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Short Communication

Evisceration residues from hunted roe deer as a resource for necrophagous insect fauna in the Black Forest, Germany: a preliminary study

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Carrion of wild ungulates is an important resource for microbes, invertebrates and vertebrates, and affects local plant communities and soils. Most wild ungulates in central Europe, however, are intensely hunted and removed from the ecosystem, thus not available as carrion. This study explores the use of evisceration residues as a resource by necrophagous insects in a temperate mountainous forest in Germany. We experimentally compared the relative abundance of necrophagous insects between sites of caged roe deer carcasses and evisceration residues of roe deer using pitfall-traps. While evisceration residues were used by necrophagous insects, significantly more individuals were sampled at entire deer carcasses; when corrected for biomass, however, no significant difference in abundance for Coleoptera groups was found. Overall, evisceration residues were used earlier and for a shorter period than entire deer carcasses. Leaving evisceration residues on site where game animals are obtained might help maintain specialized necrophagous insect communities, although their ecological role cannot completely replace that of whole carcasses of wild ruminants.

Keywords: *Capreolus capreolus*, carcass, carrion, evisceration residues, hunting, necrophagous insects, Silphidae

Introduction

Carrion is the most nutrient rich form of detritus – it serves as a food resource for microbes, vertebrate and invertebrate scavengers, and affects vegetation and nutrient availability in soils (Towne 2000, Matuszewski et al. 2010, DeVault et al. 2011, Barton et al. 2013, Hammermeister 2020, Stiegler et al. 2020). Insects, particularly Diptera and Coleoptera, facilitate the decomposition and nutrient cycling of carrion (Barton et al. 2013, von Hoermann et al. 2018). The most abundant dipteran families on carcasses are: carrion flies (Calliphoridae), flesh flies (Sarcophagidae) and stable flies (Muscidae) (Matuszewski et al. 2010, Grzywacz et al. 2017, Buenaventura et al. 2021). The coleopteran community on carrion is dominated by: burying beetles



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(Silphidae: Nicrophorinae), clown beetles (Histeridae), rove beetles (Staphylinidae), round fungus beetles (Leiodidae) and dung beetles (Geotrupidae and Scarabaeidae) (Watson and Carlton 2005, Matuszewski et al. 2011, Prado e Castro et al. 2012, Mađra et al. 2015, von Hoermann et al. 2018, 2020b, Weithmann et al. 2021).

Roe deer *Capreolus capreolus* is the most common and wide-spread large mammal species in central Europe (Andersen 1998, Linnell et al. 2004, Aulagnier et al. 2018). In Germany, roe deer are intensively hunted to reduce browsing damage in forests and agricultural fields (Putman and Moore 1998, Hothorn and Müller 2010). Approximately 40% of the roe deer population is culled each year (estimated population: 2.5 million, annual hunting bag: > 1.2 million (Deutsche Wildtierstiftung 2021, DJV 2021). Roadkill is the second largest cause of roe deer mortality (Pagany 2020, von Hoermann et al. 2020a), e.g. in 2019/2020, 22 060 of the 154 869 roe deer reported dead in the state of Baden–Württemberg were due to road collisions. While it is permitted to leave roadkill carcasses in the field (if potential disease propagation can be ruled out) roadkill is generally discarded by incineration (Landesuntersuchungsamt Rheinland Pfalz 2017a, Bundesministerium für Ernährung und Landwirtschaft 2022). Thus, due to hunting and roadkill, deer carcasses are often removed from the ecosystem and not available as carrion for necrophagous insects (Wilson and Wolkovich 2011). Since retention of livestock carcasses on fields or meadows is also prevented (Regulation (EC) No 1069/2009), resource availability for necrophagous community is restricted, which can, in turn, affect the dynamics of the whole food web (Barton et al. 2013). Retaining carrion in ecosystems could contribute to maintaining specialized necrophagous species (Barton et al. 2013, von Hoermann et al. 2021), for example, *Necrodes littoralis* (Coleoptera: Silphidae) that depends on muscle and fat tissue for successful larval development (Charabidze et al. 2016, Matuszewski and Mađra-Bielewicz 2021). However, it is currently unclear how much carrion biomass and in which spatiotemporal distribution is necessary to maintain necrophagous insect communities (Barton et al. 2019).

Evisceration residues of deer, i.e. soft tissue thoracic and abdominal viscera that are not protected by skin and fur, make up for about 22–30% of deer body mass (Becciolini et al. 2016). While it is common hunting practice in Germany, and across Europe, to leave evisceration residues of killed ungulates in the field, threats of potential spread of diseases (e.g. African swine fever in wild boar *Sus scrofa*), and complications in practicality and food-hygiene, mean that hunters are increasingly choosing to eviscerate and dispose of residues ex-situ (Bartels and Bülte 2011, Mirceta et al. 2017, Gomes-Neves et al. 2021). Thus, even the reduced resources that may be available to necrophagous insects are increasingly removed.

In this paper, we report the results of a pilot study in which we investigated the function of evisceration residues from hunting as a resource for necrophagous insects. We used an experimental approach comparing abundances of dipterans and necrophagous coleopteran families and species richness

of Silphidae caught by pitfall-traps baited with entire roe deer carcasses, evisceration residues and unbaited controls. Overall, we expect that evisceration residues will be used by necrophagous insects but cannot fully replace entire carcasses as a resource. We expect that the abundance of necrophagous insects will be lower on evisceration residues than carcasses since evisceration residue have lower biomass, nutrient contents and facilitated access, which will lead to quicker decomposition compared to carcasses with large proportions of muscle and fat tissue. Furthermore, we specifically expect the abundance of necrophagous insects corrected for carrion biomass as well as species richness of Silphidae to be higher at carcass sites compared to residue sites, since many necrophagous species rely on muscle and fat tissue for larval development. Finally, while we expect that evisceration residues provide a resource for necrophagous insects, we expect that they are used earlier but for less time compared to entire deer carcasses, due to greater accessibility, lower biomass and quicker decomposition.

Material and methods

We conducted this experiment from 29 July to 4 September 2021, when male roe deer are intensively hunted in Germany (in mating season, July–August) and the necrophagous insect community is most complete (Dekeirsschietter et al. 2013). The study was conducted in the southern Black Forest, Germany, in a mountainous mixed forest stand dominated by Norway spruce *Picea abies*, silver fir *Abies alba* and beech *Fagus sylvatica* (47°53'13.8"–47°52'53.5"N, 8°05'27.3"–8°06'07.1"E, 960–1150 m a.s.l.). In the study area, we selected nine experimental sites with little slope, high distance to hiking paths and an herb layer dominated by *Vaccinium myrtillus*. We randomly assigned three of the experimental sites to our treatment categories: 1) entire roe deer carcass, 2) roe deer evisceration residues, 3) unbaited controls (adapted following von Hoermann et al. 2018). Roe deer that were used in the experiment were shot in May 2021 and stored at –27°C until two days before exposure. Carcass and residue samples had an average mass of 17.3 kg (15.3–20.6 kg) and 4 kg (3.2–5 kg) respectively. The carcasses were unopened apart from the gunshot wounds from culling. The evisceration residues consisted of all internal organs: lungs, heart, rumen, liver, kidneys, spleen, bowel, bladder, reproductive organs and connecting tissues. While an average spacing of 50 m between experimental sites is common practice in forensic studies (Anderson and VanLaerhoven 1996, Michaud et al. 2012, Jarmusz and Bajerlein 2019), we opted for spacing of at least 100 m distance between experimental sites to avoid overlaps of individual carcass odour bouquets (von Hoermann et al. 2018, 2020b).

At every site, we placed northward facing metal cages (62 × 93 × 69 cm, mesh 4 × 12 cm) with two pitfall-traps (9 cm diameter openings), at the northwest and southeast corner of the cages to trap Diptera and Coleoptera (Weithmann et al. 2020, 2022, von Hoermann et al. 2021).

At carcass and residue sites, we placed the roe deer samples in the cages, to prevent vertebrate scavengers from dragging them away. Carcass and viscera were placed inside the metal cage right before the first trapping interval. We used distilled water with odourless detergent as trapping liquid. While pitfall-traps are mostly used to sample non-flying insects, for carrion studies pitfall-traps are also successfully applied to sample flying taxa like Diptera or flying Coleoptera (Weithmann et al. 2020, 2022, von Hoermann et al. 2021). We collected insect samples from the pitfall-traps in two-day (48 h) intervals for a total of 18 sampling intervals (I01–I18).

All invertebrates sampled by pitfall traps were transferred to 70% ethanol solution and later identified in the laboratory. Non-beetle groups were sorted to order level, while beetles were sorted to family level. Within Coleoptera, we focused on the necrophagous groups: Silphidae, Staphylinidae, Histeridae, Leiodidae and dung beetles (Watson and Carlton 2005, Matuszewski et al. 2011, Prado e Castro et al. 2012, Mađra et al. 2015, von Hoermann et al. 2018, 2020b). Silphidae and dung beetles were further identified to species level. We compared insect abundances and Silphidae species richness among treatments, summed over the whole sampling period. To assess possible effects of carrion quality we also compared insect abundances corrected for carrion biomass (individuals/kg carrion biomass). We tested for differences in insect abundances and species richness using Kruskal–Wallis tests to compare all three treatments and Holm-corrected–Wilcoxon-rank-sum-tests to compare treatment pairwise. Due to the low sample size, we used the insect abundances on the level of the individual traps (non-independent) in each site rather than the combined abundance and species richness for each experimental site. To assess the temporal development of insect visitation we also tested for differences in insect abundance for all individual trapping intervals for necrophagous Coleoptera combined, Diptera and their larvae. All analyses were done in R (<www.r-project.org>). At carcass sites a total of three samples were made unusable by a pine marten *Martes martes* during intervals I06 and I07 by displacing the pitfall-trap and feeding on its content. For the sake of adequate representation, values for these samples were set at averages of other carcass traps from the same interval. Consequently, absolute numbers of insects sampled at carcass sites maybe considered to be slightly higher than presented here.

Results

We sampled a total of 52 527 insects across all treatments. Diptera and Coleoptera accounted for 49 365 and 2664 individuals respectively, including 45 029 dipteran larvae. Of the 2370 adult beetles, 2185 were of the five groups focused on in this experiment (Table 1). Most of the remaining adult beetles were non-necrophagous carabids (Carabidae) and weevils (Curculionidae), which are not further considered in this study.

Table 1. Individuals of relevant taxa sampled between treatments. For beetle families only adults are considered.

	Carcass	Residues	Control	Total
Silphidae	220	35	0	255
Staphylinidae	643	229	10	882
Histeridae	474	82	0	556
Leiodidae	177	54	0	231
Dung beetles	179	82	0	261
Other beetles	312	83	84	479
Adult Diptera	2891	1339	106	4336
Diptera larvae	37 675	7354	0	45 029
Other insects	204	172	122	498
All	42,775	9430	322	52 527

The Kruskal–Wallis tests showed that abundance of sampled individuals differed significantly among treatments for all considered groups (Silphidae: $\chi^2 = 15.76$, $p < 0.001$; Staphylinidae: $\chi^2 = 15.19$, $p < 0.001$; Histeridae: $\chi^2 = 15.30$, $p < 0.001$; Leiodidae: $\chi^2 = 13.74$, $p < 0.01$; dung beetles: $\chi^2 = 14.73$, $p < 0.001$; adult Diptera: $\chi^2 = 14.38$, $p < 0.001$; Diptera larvae: $\chi^2 = 14.17$, $p < 0.001$) Abundance tended to be highest at sites with entire carcasses (Fig. 1). Carcass sites had significantly more Silphidae compared to residues sites and controls ($W_{\text{carcass:residue}} = 36$, $p < 0.001$; $W_{\text{carcass:control}} = 36$, $p < 0.01$, Fig. 1), while residue sites had significantly more Silphidae than controls ($W_{\text{residue:control}} = 36$, $p < 0.01$, Fig. 1).

In total, six species of Silphidae were caught (*Nicrophorus investigator* $n = 30$, *N. humator* $n = 3$, *N. vespilloides* $n = 76$, *Necrodes littoralis* $n = 12$, *Oiceoptoma thoracicum* $n = 45$, *Thanatophilus sinuatus* $n = 89$). Staphylinidae and Histeridae were the most abundant beetle families and were significantly more abundant at carcass sites compared to residues ($W_{\text{carcass:residue}} = 36$, $p < 0.01$ and $W_{\text{carcass:residue}} = 35$, $p < 0.01$, Fig. 1) and controls, respectively ($W_{\text{carcass:control}} = 36$, $p < 0.01$ and $W_{\text{carcass:control}} = 36$, $p < 0.01$, Fig. 1), and more abundant at residue sites compared to controls ($W_{\text{residue:control}} = 36$, $p < 0.01$ and $W_{\text{residue:control}} = 36$, $p < 0.01$, Fig. 1). Leiodidae were significantly more frequently sampled on carcass sites compared to residue sites and controls ($W_{\text{carcass:residue}} = 33.5$, $p < 0.05$ and $W_{\text{carcass:control}} = 36$, $p < 0.01$, Fig. 1), while also being more common on residue sites than at controls ($W_{\text{residue:control}} = 33$, $p < 0.05$, Fig. 1). Two species of dung beetles, *Anoplotrupes stercorosus* (Geotrupidae) and *Aphodius rufipes* (Scarabaeidae), were most common at carcass sites ($W_{\text{carcass:residue}} = 33.5$, $p < 0.05$ and $W_{\text{carcass:control}} = 36$, $p < 0.01$, Fig. 1), but also showed higher abundance at residues sites ($W_{\text{residue:control}} = 36$, $p < 0.01$, Fig. 1) compared to controls.

Comparing abundances of Diptera, we found the same pattern as for beetles: adult Diptera and larvae were more abundant at carcass sites compared to residues ($W_{\text{carcass:residue}} = 34$, $p < 0.05$ and $W_{\text{carcass:residue}} = 32$, $p < 0.05$, Fig. 1) and controls, respectively ($W_{\text{carcass:control}} = 36$, $p < 0.05$ and $W_{\text{carcass:control}} = 36$, $p < 0.01$, Fig. 1), with higher abundances at residue sites compared to controls ($W_{\text{residue:control}} = 33$, $p < 0.05$ and $W_{\text{residue:control}} = 33$, $p < 0.01$, Fig. 1). Of the total 4184 adult dipterans sampled, only 1.1% did not belong to the taxon Brachycera.

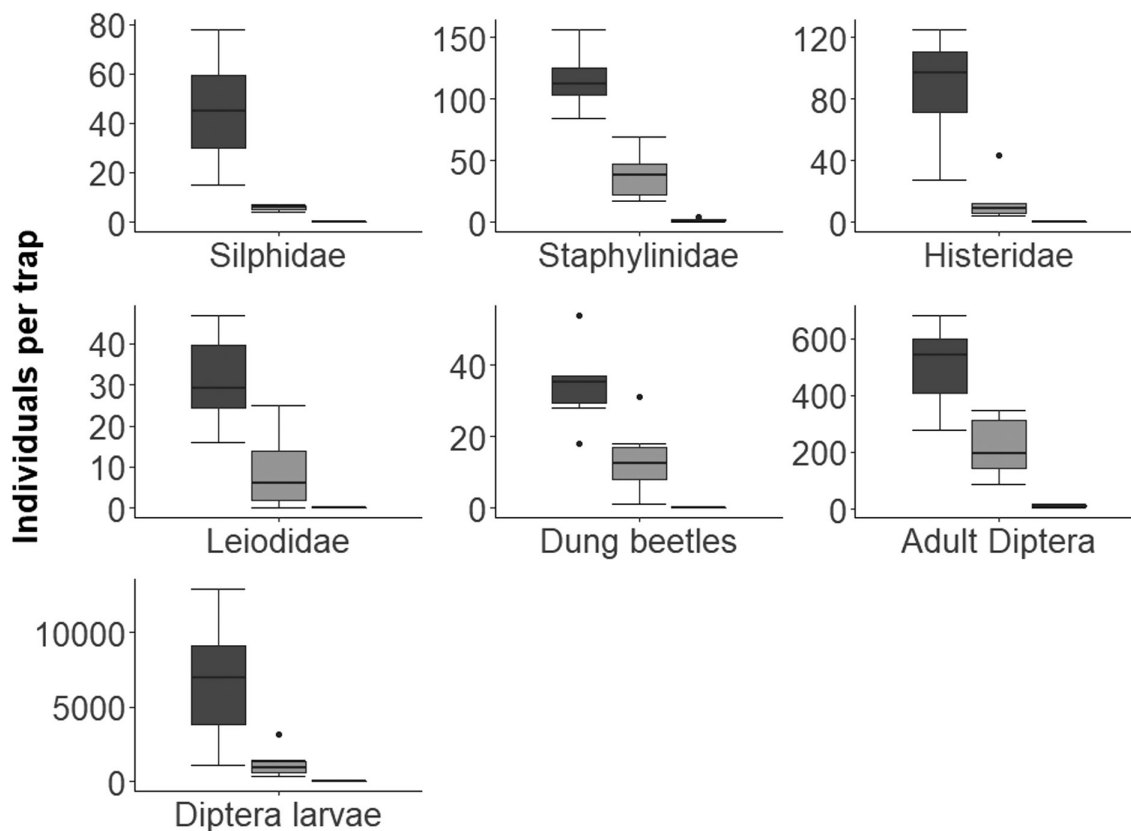


Figure 1. Boxplot presenting variation in adult beetle and dipteran abundances between treatments separated by taxon. Pairs of non-independent traps are included. Dark grey fill represents carcass sites, light grey fill represents sites with evisceration residues and white fill represents controls.

When correcting the insect abundances for biomass of the carrion samples, only dipterans showed significant differences. While adult Diptera were more abundant at residue sites ($W_{\text{carcass:residue}} = 34$, $p < 0.01$, Fig. 2), larvae were relatively more abundant at carcass sites ($W_{\text{carcass:residue}} = 32$, $p < 0.05$, Fig. 2). Dung beetles and Staphylinidae also tended to be more abundant at residue sites than carcass sites, however this trend was not significant. In contrast, Silphidae and Histeridae showed a non-significant tendency to be more abundant at carcass sites than residue sites. Species richness of Silphidae was higher at carcass sites compared to residue sites ($W_{\text{carcass:residue}} = 36$, $p < 0.01$, Fig. 3), while no Silphidae were sampled at controls.

Using Wilcoxon-rank-sum tests, trapped beetle abundance was significantly higher at residue sites than control sites in intervals I01–I08, I10, I13 and I14 with a peak in I04 ($W_{\text{residues:control}} = 21\text{--}36$, $p < 0.05$, Fig. 4). Numbers of sampled beetles at carcass sites peaked in intervals I06–I08 and were significantly different from control sites from interval three to 18 (I03–I18, $W_{\text{carcass:control}} = 24\text{--}36$, $p < 0.05$). In interval I04, more necrophagous beetles were sampled at residue sites compared to carcass sites ($W_{\text{carcass:residue}} = 1$, $p < 0.01$), while afterwards significantly more beetles were always sampled at carcass sites ($W_{\text{carcass:residue}} = 23\text{--}36$, $p < 0.05$). In contrast to carcass sites, beetle abundance was significantly higher at

residue sites compared to control sites in the first two trapping intervals ($W_{\text{residues:control}} = 31.5\text{--}33$, $p < 0.05$).

The peaks of adult Diptera and their larvae were detected earlier on residue sites (I03–I05) than carcass sites (I06 and I07). Abundances of adult dipterans on residue and control sites did not significantly differ after interval I08; however, the abundance at carcasses remained significantly higher than at control sites for the entire experiment ($W_{\text{carcass:control}} = 24\text{--}36$, $p < 0.05$). In intervals two and three, more dipterans were sampled at residue sites than at carcasses sites ($W_{\text{carcass:residues}} = 5$, $p < 0.05$ and $W_{\text{carcass:residues}} = 1$, $p < 0.01$), while there was no difference in intervals I04–I06 and I08. Dipteran larvae were most abundant in interval I05 at residue sites, while abundance at residue sites differed significantly from controls for three intervals ($W_{\text{carcass:control}} = 0\text{--}3$, I05–I07, $p < 0.05$). Larvae abundance at carcass sites significantly differed from controls for six intervals (I06–I11, $W_{\text{carcass:control}} = 21\text{--}36$, $p < 0.05$). In interval I05, more Diptera larvae were found at residue sites compared to carcass sites ($W_{\text{carcass:residues}} = 1$, $p < 0.01$).

Discussion

Evisceration residues are a resource for necrophagous insects. While significantly more coleopterans and dipterans were

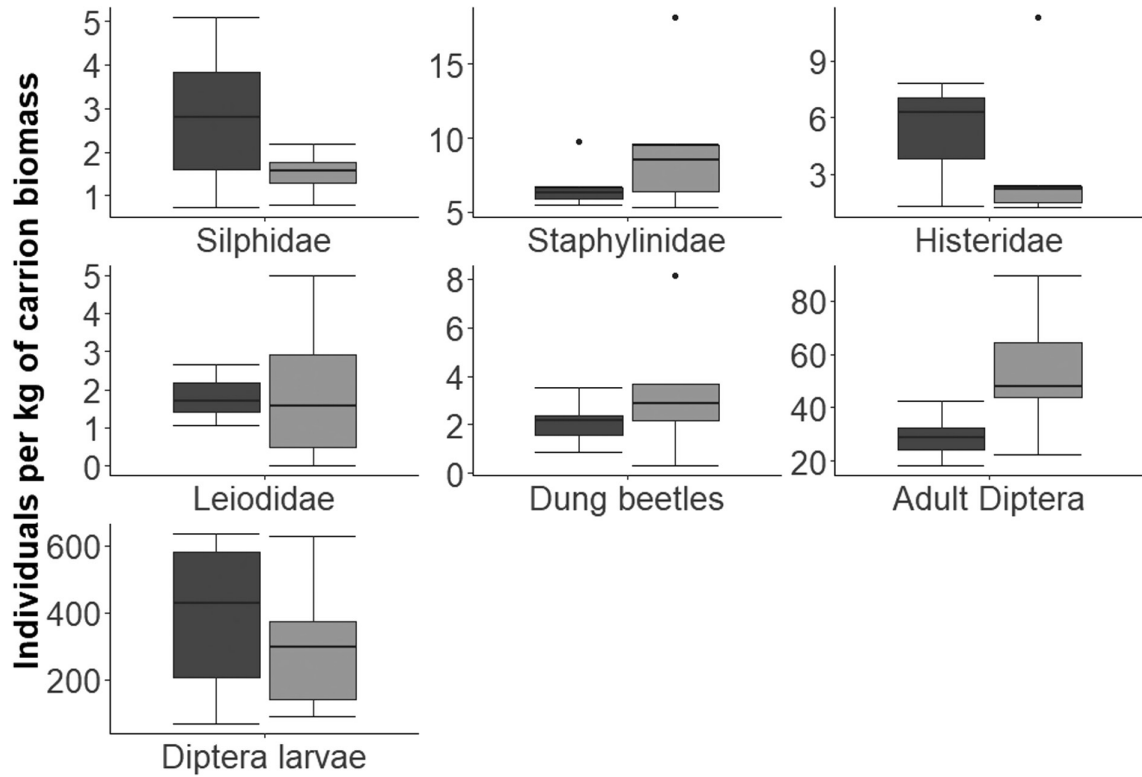


Figure 2. Boxplot presenting the variation of adult beetle and dipteran abundance between carcasses and evisceration residues corrected for sample weight and separated by taxon. Pairs of non-independent traps are included. Dark grey fill represents carcass sites, light grey fill represents sites with evisceration residues.

found on sites with entire roe deer carcasses for all taxonomic groups, they were also significantly more abundant on residue sites compared to control sites. Carcass samples have, on average, four times the biomass of evisceration residues, which in turn can influence the relative abundance of necrophagous insects. To account for this, we corrected insect abundance for carrion biomass. Contrary to our expectations, Coleoptera abundance did not differ between residue and carcass sites. Adult Diptera, were significantly

more abundant at residue sites than carcass sites, when corrected for sample weight. This may be because the lack of fur and skin results is a strong olfactory cue attracting many adult dipterans. Furthermore, the immediate presence of blood may have been highly attractive and accelerate egg laying of adult blowfly females (Bhadra et al. 2014). However, our expectations did hold true for dipteran larvae, where significantly higher abundances were sampled at carcass sites than residue sites. This is probably because dipteran larvae require high levels of protein from muscle tissue (El-Moaty and Kheirallah 2013), which is absent in residue samples. While we found no significant difference for Histeridae and Silphidae between treatments, when corrected for sample weight, there was a tendency towards higher abundances at carcass sites. As Histeridae and Silphidae are typical predators of dipteran larvae, this trend may be an indirect response to the higher prey availability (Bajerlein et al. 2011, Battán Horenstein and Linhares 2011, von Hoermann et al. 2013, Trumbo and Dicapua 2021). The opposite, albeit non-significant trend, can be observed for dung beetles and Staphylinidae. While dung beetles are also attracted to carrion (von Hoermann et al. 2020b), the remaining rectal content in evisceration residues may have attracted dung beetles to residue sites (Weithmann et al. 2020). Finally, Staphylinidae were more abundant at residue sites, when corrected for sample weight. Even though Staphylinidae predate on dipteran larvae (Greene 1996, Krawczynski et al.

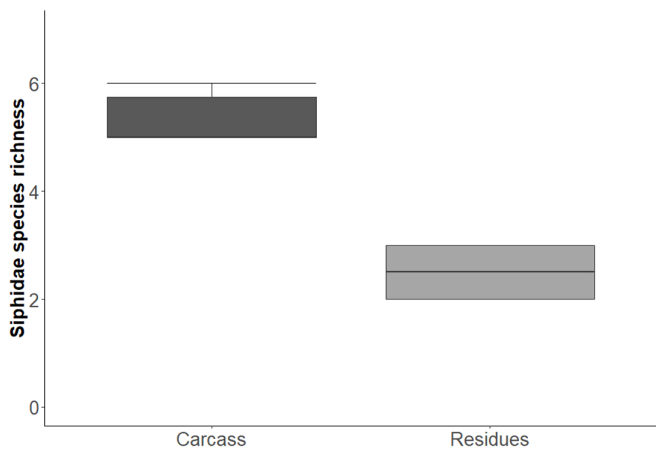


Figure 3. Boxplot representing Silphidae species richness between carcass and residues sites. Pairs of non-independent traps are included.

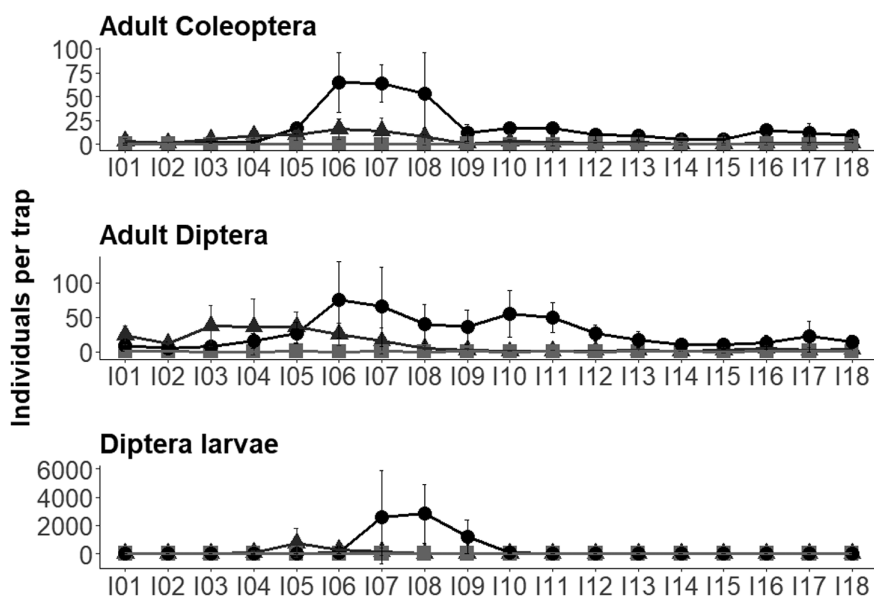


Figure 4. Temporal development of sampled Coleoptera, dipteran adults and Diptera larvae. Each interval represents a trapping interval of two days. For Coleoptera, Silphidae, Histeridae, Staphylinidae, Leiodidae and dung beetles (Geotrupidae and Scarabaeidae) are included. Black lines and circles represent carcasses sites, dark grey lines and triangles represent evisceration residues and light grey lines and squares represent controls.

2011), they may have been attracted to residue sites as they also prey on dung beetles (Freude et al. 1971, Young 1998, Biel et al. 2014).

As expected, evisceration residues were used by all insect groups earlier and for a shorter time than entire carcasses. Since residues are not protected by fur and skin, they may emit stronger olfaction cues that are attractive to insect in early intervals. Furthermore, the lack of skin and fur can facilitate insect access to the residues. Since evisceration residues have lower biomass than carcasses, they are likely depleted quicker by insects than entire carcasses (Komar and Beattie 1998, Matuszewski et al. 2016). This may be why residues are used earlier but over a shorter period of time.

In this study only Silphidae and dung beetles were determined to species level. While both species of dung beetles were found at residues and carcasses, two Silphidae species, *Thanatophilus sinuatus* and *Nicrophorus humator*, were only found at carcasses. Due to the small sample size and the difference of carrion biomass between treatments however, this result needs further investigation. Studies with larger sample sizes should additionally assess community composition and diversity of necrophagous insects over a wider range taxonomic range.

We chose to protect our samples by metal cages to avoid interference by vertebrate scavengers. Without this protective measure and due to the small sample size, vertebrate scavengers like red foxes *Vulpes vulpes* could have impeded the entire experiment by dragging the evisceration residues off the experimental sites. Moreover, it is common practice to use protective cages in carrion studies focusing on insect infestation (Melis et al. 2004, Haelewaters et al. 2015, von Hoermann et al. 2018). Under natural conditions vertebrate scavengers would likely use a high percentage of evisceration

residues, excluding it, at least partially, for use by necrophagous insects (DeVault et al. 2004, DeVault et al. 2011). Gomo et al. (2017) investigated the use of evisceration residues of moose *Alces alces* in autumn – while 85% of high-quality carrion was used up by vertebrate scavengers after ten days, more than 80% of low-quality carrion remained. In our study the activity peak for insects was between 4 and 14 days after exposure. This finding suggests, that even under natural conditions, evisceration residues might only be partly available to invertebrates, especially in summer, as vertebrate scavenging is positively affected by cold temperatures (Selva et al. 2005, Stiegler et al. 2020). Future studies could investigate the availability of evisceration residues for insects under natural conditions in summer, e.g. by exposing residues in front for camera traps and observing how long it takes for vertebrates to remove the samples.

Differences in biomass between carrion and residues was one possible bias in our study design, however we accounted for this by correcting for biomass. Another possible bias was that the carcasses used in our experiment came from regular hunting, and thus had openings due to the bullets. However, it is not uncommon to use carcasses from ungulates killed by hunting or wildlife–vehicle collisions (Haelewaters et al. 2015) for comprehensive diversity surveys of their vertebrate and invertebrate visitors, likewise not being closed (Watson and Carlton 2003, Stiegler et al. 2020, von Hoermann et al. 2021). Moreover, also under natural conditions necrophagous insects will often use carrion that has previously been predated and even scavenged upon by vertebrates (Barton et al. 2013, Fielding et al. 2014, Barry et al. 2019). Thus, while we were unable to comment on the role of naturally dying roe deer, our results are still applicable and demonstrative of the majority of roe deer carcasses that would be available in the ecosystem.

Despite our small sample size our findings indicate, that retained evisceration residues from hunting can be a valuable resource for necrophagous invertebrates. Artificially supplying carrion to vultures for example, is an already practiced conservation approach (Gilbert et al. 2007, Fielding et al. 2014). Similarly, carrion supplements in form of large herbivore viscera from hunting may support necrophagous invertebrates, and are conceivable as a conservation measure where, as in Germany, when the spread of diseases is unlikely (Landesuntersuchungsamt Rheinland Pfalz 2017b), legislation allows viscera retention. On the other hand, retention of evisceration residues can support numerous species of vertebrate scavengers in the absence of large carnivores which supply carrion with their kills or under low natural mortality of ungulates (Selva et al. 2005).

Conclusions

In a first preliminary approach, we investigated the role of evisceration residues as a resource for specialised necrophagous insect fauna, in direct comparison to whole, exposed wildlife carcasses. Overall, we found that evisceration residues were used by all observed taxonomic groups of necrophagous insects, while their abundance was generally higher at sites baited with entire carcasses. Correction for biomass only demonstrated higher relative abundances of adult Diptera at carcass sites, thus not supporting our expectations that carrion from evisceration residues is of inferior quality for necrophagous insect visitors. While more detailed research, with stronger focus on insect diversity and community composition, is necessary, our results suggest that the retention of evisceration residues might be beneficial as a conservation measure to support and maintain the necrophagous insect community.

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Ethics statement – All necessary permits were obtained for the described field study. Roe deer were culled within regular hunting management in the area and were not killed for the purpose of the experiment. As the deer were culled locally and examined before culling, carcass exposure was of no veterinary concern. For field sampling of arthropods, an exemption existed concerning §4 BArtSchV and species protection legislation according to § 45 BNatSchG (RPF55-56-8852-133/1/5).

Author contributions

Sebastian Schwegmann: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (lead). **Nikolas Binder:** Conceptualization (supporting); Investigation

(supporting); Methodology (supporting); Visualization (supporting); Writing – original draft (supporting). **Christian von Hoermann:** Conceptualization (supporting); Methodology (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Manisha Bhardwaj:** Formal analysis (supporting); Supervision (supporting); Writing – review and editing (supporting). **Ilse Storch:** Conceptualization (supporting); Funding acquisition (lead); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.q573n5tkh>> (Schwegmann et al. 2022).

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