The underestimated role of carrion in vertebrates' diet studies

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Abstract

Aim: Despite the increasing scientific evidence on the importance of carrion in the ecology and evolution of many vertebrates, scavenging is still barely considered in diet studies. Here, we draw attention to how scientific literature has underestimated the role of vertebrates as scavengers, identifying the ecological traits that characterize those species whose role as scavengers could have gone especially unnoticed.

Location: Global.

Time period: 1938-2022.

Major taxa studied: Terrestrial vertebrate scavengers.

Methods: We analyzed and compared a) the largest database available on scavenging patterns by carrion-consuming vertebrates, b) 908 diet studies about 156 scavenger species, and c) one of the most complete databases on bird and mammal diets (*Elton Traits* database). For each of these 156 species, we calculated their *scavenging degree* (i.e., proportion of carcases where the species is detected consuming carrion) as a proxy for carrion consumption, and related their ecological traits with the probability of being identified as scavengers in diet studies and in the *Elton Traits* database.

Results: More than half of the species identified as scavengers at monitored carcasses were not assigned carrion as food source in their diet studies nor in the *Elton Traits* database. Using a subset of study sites, we found a direct relationship between a species' *scavenging degree* and its rate of carrion biomass removal. Also, scavenger species which were classified as non-predators and mammals had a lower probability of being identified as scavengers in diet studies and in the *Elton Traits* database, respectively.

Main conclusions: Our results clearly indicate an underestimation of the role of scavenging in vertebrate food webs. Given that detritus recycling is fundamental to ecosystem functioning, we encourage further recognition and investigation of the role of carrion as a food resource for vertebrates, especially for non-predator species and mammals with higher *scavenging degree*.

KEYWORDS

Biases studies, carnivory, omnivory, predator, prey items

1. INTRODUCTION

Food webs are structured by complex connections among and within trophic levels that are fundamental for ecosystem functioning (Allesina et al., 2009). However, while predation and herbivory links have been widely acknowledged in food webs (e.g., Coley & Barone, 1996; Abrams, 2000), the consumption of animal and plant detritus have received less scientific attention (Moore et al., 2004; Halnes et al., 2007). Failing to recognize the role of detritus in food webs may notably hinder the understanding of both top-down and bottom-up processes, and, consequently, food-web dynamics (Moore et al., 2004; Halnes et al., 2007).

Carrion is an exceptionally nutritive kind of detritus (DeVault et al., 2003). Not surprisingly, scavenging is widespread among vertebrates (Sebastián-González et al., 2019). However, facultative scavenging has traditionally been ignored in terrestrial food web studies (Wilson & Wolkovich, 2011). Disregarding scavenging may preclude our understanding of how ecosystems are structured and function in different aspects. First, scavengers have an essential role in the movement of nutrients among and within ecosystems (DeVault et al., 2003), with this role being greatly dependent on several scavengers' ecological traits (e.g., size and home range; Gutiérrez-Cánovas et al., 2020). Second, scavenging-predation trade-offs may have direct and indirect botton-up and top-down effects on prey populations and vegetation, thus potentially leading to a restructuration of the entire food web (Barton et al., 2013; Moleón et al., 2014; Baruzzi et al., 2018). Third, multi-channel feeding and increased number of inter-specific interactions around carrion help to stabilize food webs (Wilson & Wolkovich, 2011; Moleón et al., 2014). Thus, by underestimating scavenging, we may overlook many nutrient transfer paths, places of nutrient deposition and multi-trophic effects of scavengers.

Though scavenging research has flourished in the last two decades (Moleón & Sánchez-Zapata, 2015), the scavenging role in carnivore diets is still widely neglected in diet studies for most scavenger species, especially those that do not scavenge regularly. Here, our general goal is to show that facultative scavenging by vertebrates occurs at a higher frequency than previously recognized by traditional diet studies. We used the largest database available on carrion consumption by vertebrate scavengers from camera-trapping and other procedures (Sebastián-González, 2021) and conducted a scientific literature review on the diet of these scavenger species. This allowed us to highlight that many vertebrate scavengers that were frequently observed consuming carrion are rarely identified as scavengers in traditional diet studies. We also evaluated how scavenging is treated in one of the most detailed databases on bird and mammal diets: the *Elton Traits* database (Wilman et al., 2014). Finally, we identified the ecological traits that characterize those species that have been found scavenging in monitored carcasses, but not in diet studies or in the *Elton Traits* database.

2. METHODS

2.1 Scavenger species and scavenging degree

To identify *scavenger species*, we used the database on carrion consumption by vertebrates, available at *Figshare* (Sebastián-González, 2021). This database provides information about scavenger species recorded at 2629 vertebrate carcasses (from rodents to large ungulates) in 53 terrestrial assemblages in 22 countries worldwide (Figure 1a). The database includes 177 scavenger species (95 birds, 75 mammals and seven reptiles; see Appendix S1 for more details on the database). Given that their diet is formed mostly or exclusively of carrion, we excluded vultures from the analyses (N=19 species). We also excluded domestic species (N=2). Thus, the final dataset includes 156 scavenger species.

For each scavenger species, we calculated the *scavenging degree* as the average percentage of monitored carcasses where the species was detected consuming carrion. The *scavenging degree* is equivalent to the *normalized degree* used in network analyses (Sebastián-González et al., 2021). To calculate the *scavenging degree*, we first calculated the *local scavenging degree* of each species at each study site (i.e., the percentage of monitored carcasses where the species was detected consuming carrion at a given site; Sebastián-González et al., 2021), and then averaged values when a species appeared in more than one site. We selected the *scavenging degree* as a potential proxy of carrion consumption because it can be calculated for all assemblages and species in our scavenging database, providing a global view of the process. To check if the *scavenging degree* is actually a good proxy of the amount of carrion that is removed by a given scavenger species, we related this metric with the proportion of the total carrion biomass monitored that was consumed by each species in a study site. However, this information is not available for all the sites, as it is not straightforward to calculate. Therefore, we used a subset of nine sites in two continents (Europe and Africa) and three biogeographical regions (Temperate, Mediterranean, and Subtropical) for which the amount of biomass consumed had already been calculated and published (Mateo-Tomás et al. 2017), which includes 46 scavenger species (18 mammals, and 28 birds). Details on this calculation and raw data can be found in Mateo-Tomás et al. (2017). Briefly, the total carrion consumed by each scavenger species was estimated by multiplying the average daily food intake of each species (calculated following Crocker, Hart, Gurney, & McCoy, 2002) by the number of individuals of that species in each carcass and by the total number of days that each carcass was consumed by the species. Then, we added up all the biomass consumed by each species in all the monitored carcasses, and calculated the percentage of the biomass consumed by each species related to the total carrion biomass monitored. We used Spearman correlations in R to correlate the *scavenging degree* and the percentage of carrion biomass consumed. This analysis revealed that this metric clearly identifies species with an important role as carrion recyclers (see Results), i.e., those species that consume most of the carrion in an assemblage.

2.2 Carrion consumption from diet studies and *Elton Traits* database

First, we reviewed studies on the diet of the 156 scavenger species to identify to which extent these studies explicitly consider (i.e., quantify) carrion consumption by these species. From those studies, we extracted the percentage of carrion in the diet of the species, as estimated by the authors (see details on the literature search in Appendix S2). We also extracted the percentage of vertebrates in the diet, as a measure of the maximum potential amount of vertebrate carrion in the diet of the species (if all those vertebrates were eaten as carrion). The studies estimated diet from scats, pellets, stomachs' and gizzards' content, nest remains, camera-trapping observations and/or direct observations.

The percentage of carrion and vertebrates in the diet was presented using the four more widely used metrics in dietary studies: a) *frequency of occurrence* (% FO), which is calculated as the percentage of scats/stomachs/pellets/gizzards where a given prey item (in our case, carrion and vertebrates) was found. This is the most widespread metric, but it has the drawback that calculations cannot be directly done without raw data. That is, if we need to calculate the FO of vertebrates in the diet of a species, but data is separated in mammals and birds, it is not correct to sum the FO values for these two categories, as more than one category can be present in an individual sample. Thus, for this metric, we identified the minimum carrion or vertebrate consumption as the highest FO for a given category. For example, if a study indicated that the FO of mammals (or mammalian carrion) was 60% and the FO of birds (or avian carrion) was 50%, we estimated that the minimum FO of vertebrates (or carrion) was 60%; b) *relative frequency of occurrence* (% RFO), which is calculated as the percentage of the total diet items that belong to carrion or vertebrates; c) *percentage of ingested biomass* (% Biomass), which is calculated as the percentage of the total ingested biomass that belongs to carrion biomass or vertebrate biomass in the diet of the species; and d) *percent volume* (% Volume), as the percentage of the volume of the scats/stomachs/pellets/gizzards content that belongs to carrion or vertebrates. See methodological details on these metrics in articles included in this study (see Data Availability section).

Given that each diet metric may be biased in a different direction and our aim was to have a general idea (not a precise estimation) of the amount of carrion and vertebrates in the diet, we averaged the percentage of carrion and vertebrates obtained with different metrics and used this averaged metric (hereafter, *% carrion-diet studies* and *% vertebrates-diet studies*, respectively) in further analyses.

Second, we extracted the percentage of carrion and vertebrates in the diet of the abovementioned 156 scavenger species from *Elton Traits* database (Wilman et al., 2014).

This database describes the percentage of different food categories in the species' diet in percent relevance. To calculate the percentage of vertebrates in the diet (*% vertebrates-Elton Traits*), we summed the columns representing the percentage of mammals, birds, reptiles, amphibians, fish and unknown vertebrates. The percentage of carrion in the diet *(% carrion-Elton Traits*) is specified in an independent column in the database.

2.3 Scavenger ecological traits

We extracted five scavenger ecological traits from Sebastián-González et al. (2021) that can be related with the species role as a scavenger: 1) animal group (bird, mammal, reptile), 2) home range (km^2), 3) predatory behavior (top-, meso- or non-predator), 4) diet (carnivorous or omnivorous) and 5) body mass (in kg; See Appendix S3: Table S2 for details).

2.4 Statistical analyses

First, we compared the *scavenging degree* among those species identified as scavengers in diet studies and in the *Elton Traits* and in those not identified as scavengers using a t-test.

Then, we evaluated the existence of a possible bias due to sample size by correlating the number of reviewed diet studies with the *% carrion-diet studies*. Given that these two variables were uncorrelated (Spearman correlation coefficient = -0.045, p-value= 0.628), we used Spearman's correlations to relate a) *% carrion-diet studies* of each scavenger species with *% carrion-Elton Traits*, b) *% vertebrates-diet studies* with *% vertebrates-Elton Traits*, c) *scavenging degree* with *% carrion-diet studies*, and d) *scavenging degree* with *% carrion-Elton Traits*.

Finally, we used one-predictor generalized linear models (binomial distribution, logit link) to identify the ecological traits characterizing those scavenger species that were detected in the monitored carcasses but were not identified as scavengers in the diet studies or the Elton Traits. The body mass was log-transformed. Coefficients with confidence intervals not overlapping with the zero were considered to have statistical support.

3. RESULTS

3.1 Scavenging degree and scavenging in diet studies

On average, the *scavenging degree* was 16.9 % for birds (SD = 20.9; range = 0.8-95), 19.6 % for mammals (SD = 18.2; range = 0.5-71.4), and 20.8 % for reptiles (SD = 33.2; range = 1.03-95; see Appendix S3: Table S1 for the list of species and their *scavenging degree*). Many species only appeared in one study site, while some appeared in many sites and carcasses, such as the red fox *Vulpes vulpes* (31 sites and 801 carcasses) or the wild boar *Sus scrofa* (23 sites and 452 carcasses). The scavenging behavior of some species was anecdotal, such as the stoat *Mustela erminea*, which was found in a single carcass. Other species appeared in more than 90% of the carcasses monitored in an assemblage, such as the lace monitor *Varanus varius*. Importantly, the *scavenging degree* was significantly corelated to the percentage of carrion biomass consumed by each species in each study site (Spearman's rho = 0.675, p<0.001), suggesting that it is a good proxy of the role of a species as carrion recycler in an ecosystem.

We found diet studies for 121 species out of the 156 species evaluated. In total, we reviewed 908 diet studies (Figure 1b). Carrion was poorly represented in diet studies (average *% carrion-diet studies*: 2.5%; Appendix S3: Figure S1). In contrast, vertebrates represented more than 50% of the average diet in birds and mammals and c. 10% in reptiles.

The pattern was similar when using the four different diet metrics (Appendix S3: Table S3, Figure S2).

3.2 Comparing scavenger species in different databases

We identified 86 species (62.8% of the 137 species evaluated; 32 birds and 54 mammals) that had not been assigned carrion in the *Elton Traits* database (Appendix S3: Table S1), and 65 species (53.2% of 121 species for which we found diet studies; 28 birds, 33 mammals and four reptiles) that had not been assigned carrion in diet studies. The *scavenging degree* was larger for those species identified as scavengers in diet studies and in the *Elton Traits* than in those not identified as scavengers (t-test: t = -2.130, df = 107.9, p = 0.035 for diet studies; t = -2.481, df = 77.6, p = 0.015 for the *Elton Traits,* Figure 2).

The *% vertebrates-diet studies* was highly related to the *% vertebrates-Elton Traits* (Figure 3b), but this relationship was not significant for the *% carrion-diet studies* (Figure 2a). The correlations between the *scavenging degree* and *% carrion-diet studies* (Figure 3c) and *% carrion-Elton Traits* (Figure 3d) were both significant, though correlation coefficients were lower than 0.35. These results are maintained when using each of the four diet metrics independently (Appendix S3: Figure S3).

3.3 Scavenger ecological traits

We found that species that are not predators had a lower probability of being identified as scavengers in diet studies than mesopredators and, mostly, top predators (Figure 4a, Appendix S3: Table S4). Also, mammals had a lower probability of being identified as scavengers in the *Elton Traits* database than birds (Figure 4b, Appendix S3: Table S5).

4. DISCUSSION

Our results corroborate the general perception that carrion consumption by vertebrates has largely been underestimated in the scientific literature. We identified many scavenger species whose scavenging habits had not been recognized in diet studies nor in the studied diet database, indicating that this underestimation is generalized across mammalian and avian taxa. Nevertheless, all carnivorous and many omnivorous species may be placed at some position of the scavenging spectrum, which ranges from species obtaining meat primarily through scavenging (e.g., vultures) to those that mostly kill their prey and rarely scavenge (e.g., cheetahs *Acinonyx jubatus*; DeVault et al., 2003; Pereira et al., 2014), and this scavenging behavior has important eco-evolutionary implications (DeVault et al., 2003; Wilson & Wolkovich, 2011; Barton et al., 2013; Moleón et al., 2014). Also, our results are relevant to adequately assess the process of carrion recycling. According to the traditional sources of diet data, it can be concluded that most mammal and bird species are unimportant to recycle carrion. Our study clearly shows the opposite, which is in line with the many scavenging studies conducted in the last few years (e.g., Sebastián-González et al. 2019, 2021). Thus, we claim for a more generalized consideration of scavenging in ecological research.

The global *Elton Traits* database precisely described the vertebrate consumption of the scavenger species evaluated (i.e., the *% vertebrates-diet studies* was highly correlated to the *% vertebrates-Elton Traits database*), but it showed a clear bias, as part of those vertebrates must have been scavenged rather than predated. Diet at the *Elton Traits* database is estimated in percent relevance in 10% steps, recorded as integers, so species that scavenge very opportunistically would not be assigned a scavenging role in this database. This may explain why the correlation between *scavenging degree* and *% carrion-Elton Traits* (Figure

1c) was weaker (i.e., lower rho) than between *scavenging degree* and *% carrion-diet studies* (Figure 1d), and why the percentage of carrion was uncorrelated between diet studies and the *Elton Traits* database (Figure 1a). However, the bias is substantial for other species, such as the red fox, which scavenged more than 80% of the monitored carcasses in some study areas (Sebastián-González et al., 2021) but is not described as a scavenger in the *Elton Traits* database.

It is important to state that, with the data presented in this study, it is not possible to calculate the percentage of carrion in the diet of any of the species, as we only have information on the percentage of carcasses where the species appears scavenging (i.e., the *scavenging degree*). For example, a *scavenging degree* of 60% does not mean that carrion represents 60% of the diet of a given species. Thus, the *scavenging degree* should not be regarded as a direct indicator of the amount of carrion in the diet, as it can be low for obligate scavengers (i.e., vultures), which exclusively feed on carrion, and large for some facultative scavengers, even if they also include other items in their diets. The *scavenging degree* may depend on factors such as carcass abundance (Morant et al., 2022), availability (Moleón et al., 2019), size (Moleón et al., 2015), and location (Smith et al., 2017), or interspecific interactions (Hill et al., 2018). In addition, the local density of the scavenger species could influence its *scavenging degree*. However, a previous study (Sebastián-González et al., 2020) showed that two good proxies of animal density (body size and home range; e.g., Johnson, 1999) were not related to the *scavenging degree*, suggesting that species density is probably not the main driver of the *scavenging degree* patterns observed in the present study. Further research is needed to establish the relationship between the *scavenging degree* of a species and its scavenging habits, which may be regarded as one of the major challenges in carrion ecology.

We are aware that it is not straightforward to know whether an item in a diet study has been scavenged or predated, neither using traditional methods (e.g., scat analysis, stomach content) nor the latest techniques (e.g., DNA analyses, stable isotopes; e.g., Nielsen et al., 2018). Carrion consumption has traditionally been mostly assigned to obligate scavengers (i.e., vultures) and major facultative scavengers (e.g., hyaenas). This clearly overestimates the predatory facet of many carnivore species (e.g., DeVault & Rhodes, 2002; Sebastián-González et al., 2021). However, diet studies can still recognize diet items in scats, pellets or stomachs as carrion when they are too large to be predated, something already done by many authors (e.g., Loveridge & Macdonald, 2003). Besides, diet studies should not rule out the possibility that smaller prey have been scavenged (e.g., van der Merwe et al., 2009), especially when the consumer has been detected scavenging somewhere else. We encourage authors studying vertebrates' diets to include some discussion in this line, so that readers are aware on the possible origin of the food. Citing scavenging at research papers may also be important for research projects that rely on qualitative information, such as the compilation of the *Elton Traits* database. Also, a combination of traditional methods for dietary studies (e.g., scat analysis, stomach content) with new analytical techniques such as RNA, GPS telemetry, including accelerometer data, camera trapping or drones, may help to obtain more accurate information on the relative role of carrion in the diet of these species (e.g., Lesmerises et al., 2015; Neidel et al., 2022).

Interestingly, we have found here that species with a large *scavenging degree* are also the ones consuming the largest proportion of the available carrion in experimental studies, and thus can be considered the main carrion recyclers in their ecosystems. Even if our database is unable to estimate the amount of carrion in diet at the species level, its global character may be useful to identify potential scavengers with a key role in a given study area. Also, as done here, it can be used to identify species that, at least locally, can consume carrion in large quantities. We found that scavenging tends to be relatively more underestimated in non-predator species and mammals. On the one hand, non-predators are often assumed to have a predominantly non-carnivorous diet. On the other hand, diet for mammals is mainly derived from scats (90.1% of the studies reviewed here; Appendix S3: Table S1), where food remains are more degraded than in birds' pellets, as they go through the entire digestive system and could be more difficult to identify (Caviedes-Vidal et al. 2007). Therefore, further research attention on the carrion component of diet should especially focus on these species.

Our study has also revealed the lack of field studies that provide insights into the natural history of certain species (Tewksbury et al., 2014). We were unable to find suitable diet studies for up to 23% of the species detected as scavengers in the scavenging dataset. This lack of basic biological knowledge may hamper detecting relevant ecological patterns (Damgaard & Weiner, 2017) and establishing adequate conservation actions (Xiao et al., 2017) for such species. This suggests that the ecological and management application of large databases of biological traits and the results obtained in the works analyzing these traits should be treated with caution. Finally, we also detected some geographical biases in the available data for both carcass monitoring and diet studies (see Fig. 1). Some regions of the Global South were underrepresented in our study, especially in Africa and Asia for both datasets and also in Central America for the carcass monitoring studies. These geographical biases associated with our sources of information could also partially bias our results. For example, including new study areas could reveal additional ecological traits that may characterize species with low probability of being detected as scavengers in diet studies and the *Elton Traits* database. Thus, our conclusions should be taken with caution, especially regarding the species inhabiting these underrepresented areas.

4.1. Concluding remarks

Our results have revealed that the current scientific knowledge of terrestrial vertebrate diets is strongly biased towards predation in detriment of scavenging, and that this pattern is associated with certain ecological traits of the species. While accurately estimating the proportion of meat that is predated *vs*. scavenged by a species is an outstanding research challenge, current scavenging data may be used to approach the species' role in the ecological process of carrion removal. We provide a metric, namely *scavenging degree*, that can be easily obtained in any terrestrial ecosystem (either extracted from the scavenging dataset or by new field studies) and could be used as a proxy of a species' role as carrion recycler. This metric has already proven successful in inferring ecological patterns in scavenging communities (see Sebastián-González et al., 2021). Due to its large impact on ecosystem functioning, a bigger effort is needed to increase our knowledge about the importance of scavenging in vertebrates' diets and to account for the current underestimation of the ingestion of carrion.

DATA AVAILABILITY STATEMENT

Part of the data used in this study is available from a previous study in Sebastián-González (2021, Figshare). The remaining data can be viewed at Sebastian-Gonzalez (2023, Figshare). We used 908 previously published data sets to put together the scavenger species diet database. The complete list of diet studies can be found in the "Database 2. Raw data diet of scavenger species_R1.xls" database at the above Figshare link.

Sebastian-Gonzalez, E. 2021. “Functional traits driving species role in the structure of terrestrial vertebrate scavenger networks.” Figshare Dataset. https://doi.org/10.6084/m9.figshare.14672250.v1

Sebastian-Gonzalez, E. 2023. “The underestimated role of carrion in diet studies.” Figshare Dataset. https://doi.org/10.6084/m9.figshare.19411055

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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AUTHORS CONTRIBUTIONS

Conceptualization: ESG & EA, Data curation: All, Formal analysis: ESG, Visualization JM, Writing – original draft: ESG, Writing – review & editing: All.

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Figures captions

Figure 1. Geographic distribution of the datasets used for this study. a) Number of diet studies of scavenger species by country; b) number of study sites where experimental carcasses were monitored by country. Countries without any study are represented in grey.

Figure 2. Violin plots comparing the *scavenging degree* for those species identified as scavengers or as not scavengers in a) diet studies and in b) the *Elton Traits* database.

Figure 3. Relations between a) *% carrion-diet studies* and *% carrion-Elton Traits*; b) *% vertebrates-diet studies* and *% vertebrates-Elton Traits*; c) *% carrion-diet studies* and *scavenging degree*; and d) *% carrion-Elton Traits* and *scavenging degree*. Each point represents one species, with different color points for birds, mammals and reptiles. The red line shows the regression line (± SD) for significant correlations and are included to help visualizing the correlation trend. In plots c) and d), note that there are many scavenger species for which no single study included carrion among the identified food items. We show the Spearman correlation coefficient (ρ) and p-value (p) for all correlations.

Figure 4. Predicted probability of being detected as an scavenger in a) diet studies and b) *Elton Traits*. We show the probability only for those traits with statistical support. See Appendix S3 Table S4 for model details.

Figure 1

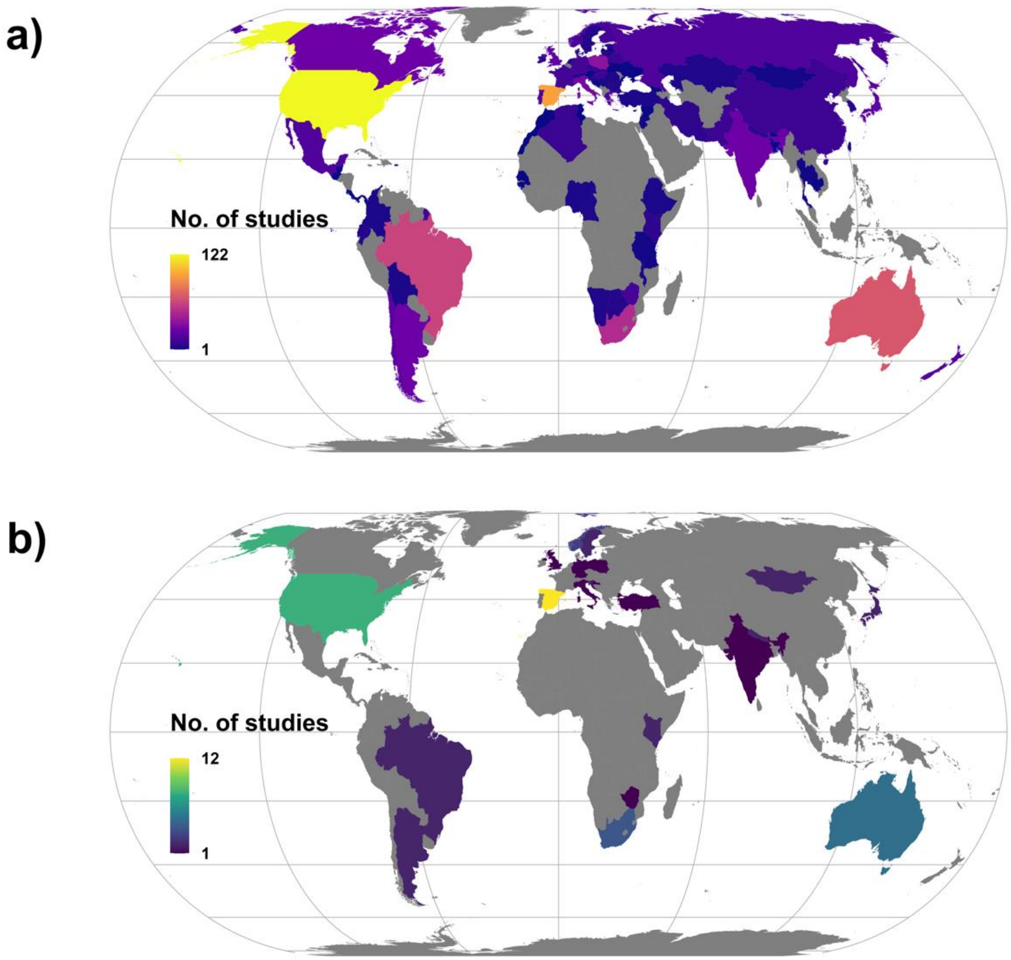
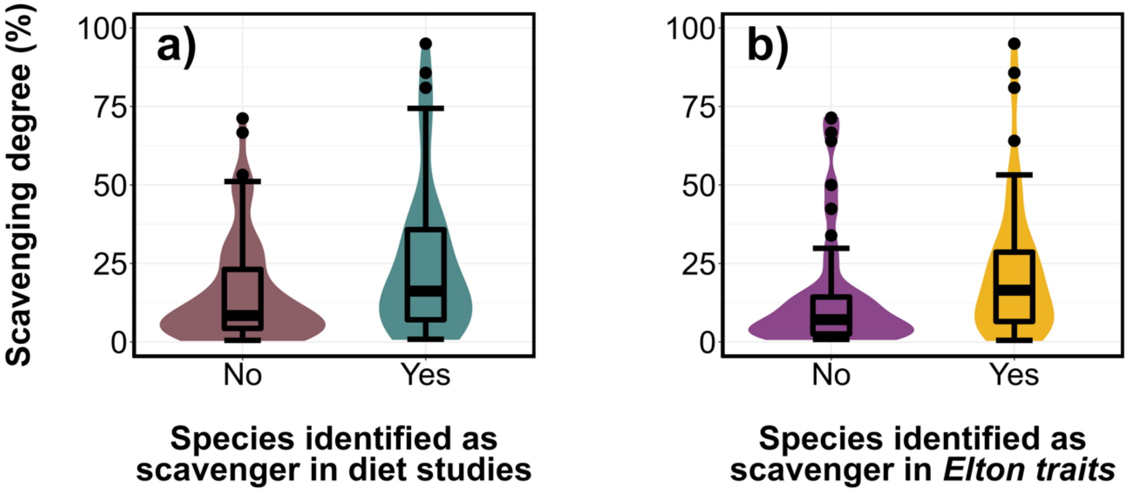


Figure 2


a)
b)
Scavenging degree (%)
100
75
50
25
0
No
Yes
Species identified as scavenger in diet studies
Species identified as scavenger in *Elton traits*

504 **Figure 3**

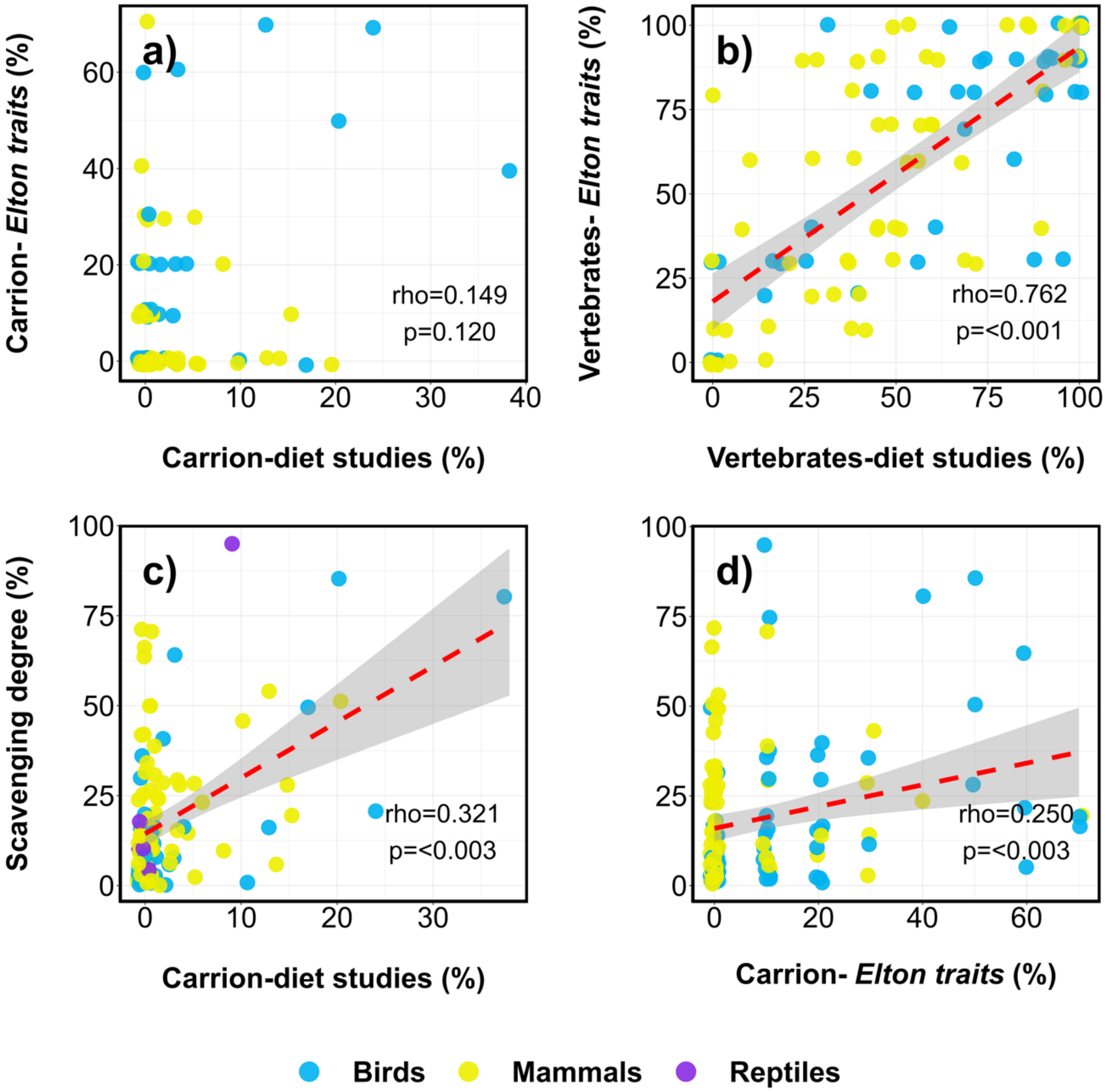


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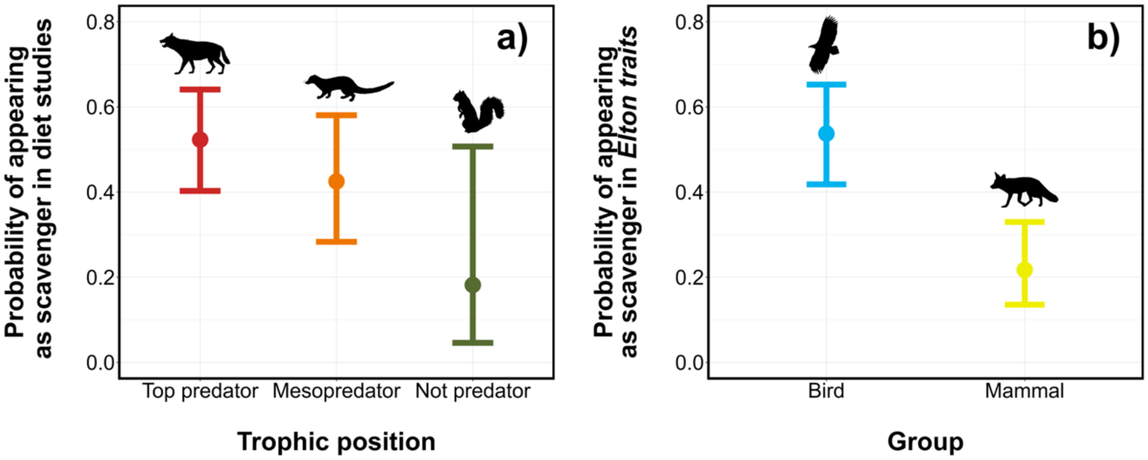
Figure 4


a)
Probability of appearing as scavenger in diet studies
0.8
0.6
0.4
0.2
0.0
Top predator
Mesopredator
Not predator
Trophic position
b)
Probability of appearing as scavenger in *Elton traits*
0.8
0.6
0.4
0.2
0.0
Bird
Mammal
Group