to people's houses, are more likely related to solitary wolves that might be searching for food, nevertheless, it can easily be prevented if dog owners don't let their pets outside alone and unprotected. Owners of domestic dogs, such as hunting and sled dogs, that have greater probabilities of undesired encounters with wolves and might be perceived as competitors, should work on new suitable techniques or gadgets to protect their pets. In cases where feral dog populations are not properly controlled and, especially, where feral dogs might represent a risk to people's and wildlife's health and safety, wolf predation on feral dogs can be an important ecosystem service.

5. Conclusions and future perspectives

This study brought relevance and provided knowledge about Intraguild predation by wolves, a topic poorly addressed on one of the most studied species worldwide. Bibliographic reviews that imply gathering huge quantity of information, such as the present one, are crucial to compile data and obtain global patterns. Carnivores seem to be an occasional food for wolves, and only rarely become relevant as supplementary food resources. However, wolves can eat almost anything and rarely kill and don't eat (Mech *et al.*, 2015). Sometimes wolves might feed on the victims' resultant of competition only because they already waste energy doing it. Thus, it may be the reason why carnivores are mostly represented by lower classes of consumption by wolves. The same happened among the most common Families and species eaten by wolves, reflecting that rarely a carnivore (or a specific species of carnivore) constitutes an important supplement on wolf diet. Our results suggest that, due to wolf's high territoriality and to the fact carnivore species most consumed exhibit scavenging behaviors, that scavenging wolf kills and competition for prey carcasses, particularly in human-dominated landscapes, can be a very important factor triggering intraguild predation in wolves. In fact, Human density seems to be a key-factor influencing wild ungulate and mesopredators abundances, potentially driving wolves to intraguild predation. By this mean, the occurrence of high values of carnivore consumption by wolves can indicate modified ecosystems that are subjected to human's presence and activities**.** Nevertheless, the consumption of carnivore species by wolves is a very complex interaction, and more studies on this topic are needed in order to understand more specific patterns and drivers. Other possible drivers should be explored in order to better understand what determines intraguild predation by wolves such as: wolf densities and territory sizes. These can represent, in some circumstances, a limiting resource for wolves (space) and a potential driver for competition, even when prey is abundant (Cubaynes *et al.*, 2014).

The increased number of different carnivore species in wolf diet might be reflecting possible struggles in mesopredators populations as well, as their main prey (small mammals) might be less abundant. The increased number of different carnivore species in wolf diet can also signalize loss of biodiversity and instable habitats, as it is related to low NDVI values and non-protected areas. In these areas, the possibility of generalist predators to rely on human wastes increases due to lack of prey, releasing abundances of mesopredator species that can enter in conflict with wildlife and humans. Nevertheless, to better understand and explore these types of interspecific interactions between wolves and other carnivore species, it would be interesting to evaluate the diet of the consumed mesopredators, in order to evaluate if possible variations on their food resources, such as carrion or human-related food, are connected to intraguild predation due to increased competition scenarios with wolves.

Whenever mesopredators or stray/feral dogs represent a danger to wildlife and to humans, the predation on these species it's an important ecosystem service provided by wolves. Human populations should be informed and aware of the present findings, in order to construct a greater tolerance towards wolves. More studies on intraguild predation based on extensive literature reviews should be performed on other species of large carnivores. These findings can raise awareness in human populations not only about the consequences of human actions to wildlife but to wipe off the bad reputation that large carnivores, like the wolf, gained through times and appeal to their conservation.

6.References

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7.Appendices

Appendix I

Table S1 – List of reviewed studies on wolf diet to assess carnivore consumption by wolves, with reference to Country, Region and Bibliographic source.

Country	Region	Bibliographic source*
PORTUGAL (PT)	Peneda-Gerês	**Álvares, 2011**
		Álvares, 1995
		Guerra, 2004
		Petrucci-Fonseca, 1990
		Vos, 2000
		Lançós, 1999
		Roque *et al.*, 2001
	Alvão-Padrela	**Carreira, 1996**
		Silva, 2006
		Carreira, 2010
	South Douro	**Quaresma, 2002**
		Vos, 2000
		Vingada *et al.*, 1997
		Quaresma, 2002; Roque *et al.*, 2003
		Torres, *et al.*, 2015
	Bragança	**Petrucci-Fonseca, 1990**
		Moreira, 1992
		Pimenta, 1998
SPAIN (ES)	Galicia	**Barja, 2009**
		Lagos, 2013
		Guitián *et al.*, 1979
		Cuesta *et al.*, 1991
		Llaneza and López-Bao, 2015
	Basque Country	**Echegaray *et al.*, 2007**
	Asturias	Llaneza *et al.* 2000
		Llaneza *et al.* 1996
		Nores *et al.*, 2008
		Cuesta *et al.*, 1991
		Braña *et al.*, 1982
	Castile-León	**Vicente *et al.*, 2000**
		Vilà *et al.*, 1990
		Cuesta *et al.*, 1991
		Barrientos, 1994
	Léon	**Salvador and Abad, 1987**
	La Rioja	Cuesta *et al.*, 1991
	Estremadura/Morena's Sierra	Cuesta *et al.*, 1991
	North Spain	**Castroviejo *et al.*, 1975**

* In bold are the bibliographic resources that reported carnivore consumption by wolves in the respective region/country.

Table S1 – List of reviewed studies on wolf diet to assess carnivore consumption by wolves, with reference to Country, Region and Bibliographic source. (continuation).

Country	Region	Bibliographic source*
ITALY (IT)	Pollino National Park	**Ciucci *et al.*, 2004**
	Cuneo (Reaches France)	**Marucco,2003**
	Turin	Gazzola *et al.*, 2007
		Gazzola *et al.*, 2005
	Aosta	Palmegiani *et al.*, 2013
	Tuscany	Mattioli *et al.*, 1995
		Davis *et al.*, 2012
		Ståhlberg *et al.*, 2016
		Mattioli *et al.*, 2011
	Arezzo	Bassi *et al.*, 2012
	Appenines	**Boitani, 1982**
	Northen Apennines	**Meriggi *et al.* 1991**
	Orecchiella Natural Park	**Ciucci *et al.*, 1996**
	Abruzzo National Park	**Patalano and Novari, 1993**
	Central-East Italy	**Pezzo *et al.*, 2003**
POLAND (PL)	Southeastern Poland	Smietana *et al.*, 1993
		Jędrzejewski *et al.* 2012
	South Poland	**Nowak *et al.*, 2005**
	Northeastern Poland	**Jędrzejewski *et al.* 2012**
	Eastern Poland	**Jędrzejewski *et al.* 2012**
	Central Poland	**Nowak *et al.*, 2011**
	Northwest Poland	
	North and West Poland	
	Podlaskie	**Jędrzejewski, *et al.*, 2000**
		Jędrzejewski *et al.*, 2002
	Biatowieza Primeval Forest	**Jędrzejewski *et al.*, 1992**
GREECE (GR)	Greece	**Papageorgiou, *et al.*, 1994**
GERMANY (DE)	Eastern German	**Wagner *et al.*, 2012**
	Northeastern Saxony	Ansorge *et al.*, 2006
BELARUS (BY)	Northeastern Belarus	**Sidorovich *et al.*, 2003**
HUNGARY (HU)	Northeastern Hungary	**Lanszki *et al.*, 2012**
ESTONIA (EE)	Southern Estonia	**Kübarsepp and Valdmann, 2003**
	Middle and South-eastern Estonia	**Valdmann *et al.*, 1998**
LATVIA (LV)	North-eastern and Western Latvia	**Valdmann *et al.*, 2005**
	Latvia	**Žunna *et al.*, 2009**
		Andersone and Ozolins, 2004
SCANDINAVIA PENINSULA (SCAN)	Sweden and Norway	**Müller, 2006**
		Ståhlberg *et al.*, 2017
FINLAND (FI)	North Karelia	**Gade-Jorgensen and Stagegaard, 2000**
ROMANIA (RO)	Eastern Romanian Carpathians mountains	**Corradini, 2015**

* In bold are the bibliographic resources that reported carnivore consumption by wolves in the respective region/country.

Table S1 – List of reviewed studies on wolf diet to assess carnivore consumption by wolves, with reference to Country, Region and Bibliographic source. (continuation).

Country	Region	Bibliographic source*
GREECE (GR)	Central Greece	Migli *et al.*, 2005
SLOVAKIA (SK)	North Central Slovakia	**Rigg and Gorman, 2012**
SWITZERLAND (CH)	Swiss Alps	Weber and Hofer, 2010
TURKEY (TR)	Kars	**Capitani *et al.*, 2016**
IRAN (IR)	Northwest Isfahan	Hosseini-Zavarei *et al.*, 2013
	Yazd	Tourani *et al.*, 2014
PAKISTAN (PK)	Gilgit Baltistan	Anwar *et al.*, 2012
	Khyber-Pakhtunkhwa	**Shabbir *et al.*, 2013**
INDIA (IN)	Maharashtra	**Habib, 2007**
	Gujarat	**Jhala, 1993**
		Jethva and Jhala, 2004
CHINA (CN)	Qinghai	**Liu and Jiang, 2003**
	Harbin	**Gao, 1990**
	Inner Mongolia	**Gao, 1990**
		Zhang *et al.*, 2009
		Chen *et al.*, 2011
KYRGYZSTAN (KG)	Issyk-Kul Region	**Jumabay-Uulu *et al.*, 2014**
MONGOLIA (MN)	Hustai National Park	Van Duyne *et al.*, 2009
		Hovens and Tungalaktuja, 2005
ALASKA (AK)	Kenai Peninsula	Peterson *et al.*, 1984
	Juneau	**Fox and Streveler, 1986**
	Northwest Alaska	Spaulding *et al.*, 2000
		Stephenson *et al.*, 1982
	South Central Alaska	**Ballard *et al.*, 1987**
		Murie, 1944
	Glacier Bay	**Lafferty *et al.*, 2014**
CANADA (CA)	Canada's Artic	**Kuyt, 1969**
	Yukon	**Theberge and Cotrell, 1977**
	British Columbia	**Darimont *et al.*, 2004**
		Bryan *et al.*, 2006
		Milakovic and Parker, 2011
		Steenweg, 2011
	British Columbia and Alberta	**Cowan, 1947**
	Alberta	**Fuller and Keith, 1980**
		James, 1999
		Morehouse and Boyce, 2011
		Carbyn *et al.*, 1993
	Western Manitoba	Sallows, 2007
	Québec	**Messier and Crête, 1985**
		Tremblay *et al.*, 2001

* In bold are the bibliographic resources that reported carnivore consumption by wolves in the respective region/country.

Table S1 – List of reviewed studies on wolf diet to assess carnivore consumption by wolves, with reference to Country, Region and Bibliographic source. (continuation).

Country	Region	Bibliographic source*
CANADA (CA)	Outaouais	Potvin *et al.*, 1988
	Ontario	Forbes and Theberge, 1996
		Theberge *et al.*, 1978
		Pimlott *et al.*, 1969
		Voigt *et al.*, 1976
UNITED STATES (US)	Montana	**Arjo *et al.*, 2002**
		Derbridge *et al.*, 2012
	Minnesota	**Van Ballenberghe *et al.*, 1975**
		Fritts and Mech, 1981
		Chavez and Gese, 2005
	Arizona and New Mexico	Reed *et al.*, 2006
		Carrera *et al.*, 2008
		Merkle *et al.*, 2009
	Isle Royale	**Mech, 1966**
	Grand Teton	**Trejo, 2012**
	Yellowstone	
GREENLAND (GL)	Nansen Land	**Marquard-Petersen, 1988.**

* In bold are the bibliographic resources that reported carnivore consumption by wolves in the respective region/country.

Appendix II

Table S2 – Biological characteristics of each carnivore species reported to be consumed by wolves.

Species	Scientific name	Family	Average adult weight (Kg)	Weight Class[(a)]	Primary Diet	Scavenging[(b)]	Nº of Studies	Nº of Sampling Sites	Mean F.O.	Mean Biomass	Continent
Domestic Dog	*Canis familiaris*	Canidae	31,0	4	Omnivore	1	42	70	5,2%	1,9%	North America/Europe/Asia
Red Fox	*Vulpes vulpes*	Canidae	7,0	3	Omnivore	1	33	39	0,6%	0,4%	North America/Europe/Asia
Wolf	*Canis lupus*	Canidae	43,3	5	Carnivore	1	15	22	0,8%	0,3%	North America/Europe/Asia
Raccoon Dog	*Nyctereutes procyonoide*	Canidae	7,7	3	Omnivore	1	10	11	2,0%	1,3%	Europe/Asia
Coyote	*Canis latrans*	Canidae	11,5	4	Omnivore	1	4	4	0,9%	NA	North America
Artic Fox	*Alopex lagopus*	Canidae	3,7	2	Carnivore	1	2	3	0,7%	NA	North America/Europe/Asia
Indian Fox	*Vulpes bengalensis*	Canidae	2,6	2	Omnivore	0	2	2	NA	1,0%	Asia
Corsac Fox	*Vulpes corsac*	Canidae	2,3	2	Carnivore	1	1	1	NA	NA	Asia
Golden Jackal	*Canis aureus*	Canidae	7,9	3	Carnivore	1	1	1	0,2%	NA	Europe/Asia
European Badger	*Meles meles*	Mustelidae	13,0	4	Omnivore	1	19	19	1,6%	2,3%	Europe/Asia
Ermine	*Mustela erminea*	Mustelidae	0,2	1	Carnivore	0	6	8	2,7%	2,7%	North America/Europe/Asia
Fisher	*Martes pennanti*	Mustelidae	3,4	2	Carnivore	1	3	5	0,8%	NA	North America
American Mink	*Neovison vison*	Mustelidae	1,0	1	Carnivore	0	3	4	1,8%	1,3%	North America
North American River Otter	*Lontra canadensis*	Mustelidae	8,2	3	Carnivore	0	3	4	3,1%	2,1%	Europe/North America
American Marten	*Martes americana*	Mustelidae	0,7	1	Carnivore	0	1	4	1,1%	NA	North America
Marten	*Martes* sp.	Mustelidae	1,5	2	-	-	3	2	2,6%	1,5%	Europe
European Pine Marten	*Martes martes*	Mustelidae	1,3	2	Carnivore	1	2	2	NA	NA	Europe/Asia
Least Weasel	*Mustela nivalis*	Mustelidae	0,1	1	Carnivore	1	2	2	NA	NA	North America/Europe/Asia
American Badger	*Taxidea taxus*	Mustelidae	7,4	3	Carnivore	1	1	1	NA	NA	North America
Long-tailed Weasel	*Mustela frenata*	Mustelidae	0,2	1	Carnivore	0	1	1	0,1%	NA	North America
Stone Marten	*Martes foina*	Mustelidae	1,7	2	Omnivore	0	1	1	NA	NA	Europe/Asia
Eurasian Otter	*Lutra lutra*	Mustelidae	9,5	3	Carnivore	0	1	1	NA	NA	Europe/Asia

Table S2 – Biological characteristics of each carnivore species reported to be consumed by wolves. (continuation).

Species	Scientific name	Family	Average adult weight (Kg)	Weight Class[(a)]	Primary Diet	Scavenging[(b)]	Nº of Studies	Nº of Sampling Sites	Mean F.O.	Mean Biomass	Continent
Wolverine	*Gulo gulo*	Mustelidae	11,8	4	Carnivore	1	1	1	0,4%	NA	North America/Europe/Asia
Domestic Cat	*Felis catus*	Felidae	4,4	2	Carnivore	0	15	17	1,3%	1,0%	North America/Europe/Asia
Jungle Cat	*Felis chaus*	Felidae	7,3	3	Carnivore	0	1	1	NA	NA	Asia
Bobcat	*Lynx rufus*	Felidae	9,3	3	Carnivore	0	1	1	NA	NA	North America
Canadian Lynx	*Lynx canadensis*	Felidae	11,2	4	Carnivore	1	1	1	NA	NA	
Palla's Cat	*Otocolobus manul*	Felidae	3,5	2	Carnivore	0	1	1	NA	NA	Asia
Black Bear	*Ursus americanus*	Ursidae	118,8	5	Omnivore	1	8	9	2,0%	5,8%	North America
Brown Bear	*Ursus arctus*	Ursidae	252,5	5	Omnivore	1	6	6	1,0%	0,6%	North America/Europe/Asia
Raccoon	*Procyon lotor*	Procionidae	6,6	3	Omnivore	1	4	7	19,0%	NA	North America/Europe/Asia
Harbour Seal	*Phoca vitulina*	Phocidae	97,5	5	Carnivore	0	2	2	6,3%	NA	North America
Seal	*Phoca* sp.	Phocidae	97,5	5	Carnivore	0	1	3	NA	2,0%	North America
Striped Skunks	*Mephitis mephitis*	Mephitidae	2,3	2	Omnivore	1	3	2	NA	NA	North America
Common Genet	*Genetta genetta*	Viveridae	2,0	2	Carnivore	0	1	1	0,3%	0,2%	Europe
Masked Palm Civet	*Paguma larvata*	Viveridae	4,0	2	Omnivore	0	1	1	10,6%	NA	Asia
Indian Gray Mongoose	*Herpestes edwardsii*	Herpestidae	2,5	2	Carnivore	1	1	1	NA	NA	Asia
Undetermined Canids	-	Canidae	13,0	4	-	-	3	6	1,9%	NA	North America/Europe/Asia
Undetermined Mustelids	-	Mustelidae	4,3	2	-	-	7	6	0,9%	1,9%	North America/Europe/Asia
Undetermined Felids	-	Felidae	7,1	3	-	-	1	2	NA	NA	North America/Europe/Asia
Undetermined Carnivores	-	-	-	-	-	-	11	13	1,1%	0,6%	North America/Europe/Asia

Each species' characteristics information not obtained through the present study was found through bibliography as described formerly in the methodology section.

(a)Weight Classes: 1 = <1kg; 2 = 1-5kg; 3 = 6-10kg; 4 = 11-35kg; 5 = >35kg.

(b)Scavengers: 1= scavenging reported; 0 = scavenging not reported.

(c) (c)* Number of studies and sampling sites reporting the consumption of the respective species.

(d) (d)* Respective means of the F.O. and biomass values of consumption by wolves on the sampling sites with carnivores' consumption. (NA: Not Available)

(e) Respective continents where the species occur.

Appendix III

Table S3 - Photographic record of each carnivore species reported to be consumed by wolves.

Photographs	Info
	**Domestic Dog** *Canis familiaris* Photo © Inês Martins
	**Red Fox** *Vulpes Vulpes* Photo © Andrew Marshall
	**Wolf** *Canis lupus* Photo © Rafael Marchante

Table S3 - Photographic record of each carnivore species reported to be consumed by wolves. (continuation).

Photographs	Info
	**Raccoon Dog** *Nyctereutes procyonoide* Photo © Alfredo Estrella
	**Coyote** *Canis Latrans* Photo © Dustin Stettler
	**Arctic Fox** *Alopex lagopus* Photo © Eric Kilby

Table S3 - Photographic record of each carnivore species reported to be consumed by wolves. (continuation).

Photographs	Info
	**Indian Fox** *Vulpes bengalensis* Photo © Arpit Deomurari
	**Corsac Fox** *Vulpes corsac* Photo © Neil McIntosh
	**Golden Jackal** *Canis aureus* Photo © Lennart Hessel

Table S3 - Photographic record of each carnivore species reported to be consumed by wolves. (continuation).

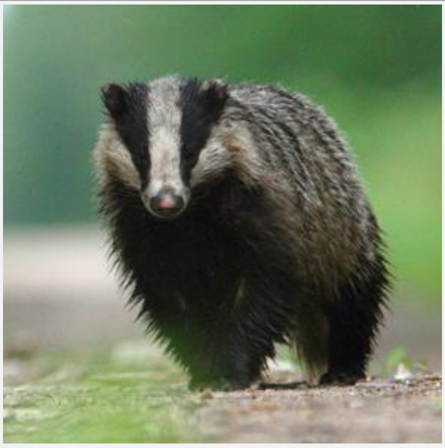
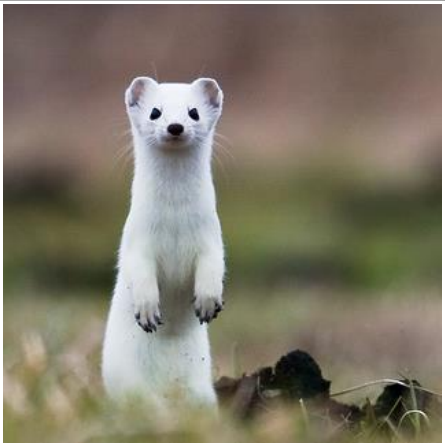
Photographs	Info
	**European Badger** *Meles meles* Photo © Silver Gutmann
	**Ermine** *Mustela erminea* Photo © Jorg Wenland
	**American Mink** *Neovison vison* Photo © Alami

Table S3 - Photographic record of each carnivore species reported to be consumed by wolves. (continuation).

Photographs	Info
	**Fisher** *Martes pennanti* Photo © Jeff Wendorff
	**North American River Otter** *Lontra canadensis* Photo © Gerry Ellis
	**European Pine Marten** *Martes martes* Photo © Andrew Marshall

Table S3 - Photographic record of each carnivore species reported to be consumed by wolves. (continuation).

Photographs	Info
	**Least Weasel** *Mustela nivalis* Photo © Bob Howdeshell
	**American Badger** *Taxidea taxus* Photo © Ryan Haggerty
	**Long-tailed Weasel** *Mustela frenata* Photo © Megumi Tedros

Table S3 - Photographic record of each carnivore species reported to be consumed by wolves. (continuation).

Photographs	Info
	**Stone Marten** *Martes foina* Photo © Domenico Pentoli
	**American Marten** *Martes americana* Photo © Tatiana Gettelman
	**Eurasian Otter** *Lutra lutra* Photo © Josh Jaggard

Table S3 - Photographic record of each carnivore species reported to be consumed by wolves. (continuation).

Photographs	Info
	**Wolverine** *Gulo gulo* Photo © Erik Mandre
	**Domestic Cat** *Felis catus* Photo © Inês Martins
	**Jungle Cat** *Felis chaus* Photo © Nirav Bhatt

Table S3 - Photographic record of each carnivore species reported to be consumed by wolves. (continuation).

Photographs	Info
	**Bobcat** *Lynx rufus* Photo © Phillip Colla
	**Canadian Lynx** *Lynx canadensis* Photo © Jeff Wendorff
	**Palla's Cat** *Otocolobus manul* Photo © James Godwin

Table S3 - Photographic record of each carnivore species reported to be consumed by wolves. (continuation).

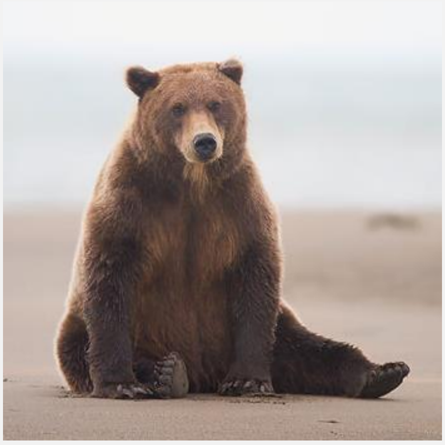
Photographs	Info
	**Brown Bear** *Ursus arctus* Photo © Ron Niebrugge
	**Black Bear** *Ursus americanus* Photo © Pam McIlhenny
	**Raccoon** *Procyon lotor* Photo © Alex Mody

Table S3 - Photographic record of each carnivore species reported to be consumed by wolves. (continuation).

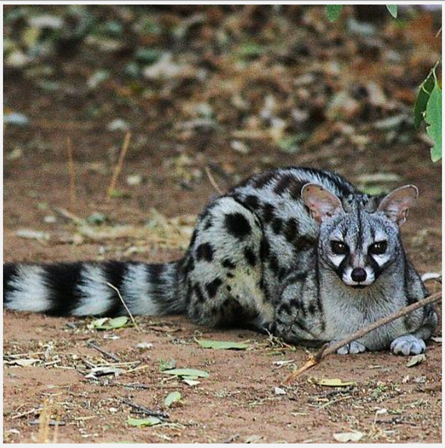
Photographs	Info
	**Harbour Seal** *Phoca vitulina* Photo © Gregory Smith
	**Striped Skunks** *Mephitis mephitis* Photo © Missouri Department of Conservation Staff
	**Common Genet** *Genetta genetta* Photo © Steve Garvie

Table S3 - Photographic record of each carnivore species reported to be consumed by wolves. (continuation).

Photographs	Info
	**Masked Palm Civet** *Paguma larvata* Photo © Tony Hara
	**Indian Grey Mongoose** *Herpestes edwardsii* Photo © Bill Coster

Appendix IV

Table S4 - Output of the one-way ANOVA to check if there were significant differences in the percentage of carnivore consumption by wolves between seasons (W- Winter and/or Autumn and S- Summer and/or Spring).

	Sum of squares	**df**	**Mean square**	**Z**	**Sig.** (p value)
Between groups	0,021	1	0,021	0,117	0,733
In groups	15,281	86	0,178		
Total	15,302	87			

Table S5 - Output of the one-way ANOVA to check if there were significant differences in the number of carnivore species consumed by wolves between seasons (W- Winter and/or Autumn and S- Summer and/or Spring).

	Sum of squares	**df**	**Mean square**	**Z**	**Sig.** (p value)
Between groups	2,426	1	2,426	1,398	0,240
In groups	196,061	113	1,735		
Total	198,487	114			

Appendix V

Table S6 - Pearson Correlation test for the F.O. and Biomass percentages of carnivore consumption by wolves in the 87 sampling sites.

		F.O.	Biomass
F.O.	Pearson Correlation (ρ)	1	0,911**
	Sig. (p value)		0,000
Biomass	Pearson Correlation	0,911**	1
	Sig. (p value)	0,000	

****.** Correlation is significant at the 0.01 level (2-tailed)

Appendix VI

Table S7 – Description of the 11 independent variables obtained from global data sets, with reference to source, period, and metrics (see Methodology section for details).

Variables	Source	Period	Citation	Metric
Roads Density	Socioeconomic Data and Applications Center; NASA; http://sedac.ciesin.columbia.edu/data/set/groads-global-roads-open-access-v1	1980-2010	Center for International Earth Science Information Network - CIESIN - Columbia University, and Information Technology Outreach Services - ITOS - University of Georgia. 2013. Global Roads Open Access Data Set, Version 1 (gROADSv1). Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC).	Number of cells
Human Density	Socioeconomic Data and Applications Center; NASA; http://sedac.ciesin.columbia.edu/data/set/gpw-v4-population-density	2000	Center for International Earth Science Information Network - CIESIN - Columbia University. 2016. Gridded Population of the World, Version 4 (GPWv4): Population Density. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC)	Mean density
Cattle Density	Global cattle density for 2005; http://www.fao.org/geonetwork/srv/en/metadata.show?id=12713andcurrTab=distribution	2005	-	Mean density
Anthromes	Anthromes version 2.0; http://ecotope.org/anthromes/v2/data/	1900-2000	Ellis, E. C., K. Klein Goldewijk, S. Siebert, D. Lightman, and N. Ramankutty. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. Global Ecology and Biogeography 19(5):589-606.	Coefficient
Agricultural Area	GlobCover 2009 v2.3; http://due.esrin.esa.int/page_globcover.php	2004-2009	-	Number of cells
Urban Area	GlobCover 2009 v2.3; http://due.esrin.esa.int/page_globcover.php	2004-2009	-	Number of cells
Forest Cover	GlobCover 2009 v2.3; http://due.esrin.esa.int/page_globcover.php	2004-2009	-	Number of cells
Mean Altitude	Worldclim; http://www.worldclim.org/	-	-	Mean
Temperature Seasonality	Worldclim; http://www.worldclim.org/	1960-1990	-	Mean
Precipitacion Seasonality	Worldclim; http://www.worldclim.org/	1960-1990	-	Mean
NDVI (Normalized Difference Vegetation Index)	https://landcover.usgs.gov/green_veg.php	2001-2012	Broxton P.D., Zeng, X., Scheftic, W., Troch, P.A., 2014b, A MODIS-Based 1 km Maximum Green Vegetation Fraction Dataset, J. Appl. Meteorol. Clim.,	Mean

Appendix VII

Table S8 - Pearson Correlation test for the 11 environmental and human related variables chosen as possible catalyzers of Intraguild predation scenarios. Significant correlations in bold.

		Mean Altitude	Temperature Seasonality	Precipitation Seasonality	NDVI	Anthromes	Cattle Density	Human Density	Urban Area	Agricultural Area	Forest Cover	Roads Density
Mean Altitude	Pearson Correlation (ρ)	1	-0,004	0,040	**-0,237****	-0,006	-0,146	-0,114	-0,129	0,064	**-0,323****	**-0,166***
	Sig. (p value)		0,962	0,604	0,002	0,941	0,060	0,144	0,096	0,409	0,000	0,032
Temperature Seasonality	Pearson Correlation (ρ)	-0,004	1	0,010	-0,023	**-0,247****	**-0,510****	0,148	0,135	**-0,367****	**0,198***	**-0,238****
	Sig. (p value)	0,962		0,899	0,771	0,001	0,000	0,057	0,082	0,000	0,010	0,002
Precipitation Seasonality	Pearson Correlation (ρ)	0,040	0,010	1	**-0,339****	0,033	**0,210****	**0,289****	**0,209****	**0,268****	**-0,448****	-0,019
	Sig. (p value)	0,604	0,899		0,000	0,673	0,007	0,000	0,007	0,000	0,000	0,807
NDVI	Pearson Correlation (ρ)	**-0,237****	-0,023	**-0,339****	1	0,086	**0,160***	**-0,181***	**-0,170***	0,023	**0,641****	**0,237****
	Sig. (p value)	0,002	0,771	0,000		0,268	0,039	0,019	0,028	0,767	0,000	0,002
Anthromes	Pearson Correlation (ρ)	-0,006	**-0,247****	0,033	0,086	1	**0,153***	-0,042	-0,067	**0,353****	-0,148	0,098
	Sig. (p value)	0,941	0,001	0,673	0,268		0,048	0,589	0,392	0,000	0,056	0,209
Cattle Density	Pearson Correlation (ρ)	-0,146	**-0,510****	**0,210****	**0,160***	**0,153***	1	-0,010	-0,021	**0,360****	-0,116	**0,349****
	Sig. (p value)	0,060	0,000	0,007	0,039	0,048		0,894	0,784	0,000	0,136	0,000
Human Density	Pearson Correlation (ρ)	-0,114	0,148	**0,289****	**-0,181***	-0,042	-0,010	1	**0,945****	0,140	**-0,228****	**0,252****
	Sig. (p value)	0,144	0,057	0,000	0,019	0,589	0,894		0,000	0,070	0,003	0,001
Urban Area	Pearson Correlation (ρ)	-0,129	0,135	**0,209****	**-0,170***	-0,067	-0,021	**0,945****	1	**0,202****	**-0,245****	**0,322****
	Sig. (p value)	0,096	0,082	0,007	0,028	0,392	0,784	0,000		0,009	0,001	0,000
Agricultural Area	Pearson Correlation (ρ)	0,064	**-0,367****	**0,268****	0,023	**0,353****	**0,360****	0,140	**0,202****	1	**-0,548****	**0,424****
	Sig. (p value)	0,409	0,000	0,000	0,767	0,000	0,000	0,070	0,009		0,000	0,000
Forest Cover	Pearson Correlation (ρ)	**-0,323****	0,198*	**-0,448****	**0,641****	-0,148	-0,116	**-0,228****	**-0,245****	**-0,548****	1	-0,048
	Sig. (p value)	0,000	0,010	0,000	0,000	0,056	0,136	0,003	0,001	0,000		0,536
Roads Density	Pearson Correlation (ρ)	**-0,166***	**-0,238****	-0,019	**0,237****	0,098	**0,349****	**0,252****	**0,322****	**0,424****	-0,048	1
	Sig. (p value)	0,032	0,002	0,807	0,002	0,209	0,000	0,001	0,000	0,000	0,536	

****.** Correlation is significant at the 0.01 level (2-tailed)
***.** Correlation is significant at the 0.05 level (2-tailed).

Appendix VIII

Table S9 – Output of the chi-square test[a] to examine the model fit of the GLM for the interaction between the percentage of carnivore consumption by wolves and the environmental and human related variables in the 87 sampling sites.

Likelihood Ratio Chi-Square	**Sig.** (p value)
24,067	0,001

Dependent Variable: Log (Carnivore consumption %)
Model: (Intercept), Protected Area, Domestic ungulates class of consumption, Wild ungulates class of consumption, Small mammals class of consumption, NDVI, Human density.
a. Compares the fitted model against the intercept-only model.

Table S10 – Output of chi-square test[a] to examine the model fit of the GLM with Poisson distribution for the interaction between the number of carnivore species by wolves and the environmental and human related variables in the 143 sampling sites.

Likelihood Ratio Chi-Square	**Sig.** (p value)
22,713	0,001

Dependent Variable: Number of carnivore species consumed
Model: (Intercept), Protected Area, Domestic ungulates class of consumption, wild ungulates class of consumption, small mammals class of consumption, NDVI, Human density.
a. Compares the fitted model against the intercept-only model.