Differences in livestock consumption by grey wolf, golden jackal, coyote and stray dog revealed by a systematic review

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Abstract:
Grey wolf (*Canis lupus*), golden jackal (*Canis aureus*), coyote (*Canis latrans*) and stray dog (*Canis familiaris*) are having increasing population trends in Europe and the United States, fuelling human-predator conflict. Predation on livestock is causing devastating losses both in terms of finance and resources to local communities. We investigated the extent to which these canine predators depend on livestock as their food source by performing a systematic literature analysis. We predicted that the wolf feeds the most on livestock and selects larger domestic animals compared to jackals, coyotes and dogs. The information retrieved from 115 scientific publications included the frequency of occurrence (%O) and biomass proportion (%B) of livestock species in the predators' diet. Our analyses revealed that wolves consumed significantly more livestock than the golden jackal and coyote. Statistical analyses indicated that in case of wolves, cattle and goats were chosen the most compared to any other species of livestock. For jackals the consumption of pig was significantly higher than equines and sheep. There was little data on coyotes and dogs, although we found higher consumption of pig compared to the cattle in case of coyotes, and no differences in livestock species consumption frequencies in case of dogs. Most studies reported that domestic species in wolf diets have been observed in areas where the wild prey availability is degraded. Predator management differs among countries and is continuously influenced by a number of unique, local factors modifying the predation rates and the intensity of this human-wildlife conflict. It is a priority to identify the real mechanism and cause of the livestock predation and set adaptive steps for its elimination.

Keywords: diet, scavenging, carnivores, human-wildlife conflict, predators, canids.

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Differences in livestock consumption by Carnivores

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1. Introduction

Characteristic wild canids have shown an increase in their distribution range and started a rapid expansion in the past few decades including grey wolf (*Canis lupus*) and golden jackal (*Canis aureus*) in Europe (Ripple *et al*., 2014; Rutkowski *et al*., 2015; Spassov & Pankov, 2019; Krofel *et al.*, 2023), and the coyote (*Canis latrans*) in the United States (Kays, 2018; Hody & Kays, 2018). Only in the last decade wolf's range has been observed to expand by over 25% in Europe (Cimatti *et al*., 2021), and currently recolonizing its now human-dominated former ranges in the continent also inducing changes in mesocarnivore communities (Kuijper *et al*., 2024). The presence of the golden jackal has been reported in recent years in Baltics (Trouwborst *et al.*, 2015), Belarus (Grichik *et al*., 2018), Czech Republic (Jirků *et al*., 2018), Germany (Trouwborst et al., 2015), Poland (Kowalczyk *et al.*, 2015), Greece (Karamanlidis *et al.*, 2023), Italy (Lapini et al., 2011), as well as in the far north in Finland (Kojola et al., 2023) and most recently in Spain (Miranda, 2024). In the United States coyotes showed expansion in their geographic range by 40% over the last 120 years (Jensen *et al*., 2022). The number of stray domestic dogs (*Canis familiaris*) has also shown an increase in the southern and eastern EU Member States (Voslářová & Passantino, 2012).

Such population increases can contribute to severe consequences like the suppression or non-recovery of game populations in areas where other factors are already limiting, for example, due to habitat deterioration, poor resource supply, diseases, and overhunting (Viñuela & Arroyo, 2002). These growing canine predator populations are now living in close proximity to many rural human settlements (Chapron *et al*., 2014). Consequently, human-predator conflicts emerge in the form of damage to livestock, private property as well as in the form of attacks on humans (Sillero-Zubiri & Laurenson, 2001). In these cases, predators tend to modify their diet and shift their prey preference to livestock, resulting in more frequent attacks on domestic species (Meriggi *et al.*, 1996; Sidorovich *et al.*, 2003).

The food habits of wolves are quite variable across the distribution area of the species (Peterson & Ciucci, 2003; Newsome *et al.*, 2016). Wolves mostly prey on large wild ungulates (e.g., moose (*Alces alces*), caribou (*Rangifer tarandus*), elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*) and other medium-sized mammals in North America, whereas in Europe they mainly consume wild ungulates such as the red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) that are supplemented by livestock or other anthropogenic food sources, where wild ungulates are scarce (Meriggi & Lovari, 1996; Newsome *et al.*, 2016). Moreover, wolves have shown a dietary shift in Europe in the past few decades by consuming more wild ungulates compared to previous records (Newsome *et al.*, 2016), which could be due to the large increase of wild prey species during this time (Burbaité & Csányi, 2009; Apollonio *et al.*, 2010; Burbaité & Csányi, 2010; Carpio *et al*., 2020; Valente *et al*., 2020). However, it is still reported that wolves consume livestock where they are available, easily accessible, and vulnerable (e.g., Migli *et al*., 2015; Gazzola *et al*., 2008; Torres *et al*., 2015), although this highly depends on livestock species and husbandry practices (Newsome *et al.*, 2016).

Compared to the wolf, the golden jackal adopts a more omnivorous lifestyle; while the golden jackal's diet consists primarily of animals, it is complemented for a significant part with plants (Markov & Lanszki, 2012, Penezić & Ćirović, 2015; Lange *et al.*, 2021). Several studies about its diet showed that the species mainly feeds on small mammals, e.g., in Bangladesh (Mukherjee *et al.*, 2004), while in Greece, the jackal primarily forages on livestock carcasses and waterfowl (Lanszki *et al.*, 2009; Giannatos *et al*., 2010; Lanszki *et al*., 2010). Similarly in Hungary, the jackals have been found to prey on small mammals as well as on young wild ungulates (Lanszki & Heltai, 2002, 2010; Lanszki *et al.*, 2006, 2010, 2015, 2018). Furthermore, a complete review on the diet composition of the species in Europe revealed that the jackal mainly consumes small mammals, whereas domestic species are especially eaten as carcasses (Lange *et al*., 2020; Lanszki *et al.*, 2020).

The coyote, like the wolf and golden jackal is a highly adaptable species which thrives in a wide range of habitats in North America, often coming in conflict with societal interests. Coyotes are blamed for inflicting agricultural damage (Berger, 2006) and suppressing white-tailed deer populations (Kilgo *et al.*, 2012; Robinson *et al.*, 2014; Chitwood *et al.*, 2015). Coyotes rely primarily on mammals, insects and fruit. Similar to wolves and golden jackals, their diet varies regionally and seasonally (McVey *et al.*, 2013; Stratman & Pelton, 1997; Turner *et al.*, 2011; Wooding *et al.*, 1984). Lagomorphs were the most common food item in South Texas USA, but white-tailed deer and rodents were the most predominant diet components in West Virginia (Crimmins *et al.*, 2012; Windberg & Mitchell, 2013). There are few studies that examine the extent to which coyotes depend on domestic livestock as their food source (Gipson *et al*., 1974; Hinton *et al*., 2017; Larson *et al*., 2020) but those revealed low consumption of livestock. Coyotes are blamed for attacking or even killing humans in extreme cases (Carbyn, 1989; Gehrt et al., 2022).

The information on livestock predation is also limited for the stray domestic dog. While many studies outline the effects of feral and stray dog predation on wildlife, only few of them mention their direct impact on livestock. Dogs can compete with medium-sized and small carnivores, but in general they do not exploit the shared food sources since most stray dog populations are highly dependent on human-derived food and gain a relatively small proportion of their diet from wild prey (Vanak & Gompper, 2009). The dog population has expanded around the globe alongside the human population. In 1993, the global population of stray dogs was estimated at 500 million individuals (Wandeler *et al*., 1993) while the most recent review conducted in 2012 estimated the global population of dogs at 700 million individuals (Hughes *et al.*, 2013). Stray dog attacks result in significant financial losses; however, the damages caused by dogs are often wrongly attributed to wolves (Kossak, 1998).

Recently, governments around the world started to invest significant efforts and resources to minimise the damages caused by large carnivores on human livelihoods and properties as a result of their growing populations (Oliveira *et al.*, 2021). The predatory behaviour of large carnivores is often the main factor that prevents the coexistence with these species, particularly the wolf is regarded as the most conflictual mammal due to its repeated attacks on livestock (Graham *et al.*, 2005; Fernández-Gil *et al.*, 2016; López-Bao *et al.*, 2017). Our study aims to describe and evaluate to what extent the four carnivores consume livestock for sustaining their diet.

Since most of the depredation cases are attributed to wolves, we predicted that the wolf is consuming livestock the most out of the four studied carnivore species. Golden jackals and coyotes are similar in their feeding behaviour, therefore their consumption of livestock was predicted to be also similar. We expected that both of these species feed on livestock, however due to their omnivorous feeding habits the proportion of the livestock matter in their diet will be lower. We predicted that the domestic dog consumes livestock the least, given their dependency on human-given food. As stray dogs are mostly found close to the human settlements, most of the food will be of anthropogenic origin (Voslářová & Passantino, 2012).

We further predicted that the wolf mostly consumes larger domestic livestock species, e.g., cattle, as they are the largest predators in size and unlike golden jackals, coyotes and stray dogs more commonly hunt in packs (Macdonald, 1983). For the golden jackal, coyote and stray dog we expected livestock consumption limited to medium- or small-sized domestic species, e.g., goats, sheep and poultry, as these predators are smaller in body size compared to the wolf, thus hunting a larger prey would not be optimal to them.

By performing a systematic literature review, our goal was to reveal 1) how frequently were the livestock species found in the diet of the wolf, golden jackal, coyote and stray dog; 2) which livestock species were consumed the most frequently by each of the four carnivores?

2. Materials and Method

2.1 Literature compilation

The study was carried out by using publications on diet analyses of the grey wolf, golden jackal, coyote and stray dog. Two major platforms were used to find publications: Web of Science and Scopus accessed in March 2023. The search terms consisted of the specific carnivore species, namely either *grey wolf, Canis lupus, golden jackal, Canis aureus, coyote, Canis latrans, stray dog, Canis familiaris*, followed by *diet, food, feeding* and finally the words for the prey, i.e., *livestock, domestic*. For example, for the grey wolf, the following search terms were used: ("Grey wolf" OR "*Canis lupus*") AND ("diet" OR "food" OR "feeding") AND ("livestock" OR "domestic"). The search was performed for the article title, abstract and keywords.

Publication dates of all years available in the database were used and in case of accessible English abstract, non-English papers were also included. Studies were conducted globally and no specific geographical region was prioritised in the publication collection phase. Articles with titles and abstracts that did not include any clues to livestock predation were excluded as it was assumed that the focus of the research was not on livestock. As a result, it was not sure that potentially mentioned results on livestock consumption could be considered reliable enough for the present analyses. However, if these search terms were mentioned in the title or abstract but livestock species did not occur in the diet, then it was valued as 0 for livestock consumption. In this way, we focused on case studies where the livestock consumption presented (or at least was considered as) a real human-wildlife conflict.

For the grey wolf, the Web of Science generated 328 papers and Scopus gave 291 papers. Two datasets were compared against each other, after removing duplicates, we were left with 419 papers. Papers were further filtered for their relevance to our topic and we kept 75 papers that were included in the analyses. Filtering for relevance in this case was defined as articles not being included in the final statistical analyses if they do not focus on livestock predation and/or note the livestock consumption using other variables than frequency of occurrence (%O) and percentage of biomass (%B). For the golden jackal, Web of Science generated 39 papers and Scopus provided 43 papers. Once the two databases were compared we ended up with 51 papers. Papers were filtered further based on the relevance. Finally, we ended up with 23 papers that were included in the analyses. For the coyote, Web of Science generated 94 papers and Scopus search resulted in 69 papers. Once the two databases were combined, we were left with 119 scientific papers. After filtering the papers 10 publications were suitable for detailed analysis. For the stray dog, the Web of Science generated 450 papers and Scopus 643 papers, respectively. The combined dataset resulted in 848 papers, of which most of them were deselected as non-relevant to our topic, including dingo studies from Australia. Therefore only 7 papers were included in the analyses. Our analysis was finally based on 115 papers (75 for wolves, 23 for golden jackals, 10 for coyotes and 7 for stray dogs); 9 of them were overlapping involving data about more than one canid species.

It is important to note that the presented method of paper selection for this review may not have led to inclusion of all possible publications on the topic. However, by following a uniform method of data collection, we were able to have a clear scope and a comparative interspecific analysis.

2.2 Variable selection

The information and metadata derived from the papers was the year of publication; the country where the study was conducted; the studied canid predator(s) and the livestock species consumed (categorised into cattle; pig; sheep; goat; horse and donkey; poultry if specified). Those cases when distinct livestock species cannot be identified; or reported only in groups (e.g., "*cattle, sheep and horse*" together) or referred only as "*livestock*" in the articles were categorised as "not specified" in our review. Additionally, we checked and categorised whether the abundance of wild ungulates and livestock species was reported or measured in the studies. This information was categorised as "*quantitative*" if exact density data (numbers of livestock, animals per km^2, transect count data) was provided, otherwise "*qualitative*" when the studies only referred to it with quantifiers or in a much more indirect way (e.g. "*wildlife stock is high*"; "*low density of wild ungulates*"; "*large flocks of goats*"). We also noted if scavenging was clearly distinguished from predation or suggested in the results or discussion sections of the articles.

The most commonly used indices expressing the diet composition of the canid species of interest in the related studies were the frequency of occurrence (%O) and percentage of biomass (%B). The frequency of occurrence of livestock was expressed as the percentage of scats or stomachs containing the livestock item considered (Vos *et al.*, 2000). The percentage of biomass is estimated by weighing the dry food remains within a sample (dry matter remains from scat or stomach) and then multiplying this mass data by an appropriate conversion factor (Reynolds & Aebischer, 1991; Lanszki *et al.*, 2006). The analysed papers used different correction factors for obtaining their results. The most frequently used methods were described by the works cited in the collected publications: Goszczyñski (1974), Floyd et al. (1978), Ackerman et al. (1984), Weaver (1993), Jedrzejewska & Jedrzejewski (1998). Hence, in order to have the largest possible dataset we opted to analyse these two indicators in our study using them as main variables. When observing the consumption of the livestock species it is critical to look at both the %O and the %B data. The %O indicates the individual variability of feeding habits of the predator, while the %B shows the actual food intake from different diet components. In other words, the first variable shows us whether consumption of livestock is a common phenomenon in the predator population or only some conflict individuals should be eliminated; meanwhile the second one determines the importance of livestock in covering food requirements of the carnivores. While both of these factors give a good insight into the general feeding habits even separately, the joint information they provide will be decisive in drafting practical measures for human-wildlife conflict mitigation.

Only studies that performed stomach content analyses or scat analyses for the diet composition were included in the statistical analysis (107 papers out of 115). Studies that have not reported these conventional indices (e.g., articles based on direct observations, frequency of depredation or summarised literature data) were excluded from statistical evaluation (8 papers out of 115); however, we present them in a summary text as additional results in the discussion section. Papers reporting data from multiple sites or repeated measures (N=34 papers out of 107) were analysed as independent studies. As a result we extracted 111 unique studies from those 34 papers that conducted repeated research, and together with one-time projects (73 papers) the final amount of available studies became 184.

In each of these studies available for statistical evaluation we handled each reported predator - livestock pair separately as a unique observation; i.e. a case when one of the prey species of interest was examined about its consumption of any type of livestock. Consequently, if one study reported the consumption of sheep, goat and pig by wolf, we considered it as three separate observations regarding wolf predation. Thereby we could separate 448 observations. If a study directly reported %O or %B as 0 for a livestock species of interest, we assumed that the authors have specifically checked it in the samples, and they wanted to emphasise that the potential prey species was not consumed at all. Consequently, we also utilised these results in our analyses.

2.3 Statistical analysis

We performed non-parametric Kruskal-Wallis test on the %O or %B data in R (R Development Core Team, 2023), to verify statistical differences in the reported livestock consumption of the studied canid species and to find the most consumed livestock species groups for each carnivore. The overall livestock consumption of canid species was compared by taking the minimum and maximum values of the reported %O data and the summarised %B data per study. In many publications, the livestock consumption was reported only broken down to livestock species, no aggregated value was given. Thus, for the %O values we could not know whether different livestock species were found in the same samples or not, *i.e.* whether they were overlapping or their values should be added. Therefore, we could only determine a range, not a specific value for the overall livestock consumption frequency. In this way we were able to reveal potential differences among canids in the magnitude of livestock remains in their diet. The "not specified" category (incorporating cases where the exact livestock species was unknown) was excluded when livestock species groups were compared with the test. For pairwise comparisons we implemented Dunn post-hoc test which is ideal for groups with unequal numbers of observations (Zar, 2010).

The p-value adjustment was performed using the Holm-Bonferroni method; and the 95% confidence intervals were calculated for the mean rank differences. When two groups were compared, we implemented Mann-Whitney U test.

In order to ensure the thorough reporting and examination of the retrieved literature, our study is in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses Statement (PRISMA Statement) that lists minimum set of items for reporting in systematic reviews and meta-analyses (Page *et al.*, 2020).

3. Results

3.1 Distribution of the researches

Most of the articles were published during the 2000s reaching a peak after 2010, when wolf and jackal - related studies became more intense (Figure 1). Compared to wolf and golden jackal, coyote and stray dog studies were rare, but equally represented in the published scientific articles.

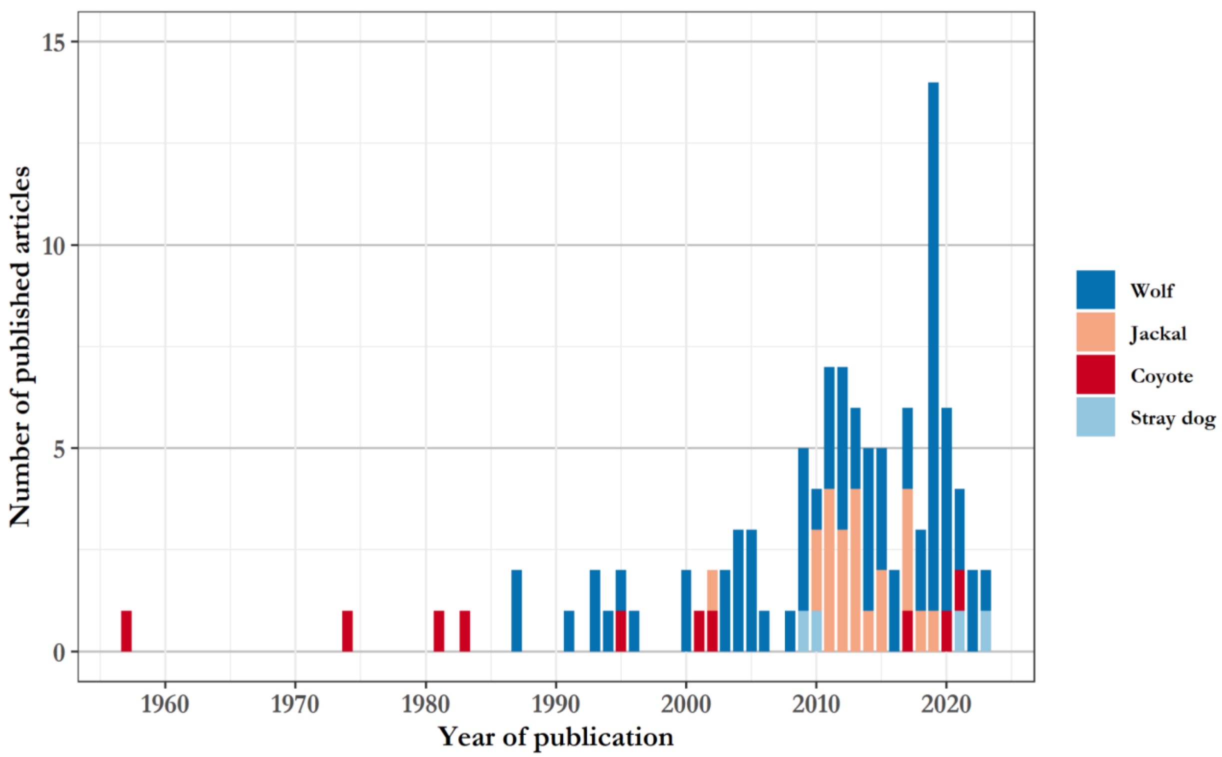

Figure 1. Scientific articles on carnivore's livestock predation published per year (from 1957 to 2022). The figure incorporates articles which were used for statistical analysis (N=107).

The majority of the studies originate from scat samples (74%), while the results based on stomach samples was 21%. Altogether, the 107 researches involved originated from 29 countries. We found more than 10 researches from the United States (USA), Italy and Pakistan; more than five from India, Spain and Bulgaria (Figure 2).

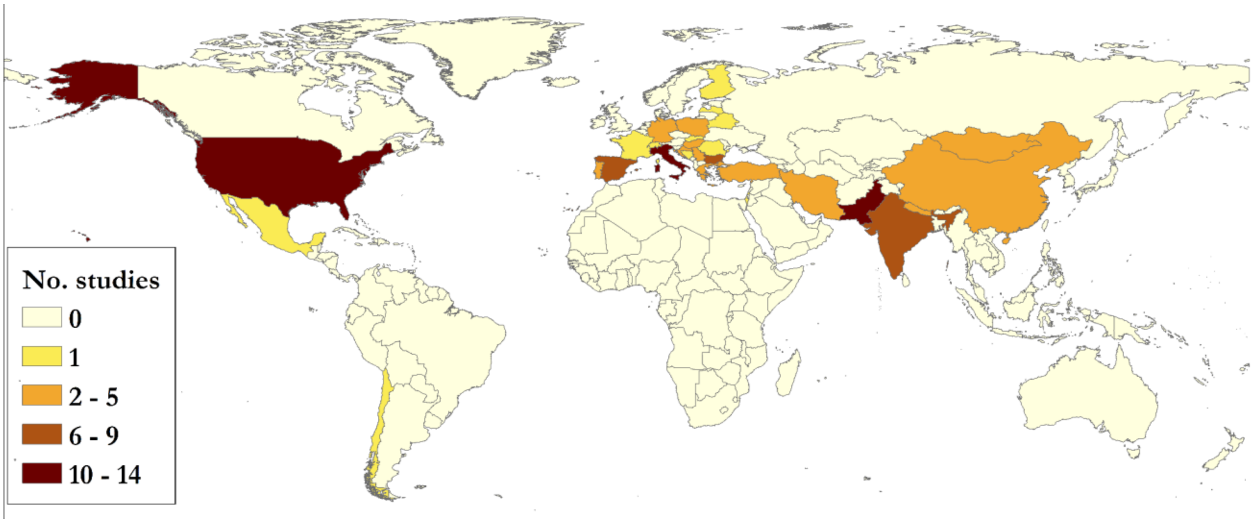

Figure 2. Location of the published researches performed on livestock consumption by canid predators. (The map is based only on papers that were included in the statistical analysis).

Approximately 55% of the countries (16 out of 29) were represented by only two or less publications about wild canines vs. livestock interactions.

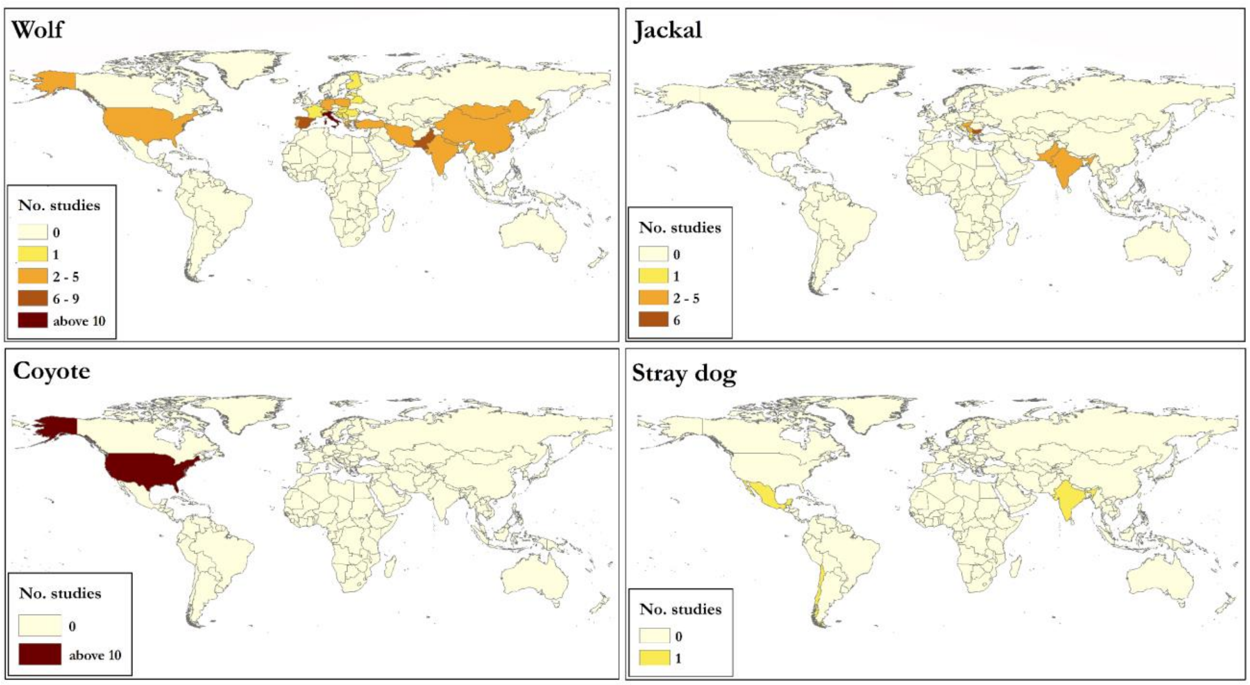

Figure 3. Location of the published studies performed on livestock consumption by grey wolf, golden jackal, coyote and stray dog. (The map is based only on papers that were included in the statistical analysis)

Considering the analysed papers, the impact of wolves on livestock was the most studied worldwide among the four canids: 65% of the papers (75 articles out of 115) were related to wolves. Especially Italy (N=13), Spain and Pakistan (both N=7) gave place for these types of studies, but a significant number of articles originated from India, Iran, Poland, Portugal, USA (all N=4) and Mongolia (N=3), as well. All coyote - related studies (N=10) originated from the USA, while many jackal studies were conducted in Bulgaria and Pakistan (N=6 and 4, respectively). The query found more than one golden jackal - related study on livestock consumption in Hungary, India and Serbia (N=3). Stray dog diet was scarcely studied worldwide and almost disappeared in this context (Figure 3).

3.2. Distribution of studies reporting scavenging and prey species abundance

Almost half of the studied articles (N=52, 49%) had referred to potential scavenging of canid predators (Figure 4). Majority of them reported scavenging in addition to predation, while in rare cases (e.g. Hosseini-Zavarei *et al.*, 2013) Authors stated that the high occurrence of livestock in the diet is mainly because of scavenging rather than depredation. But there were only two studies available where the scavenging was clearly proven and directly quantified: Gazzola *et al.* (2005) achieved this by autopsy of carcasses and distinguished direct kills from other forms of consumption; Mohammadi *et al.* (2019) evaluated prey remains based on temporal congruence between consumption and carcass condition and inspection of wounds compatible with depredation. In other cases, scavenging was only assumed or indirectly deduced when results were based on scat analysis, since a plethora of studies emphasised that the major limitation of scat analysis is that it does not distinguish between items obtained by predation and by scavenging (e.g. Rigg & Gorman, 2004; Torres *et al.*, 2015; Werhahn *et al.*, 2019; Trbojevic *et al.*, 2020).

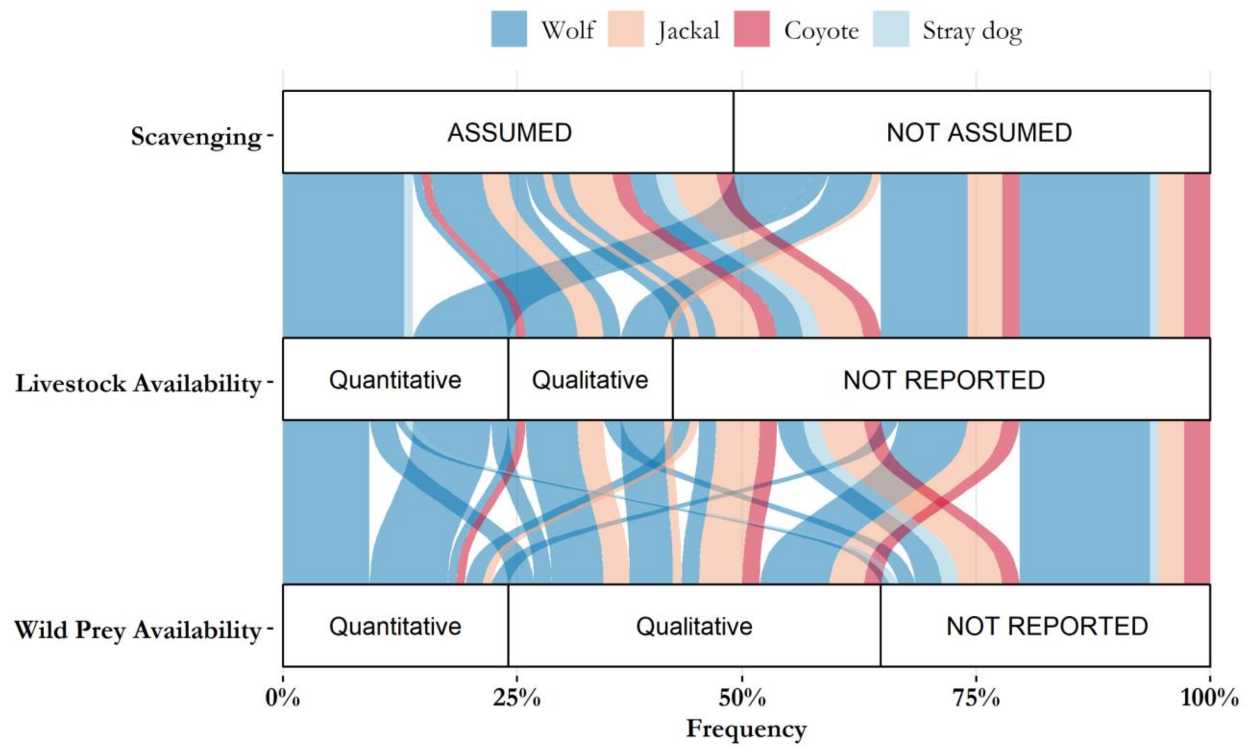

Figure 4. Alluvial diagram of articles reporting prey availability and scavenging sorted by the canid species studied. Each thread or stream represents a study coloured by the canid species of interest and the relevant level of the three categorical variables determines its flow among them. The plot also incorporates those studies that indirectly reported or only assumed potential scavenging of canid predators.

Most articles without any reference to scavenging have not reported any data about livestock or wild ungulate abundance either (N=22, 21%). On the other hand, studies which quantitatively specified wild prey availability, most likely provided exact abundance data about livestock as well (N=19, 18%) and the majority of these studies focused on wolves (Figure 4). While many articles tended to provide some information about wild ungulate availability (N=69, 64%), direct or indirect data about livestock abundance was less frequently reported (N=45, 41%).

3.3 Investigation frequency of total livestock consumption by canid species

Considering all observations (N=448) we found that wolf (N=300 observations) was the most frequently reported canid species that consumed livestock followed by the golden jackal (N=104). Coyote (N=25) and stray dog (N=19) were similar in the extent of being reported as consumers to domestic species (Figure 5).

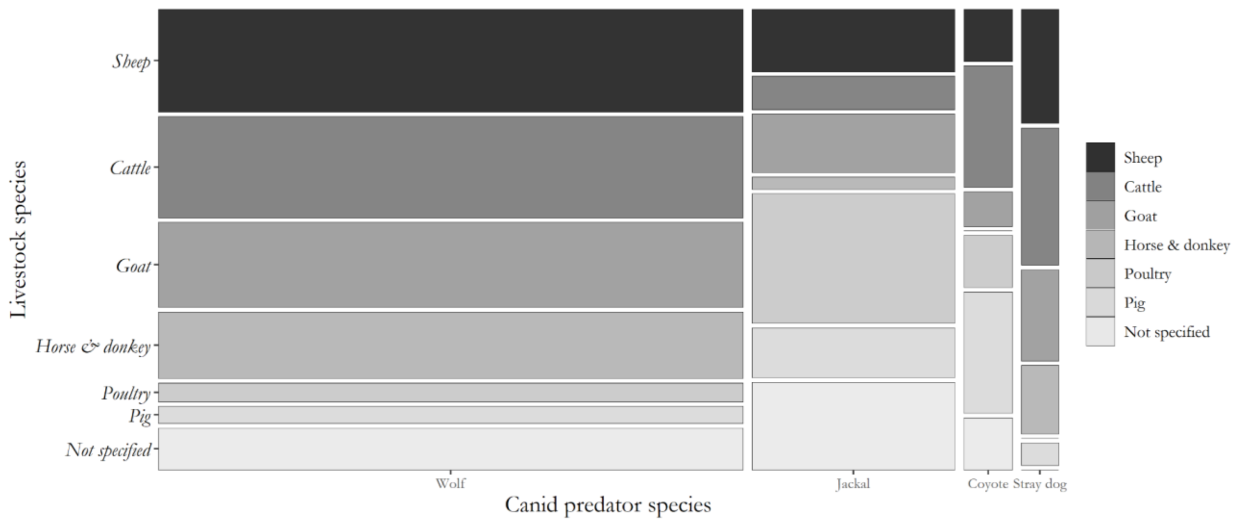

Figure 5. The relative distribution of livestock species reported as consumed by the canid species of interest in the articles. The height and width of each rectangle represent the relative proportion of the contrasting categories; i.e. how many times each livestock - predator pair occurred in the studies (number of observations).

We found that the overall livestock consumption (Figure 6) was significantly different among canid species when maximal consumption rates were compared based on the frequency of occurrence data (Kruskal-Wallis test: H(3)=18.23, p=0.0003). The Dunn post-hoc test revealed a significant difference between wolf (%O median = 32, interquartile range = 57) and jackal (%O median = 9.9, IQR = 23.4, p=0.002) ; and wolf vs. coyote (%O median = 14, IQR= 29.6, p=0.03, Table 1).

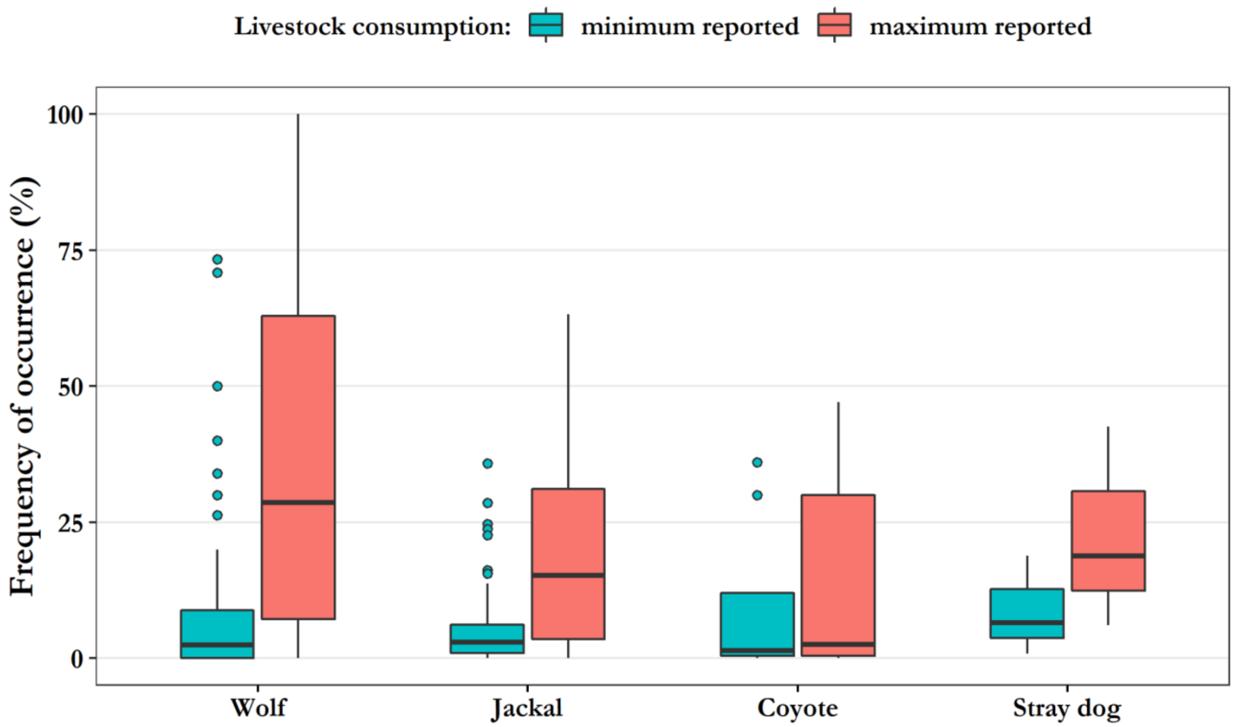

Figure 6. Minimal and maximal livestock consumption of canids based on the reported frequency of occurrence data.

The minimal consumption rates were statistically similar among canids (H(3)=1.19, p=0.75).

group	metric	comparison	mean rank difference	95% Confidence interval lower	95% Confidence interval upper	p
livestock	max. %O	jackal vs. **wolf**	-28.15	-49.76	-6.53	0.003
livestock	max %O	coyote vs. **wolf**	-31.98	-64.66	-3.41	0.012
wolf	%O	horse/donkey vs. **cattle**	-44.07	-86.49	-1.64	0.03
wolf	%O	horse/donkey vs. **goat**	-58.64	-102.27	-15.02	0.001
wolf	%B	**cattle** vs. poultry	51.18	7.79	94.57	0.008
wolf	%B	**cattle** vs. sheep	31.03	2.53	59.52	0.021
jackal	%O	horse/donkey vs. **pig**	-49.83	-94.91	-4.76	0.017
jackal	%O	**pig** vs. sheep	28.37	1.32	55.41	0.031
jackal	%B	**pig** vs. poultry	22.02	5.48	38.58	0.001

Table 1. Mean rank difference and their 95% confidence intervals for the significant pairwise comparisons. %O - frequency of occurrence data; %B - percentage of biomass data. **Bold** text indicates which group had higher mean rank scores in the comparison.

No %B data was reported in the case of stray dog and only one relevant study was found for coyote. Therefore, comparison was made between wolf and jackal only, but no difference was revealed among them for the total biomass data (Mann-Whitney test: U=394, p=0.51). The median was above 50% for jackal, and under 25% for wolf (Figure 7). But we have to consider that potential scavenging was frequently reported in the relevant studies: 3 studies out of 5 for jackal (60%) and 14 out of 31 studies for wolf (45%).

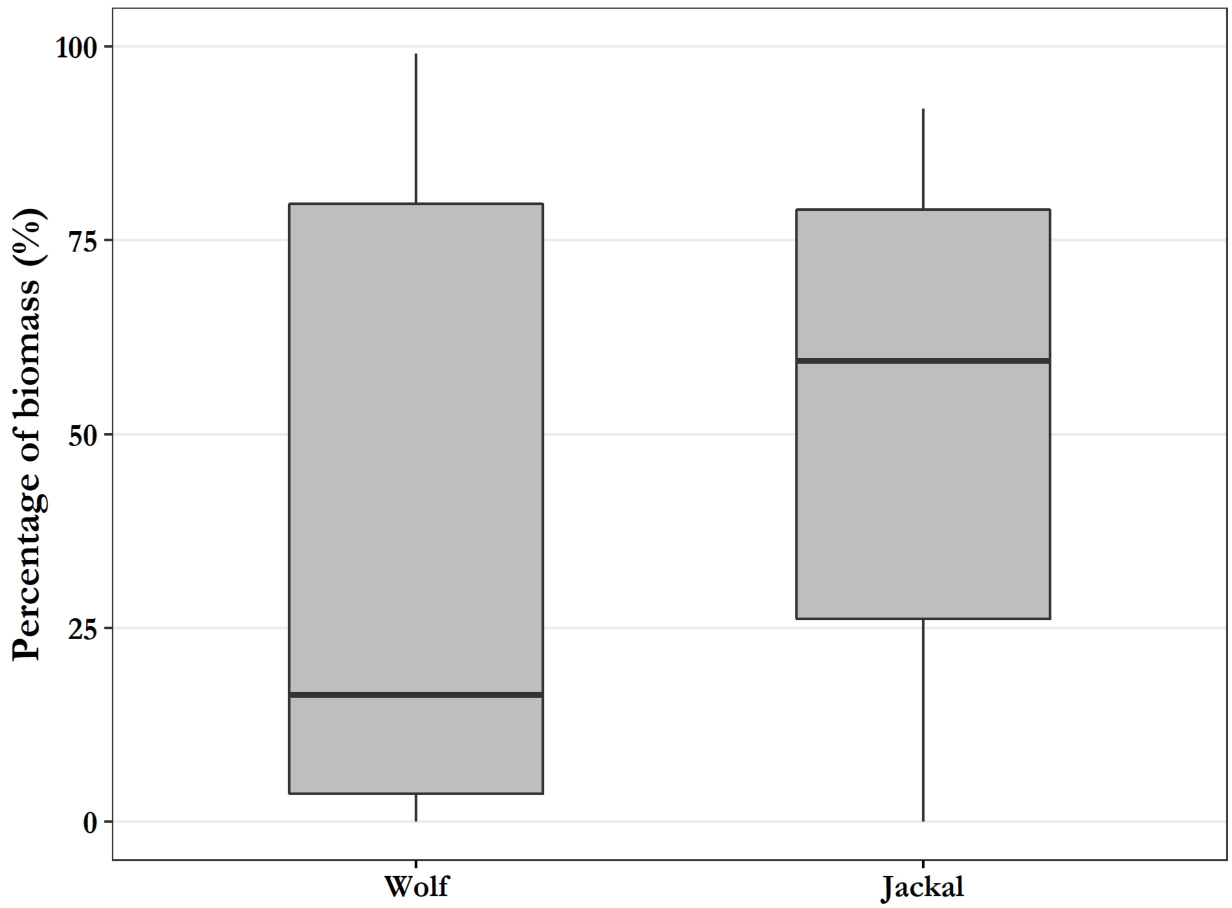

Figure 7. Livestock consumption per carnivore species as shown by the percentage of biomass.

3.4 Consumption of various livestock species by canid species

Sheep (N=94, 21% of observations) and cattle (N=91, 20% of observations) were the most frequently reported livestock species which were consumed the most by canids. Goats were the third most reported species (N=79, 18% of observations). Horse and donkey (N=52, 12% of observations), poultry (N=47, 11% of observations) and pigs (N=32, 7% of observations) were less often mentioned (Figure 5). More than 50% of observations belonged to those studies that reported direct or potential scavenging considering every single livestock species (sheep: N=59 observations - 63%, cattle: N=55 - 60%, goat: N=48 - 61%, horse: N=28 - 54%, poultry: N=30 - 64%, pigs: N=20 - 63%).

The reported %O data was significantly different among livestock species groups in the wolf's diet (Figure 8, H(5)=19.42, p=0.002). Based on 300 reported observations the %O of equines (mostly horse and donkey, median = 3.6, IQR = 11) was significantly less from cattle (median = 12, IQR = 15.6, p=0.03) and goat (median = 10.2, IQR = 23.2, p=0.001, Table 1).

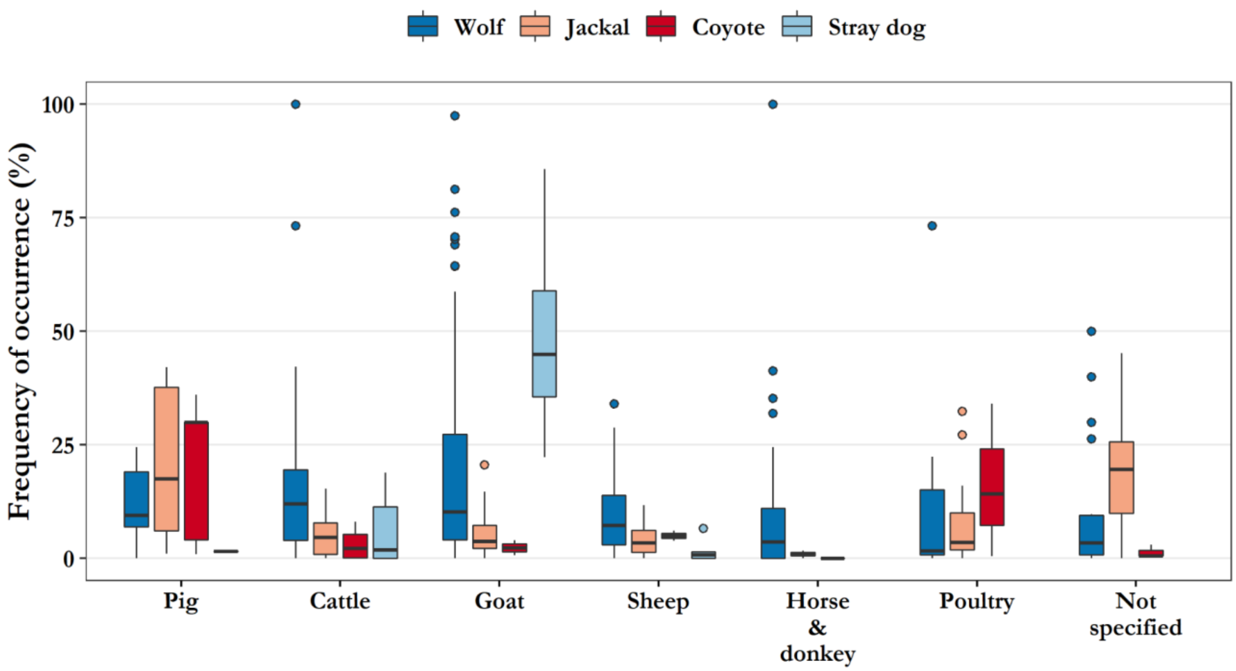

Figure 8. Consumption of livestock species by wolf, golden jackal, coyote and stray dog as shown by the frequency of occurrence.

Significant differences were also revealed in the %B data for wolf (Figure 9) based on 129 observations (H(5)=18.3, p=0.003); where the consumed biomass of cattle (median = 16.8, IQR = 46.4) was significantly higher than that of poultry (median = 0.1, IQR = 10.1, p=0.008) and sheep (median = 4.9, IQR = 9.5, p=0.019, Table 1).

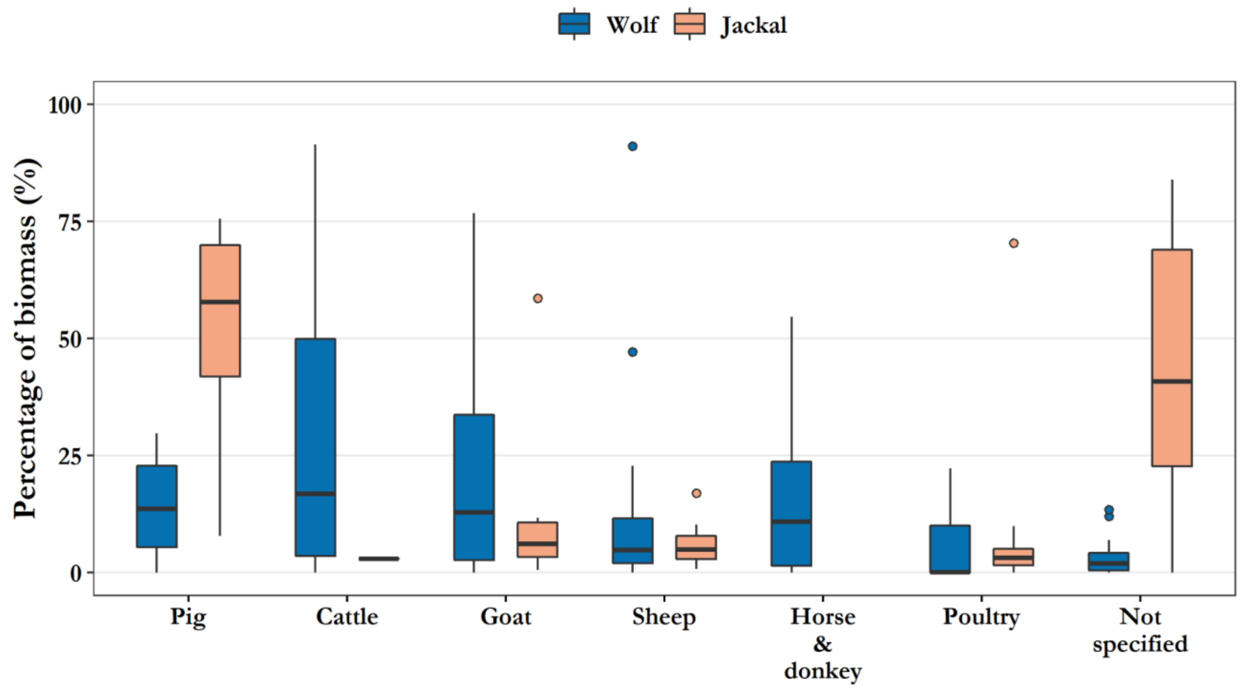

Figure 9. Consumption of livestock species by wolf and golden jackal as shown by the percentage of biomass.

Regarding to jackal (N=104 observations) %O data (H(5)=15.8, p=0.007), the consumption of pig (median = 18, IQR = 31.7) was significantly higher than equines (median = 1, IQR = 0.8, p=0.018) and sheep (median = 3.4, IQR = 4.8, p=0.03) (Figure 8). Pairwise comparisons on %B data (N=45 observations) revealed statistical difference between pig (median = 57.8, IQR = 28.1) vs. poultry (median = 3.2, IQR = 3.5, p<0.001) consumption (H(4)=15.67, p=0.004, Figure 9, Table 1).

Based on 25 observations reported by 10 articles, the amount of consumed livestock-related food items were statistically similar for different domestic species in the coyote's diet considering the %O data (H(4)=5.37, p=0.252). The contrast was the highest between cattle (median = 2.2, IQR = 5.2) and pig (median = 30, IQR = 25.9), although no significant difference was confirmed (Figure 8). Since consumed biomass data was reported by only one study, statistical test was not performed on these data.

The livestock consumption of stray dogs showed no difference between livestock species in %O data. Similar to coyote, testing on biomass data was impossible due to lack of adequate data.

4. Discussion

Most of the studies provided evidence about the wolf-related losses of livestock. The occurrence of domestic species in wolf diet has been mainly observed in areas where the wild prey availability is recognizably degraded, as it seems to be the case in some parts of Southern Europe and Asia (Torres et al., 2015; Capitani et al., 2016; Janeiro-Otero *et al.*, 2020). The diversity in the prey depends on the availability as well as the vulnerability of the prey community for each region (Marquard-Petersen 1998). In countries like Portugal and Greece where wild ungulate numbers are low, wolves feed mostly on livestock (Papageorgiou *et al*., 1994; Vos 2000), whereas in countries like Germany, the conflict is less evident due to the naturally high wild ungulate availability and prevention methods adopted by shepherds, for example surrounding pastures with electric fences in order to prevent predation on their herds (Ansorge *et al*., 2006). Even if wolf was the most reported canid predator of livestock, a vast majority of the studies emphasised that a significant amount of livestock in the diet could originate from scavenging (e.g. Capitani *et al.*, 2016; Lagos & Bárcena 2018; Ciucci *et al.*, 2020).

Livestock predation by the golden jackal also turned out to be a common issue that needs attention in order to be prevented. The diet of the golden jackal varies according to the region and depending on domestic prey availability, wild prey abundance and amount of anthropogenic food that is readily available. Moreover, golden jackals that are hunting individually will mostly be relying on small-sized prey species like rodents, hares and birds, however, forming small groups primarily for breeding also increases hunting efficiency (Mahmood *et al.*, 2013) and therefore, it can hunt larger sized prey, like medium- or large-sized ungulates (Jhala & Moehlman, 2004) including domestic ones. Furthermore, golden jackals, coyotes and stray dogs tend to utilise alternative food sources in the form of plant matter, reptiles, amphibians, smaller rodents and garbage (Lanszki *et al*., 2006, 2010; Mukherjee *et al*., 2004; Giannatos *et al*., 2010) leading to a lower proportion of domestic animal food in their diet. It has been shown by previous studies that the golden jackal, coyote and stray dog take advantage of these resources more compared to wolves (Macdonald, 1979; Vanak & Gompper, 2009; McVey *et al.*, 2013). It is also important to note that the livestock remains found in the diet of carnivores do not imply that these predators hunted the consumed livestock. While it is possible to identify whether the remains were hunted or scavenged if additional methods were implemented (Gazzola *et al.*, 2005, Mohammadi *et al.*, 2019), the majority of the studies do not mention the exact origin of the foodstuff.

In our analysed studies we saw that the small-sized and large-sized livestock consumption was rather similar in wolves but varied among the region and according to prey vulnerability. Pimenta *et al.* (2017) found that in Portugal the majority of the cattle predation occurred in a free-ranging husbandry system, where the cattle grazes on communal lands farther away from their primary shelter which are rarely confined. On the other hand, in the semi-confined husbandry systems where herds were grazed on pastures located closer to the shelter, attacks were considerably less frequent. Damages on cattle have increased in recent years by nearly 1.5 times more as shown by the compensations for wolf predation paid to farmers in countries like USA, Italy and Spain (Breck *et al.*; 2004, Dondina *et al*., 2015, Llaneza *et al*., 2015). There are few plausible explanations for this case. It may be that this increase is purely due to increased observations of wolf attacks as a result of increased awareness of wolf predation compensation programs for farmers. Alternatively, as Pimenta *et al*. (2017) described, an explanation for increased predation on cattle can be attributed to decrease in numbers of alternative livestock species such as sheep and goats. Eliminating livestock carcasses from the field as part of the implementation of the EU sanitary regulation 1774/2002, which followed the outbreak of bovine spongiform encephalopathy, reduced food resources for the predators, this may have caused the predators to shift their diet towards predating on living individuals of domestic species (Lagos & Bárcena, 2015).

Wolf preference for goats over sheep has been previously described in countries like Portugal (Torres *et al.*, 2015) and Greece (Iliopoulos, 2009), and highly depends on the area and how the livestock is handled. However, in most parts of Europe, e.g. in central Italy, sheep were the preferred livestock prey, due to the fact that in that region specifically goats' availability was in itself low (Ciucci, 1998). The goats graze more in the hilly areas which are located farther away from the settlements, these flocks are usually accompanied by very few shepherds which makes it difficult to ward off any predators (Torres *et al*., 2015). In addition, goats are mostly found in a free grazing regime, making them more vulnerable to predators. Sheep on the other hand graze closer to the villages and most of the time they stick together in tight groups, therefore this makes them less vulnerable to predators like wolves (Torres *et al*., 2015). In this article it is also noted that sheep remaining close to the settlements is crucial as the likelihood of wolves being seen and chased away by a resident is rather high. Predation on goats looks to be selected according to the flock size. Vos (2000) found that flocks of <200 goats were almost never attacked, compared to the bigger flocks of >900 goats. This can be due to the fact that larger flocks are more difficult for shepherds to control and protect. As a general principle, the use of guardian animals has been shown to be a rather effective mitigative measure tool for reducing livestock predation which should be evaluated in areas with high predation losses against the cost of changing production systems (Kurt *et al.*, 2012; Urbigkit *et al.*, 2019). On top of utilising the benefits of guard animals, it is crucial to also incorporate interventions such as electric fences, calving control and physical deterrents into the overall livestock protection (Gehring *et al*., 2011).

Golden jackal showed the highest consumption of pigs, especially in countries like Serbia during the winter months, when the slaughter of domestic pigs becomes more frequent for meat production purposes (Penezic, 2015). The remains of slaughtered animals are then dumped close to the settlements (Ćirović *et al*., 2014). Moreover in Serbia free-ranging pig grazing still occurs in marshland forests, which makes them possible to be preyed on in this habitat also preferred by jackal (Molnár *et al.*, 2021). A similar situation was observed in Greece (Giannatos *et al*., 2005) and Israel (Rotem *et al.*, 2011) where illegal dumps are located in the immediate vicinity of human settlements. In addition, cold temperature helps to keep the remains fresh for longer, providing suitable food for winter survival for predators like the golden jackal. This could attract predators close to the villages which leads to further conflict. The obvious way to resolve this issue would be to tighten the laws and legislative framework to prevent the illegal and inappropriate dumping of remains of slaughtered livestock close to the settlements (Penezic, 2015).

In contrast to the Serbian pig consumption by golden jackal, in Greece goats and pigs were the most frequently eaten (Lanszki *et al.*, 2009; Giannatos *et al.*, 2010), meanwhile in Israel poultry was the most commonly found livestock in the jackal's diet (Lanszki *et al.*, 2010). It can be argued that for the medium sized carnivores, cattle and equines seem to be too big and dangerous targets. Moreover, there are shifts in the diet of golden jackal which are mostly due to seasonal changes and variations in habitat (Jhala & Moehlman, 2004) as the broad diet of the jackal is in direct relation with the local availability of each food type (Macdonald, 1979). This can explain, among others, their low consumption of livestock in general.

Large sized domestic prey were also avoided in case of coyotes. Coyotes are similarly opportunistic feeders and will take advantage of any easy prey that becomes available (Boughton, 2020). Domestic birds such as ducks, geese, chickens and turkeys are almost always found in large groups, relatively small in size and not successful at avoiding predators, thus, those make them easy prey for coyotes. Livestock carcasses and remains being discarded near the settlements intensifying the human-predator conflict seem to be also a problem in the United States (Cypher, 1994) and can contribute to coyote-related livestock damage. While our study has the lowest sample size from coyotes, the livestock remains represented an insignificant part in their diet. In a low-productivity area, coyote diet was mostly composed of plant material and fruit, while the most common mammalian food item in coyote diet was the white-tailed deer (Swingen *et al.*, 2015; Chitwood *et al.*, 2015). Coyotes in low-productivity areas tend to shift their diets around the year and it is based on the availability of preferred food items (McVey *et al.*, 2013; Stratman & Pelton, 1997, Turner *et al.*, 2011, Wooding *et al.*, 1984).

Livestock predation by stray dogs is highly understudied, as it was reflected in the low number of studies found by the query. Literature review revealed that dogs are primarily scavengers of the waste left by humans, this is a clear case for most free-ranging or feral dog populations, in Italy (Macdonald & Carr, 1995), North America (Daniels & Bekoff, 1989; Lantis, 1980), India (Oppenheimer & Oppenheimer, 1975), southeast Asia and Australia (Corbett, 1995). Some studies suggest that, compared to wolves, stray dogs consumed more livestock (Echegaray & Vilà, 2010). According to the Polish Hunting Association, between 2004 and 2010 on average 38,924 feral and 97,290 free-ranging dogs were estimated to be killing annually on average 260 domestic animals including cattle, sheep and goats, 264 red deer, 111 fallow deer, 8,903 roe deer, 1,178 wild boars, and 16,135 brown hares (Krauze-Gryz, 2014). However, unlike the other three canid predators, dogs are more familiar and closer to humans and live in areas closer to farms. This very well explains why most of the food found in the stray dog diet is anthropogenic (Carrasco-Román *et al.*, 2021; Mitchell & Banks, 2005; Lunney, 1990; Silva-Rodríguez *et al.*, 2010; Vanak, 2009).

Conclusion

Methods of predator management and livestock handling vary among countries and largely depend on differences in habitat types, the density of wild predators, livestock management in terms of common practical protection methods against canine predators, and wild prey availability as well as national and international policy, regulations and experiences/traditions of local people from the past how to deal with predators. All of the factors have a considerable effect on the predation rates and directly influence the intensity of human-wildlife conflict.

The wolf was found to feed the most on the livestock species and showed preference to cattle and goats. Golden jackals, coyotes and dogs were less dependent on the domestic species, however pigs appeared the most frequently in jackals' (and coyote's) diet.

Throughout our analyses we found that medium sized carnivores are more problematic to smaller sized livestock species - meaning that poultry and other domestic birds, piglets, lambs and calves should be more protected against golden jackal, coyote and stray dogs. On the other hand, sheep, goats, equines and cattle should be carefully protected against a large sized predator as is the wolf in this case.

However, it is important to note that the vast majority of papers included in the analyses did not always make a clear distinction between scavenged and predated livestock when examining the scats and stomachs. Therefore, while livestock predation is indeed an issue for many local stakeholders, it is not possible to conclusively identify whether or not the livestock was scavenged or killed. It is further important to highlight that livestock predation strongly depends on wild prey availability that can shape potential preying on livestock or scavenging activities. Furthermore, changes in livestock availability or vulnerability through modifications in mitigation measures could also lead to a decrease in livestock depredation throughout the years.

When it comes to conflict mitigation, first it is important to differentiate between scavenging and livestock depredation. Secondly, the livestock loss should not be attributed to any specific predator without any evidence. It is crucial to first understand and identify the real cause of predation based on visible predation signs; then set practical and adaptive steps for its elimination. We encourage experts to use reliable methods adequate for all these purposes.

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