



RESEARCH PAPER

Seasonal variability of scavenger visitations is independent of carrion predictability

Nicolas De Pelsmaeker^{a,b}, Nicolas Ferry^a, Jonas Stiegler^c, Nuria Selva^{d,e},
Christian von Hoermann^f, Jörg Müller^{f,g,1}, Marco Heurich^{a,h,i,1,*}

^a Department of National Park Monitoring and Animal Management, Bavarian Forest National Park, Freyunger Straße 2 94881 Grafenau, Germany

^b Population Ecology Research Unit, Mammal Research Institute, Polish Academy of Sciences, Ulica Stoczek 1, 17-230 Białowieża, Poland

^c Institute of Biochemistry and Biology, Animal Ecology, University of Potsdam, Am Neuen Palais 10, 14469 Potsdam, Germany

^d Institute of Nature Conservation, Polish Academy of Sciences, Aleja Adama Mickiewicza 33 31-120 Kraków, Poland

^e Departamento de Ciencias Integradas, Facultad de Ciencias Experimentales, Centro de Estudios Avanzados en Física, Matemáticas y Computación, Universidad de Huelva 21071 Huelva, Spain

^f Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology, University of Würzburg 96181 Rauhenbrunn, Germany

^g Department of Conservation and Research, Bavarian Forest National Park, Freyunger Straße 2 94881 Grafenau, Germany

^h Chair of Wildlife Ecology and Management, Albert Ludwigs University Freiburg, Tennenbacher Straße 4 79106, Freiburg, Germany

ⁱ Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Inland Norway University of Applied Sciences 2480 Koppang, Norway

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ABSTRACT

In temperate regions, larger mammalian carrion naturally occurs in terrestrial landscapes as a pulsed resource towards the end of the winter through enhanced ungulate mortality due to starvation or exhaustion. The return of large carnivores in Central Europe provides carrion more equally throughout the year and the active enhancement of carrion for biodiversity by game managers has increased, raising the question of how different scavengers respond to the temporal variation in carrion supply. To address this question, we experimentally deployed 106 cervid carcasses throughout the year in a temperate forest of south-eastern Germany on two types of plots: permanent (i.e., site with multiple subsequent deployments) or random (i.e., site with unique deployment), and reported vertebrate scavenger visitations by camera trapping. Deployment on random or permanent sites did not affect carrion use by any single species. Generalized additive modelling revealed that vertebrate scavenging peaked in the winter season and summer independent of carrion supply. Still, different scavenger species showed different temporal patterns. While wild boar as ungulate omnivores did not display any seasonal patterns, avian scavengers showed significant variation in visitation rates. The mesopredator red fox consumed carrion significantly more often from late winter to summer, while pine marten was present at carrion only during winter. Finally, the specialist large carnivore Eurasian lynx, visited carrion sites most frequently in late winter and early spring. Our results suggest that global warming might impact some groups of vertebrate scavengers more strongly than others by reducing carrion availability in late winter, while returning carnivores could mitigate these impacts.

Introduction

Scavenging can have far-reaching effects on the food web structure, as more energy is transferred through carrion consumption than predation (Wilson & Wolkovich, 2011). Carrion provides consumers access to high-quality food resources, such that scavenging accounts for 35–75 % of biomass consumption in terrestrial ecosystems (DeVault et al.,

2003). The availability of carrion often occurs ephemerally, as a pulsed resource (Nowlin et al., 2008), and can be spatio-temporally unpredictable, which consequently affects the distribution of scavengers (Blázquez et al., 2009; Wilmers et al., 2003a). For example, vultures have been observed to follow transhumant livestock migration in the Andes (Arrondo et al., 2023). The occurrence of vertebrate carrion in a landscape provides critical subsidies of resources for many vertebrate

* Corresponding author.

E-mail address: marco.heurich@wildlife.uni-freiburg.de (M. Heurich).

¹ These authors contributed equally as senior authors.

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and invertebrate species during a period of resource scarcity (DeVault et al., 2003; Moreno-Opo & Margalida, 2013; Farrell et al., 2015). This is particularly the case during the winter in temperate regions, and during the dry season in arid ecosystems, when carrion is less prone to rapid decomposition (Read & Wilson, 2004; Rees et al., 2020; Selva et al., 2005).

In the absence of large predators, the availability of carrion throughout the year can be considered a function of the length and severity of the winter or dry season (Gese et al., 1996). The amount of snow, the duration of winter and drought, can result in large vertebrate mortality due to increased metabolic activity, decreased access to food, and higher energetic demands for movement (Parker et al., 1984). This phenomenon is most pronounced towards the end of winter or the dry season (Wilmers et al., 2003a; Sinclair et al., 1985). Facultative scavengers can increase their fitness by consuming carrion (Newton et al., 1982), and predators can compensate for a lack of prey (Parsons et al., 2022). Some scavengers also depend on carrion during specific periods of the year (e.g., grizzly bears (*Ursus arctos horribilis*) after hibernation (Green et al., 1997), bald eagles (*Haliaeetus leucocephalus*) during winter (Swenson et al., 1986), or black-billed magpies (*Pica pica*) during nesting (Dhindsa & Boag, 2008)). During winter, carrion can also enhance the survival of omnivorous scavengers by compensating for the lack of other resources (Benbow et al., 2015). As climate change is expected to lengthen the vegetation period, increase the availability of other resources, and shorten the snow period (Ćimo et al., 2020; Meehl et al., 2004), the winter mortality of ungulates may decrease, leading to reduced late-winter mortality and thus lower the carrion availability to scavengers.

The vertebrate scavenger guild consists of several functional groups that do not consistently share the same diet. Large carnivores facilitate scavenging by acquiring the kill and opening the carcass (Allen et al., 2014). Feeding by omnivores and mesopredators will further fragment the carcass. Avian scavengers, such as the common raven (*Corvus corax*), are considered true omnivores, with scavenged material found in up to 82 % of raven pellets (Rösner et al., 2005).

The consumption of carrion by many facultative scavengers has been underestimated in the past (Sebastián-González et al., 2023), and in order to support scavengers, land and wildlife managers may subsidize ungulate carrion in certain ecosystems, as is the case with vultures (e.g. *Gyps* sp.) (Cortés-Avizanda et al., 2010; Moreno-Opo et al., 2015). However, large carnivores in near-natural ecosystems will regularly predate ungulates, creating large carcasses in the landscape, which in addition to non-predatory seasonal mortality, provides scavengers with carrion on a year-round basis (Wilmers et al., 2003a). As large predators such as gray wolves (*Canis lupus*) are increasingly recolonizing areas in Europe (Chapron et al., 2014), questions arise as to whether scavengers that have adapted the timing of their carrion consumption will maintain their phenology with respect to scavenging behavior when the supply of predator-modulated carrion becomes more regular and abundant. Some species may pattern their reliance on scavenging depending on when carrion is most available (Huggard, 1993) while others may maintain their seasonal consumption of carrion.

This study examines whether scavenger species will visit carrion sites year-round or primarily towards the end of winter when carrion is regularly subsidized in the landscape of a temperate zone. We compared carrion visitation between different groups within the scavenger guild by focusing on representative species of each group. Thus, we investigated visitation rates of five scavenger species in the Bavarian Forest National Park: Eurasian lynx (*Lynx lynx*), as a specialist predator; red fox (*Vulpes vulpes*) and European pine marten (*Martes martes*), as generalist mesopredators; wild boar (*Sus scrofa*), as an omnivorous ungulate; and common ravens, as facultative avian scavengers. Given that omnivore scavengers have fewer food sources at their disposal during winter, we hypothesized an increased visitation rate at carrion sites toward the end of the season, when the variety of food sources is lowest. Thus, we expected wild boar to visit carrion sites more frequently throughout the

winter than other seasons, as their winter diet proportionally consists of more animal matter (Dardaillon, 1987). Since the diet of mesopredators such as fox correlates with the most abundant food resource (Cavallini & Lovari, 1991), and the energetic costs of hunting are higher in winter, we expected that mesopredators would more frequently visit carrion sites during winter. In the case of ravens, we predicted their superior ability to detect carrion from the air to result in equal visitation rates whenever carrion was available, with no particular seasonal differences. As a specialist, however, we expected the lynx to visit carrion during late autumn and early winter but less frequently towards the end of winter, as weakened ungulates become more vulnerable to predation. Furthermore, we expected higher visitation rates by generalist scavengers to occur at permanent sites, due to the habituation of scavengers to carrion predictability. In contrast, lynx and other specialists may be more prone to visit unique (random) carrion deployment sites (Wilmers et al., 2003a).

Materials and methods

Study area

The data for this study were collected in the Bavarian Forest National Park (BFNP; N 48° 58' 0", E 13° 23' 0", 250 km²), located in Southeastern Germany (Fig. 1). The elevational gradient of the park ranges from 600 to 1453 m.a.s.l. (meters above sea level), the mean annual precipitation from 965 to 1860 mm, and the mean annual air temperature from 3.9 to 8.6 °C, such that the climate is relatively cold and humid (Heurich et al., 2010). The forest is mainly dominated by Norway spruce (*Picea abies*), beech (*Fagus sylvatica*), and European silver fir (*Abies alba*) at lower to intermediate altitudes (Cailleret et al., 2014). Ungulates such as roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and wild boar occur in the area (Heurich et al., 2015; Janík et al., 2021). The BFNP is an important wilderness area for protecting large carnivore species, with gray wolves and Eurasian lynx as the main predators of cervids (Heurich et al., 2012, 2018). While gray wolves have recently recolonized the BFNP, they have yet to reach their full ecological functionality (Bufka et al., 2005). The BFNP is divided into a core zone (183.46 km²) and a management zone (58.67 km²), with ungulate hunting and logging occurring in the latter. The management zone represents 23.47% of the study area (Fig. 1).

Data collection

The carrion used in this study consisted of 51 roe deer and 55 red deer carcasses, either shot by hunters for management reasons or road fatalities, deployed evenly between January 2012 and October 2019. The majority of the carcasses were intact, although some hunted animals were field dressed, and some road killed animals had injuries. Carrion deployment occurred approximately bi-monthly at four permanent sites ($n = 62$, Fig. A.2), defined as those with multiple subsequent deployments (average 10.5 per site, up to 15), and at random sites ($n = 44$), defined as those with single deployments, with only one carcass (Fig. 1). Animal carrion was exposed on the ground and secured to a wooden pole by a zip tie through the hind leg. Visitations were recorded with a camera trap (Reconyx Hyperfire HC600; <https://www.reconyx.com/>), with a series of ten photos acquired at 1-s intervals once the camera was triggered. Visitation events were defined using a 30-minute threshold between visitations of a specific species, based on the methods of O'Brien (2003) and Li (2010). Carrion was deployed fresh, after the death of the animal ($n = 69$), or frozen ($n = 19$); the latter was previously shown to not affect scavenger occurrence (Stiegler et al., 2020). For 18 carcasses, the status (fresh or frozen) was unknown. Any animal recorded approaching or being present at the carrion site was classified as a visitor and was included in the analysis. Average monitoring time was 43.2 days, and deployments were spaced evenly throughout the year (Appendix A.1). The minimum duration was 30 days, and lasted until

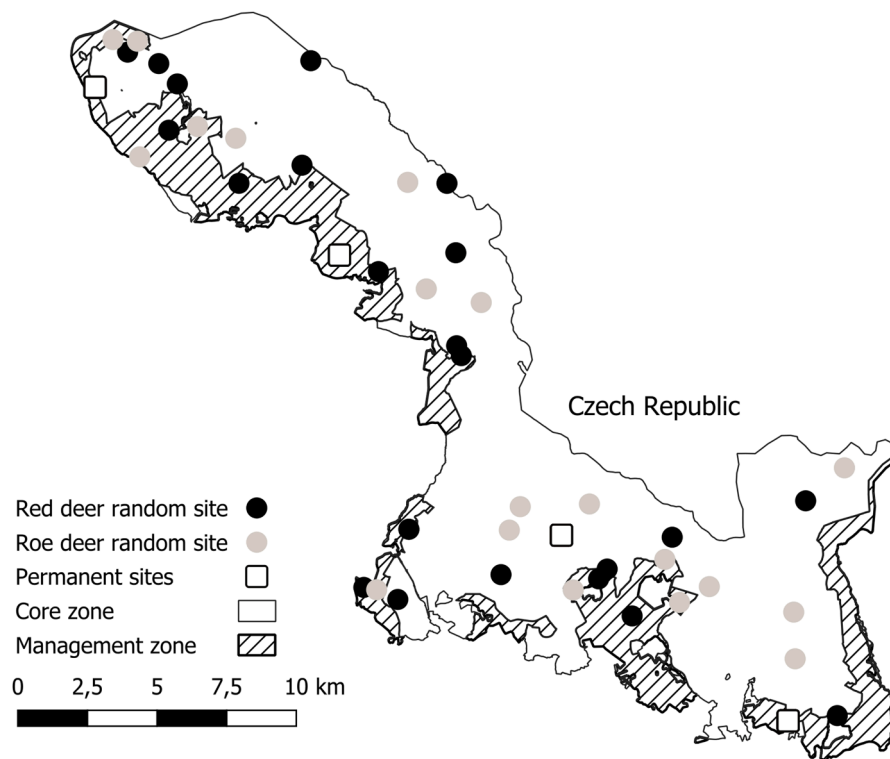


Fig. 1. Map of the Bavarian Forest National Park study area, showing the locations of the carrion deployment sites. Carrion (red deer and roe deer) was regularly deployed at permanent sites and uniquely deployed at random sites.

the carrion was considered entirely consumed (i.e. only skin and bones remained). A maximum of four carcasses were deployed simultaneously with a minimum distance of 1.1 km from each other (15.3 km on average).

In order to account for the influence of weather and climate on the visitation patterns of scavengers, we collected additional environmental data, including mean daily temperature, total daily precipitation, and snow depth, collected from the local weather station in Waldhäuser (N48° 55'47", E13° 27' 55"), located approximately at the center of the study area. Canopy openness was determined based on a survey by airborne Lidar (Latifi et al., 2016). The distance to the management zone and road density (based on the length of all roads situated within a circular buffer with a radius of 250 m around the carrion site) were calculated using QGIS version 3.22.3 (QGIS.org, 2021).

Data analysis

The data were analyzed using R version 4.2.1 (R Development Core Team, 2022). The occurrence of scavenger visitations throughout the year was calculated with generalized additive modeling provided in the *mgcv* package (Wood, 2017) using a restricted maximum-likelihood method. Data from all deployment years were pooled, and the number of visitation events per day (frequency) was used as the response variable based on a Poisson distribution. To account for overdispersion in the data, all final models used a negative binomial distribution. *Day of the year* was the primary independent variable of interest, defined using a cyclical spline smoother. Additional covariates included as fixed effects in the model were *mean daily temperature* (MeanTemp [°C]), *daily precipitation* (Precipitation [mm]), *snow depth* (Snowdepth [cm]), *plot type* (Type; [permanent/random site]), *canopy openness* (Canopy_openness [%]), *elevation* (Elevation [m.a.s.l.]), *distance to a management zone* (Distance to hunting [m]), and *road density* (Road density [km/km²]). The latter two acted as a measure for stresses that may affect animal behavior (Reimoser, 2012). To account for the number of deployments

during any given day of the year, sampling effort (i.e., the number of carcasses deployed simultaneously for any given year) was included as a fixed effect (Effort [n]) (Fig. A.1, Appendix A). Individual deployments (Carcass_ID) were included as a random factor. All numerical variables were scaled for comparability. To avoid collinearity between predictor variables in the models, all variables were checked for correlation *a priori*, using a threshold of $|r| = 0.7$. (Dormann et al., 2013). Information on species abundance, or species density in the study area was not available for the given study period.

Individual models were run for all the scavenger species detected with the camera traps ($n = 25$) (Table B.1; Appendix B), and each of the five species of interest (in order of frequency of occurrence): red fox, common raven, European pine marten, wild boar, and Eurasian lynx. Model validation was performed using the *DHARMa* package (Hartig, 2017). A p -value < 0.05 was considered significant.

Results

A total of 276,681 photos capturing animals, grouped into 3884 events (Table 1), were obtained at 49 carrion deployment sites (106 carcasses) and included in the analysis. Despite the approximately equal number of red deer and roe deer carrion, 7.2 times more events were recorded on average at red deer sites than at roe deer sites, for the five scavenger species of interest (Table 1). Along with the five most common scavengers of interest, 20 additional species, listed in Appendix B, were identified at carrion deployment sites.

Model results

The type of deployment (permanent/random), elevation, canopy openness, and distance to the management zone did not play an influential role in any of the models. When the data of all observed scavengers were pooled, we found significant variation in daily visitation rates ($\chi^2 = 37928.0$, $df = 18$, $p < 0.001$) (Fig. 2). An increase in total daily

Table 1
Number of photos and number of events of visiting scavengers, defined per carrion species.

Carrion species	Number of cadavers		Red fox		Common raven		Pine marten		Wild boar		Eurasian lynx	
	Permanent	Random	Photos	Events	Photos	Events	Photos	Events	Photos	Events	Photos	Events
Red deer	31	24	78,037	1895	31,961	434	18,703	412	64,713	291	15,966	250
Roe deer	31	20	10,545	299	25,015	124	202	30	29,991	124	1548	25
Total	62	44	88,582	2194	56,976	558	18,905	442	94,704	415	17,514	275

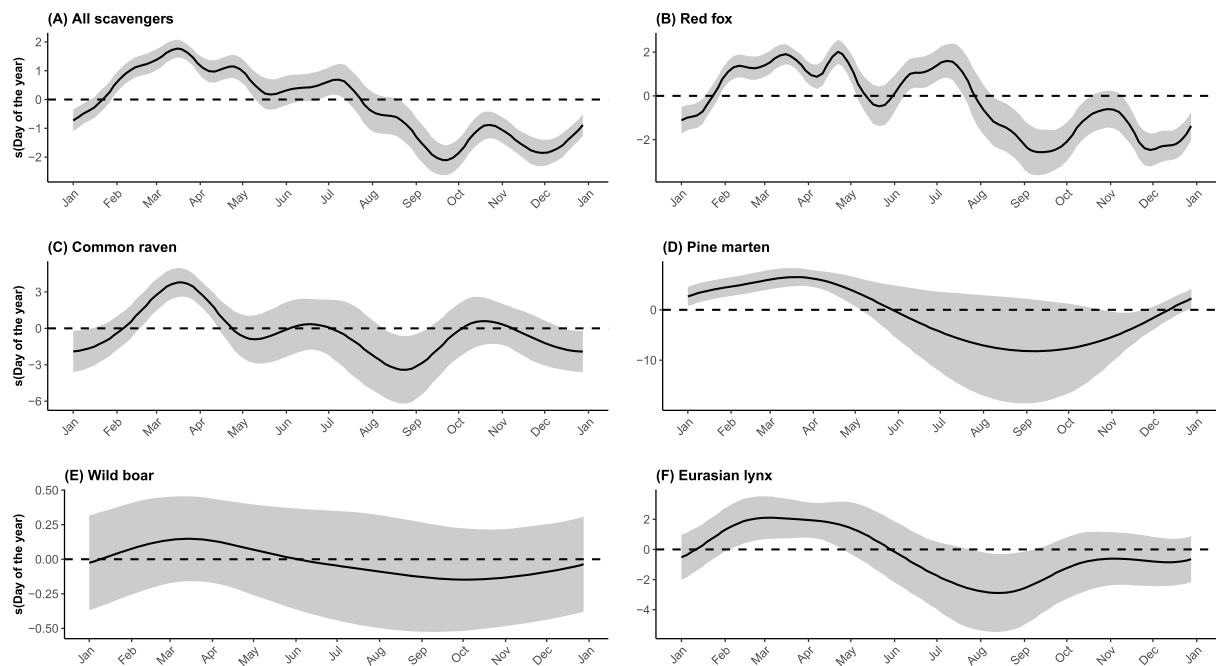


Fig. 2. Smoothing curves for the number of daily visitations over the year for (A) all scavengers (see Appendix B); (B) red fox; (C) common raven; (D) pine marten; (E) wild boar; (F) Eurasian lynx. Black lines represent regression curves for the generalized additive models. The gray ribbons represent the 95% confidence intervals. The y-axis depicts the number of events for the smoother of Day of the year. Positive values indicate an increase in visitations, and negative values indicate a decrease in visitation events at the carrion sites.

precipitation decreased the visitation rates of scavengers at carrion sites (estimate = −0.096, se = 0.028, $z = -3.380$, $p < 0.001$), as did an increase in snow depth (estimate = −0.162, se = 0.073, $z = -2.222$, $p = 0.026$) (Fig. 3; Table B.2).

Similarly, ravens visited carrion sites at different frequencies depending on the time of year ($\chi^2 = 14,492.0$, $df = 8$, $p = 0.008$) (Fig. 2), with fewer visitations during periods of increased precipitation (estimate = −0.284, se = 0.095, $z = -2.982$, $p = 0.003$) (Fig. 3; Table B.2).

By contrast, the visitation rates of wild boar did not vary over the course of the year ($\chi^2 = 15.5$, $df = 8$, $p = 0.183$) (Fig. 2), although they decreased with increasing snow depth (estimate = −0.0709, se = 0.152, $z = -4.672$, $p < 0.001$). Higher road density negatively influenced carrion visitation rates (estimate = −0.442, se = 0.187, $z = -2.342$, $p = 0.019$) (Fig. 3; Table B.2).

In mesopredators, the visitations of red foxes and pine martens to carrion sites varied seasonally ($\chi^2 = 51,658.9$, $df = 28$, $p < 0.001$; and $\chi^2 = 659.0$, $df = 8$, $p < 0.001$; respectively) (Fig. 2). Higher levels of precipitation led to fewer visitations by foxes (estimate = −0.091, se = 0.036, $z = -2.514$, $p = 0.012$), although this was only marginally significant for martens (estimate = −0.182, se = 0.098, $z = -1.849$, $p = 0.065$) (Fig. 3; Table B.2). However, marten visitations, unlike those of foxes, were negatively affected by increasing temperatures and higher snow depths (estimate = −0.373, se = 0.150, $z = -2.489$, $p = 0.013$; and estimate = −0.470, se = 0.173, $z = -2.717$, $p = 0.007$; respectively) (Fig. 3; Table B.2). Finally, significant variations in daily visitation rates were found for lynx ($\chi^2 = 1355.2$, $df = 8$, $p = 0.007$), but none of the

other covariates influenced its carrion site visitation rate.

Discussion

This study investigated the seasonal variation in carrion visitation by facultative scavengers when carrion was made available year-round through regular provision. The results show significant differences in the seasonal visitation rates between different functional groups of the scavenger guild, although carrion use generally increased towards the end of winter. When considering all scavenger species, the visitation of carrion was predominantly observed during the late winter and early spring periods. These visits persisted, albeit to a lesser extent, through the summer months, and reached their lowest point in the early autumn phase. When carrion was available year-round, large carnivores and mesopredators concentrated their visits in the late winter/early spring months. At the same time, both terrestrial (e.g., wild boar) and avian omnivores visited carrion sites more opportunistically whenever it was made an available resource. Red deer carrion was visited more often than roe deer carrion overall. This can be explained by the larger body mass of red deer (mean weight 77.4 kg and 19.8 kg for red deer and roe deer respectively), which allows a higher visitation frequency of mesopredators than for roe deer (Stiegler et al., 2020). Surprisingly, no difference in visitation frequency was observed between permanent and random sites, despite several studies finding that randomly occurring carrion promotes scavenger diversity (Cortés-Avizanda et al., 2012; Wilmers et al., 2003b), although total number of scavenger visitations

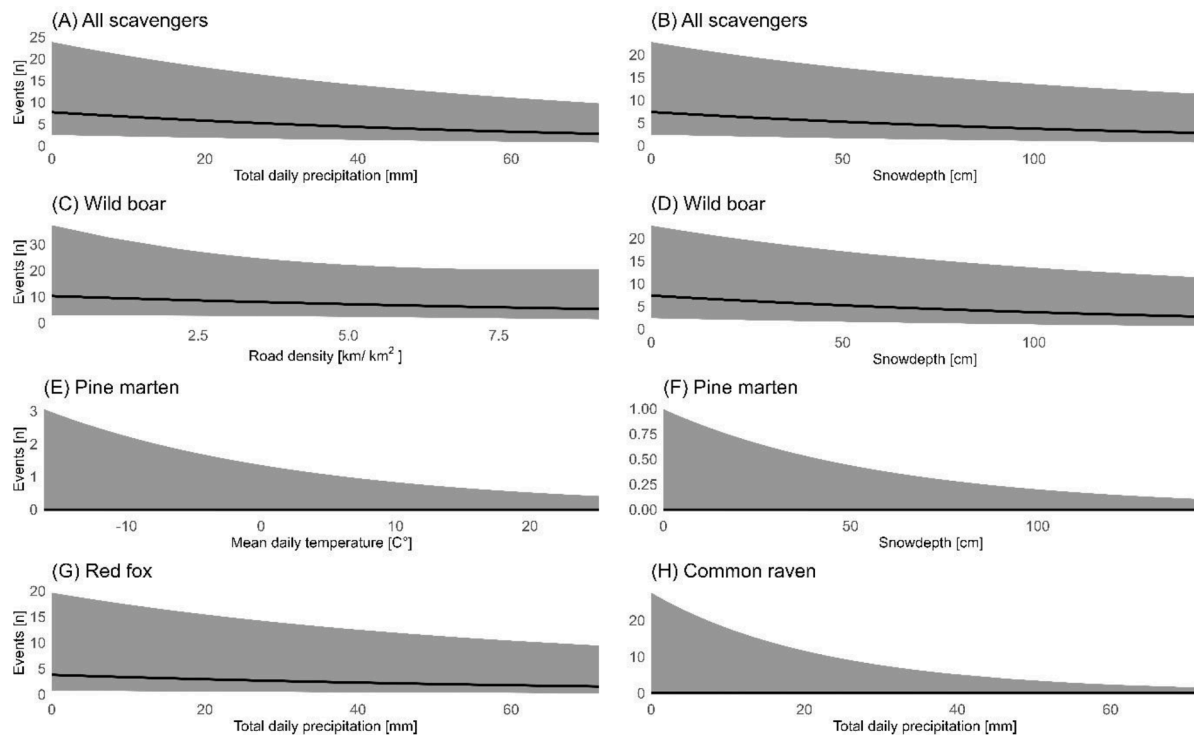


Fig. 3. Model predictions for the significant variables for (A) All scavengers - precipitation; (B) All scavengers - snowdepth; (C) Wild boar - road density; (D) Wild boar - snowdepth; (E) Pine marten - temperature; (F) Pine marten - snowdepth; (G) Red fox - precipitation and (H) Common raven - precipitation. Black lines represents the regression curves, gray ribbons represent 95% confidence intervals.

tend to be higher at predictable sites (Wilmers et al., 2003a).

Seasonal variation in scavenger occurrence

The visitation rates of common ravens varied significantly throughout the year, with peak activity at carrion sites occurring from March to April. An earlier study in Hungary found that the brood of this species is usually completed in the second half of February, with the fledging of juveniles generally occurring at the beginning of May (Bagyura et al., 2017). The observed peak may thus have coincided with the higher nutritional uptake of nestlings, as carrion is an abundant and easily accessible food source. A second (more minor) peak in visitations occurred during high summer (June–July), and a smaller third peak in late autumn (October–November). Selva (2004) described an increase in the number of ravens observed at carrion sites in the Białowieża forest (Poland) beginning in October and continuing to increase until spring (Selva, 2004). In our study, visitation rates slightly decreased from the end of November until the following spring peak.

Contrary to our hypothesis that wild boar would visit carrion sites more frequently in winter, the occurrence of wild boar at carrion sites was nearly constant throughout the year. However, higher sampling effort (i.e. more available carcasses) led to more frequent visitations. As wild boar are abundant in the BFN, the probability of carrion detection by wild boar correlates with carrion availability, and as omnivores, they may choose to consume carrion opportunistically whenever encountered. Wild boar, therefore, do not seem to have any particular phenology regarding their usage of carrion. The consumption of roe deer carrion by wild boar was observed during a study in Spain (Sáenz, 1995) and provided further evidence that these omnivores are important scavengers in their native range (Selva, 2004). Carrion site visitation by red fox showed a significantly varying seasonal pattern, with most events occurring during the second half of the winter but continuing well into the spring and early summer. The access to carrion may be critical to the health of foxes in winter and influenced by snow depth

(Selås & Vik, 2006), as scavenging appears to be primarily a winter activity. Yet, some cases of ungulate scavenging by foxes have been observed in spring (Needham et al., 2014). This coincides with our observations of the winter behavior of foxes but does not explain the peak in scavenging by foxes during July. However, red foxes typically give birth in late April (Lindström, 1988), and the energetic demands of newly independently feeding offspring may lead to increased scavenging in summer. Additionally, foxes have been observed to feed on the maggots present on carrion during the first stages of decomposition (Drygala et al., 2013), which would be abundant during the summer months. The slight drop in carrion visitations between May and June would have coincided with the nursing phase of newborn offspring, during which time males would have been the predominant foragers and hunters, and females would be less active.

The activity of pine martens depended strongly on the time of year, as carrion visits were frequent during winter but nearly absent during spring, summer, and autumn. This supported our hypothesis of more frequent winter visitations and was consistent with previous studies, in which pine marten activity at wolf-killed moose in Sweden was highest during April (Wikenros et al., 2014), with a switch primarily to vole predation or vegetal food consumption during spring and summer (Marinis & Masseti, 1995).

Although felids such as lynx are considered obligatory predators that scavenge almost exclusively on carrion that they killed themselves (e.g., King et al., 2015), scavenging by lynx on other sources of carrion has been documented in the study area (Premier et al., 2021; Ray et al., 2014) and elsewhere (Tobajas et al., 2023). Despite the year-round availability of carrion, lynx visitations varied significantly between seasons, with carrion sites visited more often during late winter and spring (February–May). While our study did not take into account the sex of the visiting individuals, the increased rate of visitation approximately coincided with the gestation period of females (Breitenmoser-Würsten et al., 2007). According to this study, lynx parturition which is in May–June (Mattisson et al., 2022), depicts a period of decreasing

carrion visitations. Carrion consumption could be more energetically advantageous than predation during the gestation period. Additionally, Peláez et al. (2020) found that, in Switzerland, the parturition period of the main prey species (roe deer) occurred simultaneously with the start of the observed decline in carrion visitations (Peláez et al., 2020). Increased availability of juvenile prey during early summer may have contributed to the lower carrion usage during that period.

Influence of environmental conditions

Some climatic conditions showed similar effects on the visitations by certain scavenger species. Total daily precipitation negatively affected the visitations of all scavengers, common ravens and red foxes, although the effect on pine marten visitations was only indicative. Ables (1969) similarly observed that foxes avoided getting wet or were reluctant to travel through wet vegetation (Ables, 1969), and Selva (2005) likewise found that pine martens were negatively affected by precipitation (Selva et al., 2005). Although there is little available information about the behavior of ravens in relation to rainfall, a reduction in their general movement during heavy rain cannot be excluded. Eurasian lynx did not appear to be influenced by precipitation.

Despite the absence of seasonal differences in the visitations of wild boar, both wild boar and marten were negatively affected by snow depth; which can be explained by the fact that deeper snow generally inhibits movement, as has been observed for wild boar and fishers (*Martes pennanti*) (Raine, 1983; Thurfjell et al., 2014). However, a thick or persistent layer of snow covering carrion may also reduce the concentrations of olfactory cues, which prevent pine martens, as well as wild boar, as a short-legged, highly olfactory foraging species (Briedermann, 1990), from successfully detecting carrion. While this would also presumably affect other scavengers, snow depth did not seem to influence visitations by the other scavenger species. Lastly, in none of the models did canopy openness have any influence on visitation rates, although a potential limitation was that the canopy openness data was based on a survey performed in the summer (Latifi et al., 2016). Canopy openness during other seasons might have yielded slightly different results in scavenger behavior.

Provisioning schedule

Somewhat surprisingly, whether carcasses were placed randomly at unique locations, or predictably at fixed locations at regular intervals did not influence the carrion visitations of any of the considered species. Stiegler et al. (2020) performed a similar experiment in the Bavarian Forest, and also found no effect of provisioning schedule. They suggested that the abundance of scavenger species may be such that carrion is detected regardless of predictability (Stiegler et al., 2020). Another study performed in the same area, found no differences in carrion detection times by foxes between provisioning schedules (Große, unpublished). Furthermore, the average duration of a carcass deployment was 43.2 days, and the time between deployments may be too long to habituate scavengers to a provisioning schedule, requiring more frequent deployments to become an effective supplementary feeding station (Cortés-Avizanda et al., 2016; Moreno-Opo et al., 2015). However, regular carrion provisioning may have potential spillover effects on species outside the scavenger guild. Tobajas et al. (2022) found in a similar experiment that an increase in experimental carrion provisioning may increase the carrying capacity of an ecosystem and thus support higher numbers of predators, which may pose a threat to other prey species (Tobajas et al., 2022).

Human disturbance

Except for wild boar, none of the investigated scavenger species displayed a change in visitation in response to human disturbance. Neither the distance to the management zone, where hunting occurs, nor

road density around the carrion sites significantly impacted visitation rates. Red foxes are generally known to tolerate human presence (Gloor, 2002) and can adapt to living close to human infrastructure (Jackowiak et al., 2021). By contrast, despite its protected status in Germany (Trouwborst, 2010), the apex predator lynx is a reclusive species and sensitive to human disturbance (Ripari et al., 2022). However, although recreational activities occur throughout the BFN, there was no indication of an influence of human-related variables on lynx visitations. While circadian patterns were not considered, lynx generally avoid trails and roads during the daytime (Filla et al., 2017), and their nocturnal activity in the study area, particularly during summer, has been observed (Große, unpublished). Nighttime visitations of carrion sites will be subject to the lowest human pressure in the park, although human recreation may reduce both the number of nights as well as the number of hours spent at a carrion site on a particular night (Belotti et al., 2018). Thus, carrion provisioning at places located further away from roads may provide a larger benefit for reclusive species.

In the BFN, wild boar is the only scavenger species hunted in the management zone. In this study, its visitation rates decreased with increasing road density. Wild boars are known to cross roads in areas used for foraging but avoid roads with heavy traffic (Thurfjell et al., 2015). The road network in the analysis consisted of motorized roads, forest trails, and pathways. Over the last few decades, wild boar populations in Germany have increased, together with the hunting effort in the BFN but also the number of traffic accidents. These latter trends can lead to an avoidance of human infrastructure by wild boar.

Conclusions

This study showed that when carrion is made available to facultative scavengers year-round, four of the five studied frequent scavengers nonetheless displayed varying seasonal visitation rates. Only wild boar showed equal visitations throughout the year, and although the common raven visited carrion in all seasons, it had an erratic visitation pattern. Our results indicate that when carrion is equally available year-round, at least experimentally, most scavengers will maintain a seasonal pattern of carrion visitation, with differences in carrion visitation depending on the functional group within the scavenger guild. Further investigation of specific behaviors, the sex of the visiting scavengers, and the demography of the studied species may shed further light on the individual needs for carrion and the motivation for carrion consumption during the preferred periods. Controlling for species abundance and investigating both inter- and intra-specific competition may also reveal additional patterns in carrion consumption. In addition, investigations of other scavenger species may reveal a carrion dependence on the broader scavenger guild. In terms of wildlife management, the deployment of carrion subsidies, whether fresh or frozen, both at permanent and random locations was beneficial. As climate change is on track to worsen for the foreseeable future (Smol, 2012), the winter period in temperate climates will likely become shorter (Meehl et al., 2004). This may lead to a more extended vegetation period, with more food resources available to ungulates, reducing their high late-winter mortality. Additionally, more alternative resources may be available to scavengers as well. As at least three of the five scavengers in this study concentrated their visitations to late winter/early spring, regardless of the year-round availability of carrion, subsidies of carrion during this period, together with the expected increase in apex predator population size, might offset some of the predicted effects of climate change on the scavenger guild, by providing a more constant and abundant source of ungulate carrion in the landscape (Wilmers & Getz, 2005).

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CRediT authorship contribution statement

Nicolas De Pelsmaeker: Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Nicolas Ferry:** Formal analysis, Investigation, Validation, Writing – review & editing. **Jonas Stiegler:** Validation, Writing – review & editing. **Nuria Selva:** Methodology, Validation. **Christian von Hoermann:** Validation, Writing – review & editing. **Jörg Müller:** Writing – review & editing. **Marco Heurich:** Conceptualization, Formal analysis, Supervision, Validation, Writing – review & editing.

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.

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Supplementary materials

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