Jonas Stiegler | Christian von Hoermann | Jörg Müller | Mark Eric Benbow | Marco Heurich

Carcass provisioning for scavenger conservation in a temperate forest ecosystem

ECOSPHERE

Carcass provisioning for scavenger conservation in a temperate forest ecosystem

Jonas Stiegler [ID],[1],† Christian von Hoermann [ID],[2] Jörg Müller [ID],[3]
M. Eric Benbow [ID],[4,5,6] and Marco Heurich [ID][2]

[1]Department of Plant Ecology and Nature Conservation, University of Potsdam, Potsdam, Germany
[2]Department of Wildlife Ecology and Management, University of Freiburg, Freiburg, Germany
[3]Department of Animal Ecology and Tropical Biology, University of Würzburg, Würzburg, Germany
[4]Department of Entomology, Michigan State University, East Lansing, Michigan, USA
[5]Department of Osteopathic Medical Specialties, Michigan State University, East Lansing, Michigan, USA
[6]Ecology, Evolutionary Biology and Behavior Program, Michigan State University, East Lansing, Michigan, USA

Abstract. Carrion plays an essential role in shaping the structure and functioning of ecosystems and has far-reaching implications for biodiversity conservation. The change in availability and type of carcasses throughout ecosystems can involve negative effects for scavenging communities. To address this issue, there have been recent conservation management measures of carrion provision in natural systems. However, the optimal conditions under which exposing carcasses to optimize conservation outcomes are still limited. Here, we used camera traps throughout elevational and vegetational gradients to monitor the consumption of 48 deer carcasses over a study period of six years by evaluating 270,279 photographs resulting out of 15,373 trap nights. We detected 17 species visiting carcass deployments, including five endangered species. Our results show that large carcasses, the winter season, and a heterogeneous surrounding habitat enhanced the frequency of carcass visits and the species richness of scavenger assemblages. Contrary to our expectations, carcass species, condition (fresh/frozen), and provision schedule (continuous vs single exposure) did not influence scavenging frequency or diversity. The carcass visitation frequency increased with carcass mass and lower temperatures. The effect of large carcasses was especially pronounced for mesopredators and the Eurasian lynx (*Lynx lynx*). Lynx were not too influenced in its carrion acquisition by the season, but exclusively preferred remote habitats containing higher forest cover. Birds of prey, mesopredators, and top predators were also positively influenced by the visiting rate of ravens (*Corvus corax*), whereas no biotic or abiotic preferences were found for wild boars (*Sus scrofa*). This study provides evidence that any ungulate species of carrion, either in a fresh or in previously frozen condition, attracts a high diversity of scavengers especially during winter, thereby supporting earlier work that carcass provisions may support scavenger communities and endangered species.

Key words: anthropogenic food subsidies; carrion ecology; diversity; nature conservation; necrobiome; vertebrate scavenger; wildlife management.

† **E-mail:** stiegler@uni-potsdam.de

INTRODUCTION

Scavenging of animal carcasses is an important ecological process that is reported to affect 45% of food web trophic links worldwide (Wilson and Wolkovich 2011). Individual carrion has been viewed as "cadaver decomposition islands" (Carter et al. 2007) or as "ephemeral resource

patches" (Finn 2001) that create spatially distinct hotspots of biological activity through both direct and indirect interactions of many necrophagous species (Finn 2001, Barton et al. 2013*b*, Benbow et al. 2018). As a part of this necrophagous network, vertebrate scavengers provide both supporting and regulating ecosystem services through nutrient cycling and carcass removal from the landscape that mediates habitat quality (DeVault et al. 2003, Parmenter and MacMahon 2009, Benbow et al. 2015). Most available carcasses are successfully scavenged if they are found before extensive decomposition by microbes and insects occurs (Putman 1983). Depending on environmental conditions, scavenging vertebrates can account for up to 90% of the carrion biomass assimilation (Houston 1986, DeVault et al. 2011). Thus, carrion plays an important role in scavenger ecology, especially during times of the year with limited alternative food sources (Selva et al. 2003, 2005).

In attempts to support populations of scavenger species, land and wildlife managers have adopted the practice of provisioning carcasses of wild or domestic herbivores in several ecosystems (Gilbert et al. 2007, John Muir Trust 2012), exemplified by the prominent supplementary feeding stations acting as important tools for conservation and supporting avian scavengers (Cortés-Avizanda et al. 2016). Ecological experiments have shown that providing carcasses can favor the coexistence of competitors (Barton et al. 2013*a*, Benbow et al. 2018) and facilitate the formation of metacommunities in and around the resource (Leibold et al. 2004). However, the optimal frequency and conditions of carrion provision are not well understood and may be influenced by both local and regional environmental (e.g., biotic and abiotic) conditions.

Due to the rapidly expanding human footprint (Venter et al. 2016), the availability of carcasses is changing worldwide. Actual numbers are rising in certain cases, for example, through intensive animal farming or hunting (Margalida et al. 2012, Oro et al. 2013, Mateo-Tomás et al. 2015). Additionally, the successful recovery of large carnivores (Chapron et al. 2014) could also contribute to a local increase of the availability of carcasses. But owing to both the ongoing decline of top predators in most ecosystems (Prugh et al.

2009, Estes et al. 2011) and management practices such as winter feeding of ungulates like roe deer (*Capreolus capreolus*; Ossi et al. 2017) or red deer (*Cervus elaphus*; Putman and Staines 2004), the spatial and temporal availability of natural carrion resources has also decreased in many regions, having far-reaching negative consequences for scavenger communities (Wilmers et al. 2003*a*, Selva et al. 2005, Cortés-Avizanda et al. 2016). In the few instances where top predators have increased, scavenger populations and communities have benefited. For example, the reintroduction of wolves in Yellowstone National Park (USA) in 1995 led to an increase in abundance of 13 species of scavengers through the regular supply of carrion from gray wolf kills (*Canis lupus*; Wilmers et al. 2003*a,b*). Also beneficial effects of regular carcass supply are shown by Margalida et al. (2007), who found that breeding effort of the Eurasian griffon vulture (*Gyps fulvus*) and the Egyptian vulture (*Neophron percnopterus*) in Catalonia (Spain) was linked to carrion availability.

Carrion undoubtedly provides feeding opportunities for a variety of species (Cortés-Avizanda et al. 2009, 2016), but to understand its role in nature conservation, including in the reintroduction of carrion-dependent species in areas where they have become extinct, a better understanding of carcass provision conditions is needed (Fielding et al. 2014). A comparison of the general structure of scavenger communities in response to carrion provision will advance conservation efforts related to anthropogenic food subsidies to ecosystems (Oro et al. 2013). However, little is known about the effects of intentionally placed carcasses as a management tool in supporting vertebrate scavenger communities (Turner et al. 2017). For instance, how do carcass species, size, condition, and introduced habitat affect scavenger diversity and activity?

One major factor affecting vertebrate scavenging is carcass size (DeVault et al. 2003, Sebastián-González et al. 2013). In a study conducted in the South African savanna, the species richness of vertebrate scavengers and carcass consumption time and rate increased with carcass size (Moleón et al. 2015). In south-central Scandinavia, carcasses of moose (*Alces alces*) were less likely to be visited by scavengers as carcass biomass decreased (Wikenros et al. 2013).

Another factor affecting scavenging is the physical condition of the carcass, namely whether it is frozen or fresh. If a carcass is frozen, vertebrate tissues may become damaged and internal bacterial activity inhibited, which favors aerobic decay over anaerobic putrefaction during the first several days of decomposition. Frost damage to the skin was also found to increase arthropod penetration of carcasses (Micozzi 1986), thereby potentially influencing carcass detection by vertebrates. Also, the surrounding habitat of the carcass may affect scavenging communities (Pardo-Barquín et al. 2019). In open habitats, birds are expected to appear more often because they use visual more than olfactory cues to detect carrion resources (Fox et al. 1976, Güntürkün 2000); accordingly, ravens and white-tailed eagles scavenge carrion placed in clearings more often than carcasses placed in forests (Selva et al. 2003). Contrary in dense habitats, mammals, for example, martens, foxes, and lynx, are expected to appear more often (Lanszki et al. 2007, Belotti et al. 2012, Walton et al. 2017).

Scavenging patterns also depend on interacting factors related to carrion availability, the local scavenging community, and abiotic conditions of the resource. For example, the scavenging species present in an area can influence the detection time, and extent or succession of invertebrate and vertebrate consumers of carrion resources (DeVault et al. 2003, Selva et al. 2005, Wilson and Wolkovich 2011). Whether a carcass is placed once at a site (single provision site) or more often at a site (continuous provision site) can also affect scavenging patterns. The scavenger community at continuous provision sites might be dominated more by generalists, whereas the scavenger community at single provision sites might be exploited more by specialists because of their abilities to track these resources as shown for common raven (*Corvus corax*) and gray jays (*Perisoreus canadensis;* Wilmers et al. 2003*b*). Alternatively, a facultative scavenging species might be able to consume a disproportionate amount of carrion simply by occurring in very high abundances relative to other species in the landscape (Ruxton and Wilkinson 2013). Of the environmental factors that affect scavenging, ambient temperature seems to be the most influential as warm conditions encourage the development of insects and the proliferation of microorganisms within and on carcasses (Benbow et al. 2013, Ray et al. 2014), and in the underlying soil (Carter et al. 2007), hence also being conducive for carrion decay (Parmenter and MacMahon 2009). During winter, when other food resources are scarce, carrion represents an essential trophic resource for the vertebrate scavenger community (Selva et al. 2005, Olson et al. 2016); for example, carrion is a more important part of the red fox diet in winter than in summer (Jędrzejewski and Jędrzejewska 1992, Needham et al. 2014).

To better understand the conditions important for carrion provision as a management tool, we evaluated the factors that affected scavenging ecology over a six-year period using camera traps at 48 carcass provision sites in the low mountain range of the Bavarian forest. We hypothesized that vertebrate scavenger species diversity and feeding would be higher during the winter and in open compared to dense forest structure and that both would increase with carcass mass, irrespective of the carcass species. Further, we posited that scavenging pressure would be lower and from fewer species on carcasses that were previously frozen and provided a single time compared to sites of continuous carrion provision.

METHODS

Field site

Fieldwork was conducted in the Bavarian Forest National Park, located in eastern Bavaria, Germany, which together with the Šumava National Park (Czech Republic) form the Bohemian Forest Ecosystem, one of the largest strictly protected woodlands of Central Europe. Altitudes range from 600 to 1450 m a.s.l. with a humid and cold climate and annual mean precipitation from 965 to 1860 mm and mean annual air temperature between 3.9 and 8.6°C. Natural vegetation is broadly divided into montane slopes with mixed mountain forest (*Luzulo-Fagetum, Asperulo-Fagetum*), subalpine *Picea* forest on peaks and high plateaus, and mixed coniferous forest (*Vaccinio-Picea*). Above the grass- and often spruce-rich mixed forests of high montane elevation are Hercynian mountain forests (*Piceion*) dominated by *Picea abies* and accompanied by *Sorbus aucuparia* and *Acer pseudoplatanus*

(Cailleret et al. 2014). Large mammals include the herbivores red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), and roe deer (*Capreolus capreolus*) and the large carnivores Eurasian lynx (*Lynx lynx*; Heurich et al. 2018) and the gray wolf with the first specimen being observed in 2015, and the first confirmed reproduction in 2017.

Experimental design

Carcasses of red deer, fallow deer, and roe deer were placed at the study sites as follows. One carcass was placed every two months on each of the five continuous provision sites and one carcass was placed once on each of the 24 single provision sites. Hind limbs of deer carcasses were fixed with a cable tied to a tree. The carcasses ranged from fresh killed to previously frozen and possessing an unharmed body to conducted field dressing (Table 1). At each site, Reconyx Hyperfire HC600 camera traps with an infrared flash were set to rapid-fire mode, which trigger every second when an animal is detected. Data were acquired from the first carcass placement in February 2012 to the last placement in July 2017 on a total of 1569 trap nights. Overall, a total of 61 carcasses were monitored. Following previous studies (Turner et al. 2017), we discarded the entire series of photographs in cases where an animal moved the carcass out of the operating range of the camera trap or because of camera malfunction. One sample event was defined as the time frame starting with carcass placement up to the date on which the carcass was entirely exploited (i.e., only skin and bones remained), which resulted in a total of 48 applicable placements (continuous provision sites and single provision sites, $n = 24$, respectively) for red deer and fallow deer (*Dama dama*; $n = 32$ and $n = 1$, respectively; analysis was not affected by combining these two groups) and roe deer ($n = 15$). The carcass visiting species recorded by the camera traps were identified by experts, and the species name was tagged into the metadata of the raw pictures via the image processing software Adobe Lightroom (Adobe Systems 2015). We declared all animals approaching carrion (e.g., scavengers, predators lured by the carcass or random appearances) as carcass visitors. After tagging was completed, the metadata containing the name of the species and the exact time of camera triggering were extracted using the R

package CamtrapR (Niedballa et al. 2016). For data analysis, we only used photographs marked as independent events. These were defined as consecutive photographs of individuals of different species or consecutive photographs of individuals of the same species taken more than 30 min apart, based on camera-trap studies of Li et al. (2010) and O'Brien et al. (2003).

Environmental variables

A total of 28 variables were used for the analysis of carcass visitors–carrion interactions (Table 1). Meteorological data (i.e., temperature, humidity, and precipitation) from recordings of five adjacent meteorological stations were taken over the course of the study. Altitude and aspect were retrieved from a digital terrain model (Aryal et al. 2017). Additional habitat parameters (cover, shrub, habitat openness, and mean height of trees) were available from LIDAR data provided by the Bavarian Forest National Park (Yao et al. 2012, Ewald et al. 2014, Latifi et al. 2015). Maps were created, habitat parameters were analyzed and mapped, and the parameters dPath (distance to next hiking trail) and dMeadow (distance to next meadow) were handled using ArcGIS 10.3.1 (ESRI 2011); data on individual tree heights were extracted using the R packages raster (Hijmans 2014) and rgdal (Bivand et al. 2017). Diversity indices and number of carcass visitor encounters were calculated by extracting camera footage using the packages CamtrapR (Niedballa et al. 2016) and vegan (Oksanen et al. 2015). The Shannon-Wiener index was calculated as $-\Sigma P_i \ln(P_i)$, where P is the proportion of individuals belonging to species i; Simpson's diversity was calculated as $1-(\Sigma pi^2)$ (Morris et al. 2014). Because Cover 10 correlated with Shrub 10 & Cover 100 (Pearson correlation coefficient > 0.7), Cover 10 was excluded from further analysis (Dormann et al. 2007).

Statistical analysis

A priori, we created a species richness curve using the R package vegan (Oksanen et al. 2015) to assess whether our sample size was sufficient to detect most of the local species that scavenge carrion. We plotted a graph of the species richness (i.e., number of scavenging species) including a 95% confidence interval against the number of placed carcasses (Moleón et al. 2015). A Shapiro-Wilk test was conducted to check the data

Table 1. Characteristics of variables used for the analysis of visitor–carrion interactions.

Variable	Variable type†	Definition	Resolution [m]	Range‡
PlotID	Independent	Study plot designation	–	1–24
Location type	Independent	Management type of the plot	–	continuous, single
Carcass detection	Both	Time until carcass was detected [d]	–	0–42
Carcass presence	Dependent	Time until carcass was depleted [d]	–	0–113
Carcass species	Independent	Animal species placed	–	*Capreolus capreolus, Cervus elaphus, Dama dama*
Carcass mass	Independent	Mass of the carcass [kg]	–	4–150
Carcass freshness	Independent	Freshness of the carcass	–	fresh, frozen, unreproducible
Carcass openness	Independent	Openness of carcass (e.g., field dressing)	–	opened, unharmed
Temperature	Independent	Mean temperature during the sampling period [°C]	–	−7.14 to 21.23
Humidity	Independent	Mean humidity during the sampling period [%]	–	62.71–98.57
Precipitation	Independent	Mean precipitation during the sampling period [mm]	–	0.02–12.29
Altitude	Independent	Altitude a.s.l. [m]	10 × 10	663.91–1323.04
Aspect	Independent	Slope direction [°]	10 × 10	1.83–334.98
Cover 100	Independent	Amount of forest cover in a 100 m radius [Index]	10 × 10	0.09–0.88
Shrub 10	Independent	Amount of shrub density in a 10 m radius [Index]	10 × 10	0.47–0.98
Shrub 100	Independent	Amount of shrub density in a 100 m radius [Index]	10 × 10	0.43–0.92
Habitat openness 10	Independent	Amount of non-mature stand in a 10 m radius [%]	10 × 10	0–100
Habitat openness 100	Independent	Amount of non-mature stand in a 100 m radius [%]	10 × 10	0.02–100
Hmean 10	Independent	Mean height of trees in a 10 m radius [m]	10 × 10	8.71–38.03
Hmean 100	Independent	Mean height of trees in a 100 m radius [m]	10 × 10	8.59–36.73
aLynx	Both	Number of independent encounters by lynx per plot	–	0–38
aMeso	Both	Number of independent encounters by mesopredators per plot	–	0–195
aWild boar	Dependent	Number of independent encounters by wild boars per plot	–	0–38
aBirds of prey	Both	Number of independent encounters by birds of prey per plot	–	0–22
aRaven	Both	Number of independent encounters by ravens per plot	–	0–81
aTotal	Dependent	Number of independent encounters by vertebrate carcass visitors per plot	–	1–217
dMeadow	Independent	Distance to next meadow [m]	10 × 10	33.02–686
dPath	Independent	Distance to next hiking trail [m]	10 × 10	1.51–448.66
Species richness	Both	Number of species per plot	–	1–9
Shannon	Both	Shannon-Wiener index per plot	–	0–1.56
Evenness	Both	Evenness index per plot	–	0.21–1
Simpson	Both	Simpson's diversity index per plot	–	0.068–1

–, means that the corresponding data were collected without remote sensing, therefore no resolution is available.
† Independent, dependent, or used as both for the generalized linear mixed models, prior to subsequent model selection.
‡ Only data from sites where carcass visitors were present were considered.

distribution of diversity indices. For normal distribution, an analysis of variance (ANOVA) was applied to test the correlation of single and continuous plots with the Shannon, Evenness, and Simpson's indices. A Kruskal–Wallis rank-sum test was applied for species richness.

Normally distributed variables were standardized using the decostand function within the package vegan (Oksanen et al. 2015), whereas not normally distributed variables were square-root-transformed to obtain a distribution approximate to normal; Tukey transformation was performed for negative values (Mangiafico 2017).

To quantify the relative importance of environmental variables in relation to dependent variables (aLynx (a = abundance), aMeso, aBirds of prey, aRaven, aWild boar, aTotal, Carcass detection, Carcass presence, Species richness, Shannon and Evenness; Table 1), we used random forest modeling (randomForest function implemented in the MASS package Mass; Venables and Ripley (2003). We classified the most important variables as the five variables (out of 20 variables for diversity indices, and 24 variables for encounters of each scavenging species, carcass detection, and carcass presence; Appendix S2: Figs. S3–S12) with the highest mean decrease Gini index (IncNodePurity factor; Kuhn et al. 2008). The results of the random forest analysis and the list of variables used for each model are given in Appendix S2: Supplementary BRT output. We then applied negative binomial generalized linear mixed models (GLMMs) with PlotID as a random effect, using the R package glmmADMB (Skaug et al. 2016). PlotID was set as a random effect to statistically consider pseudo replications resulting from multiple observations at continuous carcass placement locations. A negative binomial distribution was chosen as it corresponds to the scale parameter in a quasi-Poisson model (Hardin and Hilbe 2007) because our data were quasi-Poisson distributed. We consecutively fitted variables derived from a random forest in GLMMs in sequence according to their Gini index. Thus, some variables were used as both, dependent and independent (Table 1) for the respective models. This was followed by a model selection based on the information criterion Akaike (AIC) using the dredge function implemented in the R package MuMIn (Barton 2016). Following the studies of Anderson and Burnham (2004) and Pinheiro and Bates (2000), we used the model with the highest Akaike score (lowest AIC value) to explain our data. All models within 2 AIC units were being considered as competing models (Appendix S3: Table S1). To see whether the persistence of carrion acts as a function of biodiversity, we additionally calculated a model of carcass presence related to species richness, Shannon, Simpson's diversity, and Evenness. All analyses were conducted in R version 3.5.1 (R Core Team 2018) and R Studio version 1.1.456 (R Studio Team 2016).

RESULTS

Community richness, carcass detection, and carcass presence

We detected a total of 17 vertebrate species approaching deer carcasses, with species richness ranging from 1 (observed at the deployment of a newborn roe deer carcass) to 9 (observed at an adult red deer carcass). Image analysis revealed three of the 13 detected mammal species are currently in the Red List of threatened species in Germany (*Lynx lynx*, class 2; *Felis silvestris*, class 3; *Martes martes*, class 3; Haupt et al. 2009). Two of the observed avian species are in the Red List of threatened bird species in Bavaria (*Haliaeetus albicilla*, class R; *Milvus milvus*, class V; Rudolph et al. 2016).

On 1569 trap nights, 2943 independent encounters on 48 carcasses were detected (Table 2), revealing that species richness was higher in winter than in summer and that diversity did not significantly differ between continuous placement sites and single placement (analysis of variance for evenness df = 22, $F = 0.259$, $P = 0.938$; Shannon diversity df = 22, $F = 0.464$, $P = 0.844$; Simpson's diversity df = 22, $F = 1.493$, $P = 0.578$; and Kruskal–Wallis rank-sum test for species richness df = 6; $P = 0.6598$).

The best-fit model concerning the detection time of the carcass showed that increasing proximity to a natural meadow shortened the time until the first animal appeared (Table 3). The first species to appear was a mesopredator (*Martes martes* or *Vulpes vulpes*) in 27 cases, a wild boar (*Sus scrofa*) in 11 cases, a bird (*Corvus corax*, *Garrulus glandarius*, or *Buteo buteo*) in 9 cases, and a lynx in one case. No significant model explaining the presence time of carrion with the variables derived from the random Forest analysis was found, but all competing models relating carcass presence to diversity indices (Appendix S3: Table S1) showed an prolonged persistence time with increasing diversity of carcass visitors.

Table 2. Animal species detected at the 48 carcass placement sites between 2012 and 2017. Carcass visitors were detected with camera traps during a total of 1569 trap nights.

Species	Observations on study sites†	No. study sites observed‡	Scavenger§
Buteo buteo	147	19	+
Capreolus capreolus	6	5	−
Cervus elaphus	17	11	−
Corvus corax	364	26	+
Felis silvestris	1	1	−
Garrulus glandarius	34	6	+
Haliaeetus albicilla	11	1	+
Lynx lynx	140	15	+
Martes martes	438	15	+
Milvus milvus	2	1	+
Meles meles	8	2	+
Nyctereutes procyonoides	2	1	+
Pica pica	25	1	+
Sciurus vulgaris	9	3	+
Sus scrofa	218	34	+
Turdidae spp.	4	2	−
Vulpes vulpes	1501	44	+

† The total number of recorded encounters of the species on a site where a carcass was placed.
‡ The number of sites on which the species was detected.
§ +, Animal species classified as a potential scavenger; −, animal species not classified as a potential scavenger based on camera-trap footage.

Effects of environmental characteristics on the frequency of carcass use and scavenger diversity

The best-fit model (Table 3) indicated that cold temperatures and heavier carcasses were significant factors associated with increased carcass use for all scavenging species (Fig. 1). The best model for species richness significantly associated lower mean temperatures with increased species richness (Fig. 2). The best-fit model for Shannon diversity also identified temperature as the most determinative variable of the environmental variables (Fig. 2). The model explaining species evenness revealed increased carcass mass significantly associated with lower evenness.

Effects of environmental characteristics on the use frequency of top predators and mesopredators

Scavenging lynx were detected 150 times on 15 different camera-trap recordings. They were more likely to appear in denser forest cover, with increasing distance to the next walking path or

with larger carcass provisions (Appendix S1: Fig. S2). Mesopredators were the most common vertebrates detected at the carcasses, namely *Vulpes vulpes, Martes martes, Meles meles,* and *Nyctereutes procyonoides,* in the order of decreasing numbers of independent encounters. The presence of mesopredators was best explained by daily temperature, carcass mass, and the presence of ravens at the carcasses. The number of mesopredators feeding on the carcasses increased with the mass of the carcass and lower average daily temperatures, indicating that larger carcass provisions are more frequently used during winter months.

Effects of environmental characteristics on the carcass feeding of wild boars, birds of prey, and ravens

Wild boars (*Sus scrofa*) were detected 218 times on 34 different camera-trap recordings (Table 2) and often occurred in groups. No significant model explaining their frequency of carrion visitations was found. The most frequent bird of prey at the carcasses was the common buzzard *Buteo buteo* (147 events at 19 sites; Table 2). Other scavenging bird species visited two sites (Table 2). At one site, a single white-tailed eagle (*Haliaeetus albicilla*) was recorded 11 times, and at the other site, a red kite (*Milvus milvus*) was recorded twice. According to the best-fit model, the factor that increased the presence of these scavenging birds at the carcasses was colder temperatures. Visits of the common raven were enhanced by top predators, mesopredators, birds of prey, and the cold season.

Discussion

Our analysis of camera-trap data at sites where carcasses were placed yields new information on the potential drivers of scavenging communities in temperate ecosystems. Our models supported our hypotheses that increasing carcass size, colder temperatures (winter), and a heterogeneous surrounding habitat are major factors associated with vertebrate scavenger species richness and encounters at carrion provisions. However, contrary to our hypothesis, the condition of the carcass (fresh/frozen), the provision schedule (continuous/single), and the carcass

Table 3. Results of significant general linear mixed models with lowest AIC value and plot as random effect.

Response variable	Predictor variable	Estimate of coefficients				Model significance		
		Estimate	SE	z	Pr(>|z|)	df	Deviance	Pr(>Chi)
Species richness	(Intercept)	0.210	0.008	25.37	<0.001	1	7.020	0.008
	Temperature	−0.016	0.006	−2.68	0.007			
Shannon	(Intercept)	<0.001	0.136	0.00	1.00	1	5.565	0.018
	Temperature	−0.334	0.137	−2.43	0.015			
Evenness	(Intercept)	1.739	0.494	3.65	< 0.001	1	11.707	<0.001
	Carcass mass	−0.366	0.100	−3.63	< 0.001			
aLynx	(Intercept)	−0.493	0.162	−3.05	0.002	3	13.612	0.003
	Carcass mass	0.050	0.017	3.00	0.003			
	dPath	0.059	0.034	1.74	0.082			
	Cover 100	2.776	1.153	2.41	0.016			
aMeso	(Intercept)	0.970	0.505	1.92	0.055	3	27.358	<0.001
	Temperature	−0.645	0.132	−4.89	< 0.001			
	Carcass mass	0.214	0.105	2.04	0.041			
	aRaven	0.881	0.536	1.64	0.100			
aBirds of prey	(Intercept)	0.085	0.019	4.48	< 0.001	1	6.614	0.010
	Temperature	−0.051	0.019	−2.66	0.008			
aRaven	(Intercept)	−0.057	0.096	−0.59	0.554	4	11.255	0.024
	aBirds of prey	0.571	0.252	2.27	0.023			
	aMeso	0.072	0.036	2.03	0.042			
	Temperature	0.064	0.044	1.47	0.141			
	aLynx	0.359	0.202	1.78	0.075			
aTotal	(Intercept)	1.167	0.072	16.14	< 0.001	2	29.225	<0.001
	Temperature	−0.089	0.019	−4.69	< 0.001			
	Carcass mass	0.053	0.015	3.63	< 0.001			
Carcass detection	(Intercept)	0.065	0.069	0.94	0.345	1	90.402	<0.001
	dMeadow	0.011	0.004	2.52	0.012			
Carcass presence	(Intercept)	33.200	11.1	3.00	0.003	2	15.944	<0.001
	Evenness	42.3	10.3	4.11	< 0.001			
	Shannon	−56.4	17.2	−3.29	0.001			

species did not influence vertebrate carcass visitation or feeding at carrion.

Instead, carcass mass influenced carcass visitors community structure. Large carnivores and mesopredators preferred larger carcasses, similar to the observations of others (DeVault et al. 2003, Sebastián-González et al. 2013, Moleón et al. 2015, Turner et al. 2017). By contrast, wild boars and birds of prey had no preference for heavier carcasses. Moreover, the species evenness decreased with increasing carcass mass, which suggests that the scavenger community at large carcasses is often more diverse than at small carcasses. Surprisingly, carcass mass was not linked to the duration of the animal visitation at the carcass. In addition, carcasses did not remain longer in distinct habitats or at specific abiotic conditions but when the competition at a carcass placement was strong. This fits with findings of Turner et al. (2017), who could relate higher

species richness at carrion to a longer persistence time of the carcass.

We observed that carcass visitor diversity was not affected by carcass condition, that is, whether it was fresh or frozen. This contrasts with results from other studies which found previously frozen carcasses were associated with accelerated rates of decomposition compared to fresh ones (Micozzi 1986, Roberts and Dabbs 2015) and that arthropods can more easily enter previously frozen carcasses (Micozzi 1986). However, vertebrates are not considered to be affected by a fresh or frozen condition, as they are naturally adapted to freeze–thaw cycles of their food through the transition of the seasons (Beasley et al. 2015).

The presence of specific scavenger species at the carcasses was greatest with higher forest cover (*Lynx lynx*) and lower elevation (birds of prey). Our finding that lynx were more frequently
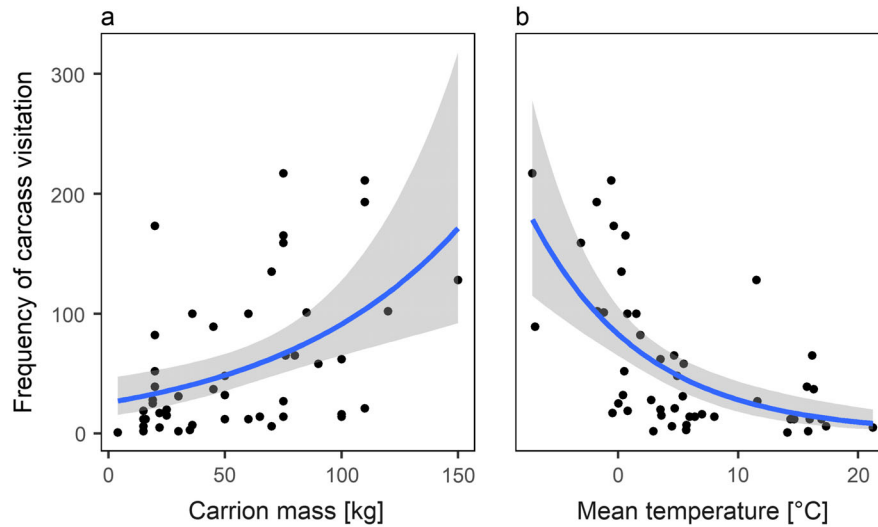
Fig. 1. Influence of (a) the mass of the carcass placed on the site and (b) mean temperature on the frequency of carcass use (*n* = 48). Observed values (circles), predicted values (connected by the blue line), and confidence intervals (gray shading) for the negative binomial GLMM; df = 2; Pr (>Chi) < 0.001. Influence of carcass mass: *z*-value = 3.63, Pr(>|z|) < 0.001. Influence of mean temperature: *z*-value = −4.69, Pr(>|z|) < 0.001.
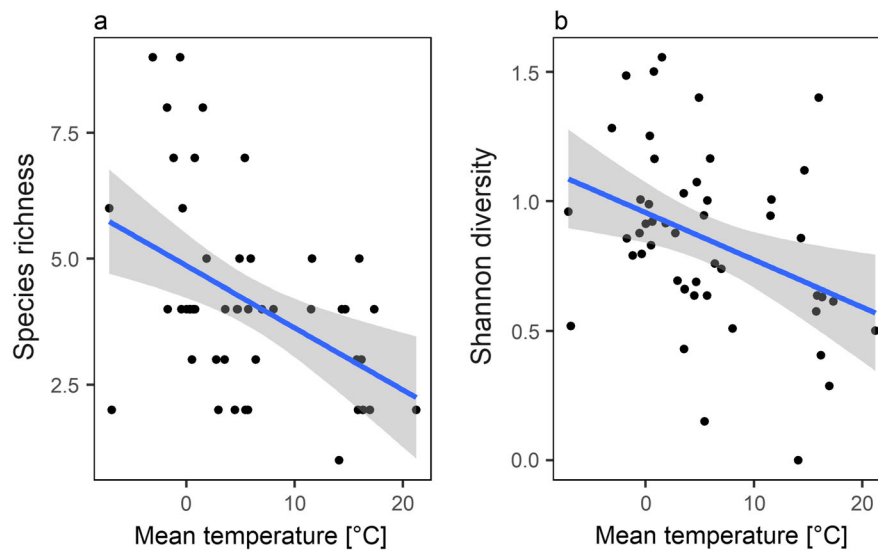

Fig. 2. Dependence of (a) species richness and (b) Shannon diversity on the daily mean temperature (n = 48). Observed values (circles), predicted values (connected by the blue line), and confidence intervals (gray shading) for the GLMMs. Species richness: negative binomial GLMM; df = 1; Pr (>Chi) = 0.008. Influence of mean temperature: *z*-value = −2.68, Pr(>|z|) = 0.007. Shannon diversity: negative binomial GLMM; df = 1; Pr (>Chi) = 0.018. Influence of mean temperature: *z*-value = −2.43, Pr(>|z|) = 0.015.

detected at carcasses in a forest with higher cover is in accordance with the findings of Belotti et al. (2018), who showed that lynx feed longer on kills in more remote areas with fewer human disturbances. The presence or absence of species in specific habitats corresponds to previous findings that habitat structure is a key factor shaping animal communities at carrion sites (Smith et al.

2017, Pardo-Barquín et al. 2019). Contrary to our expectations, birds of prey did not appear more often at carcasses in clearings than in dense forest, possibly because they are known to follow other scavengers, like the common raven, that have already located a carcass. Such behavior is known for golden eagles (*Aquila chrysaetos*; Kochert et al. 2002) and was also confirmed by three of the competing models, in which the presence of birds of prey at the carcass was positively influenced by the presence of the common raven and mesopredators. The presence of ravens was an indicator species for locating carrion, as ravens also positively influenced the presence of mesopredators at the carcass sites in our study and are known to aggregate in the proximity of carcasses (Cortés-Avizanda et al. 2009). The higher number of scavenging of birds of prey in winter can be attributed to the reduced food availability during adverse weather conditions, as natural carrion is difficult to detect when covered by snow, in accordance with the behavior of bearded vultures (*Gypaetus barbatus*) in Spain (Moreno-Opo et al. 2015). As snow cover at high altitudes in the Bavarian Forest can last up to 6 months (Cailleret et al. 2014), a higher amount of carrion feeding at low elevations is inevitable. As wild boars were present at most sites and did not prefer either specific habitats or abiotic conditions, they are acting as important scavengers throughout all seasons. This fits to their behavior of being a highly adaptive generalist species throughout their range, irrespective of their habitat (Ballari and Barrios-García 2014).

Contrary to our hypothesis, diversity and feeding frequency of carcass visitors were not affected by carcass provision schedule, that is, continuous or single placement. Leibold et al. (2004) argue that the spatial proximity of resources could favor the development of metacommunities that are less invasible by other species that compete for the same resources (Leibold et al. 2004), which means that the species present form a nested and fixed scavenger community. These metacommunities in addition to feeding site location may explain why we observed no difference in carcass visitor diversity at continuous provision and single provision sites. The existing local community might also have a saturation-like effect (Shurin and Allen 2001, Leibold et al. 2004). The species pool at both the regional level and site level may be sufficient to fully colonize and exploit carcasses provided once in the same way as carcasses provided regularly at a site. Another possibility is that the two-month interval of carcass provision could have been too long to make a difference to single placement carcasses. Scavengers may need carcasses provided more frequently, such as observed in the European vulture supplementary feeding program in Spain, where vultures were most dependent on a weekly (Donázar et al. 2009, Moreno-Opo et al. 2015) or even daily (Cortés-Avizanda et al. 2016) carrion supply.

In our study, the location of the site determined which type of potential scavenger first appeared at the carcass. When the distance between the site and the next meadow was small, mesopredators appeared first (27 events). Indeed, meadows represent the natural habitat of mesopredators (Lanszki et al. 2007), and volatile organic compounds spread faster in an open habitat than in a dense forest (Murlis 1992), which likely contributes to a shortened detection time. Despite Turner et al. (2017) found that habitat type can influence carcass detection time related to season, detection time in our study was not affected by ambient temperature.

In accordance with our hypothesis, species richness, Shannon diversity, and the presence of mesopredators, birds of prey, and ravens at the carcasses were higher at lower temperatures, supporting results of other studies (Selva et al. 2003, 2005, DeVault et al. 2004). DeVault et al. (2003) state that nearly all predators can become scavengers to some extent, especially when food becomes scarcer. Besides, carrion in temperate ecosystems is more prevalent at the end of winter, when the natural mortality rate of wild animals peaks (DeVault et al. 2003). With 1501 independent observations, the red fox (*Vulpes Vulpes*) accounted for 51% of all carcass visits in our study, concordant with results of an earlier study that revealed that carrion can account for up to 30% of a red fox diet in winter but nearly 0% in summer (Jędrzejewski and Jędrzejewska 1992). Nonetheless, we still found a higher overall Shannon diversity in winter than in summer. These findings highlight the importance of carrion as an additional food resource in the cold months of the year for a broad array of vertebrate species, including several endangered species.

Furthermore, vertebrate scavenger feeding on carrion is limited in summer by competition with insects and microbial communities (Ray et al. 2014). As microbial communities associated with carrion alter the quality of the food resource and consequently can mediate insect community assemblages, they, for instance, are attracted by the volatile organic compounds emitted (Tack et al. 2012, Davis et al. 2013, Finley et al. 2015). However, the microbes are not defenseless against vertebrates as they can produce toxins to repel vertebrate scavengers (Janzen 1977). As higher temperatures encourage microbial proliferation (Xu et al. 2009) and therefore additionally encourage insect activity (Tack et al. 2012), this interkingdom competition between microbial communities, insects, and vertebrates peaks in summer and does not even exist in winter (Benbow et al. 2018).

Management Implications

Based on our results, we suggest that in the management of vertebrate scavenger biodiversity, large carcasses of any ungulate species should be provided to vertebrate scavengers in winter. The carcasses can be fresh or frozen and can be provided at each site once or regularly. The habitat structure of the sites should, however, be heterogeneous. Further studies are needed to determine indirect effects of carrion provisions on plants, fungi, insects, and microbes that are thought to change at both short- and long-term temporal scales with lasting ecosystem effects (Yang et al. 2010, Benbow et al. 2018).

Acknowledgments

Literature Cited

Anderson, D. R., and K. P. Burnham. 2004. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Aryal, R. R., H. Latifi, M. Heurich, and M. Hahn. 2017. Impact of slope, aspect, and habitat-type on LiDAR-derived digital terrain models in a near natural, heterogeneous temperate forest. PFG – Journal of Photogrammetry, Remote Sensing and Geoinformation Science 85:243–255.

Ballari, S. A., and M. N. Barrios-García. 2014. A review of wild boar Sus scrofa diet and factors affecting food selection in native and introduced ranges. Mammal Review 44:124–134.

Barton, K. 2016. MuMIn: multi-model inference. R package version 1.15.6:1–45. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Barton, P. S., S. A. Cunningham, D. B. Lindenmayer, and A. D. Manning. 2013a. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171:761–772.

Barton, P. S., S. A. Cunningham, B. C. T. Macdonald, S. McIntyre, D. B. Lindenmayer, and A. D. Manning. 2013b. Species traits predict assemblage dynamics at ephemeral resource patches created by carrion. PLOS ONE 8:e53961.

Beasley, J. C., Z. H. Olson, and T. L. DeVault. 2015. Ecological role of vertebrate scavengers. Pages 107–127 in M. E. Benbow, J. K. Tomberlin, and A. M. Tarone, editors. Carrion ecology, evolution, and their applications. First edition. Taylor & Francis Group, LLC, Boca Raton, Florida, USA.

Belotti, E., M. Heurich, J. Kreisinger, P. Sustr, and L. Bufka. 2012. Influence of tourism and traffic on the Eurasian lynx hunting activity and daily movements. Animal Biodiversity and Conservation 35:235–246.

Belotti, E., K. Mayer, J. Kreisinger, M. Heurich, and L. Bufka. 2018. Recreational Activities Affect Resting Site Selection and Foraging Time of Eurasian Lynx. Hystrix, the Italian Journal of Mammalogy 29:181–189.

Benbow, M. E., P. S. Barton, M. D. Ulyshen, J. C. Beasley, T. L. DeVault, M. S. Strickland, J. K. Tomberlin, H. R. Jordan, and J. L. Pechal. 2018. Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. Ecological Monographs 89:e01331.

Benbow, M., A. J. Lewis, J. Tomberlin, and J. Pechal. 2013. Seasonal necrophagous insect community assembly during vertebrate carrion decomposition. Journal of medical entomology 50:440–450.

Benbow, M. E., J. K. Tomberlin, and A. M. Tarone. 2015. Introduction to carrion ecology, evolution and their applications. Pages 3–12 in M. E. Benbow, J. K. Tomberlin, and A. M. Tarone, editors. Carrion ecology, evolution, and their applications. First edition. Taylor & Francis Group, LLC, Boca Raton, Florida, USA.

Bivand, R., T. Keitt, and B. Rowlingson. 2017. rgdal: bindings for the Geospatial Data Abstraction Library. R Package version 0.8-16. https://doi.org/10.1353/lib.0.0050

Cailleret, M., M. Heurich, and H. Bugmann. 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.

Carter, D. O., D. Yellowlees, and M. Tibbett. 2007. Cadaver decomposition in terrestrial ecosystems. Naturwissenschaften 94:12–24.

Chapron, G., et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346:1517–1519.

Cortés-Avizanda, A., G. Blanco, T. L. Devault, A. Markandya, M. Z. Virani, J. Brandt, and J. A. Donázar. 2016. Supplementary feeding and endangered avian scavengers: benefits, caveats, and controversies. Frontiers in Ecology and the Environment 14:191–199.

Cortés-Avizanda, A., N. Selva, M. Carrete, and J. A. Donázar. 2009. Effects of carrion resources on herbivore spatial distribution are mediated by facultative scavengers. Basic and Applied Ecology 10:265–272.

Davis, T. S., T. L. Crippen, R. W. Hofstetter, and J. K. Tomberlin. 2013. Microbial volatile emissions as insect semiochemicals. Journal of Chemical Ecology 39:840–859.

DeVault, T. L., I. L. Brisbin Jr, and O. E. Rhodes Jr. 2004. Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. Canadian Journal of Zoology 82:502–509.

DeVault, T. L., Z. H. Olson, J. C. Beasley, and O. E. Rhodes. 2011. Mesopredators dominate competition for carrion in an agricultural landscape. Basic and Applied Ecology 12:268–274.

DeVault, T. L., O. E. Rhodes Jr, and J. A. Shivik. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102:225–234.

Donázar, J. A., A. Margalida, and D. Campión. 2009. Vultures, feeding stations and sanitary legislation: a conflict and its consequences from the perspective of conservation biology. Sociedad de Ciencias Aranzadi, San Sebastian, Spain.

Dormann, C., et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609–628.

ESRI. 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, California, USA.

Estes, J. A., et al. 2011. Trophic downgrading of planet earth. Science 333:301–306.

Ewald, M., C. Dupke, M. Heurich, J. Müller, and B. Reineking. 2014. LiDAR remote sensing of forest structure and GPS telemetry data provide insights on winter habitat selection of European roe deer. Forests 5:1374–1390.

Fielding, D., S. Newey, R. van der Wal, and R. J. Irvine. 2014. Carcass provisioning to support scavengers: evaluating a controversial nature conservation practice. Ambio 43:810–819.

Finley, S. J., M. E. Benbow, and G. T. Javan. 2015. Potential applications of soil microbial ecology and next-generation sequencing in criminal investigations. Applied Soil Ecology 88:69–78.

Finn, J. A.. 2001. Ephemeral resource patches as model systems for diversity-function experiments. Oikos 92:363–366.

Fox, R., S. W. Lehmkuhle, and D. H. Westendorf. 1976. Falcon visual acuity. Science 192:263–265.

Gilbert, M., R. T. Watson, S. Ahmed, M. Asim, and J. A. Johnson. 2007. Vulture restaurants and their role in reducing diclofenac exposure in Asian vultures. Bird Conservation International 17:63.

Güntürkün, O. 2000. Sensory physiology: vision. Pages 1–14 in G. C. Whittow, editor. Sturkie's avian biology. Fifth edition. Academic, San Diego, California, USA.

Hardin, J. W., and J. M. Hilbe. 2007. Generalized linear models and extensions. Stata Press Publication, College Station, Texas, USA.

Haupt, H., G. Ludwig, H. Gruttke, M. Binot-Hafke, C. Otto, and A. Pauly. 2009. Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands. Band 1: Wirbeltiere. – Münster (Landwirtschaftsverlag). Naturschutz und Biologische Vielfalt 70:386.

Heurich, M., J. Schultze-Naumburg, N. Piacenza, N. Magg, J. Červený, T. Engleder, M. Herdtfelder, M. Sladova, and S. Kramer-Schadt. 2018. Illegal hunting as a major driver of the source-sink dynamics of a reintroduced lynx population in Central Europe. Biological Conservation 224:355–365.

Hijmans, R. J. 2014. raster: geographic data analysis and modeling. https://CRAN.R-489project.org/package=raster

Houston, D. C. 1986. Scavenging efficiency of Turkey Vultures in tropical forest. Condor 88:318–323.

Janzen, D. H. 1977. Why fruits rod, seeds mold, and meat spoils. American Naturalist 111:691–713.

Jędrzejewski, W., and B. Jędrzejewska. 1992. Foraging and diet of the red fox Vulpes vulpes in relation to variable food resources in Białowieża National Park, Poland. Ecography 2:212–220.

John Muir Trust. 2012. Wild Land Management Standards:13. http://www.wildlandmanagement.org.uk/wp-content/uploads/2012/01/JMT_WLMS_Handbook.pdf

Kochert, M., K. Steenhof, C. McIntyre, E. Craig, A. Poole, and F. Gill. 2002. Golden eagle (*Aquila chrysaetos*). Birds of North America. https://doi.org/684.50210.2173/bna.684

Kuhn, S., B. Egert, S. Neumann, and C. Steinbeck. 2008. Building blocks for automated elucidation of metabolites: machine learning methods for NMR prediction. BMC Bioinformatics 9:1–19.

Lanszki, J., A. Zalewski, and G. Horváth. 2007. Comparison of red fox Vulpes vulpes and pine marten Martes martes food habits in a deciduous forest in Hungary. Wildlife Biology 13:258–271.

Latifi, H., F. E. Fassnacht, J. Müller, A. Tharani, S. Dech, and M. Heurich. 2015. Forest inventories by LiDAR data: a comparison of single tree segmentation and metric-based methods for inventories of a heterogeneous temperate forest. International Journal of Applied Earth Observation and Geoinformation 42:162–174.

Leibold, M. A., et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Li, S., W. J. Mcshea, D. Wang, L. Shao, and X. Shi. 2010. The use of infrared-triggered cameras for surveying phasianids in Sichuan Province, China. Ibis 152:299–309.

Mangiafico, S. 2017. rcompanion: functions to support extension education program evaluation. R Packag. version 1.5. 0.

Margalida, A., M. Carrete, J. A. Sánchez-Zapata, and J. A. Donázar. 2012. Good news for European vultures. Science 335:284.

Margalida, A., D. García, and A. Cortés-Avizanda. 2007. Factors influencing the breeding density of bearded vultures, Egyptian vultures and Eurasian griffon vultures in Catalonia (NE Spain): management implications. Animal Biodiversity and Conservation 30:189–200.

Mateo-Tomás, P., P. P. Olea, M. Moleón, J. Vicente, F. Botella, N. Selva, J. Viñuela, and J. A. Sánchez-Zapata. 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Diversity and Distributions 21:913–924.

Micozzi, M. 1986. Experimental study of postmortem change under field conditions: effects of freezing, thawing, and mechanical injury. Journal of Forensic Sciences 31:953–961.

Moleón, M., J. A. Sánchez-Zapata, E. Sebastián-González, and N. Owen-Smith. 2015. Carcass size shapes the structure and functioning of an African scavenging assemblage. Oikos 124:1391–1403.

Moreno-Opo, R., A. Trujillano, and A. Margalida. 2015. Optimization of supplementary feeding programs for European vultures depends on environmental and management factors. Ecosphere 6:1–15.

Morris, E. K., et al. 2014. Choosing and using diversity indices: insights for ecological applications from the German biodiversity exploratories. Ecology and Evolution 4:3514–3524.

Murlis, J. 1992. Odor plumes and how insects use them. Annual Review of Entomology 37:505–532.

Needham, R., M. Odden, S. K. Lundstadsveen, and P. Wegge. 2014. Seasonal diets of red foxes in a boreal forest with a dense population of moose: the importance of winter scavenging. Acta Theriologica 59:391–398.

Niedballa, J., A. Courtiol, and R. Sollmann. 2016. 'camtrapR': camera trap data management and preparation of occupancy and spatial capture-recapture analyses. R package version 1.0. https://CRAN.R-project.org/package=camtrapR

O'Brien, T. G., M. F. Kinnaird, and H. T. Wibisono. 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Animal Conservation 6:131–139.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. vegan: community Ecology Package. https://CRAN.R-project.org/package=vegan

Olson, Z. H., J. C. Beasley, and O. E. Rhodes. 2016. Carcass type affects local scavenger guilds more than habitat connectivity. PLOS ONE 11:e0147798.

Oro, D., M. Genovart, G. Tavecchia, M. S. Fowler, and A. Martínez-Abraín. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16:1501–1514.

Ossi, F., et al. 2017. Plastic response by a small cervid to supplemental feeding in winter across a wide environmental gradient. Ecosphere 8:e01629.

Pardo-Barquín, E., P. Mateo-Tomás, and P. P. Olea. 2019. Habitat characteristics from local to landscape scales combine to shape vertebrate scavenging communities. Basic and Applied Ecology 34:126–139.

Parmenter, R. R., and J. A. MacMahon. 2009. Carrion decomposition and nutrient cycling in a semiarid shrub-steppe ecosystem. Ecological Monographs 79:637–661.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in sand S-PLUS. Springer, New York, New York, USA. https://doi.org/10.1007/978-1-4419-0318-1

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. BioScience 59:779–791.

Putman, R. 1983. Carrion and Dung. The decomposition of animal wastes. British Ecological Society 8:627–642.

Putman, R. J., and B. W. Staines. 2004. Supplementary winter feeding of wild red deer Cervus elaphus in Europe and North America: justifications, feeding practice and effectiveness. Mammal Review 34:285–306.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

R Studio Team. 2016. RStudio: integrated development environment for R. RStudio, Boston, Massachusetts, USA. http://www.rstudio.com/