WILDLIFE BIOLOGY

Research article

Use of viscera from hunted roe deer by vertebrate scavengers in summer in central European mountainous mixed forest

Sebastian Schwegmann, Ilse Storch and Manisha Bhardwaj

Chair of Wildlife Ecology and Management, University of Freiburg, Freiburg, Germany

Correspondence: Sebastian Schwegmann (sebastian.schwegmann@gmail.com)

Wildlife Biology
2023: e01117
doi: 10.1002/wlb3.01117

Subject Editor: Nuria Selva
Editor-in-Chief:
Christian A. Hagen
Accepted 18 July 2023

Carrion is a valuable resource in forests, providing sustenance for vertebrate and invertebrate scavenger communities and contributing to ecosystem functions, such as nutrient cycling. Intensive ungulate hunting, and thereby extraction of carcasses, removes large quantities of potential carrion from the system, denying a valuable resource from scavenger fauna. It may be possible to reduce the loss and negative consequences to forest biodiversity by retaining evisceration residues from hunted deer, where full carcasses cannot be retained. However, what roll evisceration residues play as a resource for scavengers in temperate forests is not well understood. In this study, we exposed 47 carrion samples from hunted roe deer, in front of triple sets of camera traps, to examine how hunting remains are removed and fed upon by vertebrate scavengers. Overall, 70% of the samples were completely removed from experimental sites by vertebrates. We detected twelve vertebrate taxa feeding on evisceration residues, including martens (*Martes* spp.), red kites *Milvus milvus* and garden dormice *Eliomys quercinus*. Common buzzards *Buteo buteo* and Eurasian jays *Garrulus glandarius* were the most frequent feeders on carrion samples, while red foxes *Vulpes vulpes* displaced the largest proportion of samples. Finally, we found a range of insectivorous bird and mammal species using hunting remains as a source for invertebrate prey, while not scavenging on the remains directly. We demonstrate that evisceration residues can be a valuable resource for a wide range of taxa and suggest that viscera retention from hunted game may contribute to resource provisioning for scavengers in forest ecosystems.

Keywords: *Capreolus capreolus*, carcass, evisceration residues, hunting, invertebrates, scavengers

Introduction

Scavengers, in addition to having intrinsic conservation value, fulfil a range of ecosystem services, e.g. decomposition of carcasses and subsequent release of nutrients, which are important for ecosystem functioning and nutrient cycling (DeVault et al. 2003, Wilson and Wolkovich 2011, Beasley et al. 2016). Maintaining the scavenger guild, consisting of vertebrate as well as invertebrate taxa, is thus of great importance for conservation of ecological processes and functions throughout a range of ecosystems (Barton et al. 2013).

Carrion in turn is an essential resource for vertebrate and invertebrate scavenger communities (Matuszewski et al. 2010b, Barton et al. 2013, Stiegler et al. 2020). Scavengers often acquire carrion at kill sites, where large predators leave parts of carcasses behind (Wilmers et al. 2003, Helldin and Danielsson 2007, Allen et al. 2015). However, in much of central Europe, where large carnivores such as wolves *Canis lupus* or lynx *Lynx lynx* have been extirpated, carrion provisioning has consequently reduced. Despite the ongoing re-establishment of large predator populations in central Europe (Chapron et al. 2014, Herzog 2019), ungulate populations are heavily managed through hunting (Gordon et al. 2004, Hothorn and Müller 2010). Carrion can be provisioned through hunting (Wikenros et al. 2013, Mateo-Tomás et al. 2015), for example, trophy hunters can leave large parts of the game carcasses in the ecosystem, and large animals hunted for meat (e.g. moose, *Alces alces*) may be butchered on site, providing large amounts of residues to scavengers (Mateo-Tomás et al. 2015, Lafferty et al. 2016). In parts of Europe, including Germany, it is a widespread practice to leave evisceration residues, i.e. the internal organs, of large herbivores in the field, however, due to growing concerns of food hygiene and practicality, hunters are increasingly choosing to eviscerate large herbivores ex-situ, thereby extracting the entire animal carcass from the ecosystem (Bartels and Bülte 2011, Mirceta et al. 2017, Gomes-Neves et al. 2021). Furthermore, carcasses of small game and of wild boar are generally extracted completely, the latter due to reducing the risk of spreading disease like African swine fever. Thus, despite having the possibility to, current hunting practices do not provision carrion to the same rate as natural predators, and scavengers may be missing an essential resource.

While all vertebrate scavengers in central Europe, except for vultures, are facultative, many invertebrate scavengers are specialized obligatory scavengers, which means they are dependent on carrion as a resource (Charabidze et al. 2016, Matuszewski and Mądra-Bielewicz 2022, von Hoermann et al. 2021). Currently, it is unclear how much carrion in space and time and in which quality is needed to maintain native necrophagous fauna and corresponding ecosystem services (Barton et al. 2019). In a prior study, we found that roe deer *Capreolus capreolus* viscera left from hunting could in part functionally replace ungulate carcasses as a resource for necrophagous insects (Schwegmann et al. 2022). However, in the previous study, we placed the viscera samples in metal cages, which excluded vertebrate scavengers from consuming roe deer viscera before invertebrates could make use of this resource. In order to determine how limiting vertebrate scavengers can be on the access of invertebrates to carcasses, the first goal of the present study is to investigate what proportion and how quickly evisceration residues are used by vertebrate scavengers, and consequently made unavailable to invertebrates. We expect evisceration residues to be partly available to invertebrates, as evisceration residues will not always be removed or fully depleted by vertebrates. Our second goal was to describe the scavenging guild and scavenging patterns of vertebrates on evisceration residues in a temperate mountainous mixed forest in central Europe. We expect multiple facultative vertebrate scavenger taxa to use evisceration residues as a resource. While the use of hunting residues by scavengers has been studied previously (Selva et al. 2005, Mateo-Tomás et al. 2015, Gomo et al. 2017), this is, to our knowledge the first study surveying these patterns using a standardised experimental approach with camera traps in Central Europe, as well as the first study solely using evisceration residues of roe deer, the most abundant and most commonly hunted ungulate in Germany (DJV 2023).

Material and methods

Study region

We conducted this experiment in the southern Black Forest, in Baden-Württemberg, Germany (47°53′27.3″–47°52′52.3″N and 8°04′45.5″–8°06′24.5″E, 960–1150 m a.s.l.). The southern Black Forest is a mountainous mixed forest, dominated by Norway spruce (*Picea abies* H. Karst.), silver fir (*Abies alba* MILL.) and beech *Fagus sylvatica*. The average annual temperature in the region is about 7.1°C with a yearly average precipitation of 1484 mm (AM Online Projects 2018). Roe deer is the most abundant large herbivore in the region and is hunted from May until January (MLR 2019). The average hunting bag for roe deer in forests ecosystems in the federal state of Baden-Württemberg is 12.2 roe deer per 100 ha and year (MLR 2019). The scavenger community in the study region is exclusively comprised of facultative scavengers such as mesopredators (e.g. red fox, *Vulpes vulpes*), mustelids (e.g. martens, *Martes* spp.), birds of prey (e.g. common buzzard, *Buteo buteo*), corvids (e.g. Eurasian jay, *Garrulus glandarius*), other omnivorous birds (e.g. great tit, *Parus major*) and small mammals (e.g. Voles). Apex predators like wolf, lynx and non-native mesopredators racoon *Procyon lotor* and raccoon dog (*Nyctereutes procyonoides* GREY) only occur sporadically (MLR 2019).

Experimental set-up

We conducted this experiment 16 days each month from May to October 2022, on a total of 48 experimental sites spread throughout the study area. All experimental sites were in mixed-species forests with closed canopy, little understory vegetation, and away from hiking trails and forest roads to avoid interference of hikers. Each month, we placed eight residues at experimental sites, that were at least 200 m apart, maximizing distances between samples as much as possible in our study area, to minimise overlaps of individual carcass odour bouquets for terrestrial scavengers. No sites were repeated between months to avoid potential scavenger habituation effects and were at least 50 m away from previously sampled sites. We conducted the experiment from May to October because during this time roe deer are hunted in our study area and insect activity is high.

On each experimental site, we exposed roe deer evisceration residue samples 2–5 m in front of three camera traps (Bushnell Trophy Cam HD Aggressor Low Glow). Two cameras were only motion triggered, while the third continuously took pictures every hour for the entire observation time, to ensure we recorded when a scavenger removed a sample. Cameras were set to three-picture bursts with no delay between activations. Thus, pictures were taken continuously as long as movement was detected. Cameras were collected after removal of the sample or after 16 days (in accordance to previous findings indicating after 16 days necrophagous invertebrates depleted evisceration residues; Schwegmann et al. 2022).

All viscera used in this study were acquired through regular roe deer hunting in the region, and thus, no animals were killed particularly for this study. Samples contained rumen, liver, kidneys, spleen, bowel, bladder, reproductive organs, windpipe and connecting tissues, while heart and liver were only left in some samples. Samples were frozen at −27°C until two days prior to exposure. While this practice potentially affected sample microbiome, physical or chemical properties (Medić et al. 2018), it was necessary due to practical considerations and to facilitate systematic set-up of the experiment, and it is unlikely that freezing samples impacted carrion use by vertebrate scavengers (Stiegler et al. 2020). The average weight of each sample was 4.0 kg (range: 2.5–5.5 kg).

Analysis

We aggregated camera trap pictures into 'events,' i.e. a sequence of pictures of the same scavenger species. We assumed events were independent if there was an interval of more than 20 min between consecutive pictures (O'Brien et al. 2003). For each event, we recorded the species and days after exposure (i.e. when the residues were placed at the sites). We also classified the type of interaction the species had with the viscera sample: 1) visit: no direct feeding on sample (but could have been e.g. feeding on insects or around the sample); 2) feeding: Observed fang or beak of the scavenger touching the carrion samples; 3) removal: Observed displacement of the sample, completely outside the view of the camera trap by the animal. For an event to be included in the dataset it only needed to be detected by one of the cameras. We considered a sample removed when no parts of the sample remained visible in any later camera recordings. Thus, events were scavengers only removed a part of the carrion sample were recorded as feeding events. Detecting feeding behaviour for small mammals was difficult due to the quality of camera trap pictures and the size of the animals. As a conservative approach, we only considered small mammals to be feeding when animals were dragging or moving parts of the sample. It is, however, possible that a significant part of small mammal feeding events were overlooked. Events after a sample was removed were not classified or included into analysis, even when the event occurred within the 16 day observation period. We included all species known to be predators or facultative scavengers, or those that we observed feeding on the carrion sample. Herbivores, like brown hare (*Lepus europaeus* PALLAS), or birds feeding on insects (e.g. blackbird, *Turdus merula*) were not included in the dataset. Marten species (*Martes martes* and *Martes foina* ERXLEBEN) could not always be determined to species level, in which case we recorded the event as 'Marten'. Mice, voles, and shrews could not be determined to species level, therefore we summarized them into one category, 'Small mammals'. The only exceptions to the small mammal category were garden dormice *Eliomys quercinus*, and red squirrels *Sciurus vulgaris*, which were determined separately. One sample was excluded from analysis due to technical failure of the cameras.

We summarized all detected events per species and event type to assess which taxa were frequently responsible for the removal of evisceration residues, and which taxa frequently visited or fed upon the viscera samples and compare these frequencies among taxa. Additionally, we assessed the removal of samples over the course of the experiment and the daily activity patterns of the different scavenger groups (birds, mesopredators and small mammals) by calculating the temporal overlap of activity.

To assess feeding and visit rates over time we fitted generalized linear models (GLMs). In separate models, we used the number of visit or feeding events of all scavenger taxa per day as the response variable and the number of days after exposure as a numerical predictor. We assumed a negative-binomial distribution, as we were dealing with count data, and added an offset term for the number of samples that remained on site and were not fully displaced. To assess model fit, we compared our models with their respective null-models, and assessed the spread of residuals was visually. We deemed effects with $\alpha = 0.05$ or lower as significant. Temporal activity patterns and overlap of scavenger groups were assessed using kernel density estimates of activity throughout the day, and accounted for all, sun time corrected, visit and feeding events. We conducted all analysis and visualizations using R ver. 4.1.2 (www.r-project.org). We conducted the GLMs using the 'glmmTMB' package (Brooks et al. 2017), and the activity analysis with the 'overlap' package ver.0.3.4 (Meredith and Ridout 2021). The temporal overlap between scavenger groups was calculated using the *overlapEst* function, and we report *Dhat4* estimates which are deemed adequate for sample sizes with $n > 50$.

Results

Out of 47 viscera samples, 29.8% ($n = 14$) were not fully removed by vertebrate scavengers from experimental sites within 16 days, and at 8.5% of sites ($n = 4$) no feeding events were detected (Fig. 1). Red foxes were most frequently observed removing entire samples from experimental sites ($n = 17$, 36.2%). Five samples were removed but the animal doing so was not captured by the camera traps. Samples were removed by scavengers on average after 4.1 days of exposure; earliest removal event occurred less than three hours after the sample was exposed at the experimental site, while the latest removal was detected twelve days after exposure (Fig. 2).

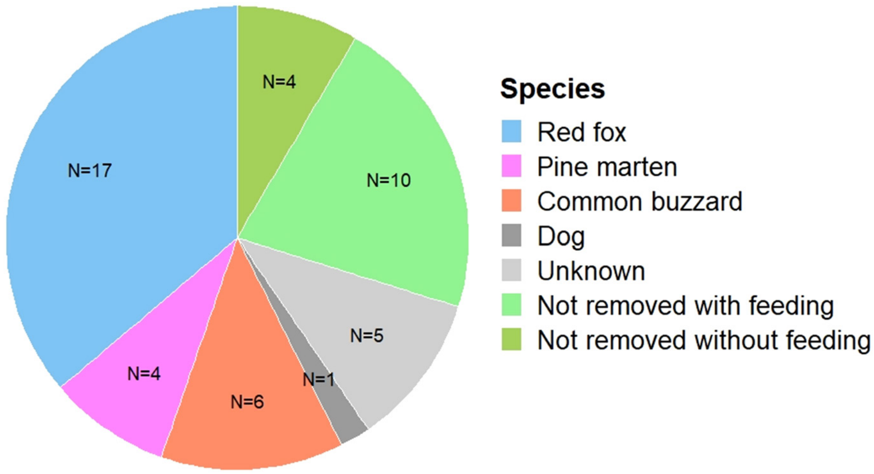

Figure 1. Number of roe deer evisceration residues removed by each vertebrate scavenger species. Light green represents samples that were fed upon but not removed (n = 10). Olive green represents samples that were not fed upon or removed (n = 4). Light grey represents samples were removed but the responsible scavenger species could not be determined (n = 5).

Of the 33 removed samples, 69.7% (n = 23) were removed within the first five days after exposure. In every month, at least one sample out of eight was not removed from the experimental sites; in May and September four of the samples were not removed.

We detected 597 events of vertebrate scavengers at our experimental sites (Table 1). On average, we detected 7.96 visit and 4.74 feeding events (including removal) per sample. The mean number of potential scavenger taxa detected at experimental sites was 2.45, while on average, 1.4 taxa were detected feeding on or removing the carrion sample.

Common buzzards (n = 77) and Eurasian jays (n = 50) were most frequently captured feeding on the carrion samples. Small mammals were most often observed at the sites (n = 206) but were only detected feeding on the sample in four out of the 206 events. Red fox removed the carcasses most often, and removed the carcass is 17 out of 20 feeding/removal events. Overall, in more than half of all marten and red fox events, the individual(s) did not show feeding behaviour or removal of the carrion sample. Finally, we detected

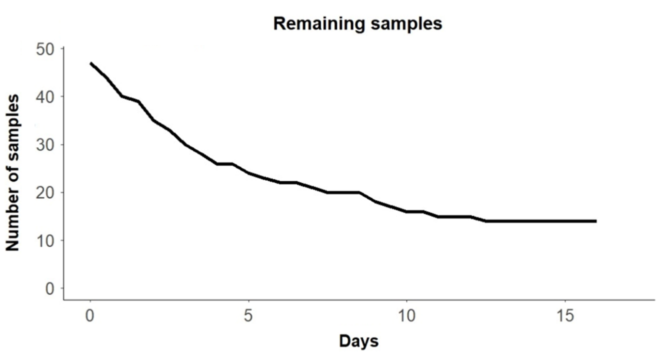

Figure 2. Removal of evisceration residues by vertebrate scavengers over time. This graph only indicates presence/absence of samples but not biomass depletion due to vertebrate or invertebrate feeding or decay.

two domesticated species scavenging (*C. lupus familiaris* and *Felis catus*), as well as two omnivores without any feeding events.

The average number of feeding events per sample, when corrected for the number of removed samples, declined significantly over the time ($p < 0.001$, Table 2, Fig. 3), while the number of visits did not change over time ($p > 0.05$; Fig. 3). Both models explaining the detections of events through time were a much better fit than the respective null-model (ΔAIC > 2 of null model relative to time model, Table 2). Small mammals and mesopredators tended to be active at night and at the same time (80.78%, Fig. 4). For mesopredators some activity including removal events was detected during daylight (Fig. 5). Avian scavengers were largely diurnal, and their activity overlapped little with mesopredators (23.67%) and small mammals (9.88%; Fig. 4).

Discussion

Evisceration residues from hunted roe deer can be a valuable resource for necrophagous invertebrates (Schwegmann et al. 2022). Here, we assessed the level of use and displacement of viscera from hunted roe deer by vertebrate scavengers, to understand whether viscera are available to invertebrates despite vertebrate scavenging. In our present study, we show that a substantial amount of evisceration residues from hunted roe deer remained available for necrophagous insects and other invertebrates even when numerous species of vertebrate scavenger make use of the same resource. We assumed that removed samples (i.e. samples that were carried out of frame of view of the camera traps) were fully consumed by vertebrates, however, it is possible that the removing taxa (red fox, pine marten, common buzzard) left fractions of the samples unconsumed in other locations and therefore still available as a resource for invertebrates and other vertebrate scavengers.

Table 1. Overview of all detected events per species as well as proportion of samples visited or fed upon. For five removal events the responsible species was not detected, thus these events are not included in the table.

	All events	Visit events	Feeding events	Removal events	Prop. samples with visit events	Prop. of samples with feeding or removal events
Red fox (*Vulpes vulpes*)	44	24	3	17	0.45	0.43
Pine marten (*Martes martes*)	27	11	12	4	0.28	0.13
Stone marten (*Martes foina*)	17	13	4	0	0.17	0.06
Marten (*Martes* spp)	17	14	3	0	0.19	0.04
Badger (*Meles meles*)	2	2	0	0	0.04	0
Red squirrel (*Sciurus vulgaris*)	15	15	0	0	0.13	0
Garden dormouse (*Eliomys quercinus*)	75	67	8	0	0.17	0.04
Small mammals (Rodentia and Soricidae)	206	202	4	0	0.30	0.04
Common buzzard (*Buteo buteo*)	90	7	77	6	0.32	0.32
Red kite (*Milvus milvus*)	25	2	23	0	0.09	0.09
Raven (*Corvus corax*)	1	0	1	0	0.02	0.02
Eurasian jay (*Garrulus glandarius*)	64	14	50	0	0.17	0.17
Great tit (*Parus major*)	9	0	9	0	0.02	0.02
Dog (*Canis lupus familiaris*)	2	1	0	1	0.04	0.02
House cat (*Felis catus*)	3	2	1	0	0.04	0.02
Total	597	374	195	28		

Our results on the vertebrate scavenger guild using evisceration residues are generally in line with studies published from other areas of Europe (Selva et al. 2005, Wikenros et al. 2013, Mateo-Tomás et al. 2015, Gomo et al. 2017). As previously described in the literature, we found that red fox was the mammalian scavenger that most intensively using viscera samples (DeVault et al. 2011, Killengreen et al. 2012). In contrast to other studies, where common ravens *Corvus corax* were the most frequent scavengers (Selva et al. 2005, Wikenros et al. 2013, Mateo-Tomás et al. 2015, Gomo et al. 2017), we only detected one feeding event of ravens in our experiment. This may possibly be due to the lack of acoustic cues, such as the sound of gunshots, that are suspected to lure ravens to carcasses (White 2005, Gomo et al. 2017), however alternatively it is also possible that ravens avoided approaching due to suspicion of triple sets of camera traps. Similarly, we also did not detect corvids like carrion crow *Corvus corone* and Eurasian magpie *Pica pica* on our camera traps, as would be expected from the findings of other studies, but it is likely that this is because, while common in the region, these birds are rarely found within the higher elevations of the Black Forest, where our experiments took place. Interestingly, while small mammals like rats, mice, voles, and shrews are known to display opportunistic scavenging behaviour (DeVault and Rhodes 2002, Henrich et al. 2017, Selva et al. 2019), few studies describe the extent of their scavenging behaviour and, to our knowledge, our study is the first report of garden dormouse (*E. quercinus*; Díaz-Ruiz et al. 2018), scavenging on ungulate carrion. Other predator or facultative scavenger species that occur in the region but were not detected on our experimental site are wild boar *Sus scrofa*, polecat *Mustela putorius*, and great spotted woodpecker *Dendrocopos major* (DeVault and Rhodes 2002, Mateo-Tomás et al. 2015, Selva et al. 2019).

The feeding activity per carrion sample decreased over the course of the experiment. This indicates that viscera samples were depleting and/or rendered unattractive as a resource for vertebrate scavengers through decay, microbes, and consumption by invertebrates (Janzen 1977, Schwegmann et al. 2022). Similar to our results, previous studies detected very

Table 2. Negative Binomial regressions results for number of events over time. Significant effects ($\alpha = 0.05$) are shown through bold text.

		Coefficient	Std-error	t-value	p-value	R^2	AIC
Visits	*Events ~ Time*					0.14	221.3
	Intercept	−0.265	0.346	−0.766	0.444		
	Time	−0.072	0.039	−1.845	0.065		
	Events ~ Null					0	327.4
Feeding	*Events ~ Time*					0.40	162.2
	Intercept	−0.445	0.204	−2.187	**0.029**		
	Time	−0.148	0.029	−5.144	**< 0.001**		
	Events ~ Null					0	258.7

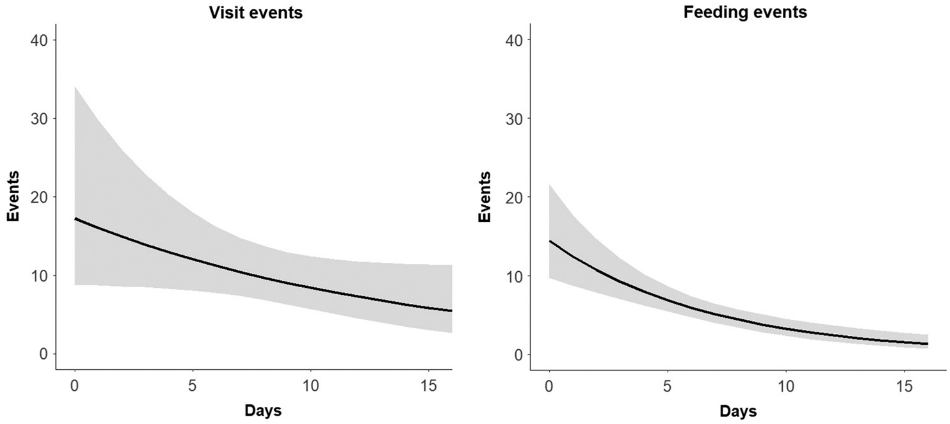

Figure 3. Visit and feeding events (including removal) over time corrected for the number of carrion samples removed.

few scavenging events by vertebrates around after 20 days past exposure, indicating over the warm period most carrion will be depleted after this time (Inagaki et al. 2022, Mctee and Stone 2022).

We were unable to directly compare carcass use by vertebrate relative to invertebrate scavengers, however, similar to entire carcasses, invertebrates were able use a significant proportion of carrion (Ray et al. 2014, Sawyer et al. 2022, Schwegmann et al. 2022). Competition between vertebrates and invertebrates at carrion may be mediated by environmental conditions, such as season/temperature, and forest structure. While invertebrates only make use of carrion outside winter, vertebrates tend to scavenge more in periods of lower temperatures (DeVault et al. 2004, Selva et al. 2005, Turner et al. 2017). Forest structure can affect invertebrate activity through changes in microclimate

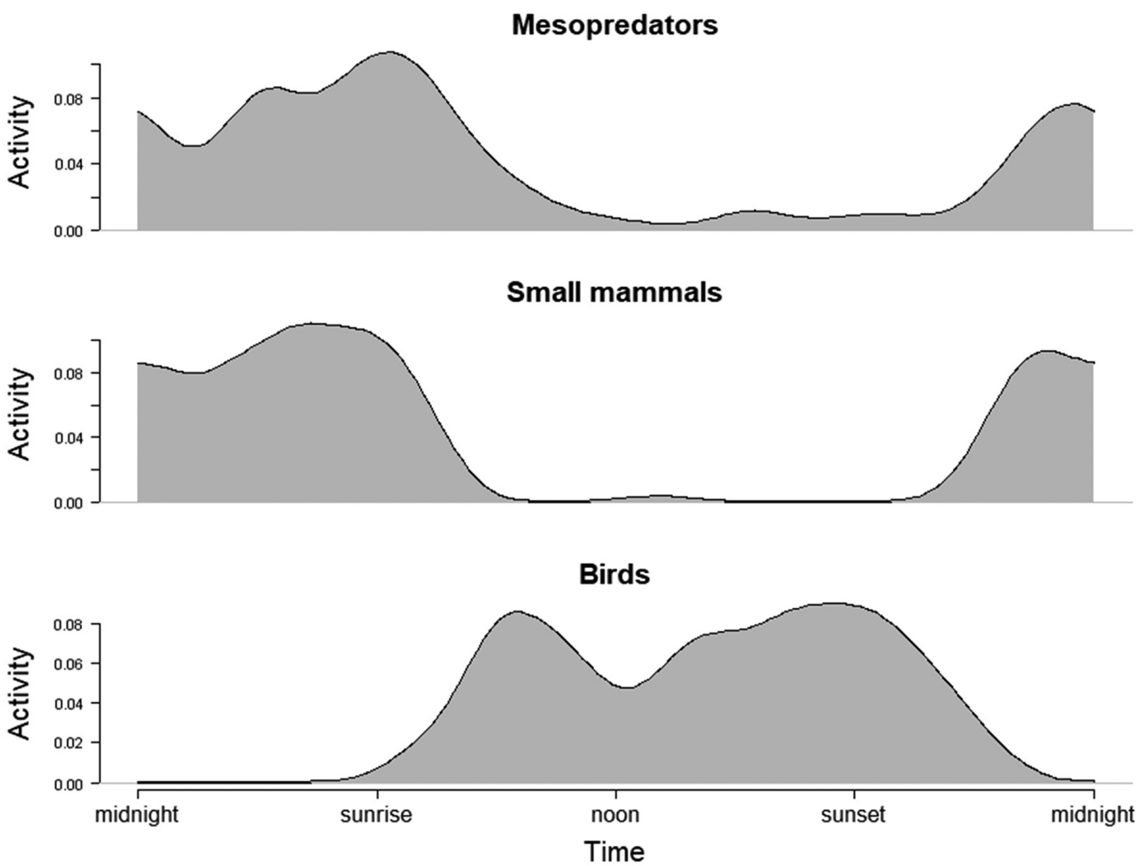

Figure 4. Temporal activity patterns of vertebrate scavengers with feeding and visit events combined. *Mesopredators* include red foxes and marten species; small mammals include garden dormice and undetermined mice and voles; birds include common buzzards, red kites, Eurasian jays, and ravens. Density curve is corrected for sun time.

Figure 5. Feeding and removal events by vertebrate scavengers captured by camera traps: (A) red kite, (B) red fox, (C) Eurasian jay and (D) garden dormouse.

and vegetation characteristics (Matuszewski et al. 2010a, von Hoermann et al. 2020, Sawyer et al. 2022), or influence carrion detection by vertebrate scavengers (e.g. high canopy closure diminishes detection by avian scavengers, Inagaki et al. 2022). Thus, different forest types may functionally exclude competition between vertebrates and invertebrates. To understand the extent of direct competition between vertebrate and invertebrate scavengers on carrion, future studies should investigate upon the effects of forest structure on the relative carrion by vertebrate and invertebrate scavengers. Additionally, to assess the relative use of carrion by different vertebrate scavengers, the number of feeding events detected per species needs to be corrected by respective relative abundances or population densities in the study area. In our study area, these data are not available, however, in the future this should be assessed to evaluate the importance of carrion for different scavenger species.

We argue that viscera retained from hunting can be a localized 'ecological hotspot'. The ecological importance of carrion goes beyond the direct provisioning of resources to vertebrate and invertebrate scavengers, as carcasses also enrich nutrients in the soil and thereby affect plant communities (Towne 2000, Melis et al. 2007, Barton et al. 2013, Teurlings et al. 2020). Carrion also offers suitable resources for insects such as Diptera to lay eggs, the larvae of which can be in turn consumed by predatory beetles like Histeridae and Staphylinidae (Greene 1996, Battán Horenstein and Linhares 2011). Finally, we also detected a range of vertebrate species clearly feeding on insects on and around our carrion samples on our camera traps. While we found some feeding events of small mammals and garden dormice, most detections were classified as visits (i.e. lacking clear evidence of feeding), due to quality of the camera trap pictures, thus likely underestimating the number of feeding events by small mammals. However, we often detected small mammals including dormice feed on insects on the carcass sites (detected by removal of large beetles). Beyond that, we detected common blackbird, song thrush (*Turdus philomelos* BREHM), mistle thrush *Turdus viscivorus* and European robin *Erithacus rubecula* feeding on insects on and around evisceration residues. Due to the quality of camera trap pictures it was not possible to always clearly distinguish these events from visits and thus reliably quantify insect feeding events. It is clear that carrion provide a range of direct and indirect resources, and future studies exploring these patterns would enrich our understanding of the extent to which carrion serves the ecosystem.

Our results show that carrion from hunting can be beneficial for scavenger communities, however when considering viscera retention as a conservation measure some points have to be considered. Firstly, the type of ammunition used during hunting matters. In the German federal state of Baden-Württemberg, where we conducted our experiment, lead ammunition for hunting is forbidden (JWMG § 31 2014). This is however not the case everywhere and lead from bullet fragments, retained in the evisceration residues, might be consumed by scavengers and thereby enter the food chain and potentially causing lead poisoning in wildlife (Kalisinska et al. 2016, Mctee et al. 2019, Pain et al. 2019). Secondly, scavenging processes on carrion can also facilitate disease propagation (Vicente et al. 2011, Moleón and Sánchez-Zapata 2021). Specifically, the outbreak of African swine fever in Europe calls for extraction of wild boar entrails. However, retention of hunting remains of herbivores like deer will mostly be unproblematic, especially alongside close inspection of carcasses for diseases during evisceration. Lastly, subsidising carrion to facultative scavengers that are generally also predators may lead to increased predation pressure for other species. Red foxes for example historically profited from anthropogenic influences on temperate ecosystems, e.g. the removal of apex predators as well as the provisioning of additional resources (Prugh et al. 2009). At the same time red foxes can be problematic for conservation of their prey, such as ground breeding birds (Kämmerle et al. 2017). A recent study by Tobajas et al. (2022) suggested that carrion provisioning to mesopredator communities, especially in winter, might increase predation pressure on threatened western capercaillie *Tetrao urogallus*, as carrion subsidies allow for higher mesopredator densities. Overall, the practicability of providing hunting remains to the scavenger community depends on local circumstances that determine whether the above-mentioned risk factors can be problematic.

Conclusion

We observed the vertebrate scavenger community using evisceration residues from hunting in a mountainous mixed forest in central Europe. In total, 12 vertebrate taxa used hunting remains including, mesopredators, birds of prey, corvids and small mammals. While red foxes, common buzzards and pine martens removed some of carrion samples, a substantial amount of hunting residues was available for necrophagous insects as well. Although we did not find all potential scavengers of our study region to be feeding on hunting remains, the observed scavenging patterns are mostly in line with reports from other studies from European boreal forests. Additionally, we observed that a range of insectivorous mammal and bird species were also attracted to carrion and used it as a source of prey. Our studies show that a wide range of vertebrate (this study) as well as invertebrate (Schwegmann et al. 2022) taxa use evisceration residues directly or indirectly as a resource. Carrion subsidies from hunting might help maintaining vertebrate and invertebrate scavenging communities as well as scavenging as ecosystem function. Using evisceration residues as a conservation measure is possible as long as some circumstantial factors like the use of adequate ammunition and the risk of diseases are considered.

Acknowledgements – We thank the forestry office Kirchzarten, as well as Hansjörg Frei and Valentin Platten, for supporting us in sample collection. We thank Dr Nuria Selva as well as three anonymous reviewers for valuable comments and suggestions. We gratefully acknowledge support by the the German Science Foundation (DFG), Research Training Group ConFoBi (GRK 2123). Open Access funding enabled and organized by Projekt DEAL.
Funding – This study was funded by the German Research Foundation (DFG), ConFoBi project no. GRK 2123.

Author contributions

Sebastian Schwegmann: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Ilse Storch**: Funding acquisition (lead); Methodology (supporting); Supervision (supporting); Writing – review and editing (supporting). **Manisha Bhardwaj**: Formal analysis (supporting); Methodology (supporting); Supervision (lead); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1002/wlb3.01117.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.q573n5tpp (Schwegmann et al. 2023).

References

Allen, M. L., Elbroch, L. M., Wilmers, C. C. and Wittmer, H. U. 2015. The comparative effects of large carnivores on the acquisition of carrion by scavengers. – Am. Nat. 185: 822–833.
AM Online Projects. 2018. Climate-Data.org. AM online projects – Alexander Merkel. https://de.climate-data.org/.
Bartels, A. C. and Bülte, M. 2011. Verocytotoxigenic *Escherichia coli* (VTEC) in wild ruminants in Germany. – In: Paulsen, P., Bauer, A., Vodnansky, M., Winkelmayer, R. and Smulders, F. J. M. (eds), Game meat hygiene in focus. Microbiology, epidemiology, risk analysis and quality assurance. Wageningen Academic Publishers.
Barton, P. S., Cunningham, S. A., Lindenmayer, D. B. and Manning, A. D. 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. – Oecologia 171: 761–772.
Barton, P. S., Evans, M. J., Foster, C. N., Pechal, J. L., Bump, J. K., Quaggiotto, M.-M. and Benbow, M. E. 2019. Towards quantifying carrion biomass in ecosystems. – Trends Ecol. Evol. 34: 950–961.
Battán Horenstein, M. and Linhares, A. X. 2011. Seasonal composition and temporal succession of necrophagous and predator beetles on pig carrion in central Argentina. – Med. Vet. Entomol. 25: 395–401.
Beasley, J. C., Olson, Z. H. and DeVault, T. L. 2016. Ecological role of vertebrate scavengers. – In: Benbow, M. E., Tomberlin, J. K. and Tarone, A. M. (eds), Carrion ecology, evolution, and their applications. CRC Press Taylor and Francis Group.
Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M. and Bolker, B. M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – R J. 2017: 378–400.
Chapron, G. et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. – Science 346: 1517–1519.
Charabidze, D., Vincent, B., Pasquerault, T. and Hedouin, V. 2016. The biology and ecology of *Necrodes littoralis*, a species of forensic interest in Europe. – Int. J. Legal Med. 130: 273–280.
DeVault, T. L. and Rhodes, O. E. 2002. Identification of vertebrate scavengers of small mammal carcasses in a forested landscape. – Acta Theriol. 47: 185–192.

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

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

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

Díaz-Ruiz, F., de Diego, N., Santamaría, A. E., Domínguez, J. C., Galgo, A., García, J. T., Olea, P. P. and Viñuela, J. 2018. Direct evidence of scavenging behaviour in the garden dormouse (*Eliomys quercinus*). – Mammalia 82: 486–489.

DJV. 2023. Jagd und Wildunfallstatistik. – Deutscher Jagdverband.

Gomes-Neves, E., Abrantes, A. C., Vieira-Pinto, M. and Müller, A. 2021. Wild game meat – a microbiological safety and hygiene challenge? – Curr. Clin. Microbiol. Rep. 8: 31–39.

Gomo, G., Mattisson, J., Hagen, B. R., Moa, P. F. and Willebrand, T. 2017. Scavenging on a pulsed resource: quality matters for corvids but density for mammals. – BMC Ecol. 17: 22.

Gordon, I. J., Hester, A. J. and Festa-Bianchet, M. 2004. Review: the management of wild large herbivores to meet economic, conservation and environmental objectives. – J. Appl. Ecol. 41: 1021–1031.

Greene, G. L. 1996. Rearing techniques for *Creophilus maxillosus* (Coleoptera: Staphylinidae), a predator of fly larvae in cattle feedlots. – J. Econ. Entomol. 89: 848–851.

Helldin, J.-O. and Danielsson, A. V. 2007. Changes in red fox *Vulpes vulpes* diet due to colonisation by *lynx Lynx* lynx. – Wildl. Biol. 13: 475–480.

Henrich, M., Tietze, D. T. and Wink, M. 2017. Scavenging of small bird carrion in southwestern Germany by beetles, birds and mammals. – J. Ornithol. 158: 287–295.

Herzog, S. 2019. Return of grey wolf (*Canis lupus*) to Central Europe: challenges and recommendations for future management in cultural landscapes. – Ann. Forest Res. 61: 203.

Hothorn, T. and Müller, J. 2010. Large-scale reduction of ungulate browsing by managed sport hunting. – Forest Ecol. Manage. 260: 1416–1423.

Inagaki, A., Allen, M. L., Maruyama, T., Yamazaki, K., Tochigi, K., Naganuma, T. and Koike, S. 2022. Carcass detection and consumption by facultative scavengers in forest ecosystem highlights the value of their ecosystem services. – Sci. Rep. 12: 16451.

Jagd- und Wildtiermanagementgesetz. 2014. §31 Sachliche verbote.

Janzen, D. H. 1977. Why fruits rot, seeds mold, and meat spoils. – Am. Nat. 111: 691–713.

Kalisinska, E., Lanocha-Arendarczyk, N., Kosik-Bogacka, D., Budis, H., Podlasinska, J., Popiolek, M., Pirog, A. and Jedrzejewska, E. 2016. Brains of native and alien mesocarnivores in biomonitoring of toxic metals in Europe. – PLoS One 11: e0159935.

Kämmerle, J.-L., Coppes, J., Ciuti, S., Suchant, R. and Storch, I. 2017. Range loss of a threatened grouse species is related to the relative abundance of a mesopredator. – Ecosphere 8: e01934.

Killengreen, S. T., Strømseng, E., Yoccoz, N. G. and Ims, R. A. 2012. How ecological neighbourhoods influence the structure of the scavenger guild in low arctic tundra. – Divers. Distrib. 18: 563–574.

Lafferty, D. J. R., Loman, Z. G., White, K. S., Morzillo, A. T. and Belant, J. L. 2016. Moose (*Alces alces*) hunters subsidize the scavenger community in Alaska. – Polar Biol. 39: 639–647.

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

Matuszewski, S., Bajerlein, D., Konwerski, S. and Szpila, K. 2010a. Insect succession and carrion decomposition in selected forests of Central Europe. Part 1. Pattern and rate of decomposition. – Forensic Sci. Int. 194: 85–93.

Matuszewski, S., Bajerlein, D., Konwerski, S. and Szpila, K. 2010b. Insect succession and carrion decomposition in selected forests of Central Europe. Part 2. Composition and residency patterns of carrion fauna. – Forensic Sci. Int. 195: 42–51.

Matuszewski, S. and Mądra-Bielewicz, A. 2022. Competition of insect decomposers over large vertebrate carrion: Necrodes beetles (Silphidae) vs blow flies (Calliphoridae). – Curr. Zool. 68: 645–656.

Medić, H., Djurkin Kušec, I., Pleadin, J., Kozačinski, L., Njari, B., Hengl, B. and Kušec, G. 2018. The impact of frozen storage duration on physical, chemical and microbiological properties of pork. – Meat Sci. 140: 119–127.

Mctee, M. and Stone, K. 2022. The scavenger spyglass: how recruiting hunters to watch carrion boosts wildlife research. – J. Wildl. Manage. 86: e22255.

Mctee, M., Hiller, B. and Ramsey, P. 2019. Free lunch, may contain lead: scavenging shot small mammals. – J. Wildl. Manage. 83: 1466–1473.

Melis, C., Selva, N., Teurlings, I., Skarpe, C., Linnell, J. D. C. and Andersen, R. 2007. Soil and vegetation nutrient response to bison carcasses in Białowieża Primeval Forest, Poland. – Ecol. Res. 22: 807–813.

Meredith, M. and Ridout, M. 2021. Package overlap. – https://CRAN.R-project.org/package=overlap.

Mirceta, J., Petrovic, J., Malesevic, M., Blagojevic, B. and Antic, D. 2017. Assessment of microbial carcass contamination of hunted wild boars. – Eur. J. Wildl. Res. 63: 37.

MLR. 2019. Wildtierbericht für Baden-Württemberg 2018. – Ministerium für Ländlichen Raum und Verbraucherschutz (Hrsg.), Stuttgart.

Moleón, M. and Sánchez-Zapata, J. A. 2021. The role of carrion in the landscapes of fear and disgust: a review and prospects. – Diversity 13: 28.

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

Pain, D. J., Mateo, R. and Green, R. E. 2019. Effects of lead from ammunition on birds and other wildlife: a review and update. – Ambio 48: 935–953.

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

Ray, R.-R., Seibold, H. and Heurich, M. 2014. Invertebrates outcompete vertebrate facultative scavengers in simulated lynx kills in the Bavarian Forest National Park, Germany. – Anim. Biodivers. Conserv. 37: 77–88.

Sawyer, S. J., Eubanks, M. D., Beasley, J. C., Barton, B. T., Puckett, R. T., Tomeček, J. M. and Tomberlin, J. K. 2022. Vertebrate and invertebrate competition for carrion in human-impacted environments depends on abiotic factors. – Ecosphere 13: e4151.

Schwegmann, S., Binder, N., von Hoermann, C., Bhardwaj, M. and Storch, I. 2022. Evisceration residues from hunted roe deer as a resource for necrophagous insect fauna in the Black Forest, Germany: a preliminary study. – Wildl. Biol. 2022: e01055.

Schwegmann, S., Storch, I. and Bhardwaj, M. 2023. Data from: Use of viscera from hunted roe deer by vertebrate scavengers in summer in central European mountainous mixed forest. – Dryad Digital Repository, https://doi.org/10.5061/dryad.q573n5tpp.

Selva, N., Jędrzejewska, B., Jędrzejewski, W. and Wajrak, A. 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. – Can. J. Zool. 83: 1590–1601.

Selva, N., Moleón, M., Sebastián-González, E., DeVault, T. L., Quaggiotto, M. M., Bailey, D. M., Lambertucci, S. A. and Margalida, A. 2019. Vertebrate scavenging communities. – In: Olea, P. P., Mateo-Tomás, P. and Sánchez-Zapata, J. A. (eds), Carrion ecology and management. Springer, pp. 71–99.

Stiegler, J., von Hoermann, C., Müller, J., Benbow, M. E. and Heurich, M. 2020. Carcass provisioning for scavenger conservation in a temperate forest ecosystem. – Ecosphere 11: 235.

Teurlings, I. J. M., Melis, C., Skarpe, C. and Linnell, J. D. C. 2020. Lack of cascading effects of Eurasian lynx predation on roe deer to soil and plant nutrients. – Diversity 12: 352.

Tobajas, J., Oliva-Vidal, P., Piqué, J., Afonso-Jordana, I., García-Ferré, D., Moreno-Opo, R. and Margalida, A. 2022. Scavenging patterns of generalist predators in forested areas: the potential implications of increase in carrion availability on a threatened capercaillie population. – Anim. Conserv. 25: 259–272.

Towne, E. G. 2000. Prairie vegetation and soil nutrient responses to ungulate carcasses. – Oecologia 122: 232–239.

Turner, K. L., Abernethy, E. F., Conner, L. M., Rhodes, O. E. and Beasley, J. C. 2017. Abiotic and biotic factors modulate carrion fate and vertebrate scavenging communities. – Ecology 98: 2413–2424.

Vicente, J., Carrasco, R., Acevedo, P., Montoro, V. and Gortazar, C. 2011. Big game waste production: sanitary and ecological implications. – In: Kumar, S. (ed.), Integrated waste management, II. IntechOpen.

von Hoermann, C., Weithmann, S., Deißler, M., Ayasse, M. and Steiger, S. 2020. Forest habitat parameters influence abundance and diversity of cadaver-visiting dung beetles in Central Europe. – R. Soc. Open Sci. 7: 191722.

von Hoermann, C., Lackner, T., Sommer, D., Heurich, M., Benbow, M. E. and Müller, J. 2021. Carcasses at fixed locations host a higher diversity of necrophilous beetles. – Insects 12: 412.

White, C. 2005. Hunters ring dinner bell for ravens: experimental evidence of a unique foraging strategy. – Ecology 86: 1057–1060.

Wikenros, C., Sand, H., Ahlqvist, P. and Liberg, O. 2013. Biomass flow and scavengers use of carcasses after re-colonization of an apex predator. – PLoS One 8: e77373.

Wilmers, C. C., Stahler, D. R., Crabtree, R. L., Smith, D. W. and Getz, W. M. 2003. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. – Ecol. Lett. 6: 996–1003.

Wilson, E. E. and Wolkovich, E. M. 2011. Scavenging: how carnivores and carrion structure communities. – Trends Ecol. Evol. 26: 129–135.