



## RESEARCH PAPER

## Red fox cannibalism in a temperate forest ecosystem



Sandrina Muther<sup>a,1</sup>, Joe Premier<sup>b,1</sup>, Martin Gahbauer<sup>b</sup>, Christian von Hoermann<sup>c,d</sup>,  
Jörg Müller<sup>c,d,2</sup>, Marco Heurich<sup>b,e,f,2,\*</sup>

<sup>a</sup> University of Natural Resources and Life Sciences, Vienna Gregor-Mendel-Straße 33, Vienna 1180, Austria

<sup>b</sup> Department of National Park Monitoring and Animal Management, Bavarian Forest National Park, Freyunger Straße 2, Grafenau 94481, Germany

<sup>c</sup> Department of Conservation and Research, Bavarian Forest National Park, Freyunger Straße 2, Grafenau 94481, Germany

<sup>d</sup> Department of Animal Ecology and Tropical Biology, Field Station Fabrikshleichach, Julius-Maximilians-Universität Würzburg, Glashüttenstraße 5, Rauhenebrach 96181, Germany

<sup>e</sup> Wildlife Ecology and Management, Albert-Ludwigs-Universität Freiburg, Tennenbacher Straße 4, Freiburg 79106, Germany

<sup>f</sup> Institute for Forest and Wildlife Management, Campus Evenstad, Inland Norway University for Applied Science, Koppang 2480, Norway

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## ABSTRACT

Scavengers benefit from carrion and simultaneously provide essential ecosystem services. To assess benefits and risks that carrion might bring, it is crucial to understand ecosystem-specific scavenger communities. Carrion research has mostly focussed on ungulate carcasses and has rarely explored the effects of carnivore carcasses, which can be critical to understanding disease transmission pathways. Therefore, using red fox, roe deer and red deer carcasses, we investigated factors that affect facultative vertebrate scavenger assemblages visiting carnivore and herbivore carcasses in a temperate forest ecosystem. Due to potentially increased disease transmission risk associated with carnivore carrion, we predicted that carnivore carcasses would be visited less and have a reduced visiting species composition compared to herbivore carcasses. Further, we expected red foxes to exhibit less consumption behavior of conspecific carcasses. We placed 22 red fox and 22 herbivore carcasses in a temperate montane protected area in Central Europe, the Bavarian Forest National Park, and analyzed the visits of all species and the consumption behavior of red fox at carcasses to understand whether these depended on carcass type. We found no significant effects of carcass type on visitation rates, visiting species composition, or red fox behavior. Cannibalism of foxes was common and, when controlling for confounding factors, e.g., elevation, temperature, and scavenging seasonality, the predicted consumption rate of red fox at conspecifics was higher than at herbivore carrion. Foxes appeared to consume conspecifics earlier than herbivore carrion, but the difference was not significant. At the very least, our results show that carnivore carcasses and fox behavior, including cannibalism, could provide a pathway for disease transmission. We thereby provide a first impression of the patterns of vertebrate scavenger assemblages at different carcass types in a temperate ecosystem and show that red fox behavior might precipitate a disease transmission pathway.

## Introduction

Carrion has far-reaching effects on belowground soil biogeochemistry, the surrounding food web, and community dynamics (Newsome et al., 2021). Carcasses are a rich source of nutrients that can create distinct hotspots of biological activity (Benbow et al., 2019). The distribution and removal of carrion in the landscape is a vital process, which vertebrate scavengers play a key role in delivering (e.g., Ray et al. 2014). During the winter when insects and microbes are less active,

vertebrate scavengers assimilate most carrion resources (DeVault et al., 2011). Besides providing this ecosystem function, scavengers benefit from increased fitness by consuming carrion. However, this function depends on the presence of a scavenger community and hence a regular carrion regime (e.g., Sebastián-González et al. 2021).

In recent decades, the availability of carrion has declined due to the loss of predators (Chapron et al., 2014), the management of wild and domestic herbivores (e.g., Arrondo et al. 2023), and livestock health and disease legislations (Margalida et al., 2010). For this reason, wildlife

\* Corresponding author.

E-mail address: [marco.heurich@npv-bw.bayern.de](mailto:marco.heurich@npv-bw.bayern.de) (M. Heurich).

<sup>1</sup> These authors contributed equally as first authors.

<sup>2</sup> These authors contributed equally as senior authors.

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management sometimes supplements natural carrion with either wild or domestic animal carcasses to support populations of scavenger species and communities (Moreno-Opo et al., 2015). The evidence for and against the removal or provisioning of carrion depends on the ecosystem and potential risks. Indeed, consuming carrion could impact scavengers negatively if diseases are present, which could have knock-on effects across the landscape (Carrasco-Garcia et al., 2018). Therefore, it is necessary to delineate these risks to support decision-makers and managers.

A strong link is suspected between scavenging and an elevated risk of direct and indirect disease transmission, as scavengers can spread pathogens across the landscape, potentially acting as vectors for various diseases (Vicente & VerCauteren, 2019). Many fatal infectious diseases that affect animal populations can be transmitted via bodily fluids or physical contact (e.g., Brown 2011). These include, for example, mange (*scabie cadit*) (e.g., Pisano et al. 2019), canine distemper (Frölich et al., 2000), and rabies (Cliquet et al., 2014), which all occur in parts of Europe. Apart from infectious diseases, transmission of various nematodes involves carnivores as hosts, with scavenging known to play a role (Poizio, 2000). Scavengers may function as reservoirs of pathogens for wild and domesticated animals, and ultimately humans. Therefore, knowledge of the scavenger community is needed to understand the direct or indirect transmission pathways in a given ecosystem.

Different carcass types, or species, seem to influence scavenging patterns, and therefore potential transmission pathways. Some studies have reported avoidance of carnivore and conspecific carcasses as food sources by vertebrate scavengers (Moleón et al., 2017; Muñoz-Lozano et al., 2019; Selva et al., 2005), suggesting that herbivore and carnivore carcasses have distinct roles in ecosystem dynamics. In south-eastern Spain, herbivore carcasses seem to be consumed more, and by more species, than carnivore carcasses, and red fox (*Vulpes vulpes*; hereafter fox) avoided cannibalism (Moleón et al., 2017). Similarly, Selva et al. (2005) observed that wild boar (*Sus scrofa*) avoided conspecific carcasses. These studies attributed this behavior to avoidance of potentially increased disease transmission risk as parasites are often shared between phylogenetically similar host species (Huang et al., 2014). Indeed, the presence of disease or parasite transmission risk might drive scavengers to evolve with low cannibalistic tendencies (Moleón et al., 2017). Cannibalism has been observed in fox, though delayed such that carrion was only consumed weeks after first placement (González et al., 2021). In another study that used herbivore (lambs) and carnivore (foxes) carcasses of comparable size, fox's preference for herbivores was shown by more rapid depletion of lamb than fox carcasses, which increased the species richness at fox carrion due to their extended availability (Oliva-Vidal et al., 2021). These studies both concluded that cannibalism depends on specific decomposition-state and local disease prevalence that balances nutrition with risk. As such, carnivore carcasses might offer a temporally different resource availability to herbivore carcasses, independent of the weight differences typically found between carnivore and herbivore carcasses (Oliva-Vidal et al., 2022). While this could benefit scavenger communities, it may also increase the potential for disease transmission.

Understanding the role of carnivore carcasses for scavenging communities is important for the management of wildlife populations, particularly for mitigating disease transmission or providing supplementary feeding for conservation goals. To explore this, we placed carnivore (fox) and herbivore (roe or red deer) carcasses in a temperate montane ecosystem of Central Europe and monitored the visitors using camera traps. We expected that carnivore carcasses would be avoided, in terms of visitation and consumption, to reduce potential exposure to diseases. We predicted a lower visitation rate at carnivore carcasses compared to herbivore carcasses, and in turn a different species composition such that the community visiting carnivore carcasses would be a subset of the community visiting herbivore carcasses. In addition, we predicted that the temporal distribution of visits of all species would show avoidance of fox carcasses by declining more rapidly over time compared to the visits of herbivore carcasses. Further, we predicted that

the temporal distribution of fox's visitation and consumption behaviors would differ between carcass types, such that they visit and consume herbivore carcasses earlier and more frequently relative to fox carcasses - thereby showing avoidance of conspecific carrion. By testing these predictions, we seek to better understand scavenging patterns and further delineate potential direct and indirect disease transmission pathways in these ecosystems.

## Materials and methods

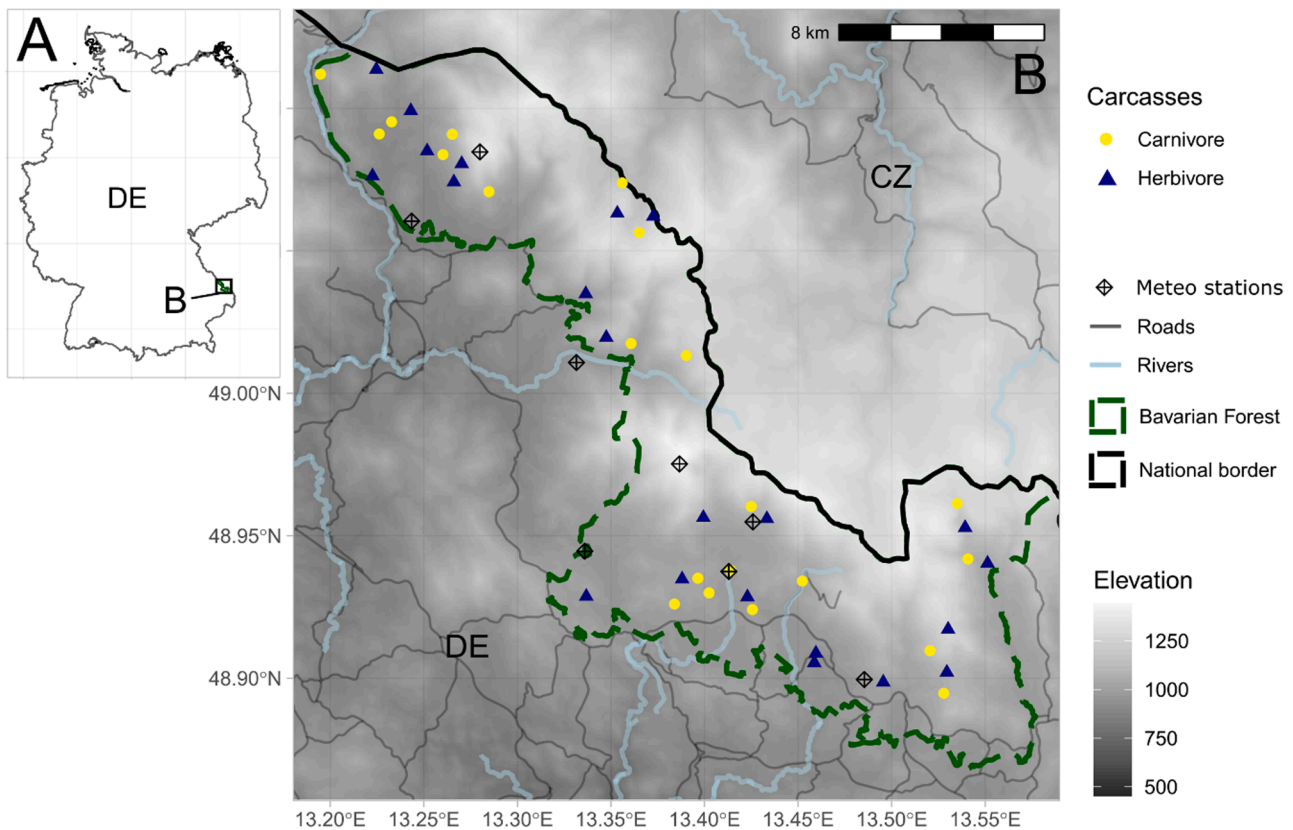
### Study region

Fieldwork was conducted in the Bavarian Forest National Park (24,396 ha) located in eastern Bavaria, Germany, along the border with Czechia, which is within one of the largest continuous areas of protected forest in Central Europe, the Bohemian Forest Ecosystem. The national park lies in an altitudinal range between 600 m and 1,453 m, and exhibits a humid and cold climate, with a mean temperature of 7.8 °C and total precipitation of 1,002 mm during 2019. The national park area is mostly forested (98%). Valley areas (650–900 m) dominated by spruce (*Picea abies*) make up 16% of the national park (van der Knaap et al., 2020). Intermediate slopes (900–1150 m) cover most of the area (68%), comprising mixed mountain forest dominated by beech (*Fagus sylvatica*), fir (*Abies alba*) and spruce. The remaining 16% belong to high altitude areas (1150–1350 m), characterised by spruce, rowan (*Sorbus aucuparia*) and sycamore maple (*Acer pseudoplatanus*) (Cailleret et al., 2014).

Large mammals like red deer, roe deer and wild boar are common in the national park. Less abundant inhabitants of the national park area include the European wildcat (*Felis silvestris*) (Beutel et al., 2017), Eurasian otter (*Lutra lutra*) (Martin et al., 2017) and Eurasian beaver (*Castor fibre*) (Orazi et al., 2022). After extirpation in the 19th century, two large carnivores have since returned. Eurasian lynx (*Lynx lynx*) returned after reintroductions during the 1970s and 1980s (Bufka & Cerveny, 1996; Palmero et al., 2021) and wolf (*Canis lupus*) returned naturally in 2015, with reproduction confirmed in 2017 (Hulva et al., 2018).

### Study design

We collected the data during a period of 18 months, from June 2018 until December 2019, with a design focussed on carcass types. During this period, a total of 44 carcasses, 22 (summer = 15, winter = 7) fox, 12 (summer = 11, winter = 1) roe deer, and 10 (summer = 4, winter = 5) red deer, were placed at various sites across the national park (Fig. 1, Appendix A: Methods 1). The mean carcass weight for carnivore carcasses was 6.2 kg, while the mean carcass weight for herbivore carcasses was 36.0 kg. Each site was used only once for carcass deployment. The sites were selected based on aerial images and visual inspection. Target habitats comprised intermediate vegetation cover (horizontal and vertical visibility of 50%) in mixed montane forests, with a distance of 1–1.5 km from trails. The minimum distance between simultaneous carcasses was 0.53 km with a median distance of 4.9 km, while the minimum distance between simultaneous carcasses of the same type was 18.3 km with a median of 18.5 km. The same person selected all deployment locations to ensure homogeneity in estimating vegetation coverage and composition. Carcass mortality causes were mainly road accidents and hunting (lead-free ammunition). We weighed the carcasses before deployment. The hind limbs of the carcasses were fixed with a cable tie to a wooden stake. The deployed carcasses were subsequently monitored for 29 days, based on previously observed carrion depletion times (Ray et al., 2014; Stiegler et al., 2020). Camera traps were mounted at a tree at 2 to 3 m distance with an approximate height of 60 cm. Automatic "Reconyx Hyperfire HC600" and "Reconyx Ultrafire XR6 Covert" cameras with infrared flash and set to 'rapid fire mode' were used, resulting in a series of 3 images each time the camera was triggered.



**Fig. 1.** Location and elevational gradient (Jarvis et al., 2008) of the study area in the Bavarian Forest National Park, Germany (DE) bordering Czechia (CZ), including sites where carnivore (fox) and herbivore (red and roe deer) carcasses were deployed, meteorological stations (temperature and precipitation data), primary and secondary roads, and major rivers (© OpenStreetMap).

#### Data preparation

From camera trap images, we identified carcass visitors with the species name, number of individuals, and image capture time. For the data analysis, images were grouped into independent events, delineated by consecutive images of different species or when consecutive images of the same species were separated by more than 30 min Li et al. (2010). Scavenger species can use carcasses for various forage resources, including the carcass itself or e.g., collecting other animal prey (Morino-Opo & Margalida, 2013). Therefore, in the analyzes all scavenging species (i.e. non-herbivore visitors) that occurred directly at a given carcass, independent of whether they utilised the carcass itself, were considered carcass visitors and, therefore, a part of the scavenging community. The visitation rate of a carcass was defined as the number of events of all scavenger species at that carcass, or for each species individually in community analyzes. To investigate whether fox behaviors differed at herbivore and conspecific carcasses, and to detect cannibalism, independent events where it could be confirmed that a fox removed tissue from the carcass were classified as “consumption” events, and as “non-consumption” events when it could not be confirmed. We did not identify the amount of carcass tissue that foxes

consumed.

Rare species, or infrequent carcass visitors, are sometimes believed to cause problems in multivariate methods and, therefore, removed (e.g., Brazner & Beals 1997). However, this can result in biased estimates (Cao et al., 1998). To overcome these issues, species with insufficient events to estimate species group compositional differences and find ordinations with adequate ‘stress’ levels were grouped with similar species until adequate stress was achieved (see *statistical analysis*). Therefore, we considered the following species groups for compositional analyzes: birds of prey, corvids, other birds, martens, Eurasian lynx, Eurasian red squirrel (*Sciurus vulgaris*), European badger (*Meles meles*), fox and wild boar (Appendix A: Table 3). Mice were excluded, as the camera trap setup was not optimised for detecting these species (De Bondi et al., 2010).

#### Explanatory variables

To compare visitation rate and species composition at deployed carcasses, our focal covariate was carcass type. We included the covariates carcass weight, elevation, mean temperature, sum precipitation, and scavenging seasonality as potentially confounding variables

**Table 1**

Overview of the explanatory variables and their characteristics used for multivariate analysis.

Predictor variable	Range
Carcass type	<i>V. vulpes</i> , <i>Capreolus capreolus</i> , <i>Cervus elaphus</i>
Carcass weight (kg)	5–110
Temperature (mean during sampling period; °C)	0.4–18.5
Precipitation (sum during sampling period; mm)	7–67
Elevation (above sea level; m)	656–1169
Scavenging seasonality (see Appendix A: Methods 2)	0.74–8.03

(Table 1). The mean temperature (°C) and sum precipitation (mm) during each 29-day sampling period were taken from meteorological stations ( $n = 8$ ) in the national park (Fig. 1). Elevation was obtained from the Shuttle Radar Topography Mission dataset (Jarvis et al., 2008) using the package ‘raster’ (Hijmans, 2019). As seasonality is known to affect scavenging in the study area (Stiegler et al., 2020), which would represent a confounding variable, we created an index of scavenging seasonality based on the temporal distribution of visits to carnivore and herbivore carcasses (Appendix A: Methods 2 and Fig. 1).

### Statistical analysis

Analyses were conducted using the statistical software R 3.5.1 (R Core Team, 2013). We assessed our predictions concerning visitation rate at herbivore and carnivore carcasses by applying negative binomial generalised linear models (GLMs), using the package ‘MASS’ (Venables et al., 2002). This distribution is appropriate for modelling over-dispersed count data (Long, 1997). We checked for non-linearity using polynomial terms and used ANOVA hypothesis tests to retain the simplest supported model (James et al., 2013). The supported model had a quadratic term for carcass weight and omitted temperature and precipitation covariates (Appendix A: Tables 4 and 5). To avoid problematic collinearity, we computed generalised variance inflation factors (GVIFs; Fox & Monette, 1992) of the covariates in models with an upper threshold of 5 (James et al., 2013) using the package ‘car’ (Fox & Weisberg, 2018) and found no potentially problematic collinearity among the covariates (Appendix A: Table 6).

We performed nonmetric multidimensional scaling (NMDS) to visualise scavenger group compositions using the ‘vegan’ package (Oksanen et al., 2019). We calculated the Bray-Curtis dissimilarity matrix using specific visitation rates (i.e. number of events per group and carcass) to quantify the compositional dissimilarity among different carcass locations (Driscoll et al., 2017). The number of dimensions was selected via scree plot, using the package ‘goeveg’ (Goral & Schellenberg, 2018), taking the lowest value with a stress value  $\leq 0.1$ . (Buttigieg & Ramette, 2014). We used analysis of similarity (ANOSIM) to check for differences in the species group compositions between carcass types. Mantel tests were used to assess whether the continuous variables correlated with species composition. Specifically, we calculated Euclidean distance matrices for each environmental variable and compared these to the species group composition Bray-Curtis dissimilarity matrix using the Spearman correlation method for non-parametric compliance (Legendre & Legendre, 1998).

An indicator species analysis was conducted, using the package ‘indispecies’ (De Cáceres & Legendre, 2009), to identify which species corresponded most to dissimilarities in species group compositions found among different carcass types. An indicator species represents the most characteristic species for a carcass type, found mainly at sites of one carcass type and at most of the sites of this carcass type (Dufrene & Legendre, 1997).

To further elucidate differences in consumption dynamics between carcass types (carnivore/herbivore), we analyzed the temporal relationship between a) carcass type and visitation rate of all species, and b) carcass type and behavior of fox. We structured the dataset according to time-to-event (i.e., survival or failure time) analysis. Each carcass entered the risk set when it was placed, this was defined as the origin time ( $t = 0$ ). Visitation event times were calculated as the number of days since placement. All carcasses were “censored” (i.e., no longer in the risk set) after 30 days to indicate that no more visitation events could be observed. Using the package ‘reda’ (Wang et al., 2022), we computed the Mean Cumulative Functions (MCFs) of the events corresponding to the groups of (a) and (b), and compared the MCFs using the constant and linear weight tests of Cook et al. (1996). We visualised the MCFs for the whole dataset and divided it by seasons to see if there were observable differences. Further, we compared the visitation and consumption behavior of fox at different carcass types with zero-inflated negative

binomial GLMs fitted using the package ‘glmmdmb’ (Fournier et al., 2012), as it is appropriate for over-dispersed count data with numerous zeros (Long, 1997). We initially used the same covariates in this GLM as those chosen for the GLM to compare visitation rates of all species at herbivore and carnivore carcasses. Elevation caused potentially problematic collinearity in the model of fox consumption rates (GVIF = 5.16, Appendix A: Table 7); therefore, the GLM was subsequently fitted with the variable omitted. Removal of elevation rendered all remaining estimates non-significant, but the coefficients were qualitatively similar (Appendix A: Table 8).

### Results

A total of 319 independent events occurred across all carcasses during 1276 trap days and nights, with a mean of 6.7 events per site at carnivore carcasses and a mean of 10 events per site at herbivore carcasses (Appendix A: Fig. 2). Visitation rates did not differ significantly between different carcass types (Table 2), which was reflected in the effect plot (Fig. 2A). Visitation rates increased with carcass weight up to 50 kg before declining (Fig. 2B). Visitation rates also had positive relationships with elevation and seasonality (Fig. 2C and D), though the latter was known a priori (Appendix A: Fig. 1).

A total of 15 scavenger species, pooled into 9 groups, were detected at all carcasses (Appendix A: Table 3). The highest visitation rate was from fox (37% of all events) followed by wild boar (22% of all events – Appendix A: Fig. 3). The group compositions were not significantly different at herbivore and carnivore carcasses according to NMDS analysis (stress = 0.098, ANOSIM  $R = -0.018$ ,  $p = 0.69$ , Appendix A: Fig. 4A). Increases in the confounding variables elevation (Mantel  $r = 0.11$ ,  $p = 0.02$ ) and precipitation (Mantel  $r = 0.25$ ,  $p = 0.001$ ) were correlated with communities with higher species abundances (Appendix A: Table 9). We did not identify any indicator species that were characteristic of group compositions at carnivore or herbivore carcasses (all  $p > 0.1$  – Appendix A: Table 10). As such, there was no statistical difference in composition of visitors at carnivore and herbivore carcasses.

The temporal distribution of all species’ visitation events did not differ significantly between carnivore and herbivore carcasses (Table 3A, Fig. 3A). The onset of consumption behavior by foxes appeared to be earlier at fox carcasses compared to herbivore carcasses (Fig. 3C). This impression remained when the dataset was divided into the two main seasonal periods (Appendix A: Fig. 5). However, there were no significant differences in the temporality of fox behavior (non-consumption and consumption) between the different carcass types (Table 3B).

Fox consumption behavior was observed at 27% of fox carcasses (visitation of 41%) and 27% of herbivore carcasses (visitation of 54%). Based on separate GLMs for visitation and consumption behaviors of fox (Appendix A: Tables 11 and 12), we found fox visitation rates did not differ significantly between different carcass types (est = -0.99,  $\pm$ SE = 1.46,  $z = -0.67$ ,  $p = 0.50$ ) but their consumption rate was significantly lower at herbivore carcasses compared to fox carcasses (est = -7.37,  $\pm$ SE

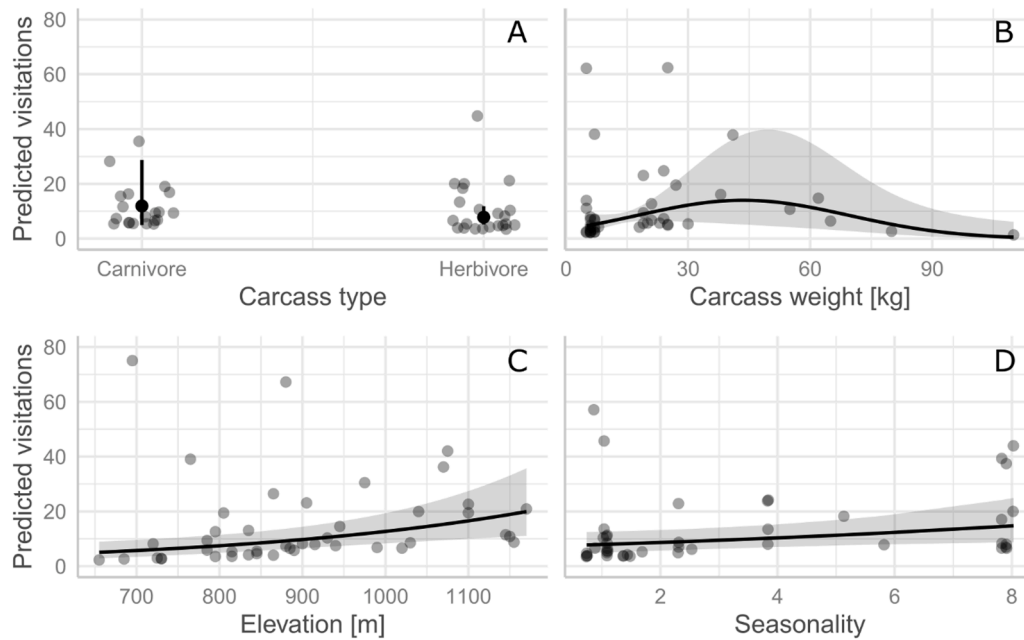
**Table 2**

Summary of negative binomial GLM for visitation rate of all species at herbivore and carnivore carcasses. The estimates, standard errors (SE), Z values and p-values ( $\Pr(>|z|)$ ) are shown for the covariates of the model (predicted response shown in Fig. 2).

Covariates	Estimate	$\pm$ SE	Z value	$\Pr(> z )$
(Intercept)	-0.55	0.78	-0.70	0.48
Carcass type (Herbivore)	-0.42	0.56	-0.76	0.45
Seasonality	0.088	0.043	2.069	0.039
poly(Weight, 2) 1 <sup>a</sup>	-0.28	1.42	-0.20	0.84
poly(Weight, 2) 2 <sup>b</sup>	-3.57	1.73	-2.068	0.039
Elevation (m)	0.0027	0.00081	3.27	0.0012

<sup>a</sup> poly(Weight, 2) 1 - first component of quadratic term.

<sup>b</sup> poly(Weight, 2) 2 - second component of quadratic term.



**Fig. 2.** Predicted visitation rate (i.e., number of visits per carcass) based on: (A) carcass type, (B) carcass weight, (C) elevation, and (D) scavenging seasonality via negative binomial GLM. Black lines indicate estimate and shaded regions the 95% CI, points are the partial residuals.

**Table 3**

Group difference tests of Mean Cumulative Functions based on (A) recurrent visitation events by all species, and (B) behaviourally specific (non-consumption vs. consumption) recurrent visitation events of fox, at herbivore and fox carcasses.

Grouping	Carcasses/behaviour	Weight	Statistic	Variance	$\chi^2$ ( $df = 1$ )	$p$
(A) All species	Herbivore vs. fox	Constant	37.50	984.15	1.43	0.23
		Linear	7.31	132.39	0.40	0.53
(B) Fox behaviour	Fox non-consumption vs. fox consumption	Constant	2.00	52.34	0.08	0.78
		Linear	1.61	7.85	0.33	0.57
	Fox non-consumption vs. herbivore consumption	Constant	1.00	63.16	0.02	0.90
		Linear	2.44	6.16	0.97	0.33
	Fox non-consumption vs. herbivore non-consumption	Constant	-4.50	65.28	0.31	0.58
		Linear	-1.79	12.68	0.25	0.62
	Fox consumption vs. herbivore consumption	Constant	-1.00	77.11	0.01	0.91
		Linear	0.83	7.46	0.09	0.76
	Fox consumption vs. herbivore non-consumption	Constant	-6.50	79.24	0.53	0.47
		Linear	-3.40	13.98	0.82	0.36
	Herbivore consumption vs. herbivore non-consumption	Constant	-5.50	90.06	0.34	0.56
		Linear	-4.23	12.30	1.45	0.23

= 1.97,  $z = -3.74$ ,  $p = 0.001$ ).

## Discussion

Our study provided the first insights into species community and fox behaviors at herbivore and carnivore carcasses in a montane temperate forest ecosystem. The results did not show any strong differences in visitation of carnivore and herbivore carcasses by scavenger species, as the visitation rates of all species and the species compositions of visitors were not significantly different at herbivore and carnivore carcasses. When considering only fox visitation rates we found the same result as for all species, however, there was an indication that the consumption rates of foxes were higher at conspecific carcasses than herbivore carcasses. Indeed, we found fox cannibalism was common, occurring at two-thirds of fox carcasses visited by foxes. The temporal differences between visitation rates of all species at herbivore and carnivore carcasses were not significant, and despite the visual impression, the temporality of fox behaviors (consumption vs. non-consumption) at herbivore and conspecific carcasses also did not differ significantly. Our results show that carnivore carcasses may influence disease transmission

pathways in this temperate montane ecosystem, at minimum due to the fox cannibalism we observed.

We found no substantial influence of carcass type on visitation rates, species group composition, or temporality of visits. This is similar to previous works with respect to species richness and detection time, such as [Oliva-Vidal et al. \(2022\)](#) and partially [Moleón et al. \(2017\)](#), when comparing results on carrion visits. However, we could not make inferences on the consumption patterns of the entire scavenging community because, apart from fox, we only analyzed their visitation rates. When consumption behavior of all visitors has been analyzed, for incomplete carcasses, the species richness of consumers was higher at herbivore than carnivore carcasses ([Moleón et al., 2017](#)). Also, for complete carcasses, the consumption time and depletion rate of herbivore carrion was greater than carnivore carrion ([Oliva-Vidal et al., 2022](#)). This indicates that the visiting community differs from the consuming community, with stronger differences observed in consumption behavior, or contact, and more subtle differences for visitation behavior ([Moleón et al., 2017](#)). At least for fox we detected no such differences between their non-consumption and consumption visits of herbivore and carnivore carcasses.

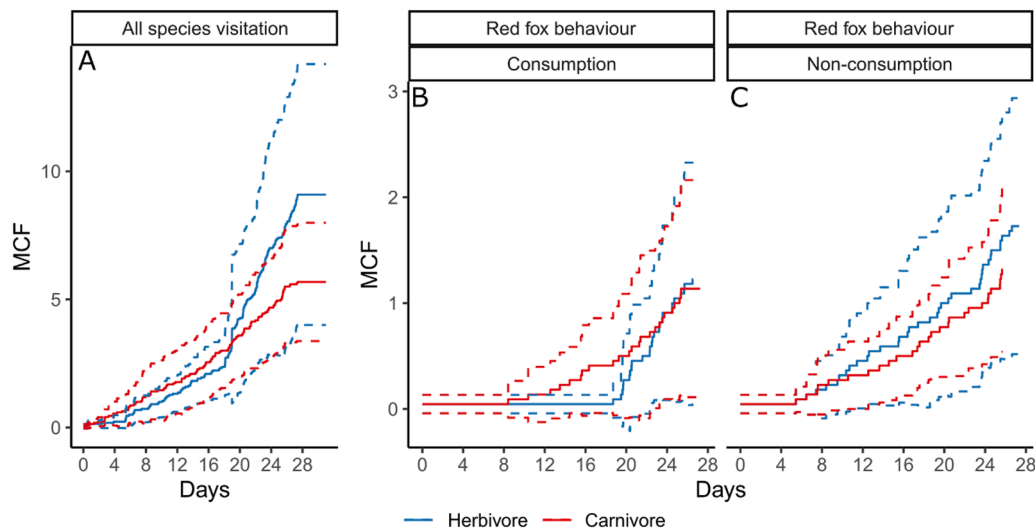


Fig. 3. Mean Cumulative Functions (MCFs – solid lines, 95% CI – dashed lines) of recurrent events at herbivore and fox carcasses, for (A) all species visitation, and (B) consumption and (C) non-consumption behaviour of fox during visitation events.

When accounting for confounding factors, we found foxes did not avoid visiting deceased conspecifics more strongly than heterospecifics and the consumption of conspecifics was predicted to be higher than herbivore carrion. At first glance, this appears to contrast with some studies. For example, the only vertebrate scavenger observed feeding on fox carcasses deployed by Muñoz-Lozano et al. (2019) was golden eagle (*Aquila chrysaetos*), otherwise, fox carcasses went untouched by other visitors. Further, Moleón et al. (2017) observed greater consumption of herbivore biomass, and by more species, than that of carnivore biomass. Although we considered only the consumption behavior of fox, and cannot compare the richness of the consuming community, in clear contrast to our study they observed no conspecific consumption of fox. However, Moleón et al. (2017) deployed only portions of the thoracic area and proximal sections of the extremities without skin, whereas we placed complete carcasses. In a later study with complete carcasses, the authors did observe cannibalism, which could indicate the importance of placing carcasses as they would occur naturally, although this depended on the carcass decomposition state and was still lower than heterospecific consumption (González et al., 2021).

In our study, fox fed on conspecifics at two-thirds of the carcasses they were observed. Fox cannibalism was also reported by González et al. (2021) and Oliva-Vidal et al. (2021), though the avoidance of consuming conspecifics, or preference for heterospecifics, was apparent in the quantity or timing of consumption they observed. A temporal delay between the consumption of heterospecific and conspecific carrion could indicate avoidance of certain states of conspecific decomposition, which might be associated with parasite potency. Our study detected no significant temporal differences between when foxes visited or consumed herbivore and conspecific carrion. Although not significant, visually we recorded a tendency for foxes to consume conspecific carrion sooner than herbivore carrion. However, the studies of González et al. (2021) and Oliva-Vidal et al. (2021), both found a delay in the consumption of conspecifics compared to heterospecifics. Varying levels of avoidance, and therefore different scavenger guilds and behaviors, could emerge due to ecosystem differences, such as parasitic loads, co-evolutionary histories, or abiotic characteristics. Specifically, a high risk of disease or parasite transmission might cause scavengers to evolve an aversion to cannibalism (Moleón et al., 2017) or a decomposition-state dependant consumption of conspecifics tuned to the local host-parasite that maximises nutrition while minimising transmission risk (González et al., 2021), the latter of which might be the case in our study.

Cannibalism can be beneficial during resource scarcity and because phylogenetically similar prey can provide nutritional advantages (Meffe & Crump, 1987). In our study area, one might assume the benefit of cannibalism outweighed the risk of disease transmission, due to low disease rates in foxes, the resource scarcity in this mountainous ecosystem, or a combination of these. This mirrors another temperate montane region, where Oliva-Vidal et al. (2021) found fox cannibalism at all carcasses ( $n = 6$ ) and rapid consumption of two of these. The drivers of cannibalism may vary among carrion studies, and it is unlikely that resource scarcity and disease risk are the only factors (Fox, 1975). Besides fox, wild boar is one of the most common scavengers in Europe and as for fox, they have also exhibited a range of behaviors towards dead conspecifics, from scavenging avoidance (Selva et al., 2005) to active consumption (Cukor et al., 2020; Oliva-Vidal et al., 2022). These differences between and within species show that many local factors can drive scavenging behavior. This discussion highlights the need for more in-depth research into vertebrate scavenging patterns on conspecifics and carnivore carcasses across ecological gradients, ideally with larger sampling schemes. Particularly a close investigation of disease and parasite transmission pathways, both present and historical, in the ecosystems concerned would help to deepen the understanding of the cannibalistic behavior observed.

Most fox carcasses deployed in this study originated from hunting. These could have conceivably had a lower incidence rate of potentially dangerous diseases, which may cause avoidance behavior, compared to natural mortality events (Hart, 1990; Huang et al., 2014). A study in Norway found diseased reindeer calves were not eaten by scavengers, while healthy calves were consumed at similar places, thereby showing the ability of scavengers to distinguish between safe and dangerous food resources (Mysterud et al., 1993). However, shot foxes should represent a random sample from a population, and hence the population's health. Furthermore, securing carcasses of diseased animals is unlikely without extreme search effort. Nevertheless, the regular visitation and consumption of fox at conspecific carcasses remains an important result because it shows that both carnivore and herbivore carcasses are resource hotspots for vertebrates and potential locations of disease transfer.

Our results seem inconclusive regarding avoidance behaviors, or lack thereof, which could be connected to the study's limitations. First, based on our camera trap images we could only confirm consumption behavior for fox, but not the amount. This meant we could only analyze the full community patterns in terms of visits and not consumption, which as

mentioned could differ (e.g., Moleón et al. 2017; Oliva-Vidal et al. 2022). To better understand the differences in visitation due to carcass type it would be informative to consider visitors' approach distances and visit durations, however we did not have the data to support these parameters. Second, although we placed carcasses throughout the year, we did not directly analyze the effect of seasons. We knew from prior work (Stiegler et al., 2020) that season affects scavenging communities, which could derive from, e.g., different food requirements or physiological constraints (Selva et al., 2005). For this reason, we ensured a balanced sample of carcass types and months and, when possible, accounted for season using confounding covariates. However, this was not possible in all analyzes, which resulted in seasonally averaged responses. It would have been more insightful to analyze the different seasons explicitly to elucidate the differences, but we would have drastically reduced the power of the dataset. Third, carcass weight plays a role in scavenging patterns (e.g., Turner et al. 2017) and, as such, has a confounding effect when trying to understand the influence of carcass type. This can be confronted practically using partial carcasses (e.g., Moleón et al. 2017), or similar-sized herbivore and carnivore carcasses (Oliva-Vidal et al., 2022). However, a near-natural and ecosystem-specific experimental design (e.g., complete carcasses, locally appropriate carrion species) is difficult to achieve without a weight disparity between carnivore and herbivore carrion. We included carcass weight in some analyzes but did not have the power to consider this in composition or temporal analyzes. The lack of difference between fox and herbivore carcasses suggests that weight did not strongly affect species composition based on visits, similar to Oliva-Vidal et al. (2022), nor the behavior of red fox (consumption and non-consumption). We know from previous studies that carcass size is an important factor in how carrion is consumed (e.g., Moleón et al. 2015), therefore we interpret our result cautiously due to our limitations. We also found that weight increased visitation rate (all species), and consumption rate (fox behavior only), although the rates declined for the heaviest carcasses. The decline is likely an artefact caused by a small sample of heavier carcasses and, by chance, a low detection rate of these particular carcasses by scavengers. Finally, we classified fox behavior based on still images, which could have led to erroneous classifications. We were conservative when classifying the images to avoid false-positives (in terms of consumption) and overestimating cannibalism. In the future, most of these limitations could be alleviated by a larger sample and video camera trapping (e.g., behavior classification and visit duration). Still, these results provide an important first impression of the effects of carcass type on scavengers within this specific ecosystem and as a foundation for further study.

## Conclusion

In this study we explored the patterns of facultative vertebrate scavenger assemblages based on visits of all species and behavior of foxes at carnivore and herbivore carcasses, thereby giving a first impression of the potential direct and indirect disease transmission pathways in this temperate mountainous ecosystem with relatively low human disturbances. We found that carcass type, i.e. herbivore or carnivore, did not significantly influence the visiting species composition, all species' visitation rates, the temporal distribution of visits from all species, or the temporal distribution of fox behaviors (non-consumption vs. consumption). Although we could not quantify feeding duration or amount, we can state that foxes did not categorically avoid cannibalism. The ubiquitous occurrence and behavior of fox in our results, and wild boar as seen in other studies (e.g., Oliva-Vidal et al. 2022), makes them possible transmission agents, which should be recognised in areas affected by wildlife diseases. Our results also show that avoidance behaviors may not always be strongly observable, especially based on visits only. Given this, it would be crucial to conduct further work that examines scavenging patterns at wild boar and fox carcasses in similar ecosystems with larger sampling schemes, video capture, and investigation of disease prevalence. This would help clarify

recommendations for wildlife management and epidemiology, especially in the context of potential African Swine Fever outbreaks.

Our results add to the evidence that local conditions are important for behavioral responses such as cannibalism. This evidence, particularly for fox (González et al., 2021; Moleón et al., 2017; Oliva-Vidal et al., 2021), calls for research that considers carrion utilisation across a gradient of resource availability to delineate the risk-reward paradigm for scavengers.

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## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2024.03.002.

## References

- Arrondo, E., Guido, J., Oliva-Vidal, P., Margalida, A., Lambertucci, S. A., Donazar, J. A., et al. (2023). From pyrenees to andes: The relationship between transhumant livestock and vultures. *Biological Conservation*, 283, Article 110081.
- Benbow, M. E., Barton, P. S., Ulyshen, M. D., Beasley, J. C., DeVault, T. L., Strickland, M. S., et al. (2019). Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. *Ecological Monographs*, 89(1), e01331.
- Beutel, T., Reineking, B., Tiesmeyer, A., Nowak, C., & Heurich, M. (2017). Spatial patterns of co-occurrence of the European wildcat *Felis silvestris silvestris* and domestic cats *Felis silvestris catus* in the Bavarian Forest National Park. *Wildlife Biology*, 2017(4).
- Brazner, J. C., & Beals, E. W. (1997). Patterns in fish assemblages from coastal wetland and beach habitats in Green Bay, Lake Michigan: A multivariate analysis of abiotic and biotic forcing factors. *Canadian Journal of Fisheries and Aquatic Sciences*, 54(8), 1743–1761.
- Brown, C. M. (2011). Compendium of animal rabies prevention and control, 2011: National association of state public health veterinarians, Inc. NASPHV (Report No. 6, pp. 1–14). *Centers for Disease Control and Prevention MMWR*. <https://www.cdc.gov/mmwr/pdf/rr/r66006.pdf>.
- Bufka, L., & Cerveny, J. (1996). The lynx (*Lynx lynx* L.) in the Sumava region, southwest Bohemia. *Journal of Wildlife Research*, 1, 167–170.
- Buttigieg, P. L., & Ramette, A. (2014). A guide to statistical analysis in microbial ecology: A community-focused, living review of multivariate data analyses. *FEMS Microbiology Ecology*, 90(3), 543–550.
- Cailleret, M., Heurich, M., & Bugmann, H. (2014). Reduction in browsing intensity may not compensate climate change effects on tree species composition in the Bavarian Forest National Park. *Forest Ecology and Management*, 328, 179–192.
- Cao, Y., Williams, D. D., & Williams, N. E. (1998). How important are rare species in aquatic community ecology and bioassessment? *Limnology and Oceanography*, 43(7), 1403–1409.
- Carrasco-García, R., Barroso, P., Perez-Olivares, J., Montoro, V., & Vicente, J. (2018). Consumption of big game remains by scavengers: A potential risk as regards disease transmission in central Spain. *Frontiers in Veterinary Science*, 5, 4.
- Chapron, G., Kaczensky, P., Linnell, J. D., von Arx, M., Huber, D., Andrén, H., et al. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346(6216), 1517–1519 (New York, N.Y.).
- Cliquet, F., Picard-Meyer, E., & Robardet, E. (2014). Rabies in Europe: What are the risks? *Expert Review of Anti-Infective Therapy*, 12(8), 905–908.
- Cook, R. J., Lawless, J. F., & Nadeau, C. (1996). Robust tests for treatment comparisons based on recurrent event responses. *Biometrics*, 557–571.
- Cukor, J., Linda, R., Václavěk, P., Mahlerová, K., Šatrán, P., & Havránek, F. (2020). Confirmed cannibalism in wild boar and its possible role in African swine fever transmission. *Transboundary and Emerging Diseases*, 67(3), 1068–1073.
- De Bondi, N., White, J. G., Stevens, M., & Cooke, R. (2010). A comparison of the effectiveness of camera trapping and live trapping for sampling terrestrial small-mammal communities. *Wildlife Research*, 37(6), 456–465.
- De Cáceres, M., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, 90(12), 3566–3574.

- DeVault, T. L., Olson, Z. H., Beasley, J. C., & Rhodes, O. E. (2011). Mesopredators dominate competition for carrion in an agricultural landscape. *Basic and Applied Ecology*, 12(3), 268–274.
- Driscoll, K., Lacey, M., & Greathouse, J. (2017). Use of camera trapping to determine spatial distribution, habitat use, and environmental factors affecting mesopredators on reclaimed mine lands at the wilds. *Journal American Society of Mining and Reclamation*, 6(1), 15–33.
- Dufrene, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological monographs*, 67(3), 345–366.
- Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N., et al. (2012). AD model builder: Using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, 27(2), 233–249.
- Fox, L. R. (1975). Cannibalism in natural populations. *Annual Review of Ecology and Systematics*, 6(1), 87–106.
- Fox, J., & Monette, G. (1992). Generalized collinearity diagnostics. *Journal of the American Statistical Association*, 87(417), 178–183.
- Fox, J., & Weisberg, S. (2018). *An R companion to applied regression*. Sage Publications.
- Frölich, K., Czupalla, O., Haas, L., Hentschke, J., Dedek, J., & Fickel, J. (2000). Epizootiological investigations of canine distemper virus in free-ranging carnivores from Germany. *Veterinary Microbiology*, 74(4), 283–292.
- González, M., Martínez-Carrasco, C., Sánchez-Zapata, J. A., & Moleón, M. (2021). Smart carnivores think twice: Red fox delays scavenging on conspecific carcasses to reduce parasite risk. *Applied Animal Behaviour Science*, 243, Article 105462.
- Goral, F., & Schellenberg, J. (2018). *Functions for community data and ordinations*. R package version 0.4.2.. <https://cran.r-project.org/web/packages/goevge/goevge.pdf>
- Hart, B. L. (1990). Behavioral adaptations to pathogens and parasites: Five strategies. *Neuroscience & Biobehavioral Reviews*, 14(3), 273–294.
- Hijmans, R.J. (2019) Raster: Geographic data analysis and modeling <https://CRAN.R-project.org/package=raster> (20 June 2019).
- Huang, S., Bininda-Emonds, O. R., Stephens, P. R., Gittleman, J. L., & Altizer, S. (2014). Phylogenetically related and ecologically similar carnivores harbour similar parasite assemblages. *Journal of Animal Ecology*, 83(3), 671–680.
- Hulva, P., Černá Bolfíková, B., Woznicová, V., Jindřichová, M., Benešová, M., Myslajek, R. W., et al. (2018). Wolves at the crossroad: Fission–fusion range biogeography in the Western Carpathians and Central Europe. *Diversity and Distributions*, 24(2), 179–192.
- James, G., Witten, D., Hastie, T., & Tibshirani, R. (2013). *An introduction to statistical learning*. 112 p. 18). New York: Springer.
- Jarvis, A., Guevara, E., Reuter, H.I., & Nelson, A.D. (2008) Hole-filled SRTM for the globe: Version 4: Data grid. <http://srtm.csi.cgiar.org/>.
- Legendre, P., & Legendre, L. (1998). *Numerical ecology* (2nd ed., pp. 205–209). Elsevier.
- Li, S., McShea, W.J., Wang, D., Shao, L., & Shi, X. (2010). The use of infrared-triggered cameras for surveying phasianids in Sichuan Province, China *Ibis*, 152(2), 299–309.
- Long, J. S. (1997). Regression models for categorical and limited dependent variables. Berk, R (1997) (Eds.). In *Advanced quantitative techniques in the social sciences*, 219, 7. London: Sage Publications.
- Margalida, A., Donazar, J. A., Carrete, M., & Sánchez-Zapata, J. A. (2010). Sanitary versus environmental policies: Fitting together two pieces of the puzzle of European vulture conservation. *Journal of Applied Ecology*, 47(4), 931–935.
- Martin, E. A., Heurich, M., Müller, J., Bufka, L., Bublly, O., & Fickel, J. (2017). Genetic variability and size estimates of the Eurasian otter (*Lutra lutra*) population in the bohemian Forest ecosystem. *Mammalian Biology-Zeitschrift für Säugetierkunde*, 86, 42–47.
- Meffe, G. K., & Crump, M. L. (1987). Possible growth and reproductive benefits of cannibalism in the mosquitofish. *The American Naturalist*, 129(2), 203–212.
- Moleón, M., Sánchez-Zapata, J. A., Sebastián-González, E., & Owen-Smith, N. (2015). Carcass size shapes the structure and functioning of an African scavenging assemblage. *Oikos*, 124(10), 1391–1403 (Copenhagen, Denmark).
- Moleón, M., Martínez-Carrasco, C., Muellerklein, O. C., Getz, W. M., Muñoz-Lozano, C., & Sánchez-Zapata, J. A. (2017). Carnivore carcasses are avoided by carnivores. *Journal of Animal Ecology*, 86(5), 1179–1191.
- Moreno-Opo, R., & Margalida, A. (2013). Carcasses provide resources not exclusively to scavengers: Patterns of carrion exploitation by passerine birds. *Ecosphere*, 4(8), 1–15 (Washington, D.C).
- Moreno-Opo, R., Trujillano, A., Arredondo, Á., González, L. M., & Margalida, A. (2015). Manipulating size, amount and appearance of food inputs to optimize supplementary feeding programs for European vultures. *Biological Conservation*, 181, 27–35.
- Muñoz-Lozano, C., Martín-Vega, D., Martínez-Carrasco, C., Sánchez-Zapata, J. A., Morales-Reyes, Z., González, M., et al. (2019). Avoidance of carnivore carcasses by vertebrate scavengers enables colonization by a diverse community of carrion insects. *PLoS One*, 14(8), Article e0221890.
- Mysterud, I., Mysterud, I., & Wikan, S. (1993). Wolf and foxes reject diseased reindeer calf. *Fauna Norvegica Series A*, 14, 57–58.
- Newsome, T. M., Barton, B., Buck, J. C., DeBruyn, J., Spencer, E., Ripple, W. J., et al. (2021). Monitoring the dead as an ecosystem indicator. *Ecology and Evolution*, 11 (11), 5844–5856.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., et al. (2019). *vegan: Community ecology package*. R Package Version, 2.5-6 <https://CRAN.R-project.org/package=vegan>.
- Oliva-Vidal, P., Tobajas, J., & Margalida, A. (2021). Cannibalistic necrophagy in red foxes: Do the nutritional benefits offset the potential costs of disease transmission? *Mammalian Biology*, 101(6), 1115–1120.
- Oliva-Vidal, P., Sebastián-González, E., & Margalida, A. (2022). Scavenging in changing environments: Woody encroachment shapes rural scavenger assemblages in Europe. *Oikos*, 2022(12), e09310 (Copenhagen, Denmark).
- Orazi, V., Hagge, J., Gossner, M. M., Müller, J., & Heurich, M. (2022). A biodiversity boost from the Eurasian beaver (*Castor fiber*) in Germany’s oldest national park. *Frontiers in Ecology and Evolution*, 10.
- Palmero, S., Belotti, E., Bufka, L., Gahbauer, M., Heibl, C., Premier, J., et al. (2021). Demography of a Eurasian lynx (*Lynx lynx*) population within a strictly protected area in Central Europe. *Scientific Reports*, 11(1), 19868.
- Pisano, S. R. R., Zimmermann, F., Rossi, L., Capt, S., Akdesir, E., Bürki, R., et al. (2019). Spatiotemporal spread of sarcoptic mange in the red fox (*Vulpes vulpes*) in Switzerland over more than 60 years: Lessons learnt from comparative analysis of multiple surveillance tools. *Parasites & vectors*, 12(1), 1–16.
- Pozio, E. (2000). Factors affecting the flow among domestic, synanthropic and sylvatic cycles of Trichinella. *Veterinary Parasitology*, 93(3–4), 241–262.
- R Core Team. (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Ray, R. R., Seibold, H., & Heurich, M. (2014). Invertebrates outcompete vertebrate facultative scavengers in simulated lynx kills in the Bavarian Forest National Park, Germany. *Animal Biodiversity and Conservation*, 37(1), 77–88.
- Sebastián-González, E., Morales-Reyes, Z., Botella, F., Naves-Alegre, L., Pérez-García, J. M., Mateo-Tomás, P., et al. (2021). Functional traits driving species role in the structure of terrestrial vertebrate scavenger networks. *Ecology*, 102(12), e03519.
- Selva, N., Jędrzejewska, B., Jędrzejewski, W., & Wajrak, A. (2005). Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Canadian Journal of Zoology*, 83(12), 1590–1601.
- Stiegler, J., von Hoermann, C., Müller, J., Benbow, M. E., & Heurich, M. (2020). Carcass provisioning for scavenger conservation in a temperate forest ecosystem. *Ecosphere*, 11(4), e03063 (Washington, D.C).
- Turner, K. L., Abernethy, E. F., Conner, L. M., Rhodes, O. E., & Beasley, J. C. (2017). Abiotic and biotic factors modulate carrion fate and vertebrate scavenging communities. *Ecology*, 98(9), 2413–2424.
- van der Knaap, W. O., van Leeuwen, J. F., Fahse, L., Szidat, S., Studer, T., Baumann, J., et al. (2020). Vegetation and disturbance history of the Bavarian Forest National Park, Germany. *Vegetation History and Archaeobotany*, 29, 277–295.
- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with s* (4th ed.). New York: Springer.
- Vicente, J., & VerCauteren, K. (2019). The role of scavenging in disease dynamics. Carrion ecology and management. *Wildlife Research Monographs*, 2, 161–182.
- Wang, W., Fu, H., & Yan, J. (2022). *reda: Recurrent event data analysis*. R package version 0.5.4. <https://github.com/wenjiej2wang/reda>.