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Consumption of Carnivores by Wolves: A Worldwide Analysis of Patterns and Drivers

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Abstract: The occurrence of carnivore species in wolf diet has been overlooked and poorly studied despite the potential implications for wolf ecology and wildlife management. We conducted an extensive literature review, focusing on 120 wolf diet studies worldwide to assess global patterns of carnivore consumption by wolves and their ecological and human-related determinants. We used a total of 143 sampling sites with data on the consumption of carnivores by wolves. In total, 35 carnivore species were reported to be consumed by wolves, comprising members of all taxonomic carnivore families represented within the gray wolf range. The carnivores were mostly limited to occasional consumption (<5% of wolf diet) but could account for as much as 25% in some study areas. The most frequently consumed carnivore species were those with reported scavenging behavior, belonging to medium-sized generalist canids. Generalized linear model (GLM) analysis revealed that higher magnitudes of carnivore consumption were related to nonprotected areas as well as lower occurrences of wild ungulates, domestic ungulates, and small mammals in wolf diet, while higher numbers of consumed carnivore species were related to nonprotected areas with low vegetation productivity and lower occurrences of domestic ungulates and small mammals in wolf diet. Our results suggest that carnivore consumption by wolves is driven by altered ecosystems and human-dominated landscapes, where mesopredator densities are often increased and prey densities decreased, which intensify competition and the need for alternative food sources.

Keywords: *Canis lupus*; competition; domestic dog; interspecific killing; mesopredators; worldwide review

1. Introduction

Interspecific interactions are the primary factor shaping the structure of ecological communities, and several are known among mammalian carnivores, including competition [1]. Competition among mammalian carnivores from the same ecological guild can be intense and lead to interspecific killing, which may be responsible for up to 68% of known mortality in some carnivore species [2–4]. Interspecific killing among carnivores is a common phenomenon across several species, and consumption of a killed carnivore may depend on the availability of other food sources [2]. Traditionally, predation and competition are assessed separately when, in reality, a carnivore species can act both as predator and competitor of other carnivores [5]. According to theoretical models, carnivore interspecific killing can result in exclusion, coexistence, or alternative stable states between species, leading to avoidance behaviors that can strongly affect species occurrence and, consequently, habitat selection [3,6]. Interspecific killing within a carnivore guild can also control mesocarnivore species, pests, and invasive species, and, through this trigger, further trophic cascades such as the reduction of predation level on smaller prey [3]. The importance of these top-down interactions can probably be best observed when apex predators are reduced or completely exterminated by humans, which results in a phenomenon known as mesopredator release, when mid-sized predators expand their distribution and may cause considerable perturbation of an ecosystem [7,8]. Furthermore, predation of top predators on mesocarnivores can also have important implications for public health and human welfare, for instance, by reducing feral dog populations, which are important vectors of potentially dangerous diseases, such as rabies [9].

Among mammalian carnivores, canids are often reported to be involved in interspecific killing as they are represented by several widespread mesocarnivores, as well as top predators such as the grey wolf (*Canis lupus*). In fact, wolves are one of the carnivore species most frequently involved in interspecific killing [2]. Wolves occur throughout most of the Northern Hemisphere in a wide range of habitats, including almost-intact wilderness areas to highly human-dominated landscapes, as long as adequate food sources are available and persecution by humans is low [10,11]. Wolf diet is extremely flexible, with large wild ungulates comprising the main prey in most regions. However, where these species are scarce, wolves often feed on domestic animals and smaller prey such as rodents or lagomorphs or even human refuse [11–14]. Wolf diet has been extensively studied worldwide, mostly on identifying prey remains in stomach content and scats [11,14]. However, in most of the studies focusing on wolf trophic ecology, occasional food items are often overlooked and pooled together as "other prey". This is the case of carnivore species consumed by wolves, which may result from direct killing due to competition and active predation or from scavenging as a complementary food source [2].

Several dietary studies across the wolf range have documented the consumption of carnivore species from different taxonomic families (e.g., [11,15,16]), including domestic dogs (e.g., [17–19]). However, to date, there has been no attempt to compile and review the evidence and assess the magnitude and general patterns related to carnivore consumption by wolves. Despite the potential implications for wildlife management, ecosystem functioning, and human welfare, wolf predation and consumption of other carnivores have been overlooked and the patterns related to the presence of carnivore species on wolf diet are poorly understood. Although wolves are one of the most studied mammals worldwide and diet is one of the most-studied topics for this large carnivore, this knowledge gap is most likely connected with the general low proportion of carnivores in wolf diet and the limitation of not being able to reliably differentiate between predation or scavenging on carnivore carcasses based on dietary studies [11,14].

This study aims to determine global patterns of carnivore consumption by wolves, including their magnitude and geographical variation, as well as ecological and human-related drivers to the consumption of other carnivores. This will help us to assess whether and when wolves use other carnivores as a food source. We conducted an extensive literature review on wolf diet across its worldwide range in order to address the following questions: (i) which and how many carnivore species are reported as wolf prey items?; (ii) what is the magnitude of carnivores as a food source for wolves?; (iii) what are the main taxonomic and ecomorphological traits (e.g., family, body size, primary diet—either strictly carnivorous or omnivorous) of the carnivores consumed by wolves?; (iv) what are the spatial and temporal patterns of carnivore consumption by wolves?; (v) what are the ecological and human-related variables that are associated with carnivore consumption by wolves? Based on our findings, we discuss the ecological and management implications of this behavior in wolves.

2. Materials and Methods

2.1. Data Collection and Organization

Data on wolf diet was collected from a literature review using Google Scholar, Web of Science (keywords used for the search include: *Canis lupus*, wolf, diet, food habits, prey selection, consumption, feeding ecology), and reference lists in obtained publications, including grey literature such as technical reports, MSc, and PhD theses (Table S1). Since some of the compiled studies included more than one sampling area, sampling sites were selected as the main unit for the analysis in this study. Depending on the available results, the magnitude of consumption of each prey species was quantified as frequency of occurrence (FO), percentage of consumed biomass (Biomass), or through both approaches (FO + Biomass). For the purpose of obtaining the full spectrum of carnivore species consumed by wolves, we also included studies reporting other types of prey item quantification, such as relative frequency of occurrence, percent of volume, crude biomass, food item identification (e.g., from kill sites), as well as studies reporting FO and/or Biomass without the exact values of prey consumption (e.g., prey items only referenced in graphics or vaguely mentioned in the text).

The geographic coordinates of each sampling site were retrieved from the study area description, whenever possible, or based on the geographical location of the sampling site described in the bibliographic source. Coordinates of sampling sites with no specific geographical location were taken approximately from areas known to be close by or from these sampling sites themselves (for example, the dietary results of a wolf pack in a certain protected area were assigned to the centroid of that protected area). All geographical operations, including estimating the coordinates for sampling sites, were performed in QGIS 2.18 (© 2004–2016 QGIS Development Team).

2.2. Assessing General Patterns of Carnivore Consumption by Wolves

Based on all sampling sites that reported consumption of carnivores by wolves, general patterns were assessed by considering the number and taxonomic family of carnivore species reported as a prey item, the ecomorphological traits of these consumed species, the magnitude of consumption of each species in wolf diet (FO and Biomass), and the geographical (continent) and seasonal variations of their consumption.

We analyzed the number of carnivore species consumed by wolves per sampling site and the number of sampling sites reporting a given species. Each carnivore species reported to be consumed by wolves was characterized according to the following ecological and morphological traits: weight (class of the average adult weight; see below), primary diet (strictly carnivorous or omnivorous), social behavior (solitary, gregarious, or small family groups), and scavenging behavior (whether scavenging was reported or not; Table S2). Average adult weights were categorized according to 5 classes: (i) ≤1 kg; (ii) 1 to 5 kg; (iii) 6 to 10 kg; (iv) 11 to 35 kg; (v) ≥35 kg. All the ecological and morphological traits related to the consumed carnivore species were obtained from [20], except for domestic dog [21] and domestic cat [22]. In order to better contextualize the behavioral patterns related to the consumption of carnivore species by wolves, we also compiled published evidence of antagonistic interactions between wolves and other carnivores, considering if the victim was consumed or not (Table S3).

To assess patterns related to the magnitude of carnivore consumption in each sampling site, we considered reported values of frequency of occurrence (FO) and percentage of consumed biomass (Biomass), which were categorized according to five classes: (i) 0% to 5%; (ii) 5.1% to 10%; (iii) 10.1% to 15%; (iv) 15.1% to 20%; (v) 20.1% to 25%. We used these classes of consumption for representing the reported values of FO whenever possible, and we used Biomass only in cases where prey item quantification by FO was not available. FO may better reflect the consumption of rare and small-to-medium-sized food items, such as carnivore species [16,23], since the measurements of Biomass for smaller prey, which are less likely to comprise the total scat content, are often overestimated [23,24]. We performed a Pearson correlation on the reported values of FO and Biomass of consumed carnivores in the wolf dietary studies reporting these two measures of prey quantification, which showed a very high correlation between them ($\rho = 0.911$; $p < 0.05$; Table S4), supporting our approach of using both measures to quantify consumption in the following analysis. Therefore, for all subsequent analyses, the dependent variable "magnitude of carnivore consumption" was constituted by all FO reported values, and Biomass values were used only in studies where FO was not available. This dependent variable is log-transformed to normalize its distribution.

Geographical patterns on carnivore consumption by wolves were assessed by categorizing sampling sites with reported carnivore consumption by continent (Europe, North America, and Asia). We then analyzed the number of carnivore prey species and the magnitude of consumption, both globally and per continent.

Seasonal patterns were analyzed for studies with reported dates or seasons of collected samples, and we categorized them into two main time periods: Winter/Autumn and Spring/Summer. We performed generalized linear models (GLMs) to assess significant differences between the seasons in the magnitude of consumption and the number of consumed carnivore species. Statistical analyses were performed using SPSS Statistics 24.0 software for Windows (IBM Corp; released in 2016). We considered $p < 0.05$ as the cut-off level for significance [25].

2.3. Assessing Factors Determining Carnivore Consumption by Wolves

To assess the ecological and human-related factors determining carnivore consumption by wolves, we used the magnitude of carnivore consumption (which we log-transformed) and the number of consumed carnivore species in each sampling site as dependent variables. GLMs were used to assess the effect of several explanatory variables (independent variables) on these two dependent variables. The GLMs were constructed by considering normal distribution and the identity link function except for the case of the dependent variable "number of consumed carnivore species", where we used Poisson distribution and the log-link function.

As independent variables, a total of 15 ecological and human-related variables were initially chosen according to their potential relevance for wolf trophic ecology, of which 4 variables were obtained directly from the compiled studies and 11 variables were obtained from available online global datasets (Table S5). Independent variables retrieved from the compiled studies included the presence or absence of protected areas (based on study area description) and the reported percentage of consumption of three food items in wolf diet, namely, domestic ungulates, wild ungulates, and small mammals. The remaining 11 variables were obtained from global datasets: roads density, human density, cattle density, anthromes as a measure of human impact and transformation in the landscape [26], proportion of agricultural areas, proportion of urban areas, forest cover, mean altitude, temperature seasonality (e.g., annual range in temperature), precipitation seasonality (e.g., annual range in precipitation), and the Normalized Difference Vegetation Index (NDVI) as a measure of vegetation productivity and primary production, as often used in macroscale analysis [27–30]. The values for these variables were obtained for each sampling site from digital maps, using as spatial resolution a pixel size of 10×10 km, which corresponds to the minimum size of wolf home ranges [11,24]. To retrieve the variable values, we also considered the time period (decade) in which the wolf diet of each sampling site was assessed. Anthromes represent the degree of long-term anthropogenic transformation of terrestrial biomes between the years 1700 and 2000 and are quantified on a scale where negative values represent habitats that have become wilder, zero values are nonaltered habitats, and positive values are habitats that have become more anthropized [26]. A Pearson correlation test on these 11 variables revealed high correlations between most of them (Table S6). Therefore, in the GLM analysis, we only included the two uncorrelated variables that were considered to be most representative of environmental and human-related conditions: NDVI and human density. Statistical analyses were performed using SPSS Statistics 24.0 software for Windows (IBM Corp., Armonk, NY, USA; released in 2016). We considered $p < 0.05$ as the cut-off level for significance [25].

3. Results

3.1. General Patterns of Carnivore Consumption by Wolves

The global review of 120 studies on wolf diet provided information on a total of 212 sampling sites, covering 27 countries (Table S1). Carnivores were reported as a prey item for wolves in 143 (67%) sampling sites (Figure 1), including 82% (n = 88) of sampling sites in Europe, 55% (n = 42) in North America, and 45% (n = 13) in Asia.

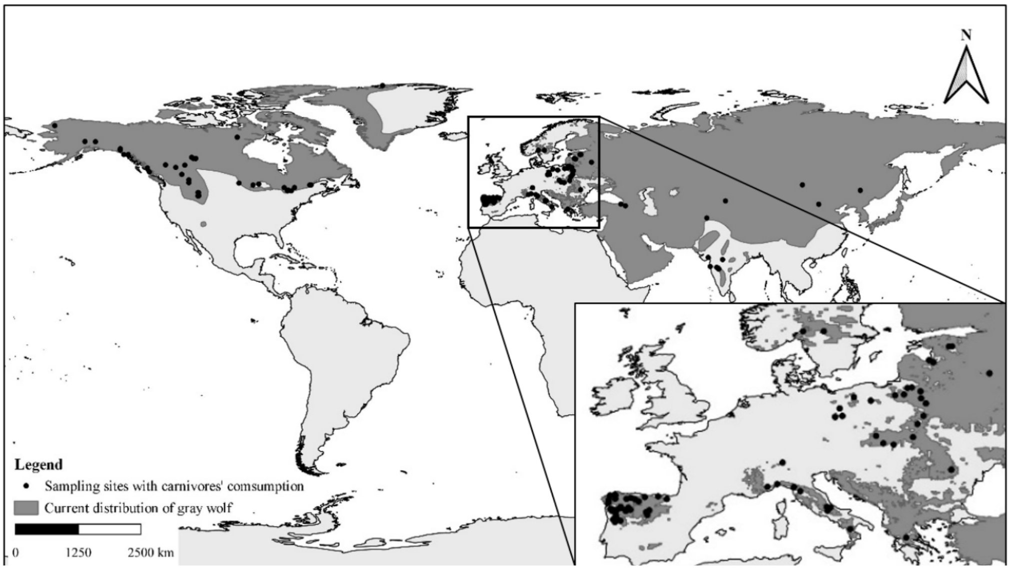

Figure 1. Location of the sampling sites reporting carnivore consumption by wolves worldwide (n = 143, black dots) based on 120 reviewed studies on wolf diet. Inset map depicts Europe, which includes most of the sampling sites reporting carnivore consumption by wolves (n = 88). Dark grey areas represent wolf range according to *The IUCN Red List of Threatened Species*™ (2017).

A total of 35 species of carnivores were reported as prey items in wolf diet studies worldwide (Europe = 12, Asia = 14, North America = 24; Figure 2). In general, domestic dogs (*Canis familiaris*) were the most common carnivore to be consumed by wolves, with consumption reported in 70 sampling sites. Most of them were located in Europe (n = 67; 96%), while only 3 (4%) were reported in Asia and none in North America. Considering the proportion of carnivore consumption among the sampling sites in each continent, domestic dogs were reported from 88% of sites in Europe, 23% of sites in Asia, and 0% of sites in North America. Besides domestic dogs, the most frequently consumed carnivores were red foxes (*Vulpes vulpes*), European badgers (*Meles meles*), and domestic cats (*Felis catus*), particularly in Europe, where they were reported from 30%, 19%, and 18% of sampling sites, respectively. The red fox was the most consumed carnivore in Asia, detected in wolf diet in 44% of the Asian sampling sites that report carnivore consumption. In North America, the most important carnivore species detected in wolf diet were the grey wolf (*Canis lupus*), black bear (*Ursus americanus*), raccoon (*Procyon lotor*), and red fox reported in 42%, 21%, 17%, and 14% of American sampling sites, respectively.

Regarding taxonomic families, canids (n = 159, considering the number of records that a species of this family appears as a wolf food item in the sampling sites), followed by mustelids (n = 61), were most frequently reported in general and for all three continents (Figure 3). In Europe, felids were also frequently reported (n = 17), although this family was only represented by a single species, the domestic cat. In North America, ursids were also frequently reported (n = 11), together with other families less represented, while in Asia, several carnivore families were scarcely but evenly reported.

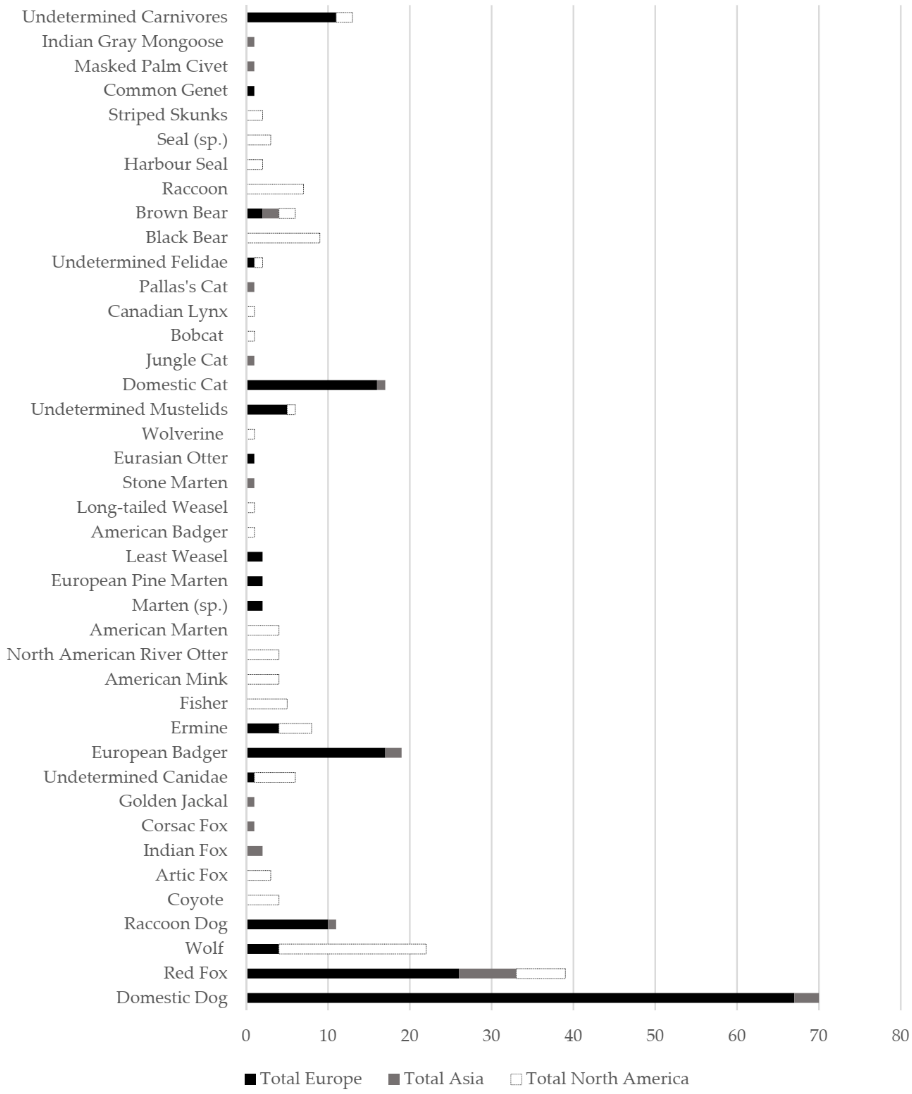

Figure 2. List of carnivore species reported to be consumed by wolves worldwide according to the number of sampling sites for each species in the three continents.

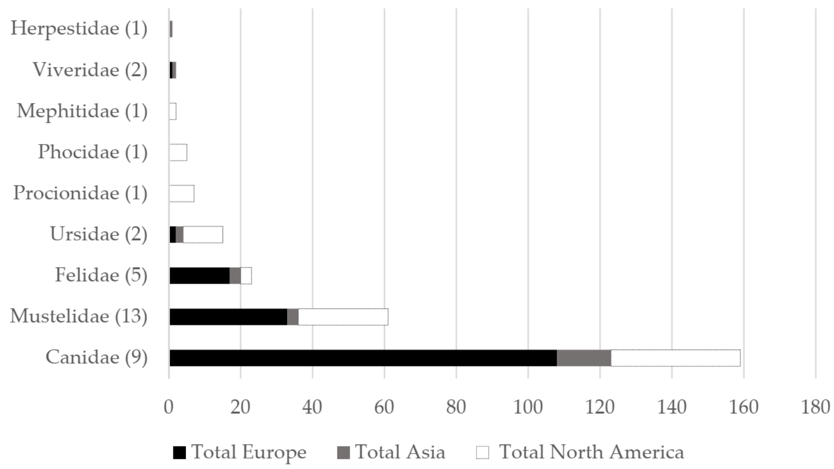

Figure 3. List of carnivore taxonomic families reported to be consumed by wolves worldwide according to the number of times a species of each family appears as a wolf food item in the sampling sites in the three continents. The number of consumed species reported for each family is represented in the parentheses.

The magnitude of carnivore consumption by wolves, expressed by reported values of FO and Biomass, was possible to retrieve from 87 (61%) sampling sites that reported carnivore consumption and was usually low, representing less than 5% of wolf diet, although it reached up to almost 25% in some sampling areas in Europe and North America (Figure 4).

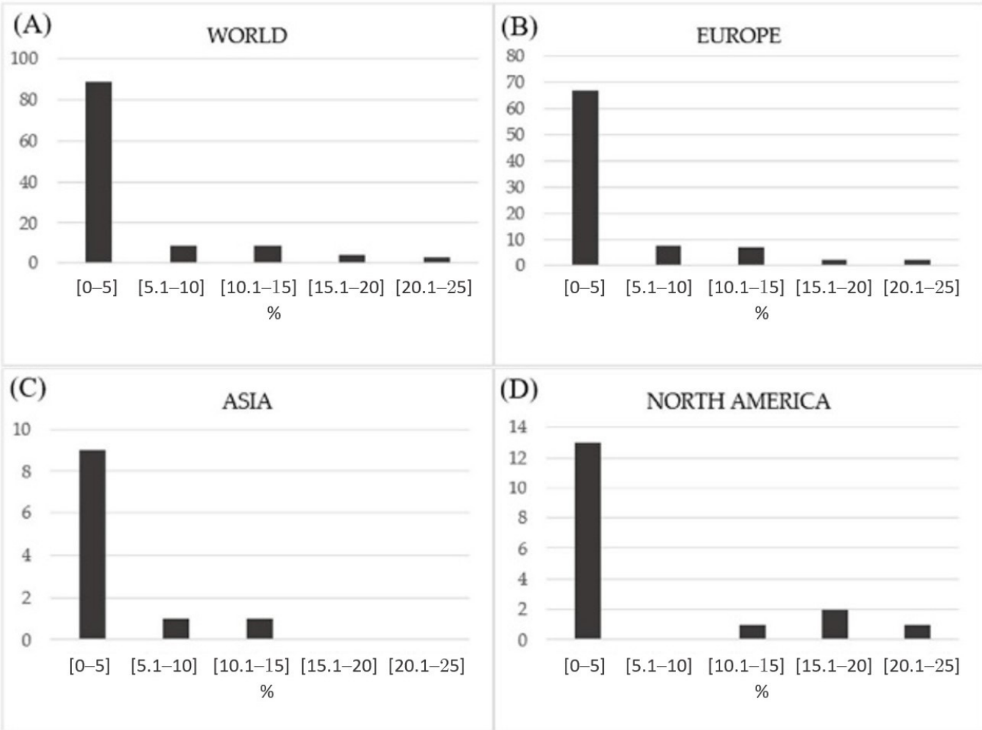

Figure 4. Distribution of classes representing the magnitude of carnivore consumption by wolves based on reported values of frequency of occurrence (FO) and percentage of consumed biomass (Biomass) according to the number each consumption class is reported to have in the sampling sites, globally (**A**) and per continent (**B**–**D**).

Considering the taxonomy of consumed carnivores, the highest values of the magnitude of consumption belong mostly to canids, particularly domestic dog (reaching up to 20% of wolf diet), while for other canid species such as red fox and other families (Mustelidae, Felidae, and Ursidae), consumption usually represents less than 5% of wolf diet (Figure 5).

According to the number of times a species of each category appeared as a wolf food item in the sampling sites, the carnivores most frequently consumed by wolves comprised middle-sized species of 6 to 35 kg (14 species, 40% of all reported species), with a generalist diet (23 species, 66%), scavenging habits (20 species, 57%), and solitary behavior (24 species, 69%). Regarding social behavior, it is important to note that although gregarious carnivore species were consumed less frequently than solitary species, the percentages of consumption were generally higher for gregarious species (3 species, 9% of all reported species; Figure S1 and Table S7).

Finally, we found complementary bibliographic evidence in a total of 24 studies that reported antagonistic interactions between wolves and 9 carnivore species, including wild canids (n = 9 studies), domestic dogs (n = 6), bears (n = 6), wolverine (*Gulo gulo*; n = 2), and domestic cat (n = 1), of which 11 (46%) studies that comprised 5 carnivore species recorded the consumption of the victims by wolves, including cannibalism of wolf pups (n = 3 studies; Table S3).

We found no significant differences between seasons in the magnitude of carnivore consumption (GLM, $p = 0.7$; Tables S8 and S9) and the number of carnivore species consumed by wolves (GLM, $p = 0.2$; Tables S10 and S11).

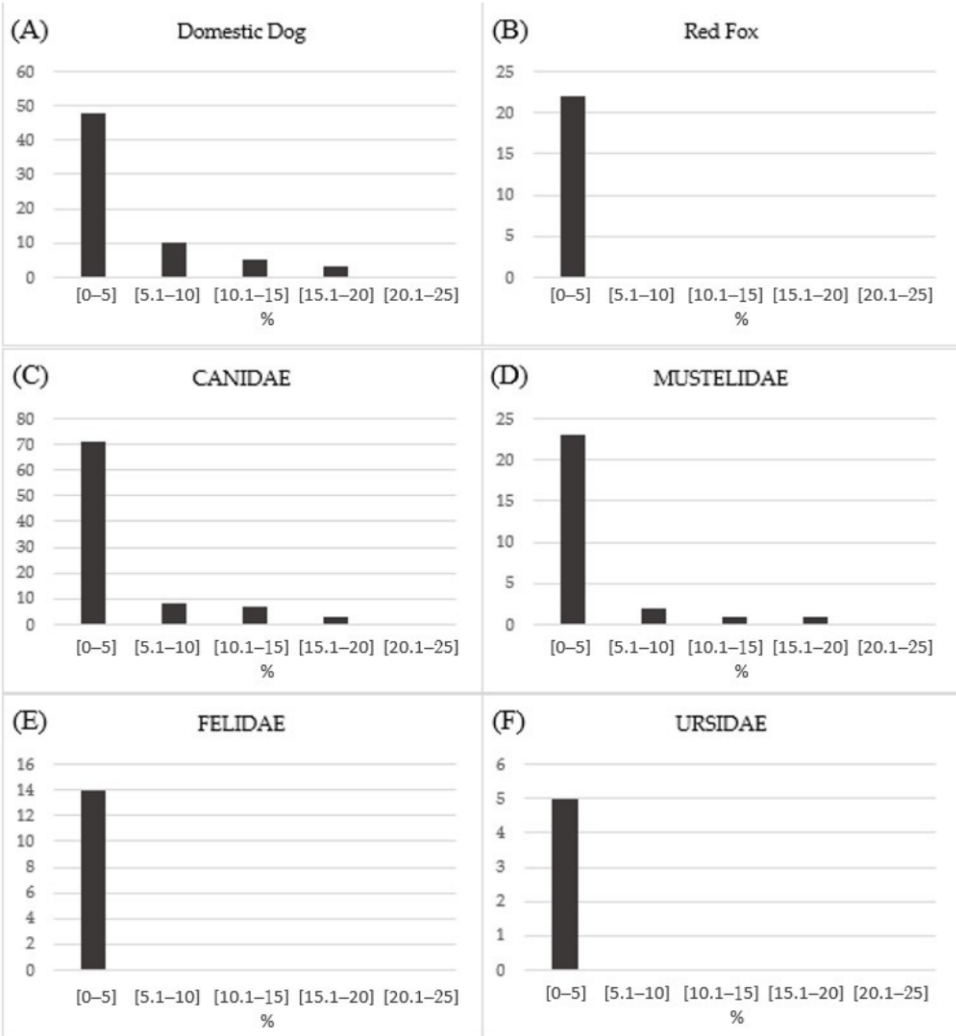

Figure 5. Distribution of classes representing the magnitude of carnivore consumption by wolves based on reported values of frequency of occurrence (FO) and percentage of consumed biomass (Biomass) according to the number of times each consumption class is reported for the two most commonly consumed carnivore species, domestic dog (**A**) and red fox (**B**), as well as for each of the most represented carnivore families, namely, Canidae (**C**), Mustelidae (**D**), Felidae (**E**), and Ursidae (**F**).

3.2. Determinants for Carnivore Consumption by Wolves

The magnitude of carnivore consumption by wolves was significantly affected by five of the variables included in the GLM analysis; the most significant were protected area and percentage of livestock, wild ungulates, and small mammals in wolf diet. Although with less significance than the other variables, human density also seems to affect the magnitude of carnivore consumption (Table 1 and Table S12). Higher values of carnivore consumption by wolves occurred in regions with nonprotected areas, low human density, and low percentages of livestock, wild ungulates, and small mammals in wolf diet. Vegetation productivity (NDVI) had no effect on the magnitude of carnivore consumption by wolves.

The number of carnivore species consumed by wolves was affected by protected area, NDVI, and percentage of livestock and small mammals in wolf diet (Table 2 and Table S13). Higher numbers of carnivore species consumed by wolves occur in regions with nonprotected areas, low values of vegetation productivity, and low percentages of livestock and small mammals in wolf diet.

Table 1. Results from generalized linear model (GLM) analysis for the effects of environmental and human-related variables on the magnitude of carnivore consumption by wolves in 87 sampling sites worldwide. Significant results are in bold.

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test		
			Lower	Upper	Wald Chi-Square	df	Sig. (p-Value)
(Intercept)	1.694	0.2536	1.197	2.191	44.655	1	**0.000**
(Protect Area = N)	0.150	0.0589	0.035	0.266	6.509	1	**0.011**
(Protect Area = Y)	·	.	.	.	.	.	.
Domestic ungulates in wolf diet	−0.009	0.0022	−0.014	−0.005	18.599	1	**0.000**
Wild ungulates in wolf diet	−0.011	0.0021	−0.015	−0.006	24.405	1	**0.000**
Small mammals in wolf diet	−0.012	0.0036	−0.019	−0.005	10.577	1	**0.001**
NDVI	−0.003	0.0022	−0.007	0.002	1.431	1	0.232
Human density	0.000	0.0001	−0.001	-3.9×10^5	5.109	1	**0.024**

Table 2. Results from GLM analysis for the effects of environmental and human-related variables on the number of carnivore species consumed by wolves in 143 sampling sites worldwide. Significant results are in bold.

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test		
			Lower	Upper	Wald Chi-Square	df	Sig. (p-Value)
(Intercept)	1.811	0.4866	0.857	2.764	13.846	1	**0.000**
(Protect Area = N)	0.316	0.1357	0.050	0.582	5.429	1	**0.020**
(Protect Area = Y)	·	.	.	.	.	.	.
Domestic ungulates in wolf diet	−0.010	0.0046	−0.019	−0.002	5.270	1	**0.022**
Wild ungulates in wolf diet	−0.005	0.0042	−0.013	0.003	1.333	1	0.248
Small mammals in wolf diet	−0.018	0.0069	−0.031	−0.004	6.667	1	**0.010**
NDVI	−0.008	0.0034	−0.015	−0.002	6.057	1	**0.014**
Human density	5.1×10^{-5}	0.0003	0.000	0.001	0.039	1	0.843

4. Discussion

This study provides the first comprehensive overview of available knowledge on the patterns and drivers related to the consumption of carnivore species by wolves, demonstrating that it is a common occurrence across the world; it has been reported from all three continents within the wolf range: Europe, Asia, and North America. Although the number and composition of carnivore species consumed by wolves vary across the continents, overall consumption was highest for generalist mesocarnivores with reported scavenging habits and solitary behavior. Furthermore, this study reveals that carnivore consumption by wolves seems to be driven by low productive ecosystems and human-dominated landscapes. These findings provide valuable insights on wolf behavioral ecology and interspecific relationships among carnivores, with important implications for wildlife management.

4.1. Searching for Patterns: What Carnivores Are Consumed by Wolves? Where and Why?

Although carnivores were included to a limited extent in wolf diets at most of the study sites, we found a surprisingly high number and diversity of consumed carnivore species. They comprise all taxonomic carnivore families represented within the gray wolf range, with weights ranging from 0.1 kg (least weasel; *Mustela nivalis*) to up to 250 kg (brown bear; *Ursus arctos*), and include both wild and domestic species. Domestic dogs were the most common carnivore species consumed by wolves, particularly in Europe. In this continent, wolf populations mostly occur in human-dominated landscapes, where the occurrence of domestic dogs, particularly feral dogs, is widespread within the wolf range and the densities of the main wild prey species (i.e., ungulates) for wolves are often low [31]. Besides ecological factors, several human-related factors may also influence dog predation by wolves, as dogs are often used for various human needs, such as hunting and livestock protection [32], which might implicate a stronger and more frequent interaction with wolves. Consequently, low wolf densities that often co-occur with a high abundance of domestic dogs in European landscapes can lead to high competition and frequent interactions between these two closely related canids. These include predation with consumption, as dogs may be perceived as alternative prey for wolves [32,33]. In contrast to Europe, very few dietary studies in Asia (and none in North America) reported domestic dogs as a wolf food item. However, particularly in North America, there are several reports of hunting or pet dogs being killed by wolves, but only a few cases involved the consumption of the victim [34,35]. This evidence suggests that dog consumption by wolves also occurs in North America, but it is likely rare and localized so that dietary studies often fail to detect it. Moreover, the frequent consumption of domestic dogs by wolves that occurs in Europe seems to be related to the reported predation on ecologically similar canids in other continents, namely, the coyote (*Canis latrans*) in North America and the golden jackal (*Canis aureus*) in Asia [6].

The red fox was the most common wild carnivore species found in wolf diet in Asia and one of the most common worldwide. Food competition between foxes and wolves is unlikely to happen, particularly in well-preserved habitats, as the overlap of their trophic niche is often low [10,36,37]. However, antagonistic interactions between wolves and foxes may occur when eating the same carcass, such as at wolf kill sites, and particularly when alternative food sources are scarce [24]. In fact, red foxes are frequent kleptoparasites of wolf kills [20,24]. This can lead to potentially fatal encounters for foxes and the consequent consumption of the victim, especially if foxes are young and inexperienced [10]. Surprisingly, grey wolves were the most common carnivore species reported in wolf diet studies in North America. Wolf hairs found in wolf scats or stomachs are usually a consequence of grooming, especially in seasons when females take care of pups [38]. For this reason, wolf hairs are often excluded from diet analysis (e.g., [39–41]). However, cannibalism among wolves cannot be discarded, as many authors have reported intraspecific aggression, leading to cannibalism and even infanticide among wolves (see Table S3). In fact, it may occasionally occur that breeding females kill and consume pups from other subordinate females or consume their own dead cubs [42,43]. Furthermore, in North America, intraspecific aggression due to territorial competition is often the primary cause of mortality among adult wolves, which frequently involves a total or partial consumption of the victim [24,44,45].

Canids were the most common taxonomic family represented in wolf diets in all three continents. Since carnivore species generally display avoidance of feeding on carcasses of carnivores found already dead, especially of conspecifics, consumption of canids by wolves could be primarily related to predation [46,47]. Moreover, canids are the carnivore family that is most often involved in interspecific killing, with the grey wolf as the most frequently reported killer [2]. Besides canids, mustelids were also frequently reported as prey species in the wolf diet. Even though some mustelids scavenge, their main food sources do not overlap with the wolf diet [48,49]. Furthermore, mustelids, which are mostly small- and medium-sized animals, are reported to be one of the most frequent victims in lethal interspecific interactions among mammalian carnivores [2]. This suggests that interspecific killing of mustelids by wolves, similar to the small number of detected species belonging to Hespestidae, Viveridae, Mephitidae, Procionidae, and Phocidae, might be primarily perceived as predation of alternative prey and not as the killing of competitors for food. The same may be true for felids, mostly represented by the domestic cat in Europe, but also several medium-sized wild felids from North America and Asia, as they are not considered scavengers and usually hunt small animals [50]. Thus, they rarely compete with wolves, particularly at kill sites, and their consumption is more likely related to food acquisition. This makes sense, particularly for domestic cats, as they are reported as frequent wolf prey in several European countries [51–53]. Ursids, one of the most frequently reported carnivore families in the diet of North American wolves, include two species that are much larger than wolves, the black bear and the brown bear. The latter species is reported to be less frequently consumed by wolves (see Table S3), probably because brown bears are less abundant, larger-bodied, and possibly more aggressive than black bears [54]. Consumption of bears by wolves seems to mainly result from direct competition for food on kill sites and predation on bear cubs [55,56]. In fact, the most frequently documented cases concerning brown bear consumption by wolves involve cubs, and one case of black bear consumption was also thought to be a cub [57–59]. Bear cubs can be considered an abundant food supply in some areas, and, among carnivores, smaller species sometimes do kill cubs or juveniles of larger species [2,24]. Still, as wolves and bears often scavenge the same kill sites, antagonist interactions between these two large carnivores can happen for food or to defend juveniles [55,60–62]. In such encounters, a pack of wolves may kill a competitor as large as adult black bear females ([56]; Table S3). Moreover, scavenging may also be involved as wolves have been reported to eat bears that have died by other causes, including human hunting [55,63].

Our approach, based on wolf dietary studies, did not allow us to clearly differentiate if the presence of carnivore species in wolf diet is a result of predation or scavenging. However, Moleón et al., (2019) [47] found that mammalian carnivores avoid the consumption of carcasses of carnivore species, probably because it embodies a much higher risk of parasite transmission [46], especially when the corpses are found dead and not predated [64]. Most of the consumed carnivores are smaller than wolves, as expected from general patterns of interspecific killing [2], considering wolf cautiousness and capacity to evaluate the cost–benefit ratio of each hunt [13,65]. Furthermore, most carnivore species eaten by wolves are generalists with an omnivorous diet and scavenging behavior, suggesting their consumption by wolves may result from active predation, particularly at wolf kill sites. No significant differences in the magnitude of consumption or number of carnivore species consumed by wolves were found between cold and warm seasons. This is surprising since abundances of wolves' main prey are usually lower in winter than in summer [11], and, consequently, higher consumption of carnivores during cold seasons due to increasing competition and/or need to consume other types of food items could be expected. Additionally, it is known that some mesopredators (e.g., the red fox) scavenge more often during winter [66]. Therefore, other factors driving carnivore consumption by wolves, such as human activities or landscape attributes, can be expected to overshadow the seasonal effects.

4.2. Searching for the Drivers: Which Factors Affect Carnivore Consumption by Wolves?

Interspecific killing among carnivores, involving the consumption of the victim, is considered to be dependent on the availability of other food items [2]. In line with this assumption, our study showed that lower percentages of ungulates, both domestic and wild, and small mammals in wolf diet are related to a higher magnitude of carnivore consumption. In addition, the consumption of a larger number of carnivore species by wolves is also related to lower percentages of domestic ungulates and small mammals in the wolf diet. These patterns are more evident in Europe, the continent with the highest proportion of sampling sites reporting carnivore consumption by wolves, and particularly in the agricultural areas of the Iberian Peninsula, Italy, and Belarus, where carnivore species can comprise up to 25% of wolf diet [53,67–70]. Domestic ungulates often become the most important wolf prey in human-dominated landscapes, where wild ungulates occur in low numbers [11,71,72]. Livestock depredation usually comes with a risk for wolves due to human persecution, and it can be considerably reduced if effective protection measures are implemented [73], which may explain the need for alternative food sources, including carnivores. In such a context of wild prey scarcity, competition levels likely increase among wolves and other predators, which, in turn, increases the probability of fatal interactions among them and consumption of the victims. Small mammals, such as rodents, seem to be an important alternative food source for wolves and may compose most of the wolf diet in agricultural or barren areas (e.g., Arctic), where ungulates are scarce [11,12]. Whenever small mammals are an important prey in wolf diet, exploitative competition between wolves and mesocarnivore species is also likely to intensify, particularly when small mammal densities are low. Therefore, under these ecological conditions, an increasing probability of lethal interactions among these predators and the consumption of the victims is to be expected [2].

The influence of agricultural landscapes can also be seen in our results, as the magnitude of carnivore consumption is related to nonprotected areas. In human-dominated and agricultural landscapes with a scarcity of wild prey, the occurrence of several species of generalist mid-size carnivores (mesopredators) is often common and abundant [8,74]. In such an ecological context, wolves increase consumption of other types of prey besides ungulates [12,14]. Although large predators, including wolves, have the capacity to survive in areas with high human densities [75], mesopredators usually deal better in human-dominated landscapes due to their smaller size and adaptive generalist behavior that help them access human waste and avoid conflicts with people [8,76,77]. Increasing mesopredator densities in areas with high human influence increases competition for food sources among co-occurring species of predators, and, therefore, lethal interactions are more likely to occur [76,78]. Moreover, in agricultural and human-dominated landscapes, scavenging can become an important food source, with mesopredators benefiting from carcasses killed by larger carnivores such as wolves [79,80] or slaughter remains provided by humans [77]. In this context, competition for food is expected to be stronger and may lead to more frequent interspecific killing of carnivores by wolves while protecting carcasses.

Another factor influencing the number of carnivore species consumed by wolves appears to be the NDVI, which reflects plant productivity and, in turn, animal population dynamics [81]. Plants have strong direct and indirect effects on higher trophic levels (herbivores and predators), so lower plant abundance and diversity influence predators by reducing their prey availability [82]. This can intensify competition among the predators and top-down control of mesocarnivores, which was previously suggested to be stronger in less productive environments [83]. Our results tend to concur with this prediction. The higher number of carnivore species in wolf diet, observed in regions with lower vegetation productivity, may also be related to the influence of regions located outside protected areas, where lower values of vegetation productivity are expected (e.g., due to deforestation and habitat loss) and the consequent lower densities of wild prey for wolves [74,82]. Nonprotected areas are also associated with higher levels of human influence, which are generally more harmful to top predators than mesopredators and may increase intraguild lethal interactions [76].

4.3. Conclusions and Management Implications

This study provides the first-ever overview of the consumption of carnivores by wolves, a topic rarely addressed for this extensively studied top predator. Although wolves can eat almost anything and rarely kill without consuming the prey [11,13], carnivores seem to be mostly a rare food item for wolves, although they can become a relevant supplementary food source in some ecological contexts. Our results suggest that competition for the remains of prey, particularly in human-dominated landscapes and/or areas where food sources are scarce, can be an important factor triggering the killing and consumption of carnivores by wolves. Nevertheless, the reasons and behaviors explaining the consumption of carnivore species by wolves may result from complex interactions between interspecific competition and food availability; thus, further research on this topic is needed in order to fully understand the specific patterns and drivers in various ecological contexts. Our literature review enabled broad spatial coverage of all wolf ranges but may have missed some wolf dietary studies providing different keywords on search engines or using languages other than English. Therefore, further research on this topic, especially focusing on a regional scale, would probably benefit from an expanded literature search that is difficult to conduct on a global scale. Additional potential factors that could influence interspecific killing and warrant further research are wolf densities and territory sizes, as space can represent a limiting resource for wolves and a potential driver for competition, even when prey is abundant [45]. Furthermore, to better understand the interspecific interactions between wolves and other carnivore species, it would be relevant to consider the local diet of the consumed mesopredators to evaluate if variation in their food sources, such as carrion or human-related food, can mediate competition with wolves.

Our findings also have implications for wildlife management, as they highlight several ecosystem services provided by wolves in controlling a vast number of mesopredators, particularly feral dogs.

In fact, feral or uncontrolled domestic dogs often raise conflicts with humans, pose a threat to human safety, disrupt ecosystems, and threaten biodiversity [84]. Most of the carnivore species consumed by wolves are medium-sized generalist carnivores, whose abundance can bring numerous issues for humans and wildlife, such as disease outbreaks and local extinctions of endangered species [8]. This includes the coyote in North America and the golden jackal in Eurasia—generalist middle-sized canids that also occur in urban areas and can potentially become overabundant near human settlements [85,86]. Recent population expansions of coyotes and golden jackals [6,87] have increased the potential for interactions among these carnivores, including interspecific killing by wolves. This will likely increase the value of ecosystem services provided by wolves in controlling mesopredator populations, especially since traditional approaches of limiting mesopredator abundance by shooting and other forms of lethal control suffer from low effectiveness and low social acceptance [88,89]. Improved appreciation of interspecific killing of carnivores as an important ecological role and service provided by wolves could benefit their conservation if used to raise awareness and to promote greater tolerance towards this top predator.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/12/12/470/s1: Figure S1: Weight classes (A), primary diet (B), reported scavenging behavior (C), and social behavior (D) of the carnivore species consumed by wolves worldwide according to the number of times a species in each category appears as a wolf food item in the sampling sites. The number of consumed species reported for each category is represented between parentheses. Table S1: List of scientific literature on wolf diet that was reviewed to assess carnivore consumption by wolves, including country, region, and bibliographic source. Bibliographic sources with reported consumption of carnivore species by wolves are marked in bold. Table S2: Ecomorphological traits of each carnivore species reported to be consumed by wolves, with reference to the number of compiled studies and sampling sites, reported magnitude of consumption (FO: frequency of occurrence; Biomass: percentage of consumed biomass), and extant range per continent. Table S3: Published evidence on observations of antagonistic interactions between wolves and carnivore species, with reference to the existence/absence of consumption of the victims (total or partial), observation method, country, and the respective continent. Table S4: Results from Pearson correlation tests between the values of frequency of occurrence (FO) and percentage of consumed biomass (Biomass) of carnivores in wolf diets in 87 sampling sites. Table S5: Description of the 15 ecological and human-related variables used to assess factors determining carnivore consumption by wolves, including the source, time period, metrics, and variable type. The uncorrelated six variables included in the GLM tests are marked in bold (see Methods section for details). Table S6: Results from Pearson correlation tests for the 11 environmental and human-related variables obtained from online data sources, which were used to assess the factors determining carnivore consumption by wolves. Significant correlations in bold (** correlation significant at $p < 0.01$; * correlation significant at $p < 0.05$). Table S7: Weight classes, primary diet, reported scavenging behavior, and social behavior of the carnivore species consumed by wolves worldwide, the number of times a species in each category appears as a wolf food item in the sampling sites, and the number of consumed carnivore species by category. Weight classes: (i) <1 kg; (ii) 1 to 5 kg; (iii) 6 to 10 kg; (iv) 11 to 35 kg; (v) >35 kg. Table S8: Results from the GLM analysis for the effects of seasons (W—winter/autumn and S—summer/spring) on the magnitude of carnivore consumption by wolves in 88 sampling sites worldwide. Table S9: Results from the chi-square test (by comparing the fitted model against the intercept-only model) to assess the fitness of the GLM for the effects of seasons (W—winter/autumn and S—summer/spring) on the magnitude of carnivore consumption by wolves in 88 sampling sites worldwide. Table S10: Results from the GLM analysis for the effects of seasons (W—winter/autumn and S—summer/spring) on the number of carnivore species consumed by wolves in 115 sampling sites worldwide. Table S11: Results from the chi-square test (by comparing the fitted model against the intercept-only model) to assess the fitness of the GLM for the effects of seasons (W— winter/autumn and S—summer/spring) on the number of carnivore species consumed by wolves in 115 sampling sites worldwide. Table S12: Results from the chi-square test (by comparing the fitted model against the intercept-only model) to assess the fitness of the GLM for the effects of environmental and human-related variables on the magnitude of carnivore consumption by wolves in 87 sampling sites worldwide. Table S13: Results from the chi-square test (by comparing the fitted model against the intercept-only model) to assess the fitness of the GLM for the effects of environmental and human-related variables on the number of carnivore species consumed by wolves in 143 sampling sites.

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