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Arthropod Succession Following a Mass Mortality Event of Reindeer *(Rangifer tarandus)* in an Alpine Ecosystem

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Preface

As this thesis marks the end of my time at the Norwegian University of Life Sciences, I would like to express my gratitude towards this great university. I also want to thank my supervisors, Tone Birkemoe, Sam Steyaert and Anders Aak, for their valuable advice. Further, I want to thank Sindre Ligaard and Geir Søli for help with the species identification, Christine Reenskaug and Bendik Ferkingstad for feedback on the text, Heidi Granum for help with the preparations of the study, and Karoline Thygesen for good company during the fieldwork. Last, but not least – thank you to everyone in the REINCAR research group for giving me the opportunity to write my thesis on such an exciting topic.

Abstract

Carcasses are of great ecological importance, especially as a resource for arthropods. However, many aspects of carrion ecology remain to be investigated. One of these aspects is the ecological significance of mass mortality events. In 2016, a natural mass mortality event gave the opportunity for an extensive study on carcass decomposition in an alpine area, as a lightning strike killed 323 wild reindeer (*Rangifer tarandus*) at the Hardangervidda mountain plateau in Norway. Two years after the incident, when the reindeer were in the dry/remains stage, twice as many arthropods were found on the site where the reindeer died as on a control site 300 m away. In this study, I investigated how much the arthropod activity changed from the second year after mass death to the third. This included examining both large-scale effects – the differences between the carrion site and the control site, and small-scale effects – the differences along a carrion density gradient on the carrion site.

Three years after the mass death, the number of arthropods on the carrion site was still significantly higher than on the control site. The positive response to carcass presence was found in several different groups: Predators, parasitoids, detritivores, Diptera, springtails and mites. Among the Diptera, *Parapiophila vulgaris* was particularly favoured numerically by the presence of carcasses. On the small scale, parasitoids, detritivores and springtails were positively correlated with carrion density. There was no decline in arthropod activity on the carrion site from the second year to the third. My study therefore shows that the large arthropod abundance the second year after the mass mortality event at Hardangervidda was maintained the third year. The large and long-lasting impact the carcasses had on the arthropod abundance is a clear sign that carrion needs to be recognized as an important element of biodiversity and biomass production in ecosystems.

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1. Introduction

Decomposition of dead animals is a fundamental ecological process. After death, a cadaver releases massive amounts of nutrients and acids into the environment (Towne, 2000; Carter et al., 2007). This makes carcasses capable of drastically altering the properties of the local vegetation, soil and fauna (Towne, 2000; Bump et al., 2009). Carcasses also attract both vertebrate and invertebrate scavengers, and the scavengers may in turn attract predators (Moleón et al., 2015; Baruzzi et al., 2018). As a result of the increased food availability, these animals might improve their breeding success. Additionally, plant seed dispersal through endozoochory by scavengers appears to be directed towards the area around the carcasses (Steyaert et al., 2018). The changes that happen when a dead animal is 'recycled' may affect a large area, and may last for a long time (Coe, 1978; Danell et al., 2002).

However, many aspects of carrion ecology have yet to be investigated properly (Gu et al., 2014). One of the reasons for the lack of knowledge about carrion ecology is the difficulties involved with studying it. Unless studied experimentally, a carcass is an unpredictable and ephemeral resource. In contrast to dead trees, which may persist in the environment for many decades before they are fully decomposed (Sinclair, 2004; Storaunet and Rolstad, 2002), it does not need to take more than days or weeks before a large carcass is reduced to hair and bones by vertebrate or invertebrate scavengers in certain environments (Moleón et al, 2015; Spicka et al., 2011). Another complication is that researchers that wish to study carrion ecology must follow the local laws for where a carcass can and cannot be left to decompose. Many countries practice a management strategy where carcasses of domestic animals are removed or destroyed for hygiene reasons, and in some countries, this practice even includes carcasses in the wild (Gwyther et al., 2011; Vantassel and King, 2018). Removal of carcasses consequently leads to the removal of the ecosystem processes that occur during decomposition (Steyaert et al., 2018; Margalida and Colomer, 2012).

Payne (1965) proposed six stages of decomposition: Fresh, bloated, active decay, advanced decay, dry, and remains. The fresh stage lasts from the moment of death until the onset of the bloated stage, in which microorganisms produce organic acids and gases that result in bloating of the cadaver (Carter et al., 2007). During active decay, cadaveric fluids and maggot activity lead to the formation of a "cadaver decomposition island". A cadaver decomposition island is commonly associated with increased microbe activity and nematode abundance, as well as excessive nutrient and acidity flow from the rotting carrion. This causes plant material underneath and around the carcass to die, which marks the onset of the advanced decay stage (Forbes and Carter, 2015; Carter et al., 2007). The last two stages, dry and remains, are difficult to tell apart and are often referred to as the dry/remains stage (Payne, 1965; Grassberger and Frank, 2004). This stage is characterised by skeletonization and increased plant growth, and may last much longer than the earlier stages (Grassberger and Frank, 2004; Carter et al., 2007; Coe, 1978).

Mass mortality events, the "rapid, catastrophic die-off of organisms" (Fey et al., 2015), are especially interesting. This is because their effects are on a larger spatial scale than the effects of a single cadaver, and because they involve a larger amount of biomass. Solitary cadavers can certainly have great impacts on their surroundings if they are large in size; for example, whale falls are believed to be of great importance for the nutrient cycling in deep-sea ecosystems (Wallace, 2015), and Coe (1978) found that a 1.6 tonne elephant carcass *(Loxodonta africana)* created a cadaver decomposition island that extended 40 cm into the soil. However, a large carcass is not equivalent to a mass mortality event. Baruzzi et al. (2018) even suggest that when carcass size increases, per capita access to carrion by scavengers decreases because of the decreasing surface area to volume ratio.

Mass mortality events are believed to occur more and more often in the future because of disease and biotoxicity (Fey et al., 2015), yet we do not know much about their impact on ecosystems. This is what motivated a research team in Mississippi to create an artificial mass mortality event and study its effects on the local biota (Baruzzi et al., 2018; Lashley et al., 2017). They found that while a single pig (*Sus scrofa*) carcass only attracted vertebrate and invertebrate scavengers and predatory beetles (Coleoptera), large numbers of carcasses also attracted insectivorous birds, anoles, hornets and armadillos (Baruzzi et al., 2018). Additionally, the large amount of carrion biomass permitted a mass dispersal of millions of blow fly (Diptera: Calliphoridae) larvae, which severely disturbed the soil and leaf litter as they dispersed (Lashley et al., 2017). It was reported that the blow flies could skeletonise a whole carcass in a matter of days.

The finding of Lashley et al. (2017) is only one of many that highlights how important arthropods are for carcass decomposition. A study conducted in South Carolina by Payne (1965) showed that carcasses where insects were excluded decomposed very slowly and kept their form for many months. In comparison, when insects were present, it only took six days before 90% of the carcass was removed. The species composition on a carcass is continuously shifting; for example, blow flies and flesh flies (Diptera: Sarcophagidae) are usually the first to colonise a carcass (Payne, 1965; Lashley et al., 2017), while skin beetles (Coleoptera: Dermestidae) and hide beetles (Coleoptera: Trogidae) are later colonisers (McKinnerney, 1978). For this reason, an examination of the arthropod fauna on a corpse can be used to determine the post-mortem interval – the time that has elapsed since the person died (Wang, 2008).

A substantial part of the knowledge we have about carrion ecology comes from forensics (Benbow et al., 2015). In forensic studies, the carcass is typically a pig because they are similar to human corpses in several aspects, and the place of decomposition is typically a forest or another low-elevation area (Barton et al., 2013). Thus, more knowledge is needed on carcass decomposition on other species and in higher elevations. High elevation areas are of special concern to carrion ecology for several reasons. They are characterised by low temperatures, which may slow the decomposition process because arthropods and microbes are limited by the cold (DeVault et al., 2004). This leaves more material available for scavengers. Additionally, the most important pollen vectors in alpine ecosystems are Diptera, which means that many of the carrion feeders in an alpine ecosystem are also that ecosystem's pollinators (McCall and Primack, 1992; Kearns, 1992). These ecosystems are also highly stressful because of the nutrient limitation, and we know little about how an alpine area would react to nutrients in amounts equivalent to what would be released from one or more carcasses. De Jong and Chadwick (1999) examined arthropod succession on carcasses at high elevations in Colorado, but only using small, solitary rabbit (*Oryctolagus cuniculus)* carcasses. There was still arthropod activity on some of the carcasses when the study was terminated seven weeks later. As a conclusion to their study, they stressed that further alpine studies on carrion is needed, preferably on larger carcasses than rabbits.

There is also an unevenly high representation of short-term studies that fully or partially neglect the later stages of decomposition. Arthropod activity typically peaks in the active decay stage and is reduced to very little in the dry and remains stages (Parmenter and MacMahon, 2009; Payne, 1965; Braack, 1981). Most arthropod experiments on carcasses are therefore ended shortly after the last stage is reached, usually after weeks or months (Payne, 1965; Grassberger and Frank, 2004; Melis et al., 2004). This is unfortunate, as research indicates that carrion can have long-term effects on their environment. For example, Towne (2000) reported that ungulate carcasses significantly raised soil nitrogen and phosphorus concentrations two years after death and continued to alter the local vegetation five years after death. Bump et al. (2009) found that moose (*Alces alces*) carcasses increased the abundance of both bacteria, fungi and soil nitrogen more than three years post-mortem. Danell et al. (2002) showed that even a ten-year-old muskox (*Ovibos moschatus*) carcass had drastic effects on the surrounding vegetation. Therefore, it is possible that carrion can have long-term effects on arthropod communities that short-term studies are incapable of detecting. The effects will most likely last longer in alpine and arctic areas, where the cold slows the decomposition process.

In August 2016, a natural mass mortality event gave the opportunity for an extensive study on carcass decomposition in an alpine area; a lightning strike killed 323 wild reindeer (*Rangifer tarandus*) at the Hardangervidda mountain plateau in Norway (Steyaert et al., 2018). Since then, the site has been monitored every summer. Mammals, birds and plants have been monitored since the beginning, but arthropods were not investigated until 2018 (Granum, 2019). At this point, the reindeer had been dead for two years, and the carcasses were in the dry/remains stage (figure 1).

Figure 1: Decompositional changes at Hardangervidda where a lightning strike killed 323 reindeer in

2016. **(a)** Shortly after the mass death (photo by Shane Frank). **(b)** One year post-mortem (photo by Rudy Badia). **(c)** Two years post-mortem (photo by Rudy Badia). **(d)** Three years post-mortem (photo by Alex Briggs).

Even though the carcasses were completely skeletonised in 2018, twice as many individuals of arthropods were found on the carrion site as on a similar control site with no carrion (Granum, 2019). Predatory arthropods were twice as abundant on the carrion site, and Diptera, analysed as a separate group due to their mixed trophic status and the difficulty of identifying them further, were thrice as abundant. The increase in the predator guild was probably because of more available prey, as they feed on Diptera (Merritt and De Jong, 2015; Harwood et al., 2007). The reason for the increased abundance of Diptera is less clear. Blow flies and flesh flies were barely present, and the rest of the Diptera were not identified to family level, so it is uncertain what resources they were utilizing. Surprisingly, the detritivore guild was not affected by the presence of carcasses. The herbivores showed no difference in abundance between the two sites either, even though they were expected to decline because of the vegetation loss.

Granum (2019) has shown that carcasses can affect the local arthropod community for at least two years in an alpine tundra ecosystem, and the striking difference the author found between the carrion site and the control site indicates that it may last even longer. By using the materials and methods described by Granum (2019) at the same study site one year later and incorporating her raw data into my study, I intend to collect one more year of data that can be compared with the previous. I will examine how the arthropod composition have changed from the second year to the third year after death. This includes examining both large-scale effects – how much the arthropod community on the carrion site differs from the control site, and small-scale effects – how much the arthropod community within the carrion site differs along a carrion density gradient. In this study, I will test the following hypotheses:

I) The differences in the arthropod community between the carrion site and the control site, and along the carrion density gradient, will be reduced the third year after the mass mortality event compared to the second year.

II) There will still be more predatory and parasitoid arthropods on the carrion site compared to the control site the third year after mass death, because of their delayed numerical response to prey density.

III) Within the carrion site, the number of predatory and parasitoid arthropods will increase with increasing carrion density both the second and the third year after mass death.

The results I find may increase our understanding of how a mass mortality event can alter an alpine ecosystem. Not only will such an event provide more food for arthropods, but as a result, it might also affect food availability for insectivorous birds, pollination services, and seed dispersal through visiting vertebrates.

2. Materials and methods

2.1. Study site

Hardangervidda, located in the southern part of Norway, is the largest mountain plateau in northern Europe. Most of the area is above the treeline. The eastern part has an average elevation of 1100 m a.s.l. and is flatter than the western part, which has mountains up to 1700 m a.s.l. The plateau has an annual precipitation ranging from 500 to 3000 mm and is rich in lakes, rivers and streams (Melvold and Skaugen, 2013). Hardangervidda houses Europe's largest population of wild reindeer (Strand et al., 2006). Other characteristic animals are arctic fox (*Vulpes lagopus*), moose (*Alces alces*), Eurasian beaver (*Castor fiber*), Norway lemming (*Lemmus lemmus*), ptarmigans (*Lagopus* spp.) and brown trout (*Salmo trutta*). The central parts of Hardangervidda have been a national park since 1981.

The lightning storm that killed 323 wild reindeer on the 26th of August 2016 happened near Vesle Saure lake in the south-eastern part of Hardangervidda (figure 2). The area is located 1220 m a.s.l. The ground layer is dominated by mosses and lichens, and the field layer by dwarf birch (*Betula nana*), ericaceous species and graminoids (Steyaert et al., 2018). Since the mass die-off, vertebrates like raven (*Corvus corax)*, golden eagle (*Aquila chrysaetos*), arctic fox, red fox (*Vulpes vulpes*), wolverine (*Gulo gulo*) and rodents have been observed scavenging the carcasses.

Figure 2: Map of the location of the study sites: A carrion site, where a herd of reindeer (*Rangifer tarandus*) died in 2016, and a control site 300 m away.

The remains of the reindeer carcasses lie in a northern hillside. They are distributed over an area of approximately 240 x 100 m, the biggest concentration being within an area of 50 x 50 m (Steyaert, 2018). The heads were removed by authorities after the die-off to check for chronic wasting disease, but the rest of the carcasses remained in site. Three years after the mass death, vegetation was still scarce in the 50 x 50 m core (personal observation). However, some plants were starting to return along the edges, especially some mosses and the grass *Avenella flexuosa* (Steyaert, 2020 – pers. comm.).

2.2. Study design and data collection

The arthropod trapping performed by Granum (2019) in 2018 (hereafter called year 2) was repeated in 2019 (hereafter called year 3), allowing for comparison between the second year after death (figure 1c) and the third (figure 1d). A detailed description of the methods from Granum (2019) were provided to make sure that the sampling equipment was identical and that the procedures were done in the same way both years.

The arthropod trapping periods started shortly after snowmelt and lasted for five weeks in year 2 (12 June-17 July) and six weeks in year 3 (22 June-3 August). A grid at approximately 120 x 60 m was made within the carrion site. Additionally, a grid at approximately 50 x 35 m was made on a control site free of carrion. Each site had 30 plots (figure 3). The two sites are approximately 300 m apart, and they are similar in that they both face north and have the same elevation, slope and vegetation communities.

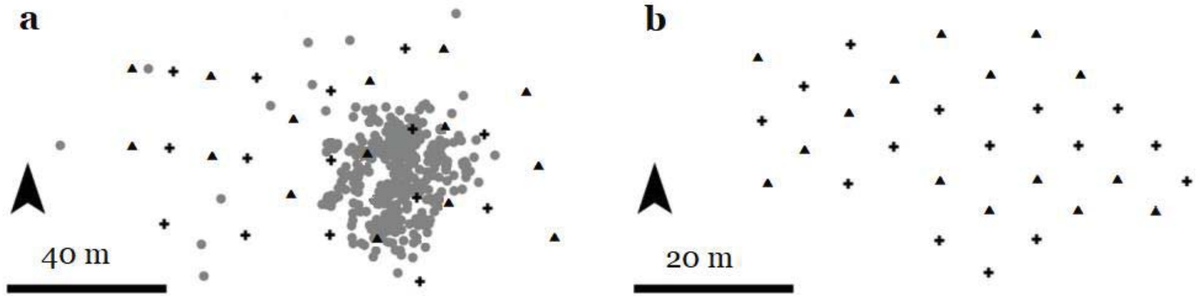


Figure 3: Map of the **(a)** carrion site and **(b)** control site at Hardangervidda. Triangles represent plots with a pitfall trap and a sticky trap, crosses represent plots with a pitfall trap only, and grey dots represent reindeer (*Rangifer tarandus*) carcasses. Figure adapted from Steyaert et al. (2018).

On each of these plots, a pitfall trap was placed in the ground (figure 4). The traps contained 125 ml of a mixture consisting of 50% propylene glycol and 50% water, in addition to some dishwashing soap. The purpose of the soap was to break the surface tension. The traps had Plexiglas square roof above them, mounted to the ground by wire. On half the plots, a sticky trap was installed next to the pitfall trap. The sticky traps were made of white plastic lids, 15 cm in diameter, covered with Tanglefoot insect glue on one side. These were placed on bamboo poles, 50-100 cm above ground.

Figure 4: Traps that were used to collect arthropods at Hardangervidda, two and three years after mass death of reindeer (*Rangifer tarandus*). **(a)** An uncovered and **(b)** covered pitfall trap, and **(c)** a sticky trap at the end of the trapping period in year 3 (photos by Lina Westermann).

At the end of the trapping periods, the pitfall traps were emptied, and the sticky traps were taken down. All the traps were stored in a freezer until the content was analysed. For the pitfall traps, the beetles were identified to species level by beetle expert Sindre Ligaard. The rest were identified to various taxonomic levels depending on the taxon (table S1; appendix). All the arthropods were then divided into functional groups: predators, parasitoids, detritivores and herbivores, in addition to the group ‘others’, which included arthropods that did not fit into any of the other groups. This group was not analysed further. Diptera were not put in any functional groups and were analysed separately. This was because of difficulties with determining which functional group an individual belonged to. Springtails (Collembola) and mites (Acari) were only counted in year 3 and were also analysed separately. For the sticky traps, parasitoids and Diptera were counted. Other individuals were ignored because of their very low abundance. Additional help from Geir Søli at University of Oslo was provided to identify Diptera individuals further, due to a particularly abundant species. For time-saving purposes, only one quadrant of each sticky trap was analysed. Sticky traps that fell down during the trapping periods (N=2) were left out of the analyses.

2.3. Data processing

The raw data from year 2 and year 3 was analysed together in the same dataset. For the large-scale effects, negative binomial regression models were fit to see how the number of arthropods was affected by site (carrion or control) and year. For each functional or taxonomic group, five models were tested: An interaction model (site * year), an additive model (site + year), a site model, a year model, and a null model. For each group, the model with the lowest AICc (Akaike's Information Corrected Criterion; Hurvich and Tsai, 1989) was chosen using the MuMIn package in R. This was done for both the pitfall trap and the sticky trap data. For springtails and mites, year was not used as a predictor variable as these groups were only counted the third year.

For the small-scale effects, carrion density on the carrion site was calculated. This was done by constructing a circle with a radius of ten m around each pitfall trap, using the carcass distribution data (figure 3a). It was then determined how much of the ground within the circle was covered with carcasses, on a scale from 0 to 1. Negative binomial regression models were fit to see how the number of arthropods in each group was best described by carrion density, year or both, using the same AICc-based model selection as described above. Carrion density analyses were done for pitfall traps on the carrion site only.

3. Results

3.1 Arthropod catch

A total of 18,622 arthropods on the carrion site and 6,715 arthropods on the control site were found in the pitfall traps in year 2 (table 1, table S2; appendix). In comparison, there were 13,750 arthropods on the carrion site and 4,268 on the control site in year 3 (springtails and mites excluded). The most abundant groups were Diptera (of which Nematocera were more abundant than Brachycera), predators and parasitoids. The predators were dominated by spiders (Araneae), harvestmen (Opiliones) and predatory beetles, and the parasitoid guild consisted of parasitoid wasps. Herbivores, dominated by true bugs (Hemiptera), were relatively rare. This was also true for the detritivore guild, consisting exclusively of detritivorous beetles, of which most can be classified as necrophagous. In year 3, the springtails were more abundant than any other group. Mites were also numerous.

Table 1: Total number of arthropods in each functional/taxonomic group found in pitfall traps (N=120) two and three years after mass death of reindeer (*Rangifer tarandus*) at Hardangervidda, sorted by year and site (carrion or control). The relative abundance of each group is colour-coded on a scale from yellow to green, from lowest to highest.

	Year 2				**Year 3**			
	Carrion		*Control*		*Carrion*		*Control*	
Predators	7782	41,8 %	2979	44,4 %	5067	36,9 %	1579	37,0 %
Parasitoids	1142	6,1 %	364	5,4 %	909	6,6 %	347	8,1 %
Detritivores	60	0,3 %	16	0,2 %	36	0,3 %	2	0,0 %
Herbivores	260	1,4 %	300	4,5 %	556	4,0 %	580	13,6 %
Diptera	9304	50,0 %	2980	44,4 %	7176	52,2 %	1705	39,9 %
Others	74	0,4 %	76	1,1 %	6	0,0 %	55	1,3 %
	18622	100,0 %	6715	100,0 %	13750	100,0 %	4268	100,0 %
Springtails	NA	-	NA	-	25387		3730	
Mites	NA	-	NA	-	2323		898	
					27710		4628	

For the sticky traps, 2,240 arthropods from the carrion site and 1,362 arthropods from the control site were counted in year 2 (table 2, table S3; appendix). In year 3, the numbers were 2,575 for the carrion site and 762 for the control site. The sticky traps caught mainly Diptera, in addition to some parasitoid wasps. *Parapiophila vulgaris* (Diptera: Piophilidae) was the most abundant species.

Table 2: Total number of arthropods in each functional/taxonomic group found on sticky traps (N=58) two and three years after mass death of reindeer (*Rangifer tarandus*) at Hardangervidda, sorted by year and site (carrion or control). The relative abundance of each group is colour-coded on a scale from yellow to green, from lowest to highest.

	Year 2				**Year 3**			
	Carrion		*Control*		*Carrion*		*Control*	
Parapiophila vulgaris	863	38,5 %	36	2,6 %	1899	73,7 %	38	5,0 %
Other Brachycera	1080	48,2 %	1048	76,9 %	397	15,4 %	483	63,4 %
Nematocera	272	12,1 %	267	19,6 %	234	9,1 %	176	23,1 %
Parasitoids	25	1,1 %	11	0,8 %	45	1,7 %	65	8,5 %
	2240	100,0 %	1362	100,0 %	2575	100,0 %	762	100,0 %

3.2. Carrion site vs. control site: Pitfall traps

The total number of arthropods in the pitfall traps was best described by the ‘site + year’ additive model (table S4, table S5; appendix). The differences in total arthropod numbers in pitfall traps between the carrion site and the control site remained the same both two and three years after death. There were 2.6 times more arthropods on the carrion site in year 2 and 3.2 times more arthropods in year 3 compared to the control site, springtails and mites excluded ($\beta = -1.058$, SE = 0.085, $p < 0.001$) (figure 5). This was caused by a larger abundance of predators, parasitoids, detritivores and Diptera on the carrion site. The total arthropod number was also higher in year 2 than in year 3 ($\beta = -0.170$, SE = 0.085, $p = 0.045$).

Figure 5: Mean number of arthropods (± SE) found in pitfall traps (N=120) two and three years after mass death of reindeer (*Rangifer tarandus*) at Hardangervidda, sorted by year and site. Springtails and mites excluded.

Predator abundance was best described by the 'site * year' interaction model (table S4, table S6; appendix). They increased in abundance from year 2 to year 3 on the carrion site, whereas they decreased in abundance from year 2 to year 3 on the control site. As a result, they were 2.0 times more abundant on the carrion site than on the control site in year 2, and in year 3, they increased to become 3.2 times more abundant (site: $\beta = -0.669$, SE = 0.099, $p < 0.001$; year: $\beta = 0.299$, SE = 0.097, $p = 0.002$; year * site: $\beta = -0.496$, SE = 0.139, $p < 0.001$). The optimal model for the parasitoids was the 'site' model (table S4, S7; appendix). They were 3.1 and 2.6 times more abundant on the carrion site compared to the control site in year 2 and 3, respectively ($\beta = -1.059$, SE = 0.135, $p < 0.001$).

Detritivore abundance was best explained by the 'site * year' interaction model (table S4, table S8; appendix). They were 3.8 times more abundant on the carrion site in year 2, and 18.0 times more abundant in year 3, than on the control site. They also decreased in abundance on both sites from year 2 to year 3 (site: $\beta = -1.322$, SE = 0.397, $p < 0.001$; year: $\beta = -0.511$, SE = 0.351, $p = 0.145$; site * year: $\beta = -1.569$, SE = 0.874, $p = 0.073$). The optimal model for

Diptera was the additive 'site + year' model (table S4, table S9; appendix). They were 3.1 and 4.2 times more abundant on the carrion site than the control site in year 2 and 3, respectively ($\beta = -1.288$, SE = 0.126, $p < 0.001$). They were also more abundant in year 2 than in year 3 ($\beta = -0.408$, SE = 0.126, $p = 0.001$).

Herbivores in total were not affected by carcass presence and were best described by the 'year' model, being more abundant in year 3 compared to year 2 ($\beta = 0.707$, SE = 0.129, $p < 0.001$) (table S4, table S10; appendix). There were, however, differences within the herbivore group (figure 7). The true bugs, representing herbivores feeding on stems or leaves, were best described by the 'site * year' interaction model (table S4, table S11; appendix). They were only 0.4 times as abundant on the carrion site than the control site in year 2, and 0.7 times in year 3. Like the herbivores in total, they increased in abundance on both sites from year 2 to year 3 (site: $\beta = 1.001$, SE = 0.266, $p < 0.001$; year: $\beta = 1.514$, SE = 0.263, $p < 0.001$; site * year: $\beta = -0.646$, SE = 0.359, $p = 0.072$). In contrast, the herbivorous beetles, of which the optimal model was the 'site + year' additive model, were 6.5 times more abundant on the carrion site in year 2, and 4.3 times more in year 3 ($\beta = -1.750$, SE = 0.255, $p < 0.001$) (table S4, table S12; appendix). Unlike the other herbivores, they were more abundant in year 2 ($\beta = -1.266$, SE = 0.235, $p < 0.001$). The herbivorous beetles were dominated by *Otiorhynchus nodosus* (Coleoptera: Curculionidae).

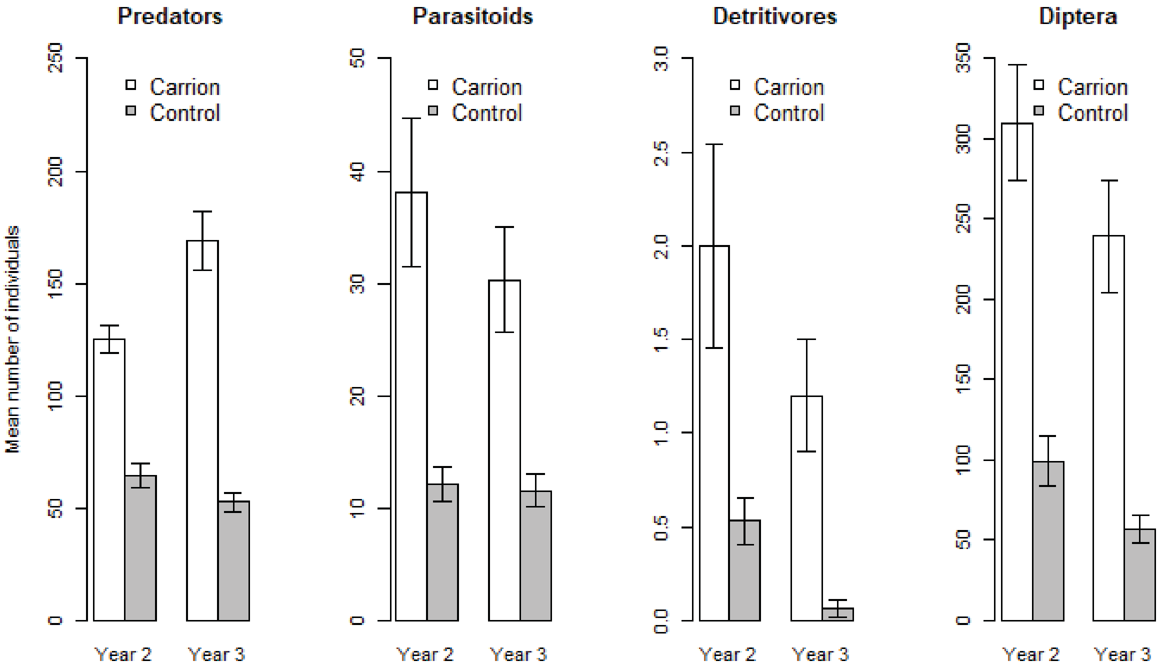


Figure 6: Mean number of predators, parasitoids, detritivores and Diptera (± SE) found in pitfall traps (N=120) two and three years after mass death of reindeer (*Rangifer tarandus*) at Hardangervidda, sorted by year and site (carrion or control).

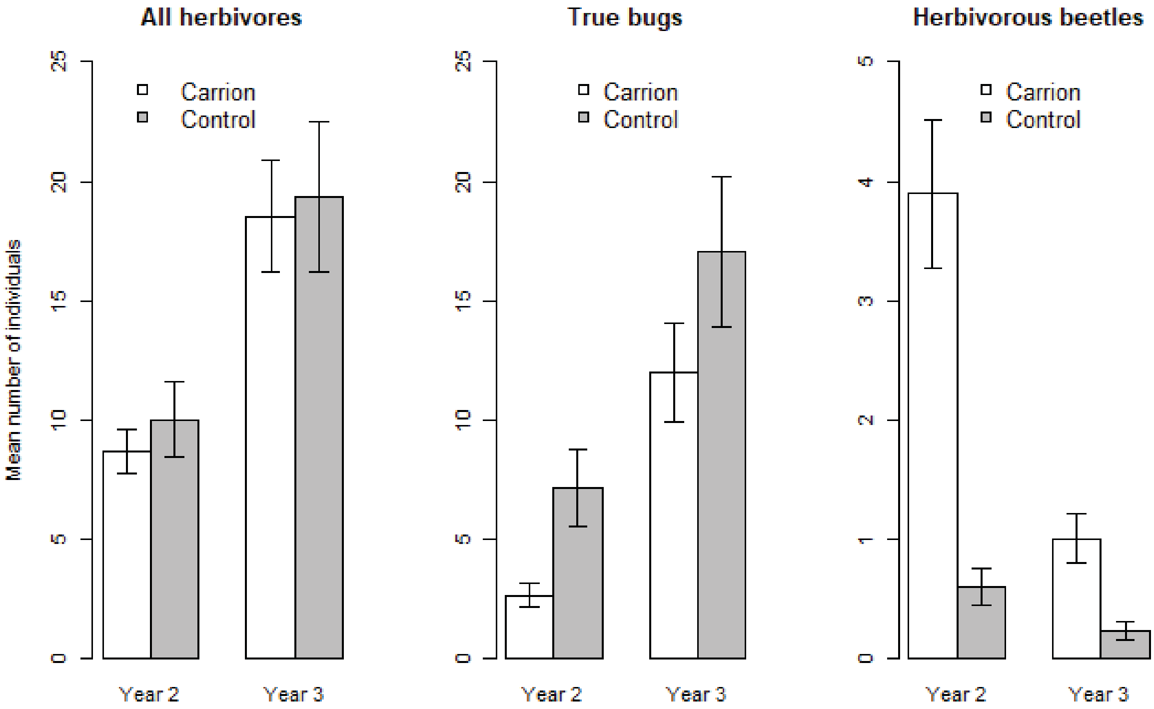


Figure 7: Mean number of all herbivores, true bugs and herbivorous beetles (± SE) found in pitfall

traps (N=120) two and three years after mass death of reindeer (*Rangifer tarandus*) at Hardangervidda, sorted by year and site (carrion or control).

Springtails and mites, not counted in year 2, were both affected by the presence of carcasses in year 3 (table S4, table S13, table S14; appendix). Springtails were 6.8 times more abundant on the carrion site than the control site (β = -1.918, SE = 0.195, p < 0.001), and mites were 2.6 times more abundant on the carrion site (β = -0.950, SE = 0.163, p < 0.001) (figure 8).

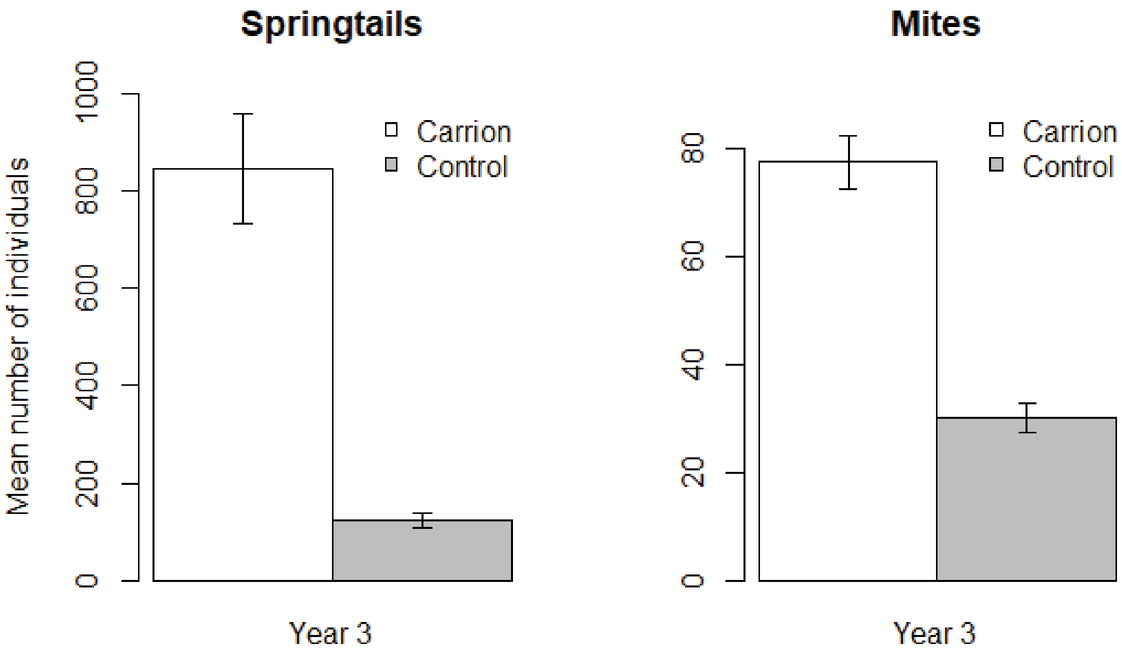


Figure 8: Mean number of springtails and mites (± SE) found in pitfall traps (N=60) three years after mass death of reindeer (*Rangifer tarandus*) at Hardangervidda, sorted by site (carrion or control).

3.3. Carrion site vs. control site: Sticky traps

The total number of arthropods on the sticky traps was best described by the ‘site * year’ interaction model (table S4, table S15; appendix). The arthropod abundance increased on the carrion site from year 2 to year 3, whereas it decreased on the control site (figure 9). This caused the sticky traps to catch 1.6 times more arthropods on the carrion site than on the control site in year 2, compared to 3.4 times more in year 3 (site: β = -0.498, SE = 0.060, p < 0.001; year: β = 0.139, SE = 0.057, p = 0.015; site * year: β = -0.577, SE = 0.089, p < 0.001).

The large catch of arthropods on the carrion site was mainly caused by *P. vulgaris*, about 40% of all individuals caught on the sticky traps. The optimal model for this group was the 'site + year' additive model (table S4, table S16; appendix). *P. vulgaris* was hardly present on the control site, yet very common on the carrion site (β = 3.474, SE = 0.200, p < 0.001). But unlike the total number of arthropods on the sticky traps, the difference in *P. vulgaris* abundance between the carrion site and the control site did not change between the years. *P. vulgaris* was, however, generally more abundant in year 3 than in year 2 (β = 0.598, SE = 0.187, p = 0.001): It comprised 25% of the Diptera in year 2 compared to 60% of the Diptera in year 3. Blow flies and flesh flies were barely present on the traps.

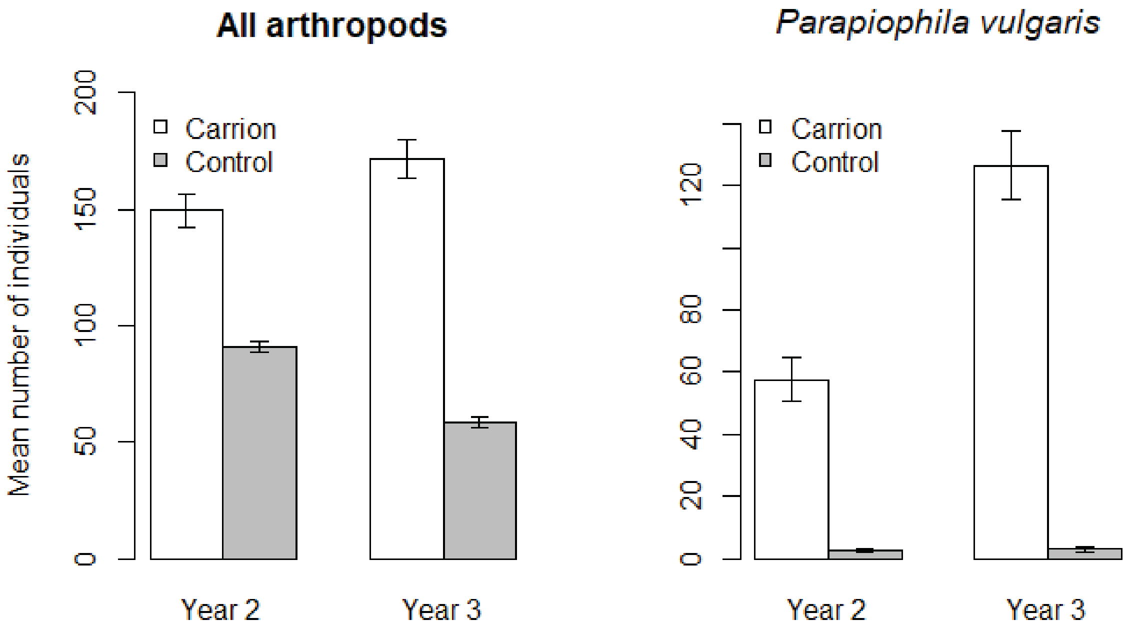


Figure 9: Mean number of all arthropods and individuals of *Parapiophila vulgaris* (± SE) found on sticky traps (N=58) two and three years after mass death of reindeer (*Rangifer tarandus*) at Hardangervidda, sorted by year and site (carrion or control).

3.4. Carrion density gradient: Pitfall traps

Within the carrion site, carrion density had an effect on several groups. The total number of arthropods in the pitfall traps was best explained by a 'carrion density' model (table S4, table S17; appendix). In general, the arthropods increased in abundance with increasing carrion density (β = 0.724, SE = 0.197, p < 0.001), and there was no difference between the years (figure 10).

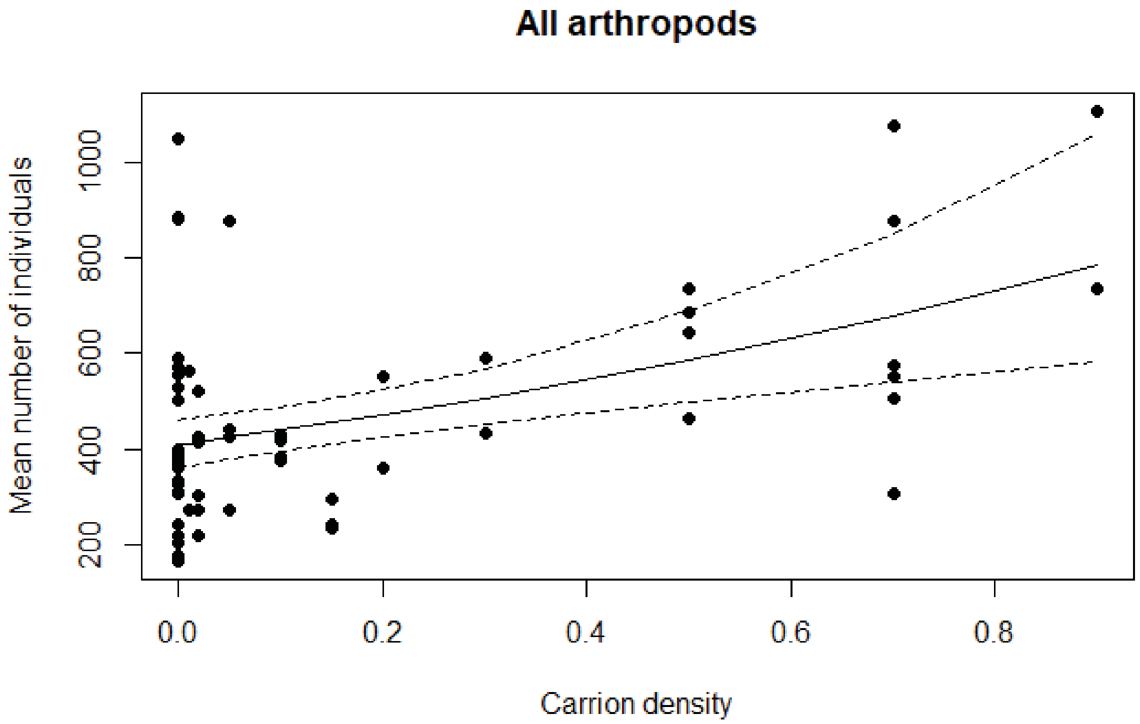
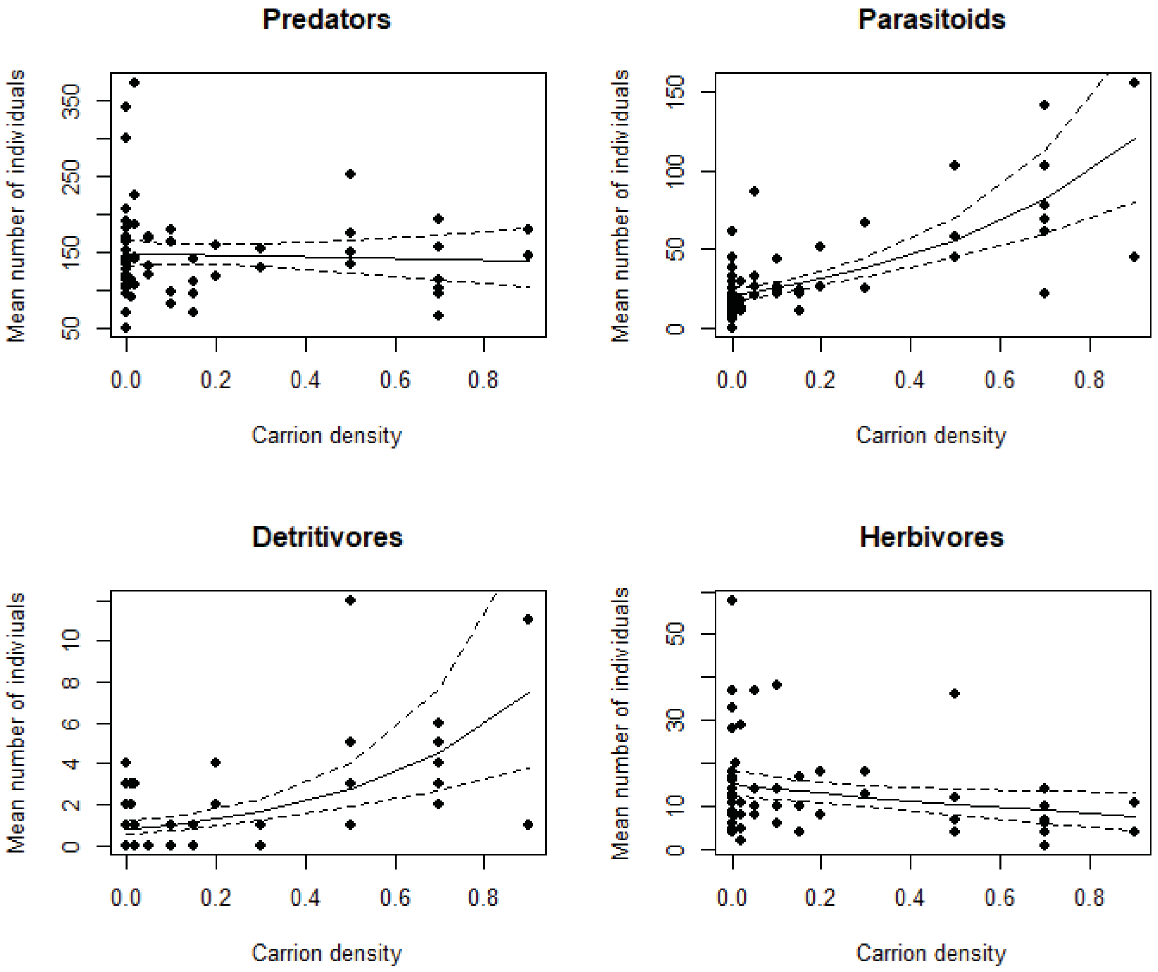


Figure 10: Mean number of arthropods (+ 95% confidence interval) found in pitfall traps (N=60) in relation to carrion density after mass death of reindeer (*Rangifer tarandus*) at Hardangervidda, year 2 and 3 combined. Springtails and mites excluded.

Predatory arthropods were not affected by carrion density and were best described by the 'year' model, being more abundant in year 3 compared to year 2 (β = 0.299, SE = 0.087, p < 0.001) (figure 12, table S4, table S18; appendix). Parasitoid abundance was best explained by the 'carrion density' model (table S4, S19; appendix). They were positively correlated with carrion density both years (β = 1.947, SE = 0.277, p < 0.001). The optimal model for the detritivores was also the 'carrion density' model (table S4, table S20; appendix), as they increased in abundance with increasing carrion density (β = 2.497, SE = 0.500, p < 0.001).

Herbivore abundance was best described by the 'carrion density + year' additive model (table S4, table S21; appendix). Although they were just as abundant on the carrion site as the control site, they decreased in abundance with increasing carrion density (β = -0.634, SE = 0.296, p = 0.032). They were also generally more common in year 3 compared to year 2 (β = 0.739, SE = 0.152, p < 0.001). The true bugs, of which the optimal model was the 'carrion density + year' additive model, responded the same way (table S4, table S22; appendix): They were also negatively correlated with carrion density (β = -1.258, SE = 0.467, p = 0.007), and were more abundant in year 3 compared to year 2 (β = 1.504, SE = 0.233, p < 0.001). The herbivorous beetles were best explained by the ‘carrion density + year’ additive model (table S4, table S23; appendix). They showed a small increase in abundance with carrion density, although not significant (β = 0.792, SE = 0.445, p = 0.075). Unlike the rest of the herbivores, they were more common in year 2 compared to year 3 (β = -1.364, SE = 0.268, p < 0.001).


Predators

Parasitoids

Detritivores

Herbivores

Figure 12: Mean number of predators, parasitoids, detritivores and herbivores (+ 95% confidence interval) found in pitfall traps (N=60) in relation to carrion density after mass death of reindeer (*Rangifer tarandus*) at Hardangervidda, year 2 and 3 combined.

Diptera were the only group that differed in their response from year 2 to year 3, and were best explained by the ‘carrion density * year’ interaction model (table S4, table S24; appendix). They had a positive correlation with carrion density in year 3, whereas they were not affected by carrion density in year 2 (figure 11) (carrion density: β = 0.431, SE = 0.389, p = 0.279; year: β = -0.560, SE = 0.178, p = 0.002; carrion density * year: β = 1.155, SE = 0.563, p = 0.040).

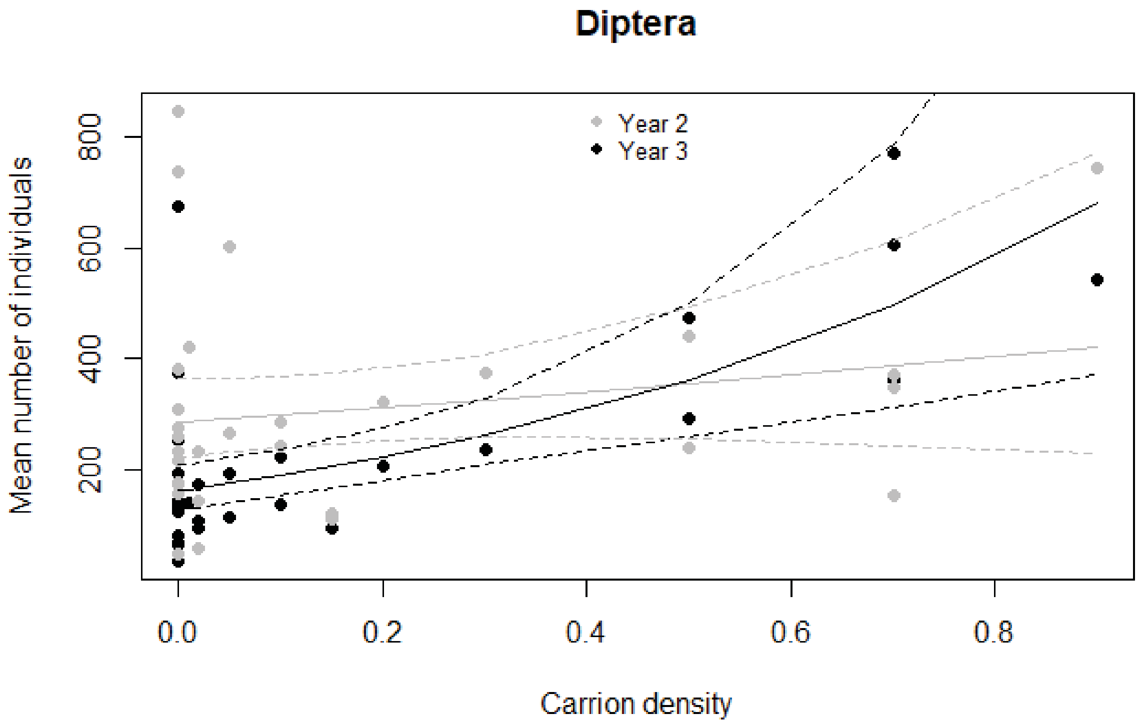


Figure 11: Mean number of Diptera (+ 95% confidence interval) found in pitfall traps (N=60) in relation to carrion density two and three years after mass death of reindeer (*Rangifer tarandus*) at Hardangervidda.

In year 3, the number of springtails was also positively correlated with carrion density (β = 1.320, SE = 0.458, p = 0.004) (figure 13, table S4, table S25; appendix). Mites were unaffected (table S4, table S26; appendix).

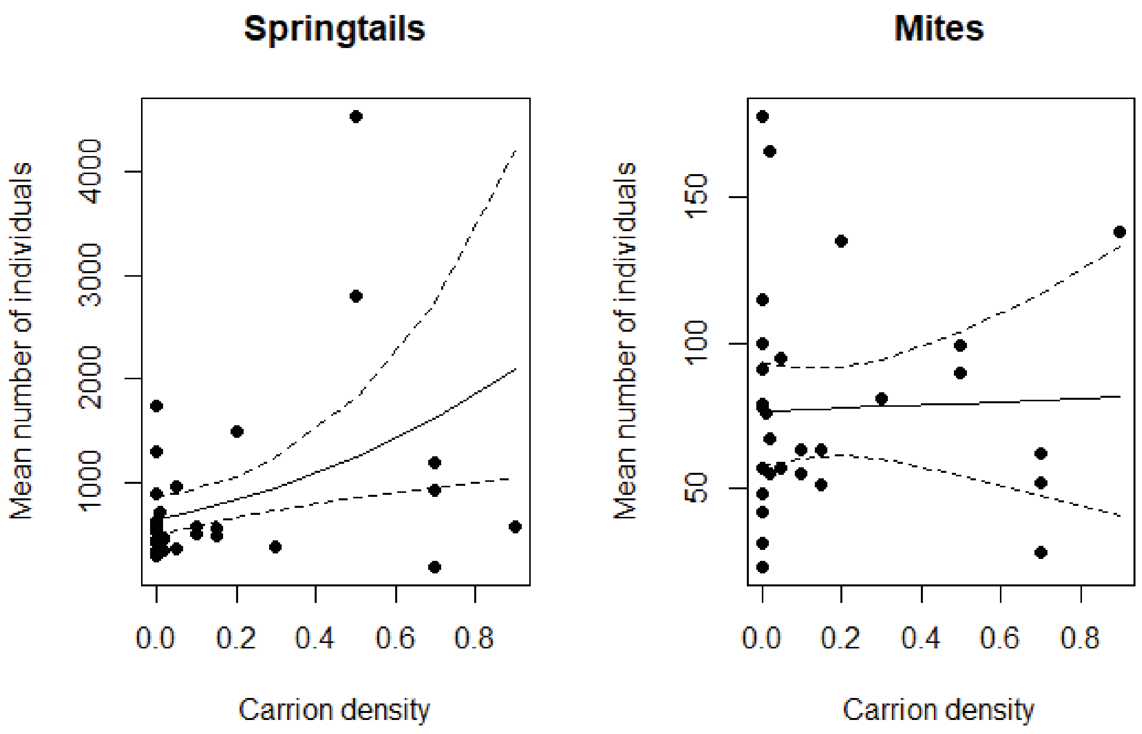


Figure 13: Mean number of springtails and mites (+ 95% confidence interval) found in pitfall traps (N=30) in relation to carrion density three years after mass death of reindeer (*Rangifer tarandus*) at Hardangervidda.

4. Discussion

The mass mortality event of reindeer had large effects on the arthropod community both two and three years post-mortem. My first hypothesis, that the effects of carrion would be smaller the third year, was refuted. There was no sign of relative decrease in arthropod activity on a large scale, nor on a small scale, from year 2 to year 3. For some groups, the activity even increased. In the large-scale analysis, the predators were more positively associated with carcass presence the third year, and in the small-scale analysis, Diptera responded more strongly to carrion density the third year.

The lack of decline in arthropod numbers around the carcasses from year 2 to year 3 are likely to be explained by the slow decomposition rate at Hardangervidda. Since most arthropods in seasonal temperate areas like Hardangervidda only have one generation per year, the arthropods here will probably need a longer time to consume a carcass than in warmer parts of the world (Füreder, 1999; DeVault et al., 2004). This might prolong the duration of the succession. Based on pictures and observations of the reindeer carcasses, the decompositional changes from the second year to the third were minimal. The carcasses were determined to be in the same decomposition stage both years, the dry/remains stage, as all that remained was bones.

The total number of arthropods was much higher on the carrion site than the control site both two and three years after mass death. Furthermore, it was positively correlated with carrion density. Previous studies that have done similar experiments have also shown that the presence of carcasses increases arthropod abundance. Sikes (1994) found more beetles on ungulate carcass plots compared to control plots in Yellowstone National Park, and the same result was found by Melis et al. (2004) in Norway. France et al. (1992) reported larger numbers of blow flies in traps mounted above buried pig carcasses than in control traps in Colorado. However, all these studies were of short duration and were done on carcasses less than a year old. Whether the arthropod activity on the carcasses ceased during the study period is not known.

In line with my second hypothesis, predators and parasitoids continued to be more abundant on the carrion site the third year after death. But surprisingly, there was a bigger difference in predator numbers between the carrion site and the control site in year 3 than it was the year before. The large abundance of predators on the carrion site was probably a numerical response caused by the unexpectedly large abundance of Diptera and other prey items. Predators like rove beetles (Coleoptera: Staphylinidae) and spiders, which were common on the carrion site, frequently feed on arthropods that can be found on carrion (Merritt and De Jong, 2015; Harwood et al., 2007). It is possible that the larger abundance of *P. vulgaris* in year 3 led to an even bigger food availability for the predators this year.

The large abundance of prey was presumably also the reason why the parasitoids preferred the carrion site. Many different arthropods can be used as hosts by parasitoid wasps, including Dipterans (Khoobdel et al., 2019; Grassberger and Frank, 2004) and spiders (Korenko et al., 2013). Both Diptera and spiders were more abundant on the carrion site. Adult parasitoid wasps also depend on nectar from flowers to feed on (Jervis et al., 1993), but since the number of flowers was reduced on the carrion site, the feeding opportunities here were limited compared to the control site.

Surprisingly, predators and parasitoids responded differently to carrion density, even though these groups were on the carrion site for the same reason. I hypothesised that predator and parasitoid numbers would increase with increasing carrion density, but this was only true for parasitoids. The reason for this difference could be that the predators move fast and are therefore not so attached to one area. Most of the parasitoid wasps caught in the traps were very small and possibly have a shorter dispersal range than the larger predators (Lei and Hanski, 1998).

Predators and parasitoids are likely to hunt the animals that are feeding on what is left of the carcasses, like detritivores and Diptera. Detritivores and Diptera showed a large increase in abundance both years, even though the carcasses were reduced to skin and bones already one year after death (Yin, 2018). Granum (2019) found that when including blow flies and flesh flies in the detritivore guild, the detritivores showed no significant change in abundance between the carrion site and the control site. Although blow flies and flesh flies are undoubtedly detritivores, they were not affected by the presence of carcasses. This is probably because the reindeer carcasses lacked the soft tissue that these flies require to oviposit (Payne, 1965; Grassberger and Frank, 2004).

Only by analysing detritivorous Diptera and detritivorous beetles separately, the latter's preference for carrion became evident. The detritivorous beetles caught in this study consisted almost entirely of necrophages. Necrophagous beetles are found to be some of the most dominant members of the carrion fauna in the later stages of decomposition (McKinnerney, 1978; Payne, 1965; Grassberger and Frank, 2004). Among these, the genera *Catops* (Coleoptera: Leiodidae) and *Omalium* (Coleoptera: Staphylinidae) were common in the pitfall traps. *Catops* have been found underneath rabbit carcasses in a montane forest (De Jong and Chadwick, 1999). *Omalium* have been found on pig carcasses in the advanced decay and the remains stages (Matuszewski et al., 2008), and on brown rat (*Rattus norvegicus*) carcasses in the decay and dry stages (Kočárek, 2003). Detritivores also increased in numbers with increasing carrion density. Since they get their food directly from the carcasses, it is likely that they prefer staying close to them.

Among the Diptera, Nematocera and Brachycera seemed to benefit equally from carrion. *P. vulgaris* was especially benefited by carrion, as it was many times more abundant on the carrion site than the control site. *P. vulgaris* belongs to Piophilidae. This is a common family on carcasses in late stages of decomposition (Muñoz-Lozano et al., 2019; Merritt and De Jong, 2015). The genera *Piophila* and *Stearibia* have even been found in the dry and remains stages (Grassberger and Frank, 2004; Martinez et al., 2006). But to my knowledge, *Parapiophila* has never been found any later than the decay stages (Fiedler et al, 2008; Matuszewski et al., 2008). My study, which suggests that *P. vulgaris* utilizes reindeer carcasses in the dry/remains stage, therefore represents a novel finding. *P. vulgaris* might exploit bones and/or antlers, similar to *Protopiophila litigate*, which only oviposits on discarded cervid antlers (Bonduriansky and Brooks, 1999), or *Thyreophora cynophila*, which feeds on bone marrow (Menier, cited in Martín-Vega et al., 2010).

For Diptera, it was only when looking at year 3 separately that a positive correlation with carrion density appeared. This might be connected to the fact that *P. vulgaris* comprised a larger part of the Diptera in year 3 than in year 2. It is possible that *P. vulgaris* is more tightly linked to the carcasses than other Diptera, although the analyses were not able to detect such a pattern. Similar to this finding, the total number of arthropods on the sticky traps was more positively associated with carcass presence in year 3 compared to year 2. *P. vulgaris* was responsible for a large part of this increasing difference, even though *P. vulgaris* itself did not respond significantly different to carcass presence the two years. It is however likely that *P. vulgaris* concealed any response that other Diptera might have had. *P. vulgaris* dominated on the sticky traps on the carrion site, and these traps were almost completely covered at the end of the trapping periods. As the traps fill up, their ability to catch arthropods is reduced.

Herbivore abundance in total was not affected by the presence of carcasses. This was as expected, as Granum (2019) found the same result. But by dividing the herbivores into more specific groups, I found that true bugs were less abundant on the carrion site. The reduction in vegetation on the carrion site, caused by the decaying carcasses, was visible both in year 2 and year 3. True bugs might be particularly affected by this because they spend more time at the plant they are feeding on than other herbivores like butterflies (Lepidoptera) and bees (Hymenoptera: Apiformes), which predominantly visit flowers for pollen and nectar. However, this finding is contradictory to Gu (cited in Gu et al., 2014), who found larger numbers of cicadas (Hemiptera: Cicadoidea) in pitfall traps closest to the carcass.

The herbivorous beetles, consisting almost exclusively of the weevil *O. nodosus,* were more common on the carrion site. This species is best known for feeding on roots and leaves of woody plants (Lemdahl, 2000; Oddsdottir et al., 2010), but may also exploit decomposing matter, whether the source is a plant, a fungus or an animal (Ligaard, 2020 – pers. comm.). Therefore, it might be that *O. nodosus* is actually feeding on decaying matter or fungi around the carcasses. An alternative explanation is that the beetles are simply easier to catch on the carrion site. *O. nodosus* is nocturnal, and on its wanderings on the carrion site, it might easily fall into the pitfall traps because of fewer obstacles like heather and shrubs than on the control site. *O. nodosus* was also found to increase in abundance after low-intensity burning of clear-cut forests in Sweden (Hjältén et al., 2010), a disturbance event that would also remove these obstacles. Even though the herbivorous beetles were more abundant on the carrion site than the control site, carrion density was of no significant importance to their abundance. This led to an overall decrease in herbivore numbers with increasing carrion density.

The third year, springtails showed a large increase in abundance from the control site to the carrion site. This is in accordance with Gu et al. (2014) and Klonowski et al. (2015), who found that springtails were positively associated with carcass presence. An explanation for this could be the large nutrient pulse. Hågvar and Klanderud (2009) found that the number of springtails increased with added nitrogen, phosphorus and potassium, nutrients that a cadaver also adds to the soil (Towne, 2000; Carter et al., 2007). In Klonowski et al. (2015), the abundance of the springtail *Hypogastrura vernalis* was positively associated with carcass presence, and also showed a positive correlation with phosphate and nitrate concentrations in the soil. According to Hågvar and Klanderud (2009), nutrients enhance the growth of graminoids, and the decomposition of graminoid litter causes high fungal activity which increases the food availability for fungivorous springtails. Therefore, it is possible that the springtails that increased in abundance in my study were fungivores. In contrast to all of these observations, Bornemissza (1957) found that the springtail community was drastically reduced after arrival of a guinea pig (*Cavia porcellus*) carcass, and that it remained that way for at least a year.

The springtails also increased in abundance with increasing carrion density. This is similar to the finding of Klonowski et al. (2015), who found that the biggest springtail abundance was near the centre of a badger carcass. However, my observations were quite few, as I only had one year of observations for springtails. More observations might have helped in making this relationship clearer. This also applies to the mites, which were not affected by carrion density. Despite their indifference to carrion density, the mites were more abundant on the carrion site than the control site. Mites are a large group with diverse feeding habits, and they may live below or above the soil surface (Bornemissza, 1957; Perotti and Braig, 2009). Soil-dwelling mites tend to disappear when a carcass is present (Merritt and De Jong, 2015). For example, Bornemissza (1957) found significantly lower numbers of mites underneath a guinea pig carcass than in the surrounding soil. Since the mites in my study were caught in pitfall traps, the majority of them was most likely surface-living. The mites that increased in abundance on the carrion site might have been parasitic or phoretic mites, arriving on the carrion site on the bodies of other arthropods, or predatory mites that feed on fly eggs, microbes, springtails or other arthropods present on the carcasses (Perotti and Braig, 2009).

A possible drawback of this study is that the trapping period in year 3 lasted a week longer than in year 2. A way to make the two years more comparable could be standardizing for trapping effort, i.e. dividing the trapped number by the number of trapping days. However, it is likely that the arthropod community at Hardangervidda changes throughout the summer. If the arthropods linked to carrion were affected differently than other arthropods during the extra week in year 3, there is a chance that this is responsible for some of the differences in arthropod composition between year 2 and year 3.

My study shows that it may take more than three years before an alpine area affected by a mass mortality event goes back to its original state. Predators, parasitoids, detritivores, Diptera, springtails and mites were still flourishing on the remains of the reindeer carcasses at Hardangervidda three years after death. Like many other carrion studies, this implies that carcasses are an important element of a diverse ecosystem. The cadaver decomposition islands they create can have an impact on the soil and vegetation for years after death, especially by elevating the nutrient levels (Bornemisszza, 1957; Coe, 1978; Towne, 2000; Carter et al., 2007). Carcasses also have an important role in providing food for scavengers and their predators (Payne, 1965; Moleón et al., 2015; Lashley et al., 2017). Because of the high soil fertility and resource availability, carcasses can support a large production of both plant and animal biomass and hence become hotspots of biodiversity (Towne, 2000; Baruzzi et al., 2018). By systematically removing or destroying carcasses, the energy source they represent will be lost from the ecosystem. This might limit the abundance of species that depend on this kind of resource.

Studies on the impact of carrion in alpine ecosystems, especially concerning the accumulation of arthropods, will be of great importance in understanding this nutrient-limited ecosystem. I recommend that the study carried out by Granum (2019) and myself gets continued, to see how the carrion site at Hardangervidda develops in the years to come.

References

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 (4): 761-772

Baruzzi, C., Mason, D., Barton, B. and Lashley, M. (2018): “Effects of increasing carrion biomass on food webs”. *Food webs*, 17: e00096

Benbow, M. E., Tomberlin, J. K. and Tarone, A. M. (2015): “Introduction to carrion ecology, evolution, and their applications”. *Carrion Ecology, Evolution, and Their Applications*. Eds. Benbow, M. E., Tomberlin, J. K. and Tarone, A. M. CRC Press.

Bonduriansky, R. and Brooks, R. J. (1999): “Why do male antler flies (*Protopiophila litigata*) fight? The role of male combat in the structure of mating aggregations on moose antlers”. *Ethology Ecology & Evolution*, 11 (3): 287-301

Bornemissza, G. F. (1957): “An analysis of arthropod succession in carrion and the effect of its decomposition on the soil fauna”. *Australian Journal of Zoology*, 5 (1): 1-12

Braack, L. E. O. (1981): “Visitation patterns of principal species of the insect-complex at carcasses in the Kruger National Park”. *Koedoe*, 24 (1): 33-49

Bump, J. K., Peterson, R. O., Vucetich, J. A. (2009): “Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses”. *Ecology*, 90 (11): 3159-3167

Carter, D. O., Tibbett, M. and Yellowlees, D. (2007): “Cadaver decomposition in terrestrial ecosystems”. *The Science of Nature*, 94 (1): 12-24

Coe, M. (1978): “The decomposition of elephant carcasses in the Tsavo (east) National Park, Kenya”. *Journal of Arid Environments*, 1 (1): 71-86

Danell, K., Berteaux, D. and Bråthen, K. A. (2002): “Effect of muskox carcasses on nitrogen concentration in tundra vegetation”. *Arctic*, 55 (4): 389-392

De Jong, G. and Chadwick, J. W (1999): “Decomposition and arthropod succession on exposed rabbit carrion during summer at high altitudes in Colorado, USA”. *Journal of Medical Entomology,* 36 (6): 833-45.

DeVault, T. L., Brisbin Jr., I. L. and Rhodes, O. E. (2004): “Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers”. *Canadian Journal of Zoology*, 82 (3): 502-509

Fey, S. B., Siepielski, A. M., Nusslé, S., Cervantes-Yoshida, K., Hwan, J. L., Huber, E. R., Fey, M. J., Catenazzi, A. and Carlson, S. M. (2015): “Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events”. *PNAS*, 112 (4): 1083-1088

Fiedler, A., Halbach, M., Sinclair, B. and Benecke, M. (2008): “What is the edge of a forest? A diversity analysis of adult Diptera found on decomposing piglets inside and on the edge of a western German woodland inspired by a courtroom question”. *Entomologie heute*, 20: 173-191

Forbes, S. L. and Carter, D. O. (2015): “Processes and mechanisms of death and decomposition of vertebrate carrion”. *Carrion Ecology, Evolution, and Their Applications*. Eds. Benbow, M. E., Tomberlin, J. K. and Tarone, A. M. CRC Press.

France, D. L., Griffin, T. J., Swanburg, J. G., Lindemann, J. W., Davenport, G. C., Trammell, V., Armbrust, C. T., Kondratieff, B., Nelson, A., Castellano, K. and Hopkins, D. (1992): “A multidisciplinary approach to the detection of clandestine graves”. *Journal of Forensic Sciences,* 37 (6): 1445-1458

Füreder, L. (1999): “High alpine streams: cold habitats for insect larvae”. *Cold-Adapted Organisms*. Eds. Margesin R. and Schinner F. Springer, Berlin, Heidelberg.

Granum, H. M. (2019): “Change in arthropod communities following a mass death incident of reindeer at Hardangervidda”. Master’s thesis. Ås: Norwegian University of Life Sciences.

Grassberger, M. and Frank, C. (2004): “Initial study of arthropod succession on pig carrion in a Central European urban habitat”. *Journal of Medical Entomology*, 41 (3), 1: 511–523

Gu, X., Haelewaters, D., Krawczynski, R., Vanpoucke, S., Wagner, H. and Wiegleb, G. (2014): “Carcass ecology - more than just beetles”. *Entomologische Berichten*, 74 (1-2): 68-74

Gwyther, C. L., Williams, A. P., Golyshin, P. N., Edwards-Jones, G., Gareth and Jones, D. L. (2011): “The environmental and biosecurity characteristics of livestock carcass disposal methods: A review”. *Waste Management*, 31 (4): 767–778

Harwood, J. D., Bostrom, M. R., Hladilek, E. E., Wise, D. H. and Obrycki, J. J. (2007): “An order-specific monoclonal antibody to Diptera reveals the impact of alternative prey on spider feeding behavior in a complex food web”. *Biological Control*, 41 (3): 397-407

Hurvich, C. M. and Tsai, C. (1989): “Regression and time series model selection in small samples”. *Biometrika*, 76 (2): 297-307

Hågvar, S. and Klanderud, K. (2009): “Effect of simulated environmental change on alpine soil arthropods”. *Global Change Biology*, 15 (12): 2972-2980

Jervis, M. A., Kidd, N. A. C., Fitton, M. G., Huddleston, T. and Dawah, H. A. (1993): “Flower-visiting by hymenopteran parasitoids”. *Journal of Natural History*, 27 (1): 67-105

Khoobdel, M., Sobati, H., Dehghan, O., Akbarzadeh, K. and Radi, E. (2019): “Natural host preferences of parasitoid wasps (Hymenoptera: Pteromalidae) on synanthropic flies”. *European Journal of Translational Myology*, 29 (2): 118-123

Klonowski, B. Rössler, A., Gu, X., Krawczynski, R. and Wiegleb, G. (2015): “Influence of a badger carcass on soil chemistry and Collembola”. *Acta Societatis Zoologicae Bohemicae*, 79 (3): 235-241

Kočárek, P. (2003): “Decomposition and Coleoptera succession on exposed carrion of small mammal in Opava, the Czech Republic”. *European Journal of Soil Biology*, 39 (1): 31-45

Korenko, S., Isaia, M., Satrapová, J. and Pekár, S. (2013): “Parasitoid genus-specific manipulation of orb-web host spiders (Araneae, Araneidae)”. *Ecological Entomology*, 39 (1): 30-38

Lashley, M. A., Jordan, H. R., Tomberlin, J. K. and Barton, B. T. (2017): “Indirect effects of larval dispersal following mass mortality events”. *Ecology*, 99 (2): 491-493

Lemdahl, G. (2000): “Late-glacial and early-Holocene Coleoptera assemblages as indicators of local environment and climate at Kråkenes Lake, western Norway”. *Journal of Paleolimnology*, 23 (1): 57-66

Margalida, A. and Colomer, M. A. (2012): “Modelling the effects of sanitary policies on European vulture conservation”. *Scientific Reports*, 2: 1-7

Martinez, E., Duque, P. and Wolff, M. (2006): “Succession pattern of carrion-feeding insects in Paramo, Colombia”. *Forensic Science International*, 166 (2-3): 182–189

Martín-Vega, D., Baz, A. and Michelsen, V. (2010): “Back from the dead: *Thyreophora cynophila* (Panzer, 1798) (Diptera: Piophilidae) ‘globally extinct’ fugitive in Spain”. *Systematic Entomology*, 35 (4): 607-613

Matuszewski, S., Bajerlein, D., Konwerski, S. and Szpila, K. (2008): “An initial study of insect succession and carrion decomposition in various forest habitats of Central Europe”. *Forensic Science International*, 180 (2-3): 61-69

McCall, C. and Primack, R. B. (1992): “Influence of flower characteristics, weather, time of day, and season on insect visitation rates in three plant communities”. *American Journal of Botany*, 79 (4): 434-442

McKinnerney, M. (1978): “Carrion communities in the northern Chihuahuan Desert”. *The Sourthwestern Naturalist*, 23 (4): 563-576

Melis, C., Teurlings, I., Linnell, J. D. C., Andersen, R. and Bordini, A. (2004): “Influence of a deer carcass on Coleopteran diversity in a Scandinavian boreal forest: A preliminary study”. *European Journal of Wildlife Research*, 50 (3): 146-149

Melvold, K. and Skaugen, T. (2013): “Multiscale spatial variability of lidar-derived and modeled snow depth on Hardangervidda, Norway”. *Annals of Glaciology*, 54 (62): 273-281

Merritt, R. W. and De Jong, G. D. (2015): “Arthropod Communities in Terrestrial Environments”. *Carrion Ecology, Evolution, and Their Applications*. Eds. Benbow, M. E., Tomberlin, J. K. and Tarone, A. M. CRC Press.

Moleón, M., Sánchez-Zapata, J. A., Sebastián-González, E. and Owen-Smith, N. (2015): “Carcass size shapes the structure and functioning of an African scavenging assemblage”. *Oikos*, 124 (10): 1391-1403

Muñoz-Lozano, C., Martín-Vega, D., Martínez-Carrasco, C., Sánchez-Zapata, J. A., Morales-Reyes, Z., Gonzálves, M. and Moleón, M. (2019): “Avoidance of carnivore carcasses by vertebrate scavengers enables colonization by a diverse community of carrion insects”. *PLoS One*, 14 (8): e0221890

Oddsdottir, E. S., Eilenberg, J., Sen, R., Harding, S. and Halldorsson, G. (2010): “Early reduction of *Otiorhynchus* spp. larval root herbivory on *Betula pubescens* by beneficial soil fungi”. *Applied Soil Ecology*, 45 (3): 168-174

Parmenter, R. R. and MacMahon, J. A. (2009): “Carrion decomposition and nutrient cycling in a semiarid shrub–steppe ecosystem”. *Ecological Monograph*, 79 (4): 637-661

Payne, J. A. (1965): “A summer carrion study of the baby pig *Sus scrofa* Linnaeus.” *Ecology*, 46 (5): 592-602

Perotti, M. A. and Braig, H. R. (2009): “Phoretic mites associated with animal and human decomposition”. *Experimental and Applied Acarology*, 49 (1-2): 85-124

Sikes, D. S. (1994): “Influences of ungulate carcasses on coleopteran communities in Yellowstone National Park, USA”. Montana State University-Bozeman, College of Agriculture

Sinclair, R. (2004): “Persistence of dead trees and fallen timber in the arid zone: 76 years of data from the T.G.B. Osborn Vegetation Reserve, Koonamore, South Australia”. *The Rangeland Journal*, 26 (1): 111-122

Spicka, A., Johnson, R., Bushing, J., Higley, L. G. and Carter, D. O. (2011): “Carcass mass can influence rate of decomposition and release of ninhydrin-reactive nitrogen into gravesoil”. *Forensic Science International*, 209 (1-3): 80–85

Steyaert, S. M. J. G., Frank, S., Puliti, S., Badia, R., Arnberg, M. P., Beardsley, J., Økelsrud, A. and Blaalid, R. (2018): "Special delivery: Scavengers direct seed dispersal towards ungulate carcasses". *Biology letters*, 14 (8): 20180388

Storaunet, K. O. and Rolstad, J. (2002): "Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest". *Canadian Journal of Forest Research*, 32 (10): 1801-1812

Strand, O., Bevanger, K. and Falldorf, T. (2006): NINA rapport 131, "Reinens bruk av Hardangervidda". Norwegian Institute for Nature Research.

Towne, E. G. (2000): "Prairie vegetation and soil nutrient responses to ungulate carcasses". *Oecologia*, 122 (2): 232–239

Vantassel, S. M. and King, M. (2018): "Wildlife carcass disposal". Wildlife Damage Management Technical Series. USDA, APHIS, WS National Wildlife Research Center. Fort Collins, Colorado.

Wallace, J. R. (2015): "Aquatic vertebrate carrion decomposition". *Carrion Ecology, Evolution, and Their Applications*. Eds. Benbow, M. E., Tomberlin, J. K. and Tarone, A. M. CRC Press.

Wang, J., Li, Z., Chen, Y., Chen, Q. and Yin, X. (2008): "The succession and development of insects on pig carcasses and their significances in estimating PMI in south China". *Forensic Science International*, 179 (1): 11-18

Yin, S. (17.08.2018): "Hundreds of reindeer died by lightning. Their carcasses became a laboratory". The New York Times. Retrieved 07.05.2020 from: https://www.nytimes.com/2018/08/17/science/reindeer-carcasses-lightning.html

Appendix

Table S1: The functional groups of which taxonomic arthropod groups were divided into, based on what was caught in pitfall traps and sticky traps two and three years after mass death of reindeer (*Rangifer tarandus*) at Hardangervidda.

Functional group	**Taxonomic groups**
Predators	Araneae, Opiliones, Neuroptera, Coleoptera (*Podistra, Rhagonycha, Carabus, Cymindis, Notiophilus, Patrobus, Dasytes, Acidota, Acrotona, Aleochara, Anthophagus, Atheta, Bryophacis, Cephalocousya, Deliphrum, Eucnecosum, Lesteva, Liogluta, Mycetoporus, Oxypoda, Philontus, Quedius, Tachinus, Omalium**)
Herbivores	Hemiptera, Lepidoptera, Symphyta, Coleoptera (*Byrrhus, Gonioctena, Otiorhynchus)*
Detritivores	Coleoptera *(Oxytelus, Catops, Protaetia, Thanatophilus, Omalium)*
Parasitoids	Evanioidea, Ichneumonoidea, Cynipoidea, Chalcidoidea, Proctotrupoidea, Sphecoidea, Pompiloidea
Others	Plecoptera, Vespidae, Siphonaptera, Coleoptera (*Amara, Cryptophagus, Agathidium*)

* The genus *Omalium* is included in both the predator group and the detritivore group.

Table S2: Total number of arthropods in each of the functional/taxonomic groups found in pitfall traps (N=120) two and three years after mass death of reindeer (*Rangifer tarandus*) at Hardangervidda, sorted by year and site (carrion or control).

	Year	**Carrion site**	**Control site**	**Total**
All arthropods	2018	18,622	6,715	25,337
Predators	2018	7,782	2,979	10,761
Parasitoids	2018	1,142	364	1,506
Detritivores	2018	60	16	76
Herbivores	2018	260	300	560

Diptera	2018	9,304	2,980	12,284
Others	2018	74	76	150
All arthropods*	2019	41,460	8,896	50,356
Predators	2019	5,067	1,579	6,646
Parasitoids	2019	909	347	1,256
Detritivores	2019	36	2	38
Herbivores	2019	556	580	1,136
Diptera	2019	7,176	1,705	8,881
Springtails	2019	25,387	3,730	29,117
Mites	2019	2,323	898	3,221
Others	2019	6	55	61

* In 2019, two additional groups (springtails and mites) were counted.

Table S3: Total number of arthropods in each functional/taxonomic group found on sticky traps (N=58) two and three years after mass death of reindeer (*Rangifer tarandus*) at Hardangervidda, sorted by year and site (carrion or control).

	Year	**Carrion site**	**Control site**	**Total**
All arthropods	2018	2,240	1,362	3,602
Parapiophila vulgaris	2018	863	36	899
Other Brachycera	2018	1,080	1,048	2,128
Nematocera	2018	272	267	539
Parasitoids	2018	25	11	36
All arthropods	2019	2,575	762	3,337
Parapiophila vulgaris	2019	1,899	38	1,937
Other Brachycera	2019	397	483	880
Nematocera	2019	234	176	410
Parasitoids	2019	45	65	110

Table S4: The optimal negative binomial regression models, and their AICc weights, that were used to explain how the abundance of different arthropods on a site with mass death of reindeer (*Rangifer* *tarandus*) and a similar control site 300 m away was affected by site (carrion or control), year, and carrion density two and three years after the mass death event.

	Carrion site vs. control site		**Carrion density**	
	Optimal model	**AICc weight**	**Optimal model**	**AICc weight**
Pitfall traps				
All arthropods	Site + year	0.453	Carrion density	0.585
Predators	Site * year	0.979	Year	0.679
Parasitoids	Site	0.539	Carrion density	0.571
Detritivores	Site * year	0.684	Carrion density	0.466
All herbivores	Year	0.627	Carrion density + year	0.457
True bugs	Site * year	0.623	Carrion density + year	0.701
Herbivorous beetles	Site + year	0.692	Carrion density + year	0.490
Diptera	Site + year	0.588	Carrion density * year	0.677
Springtails	Site	1.000	Carrion density	0.891
Mites	Site	1.000	Null model	0.771
Sticky traps				
All arthropods	Site * year	1.000	NA	NA
Parapiophila vulgaris	Site + year	0.509	NA	NA

Table S5: The optimal negative binomial regression model explaining total number of arthropods caught in pitfall traps (N=120) at Hardangervidda at a site with mass death of reindeer (*Rangifer tarandus*) and a similar control site 300 m away two and three years after the mass death event. Springtails and mites excluded.

	Estimate	**Std. error**	***p* value**
Intercept	6.244	0.073	<0.001
Site	-1.058	0.085	<0.001
Year	-0.170	0.085	0.045

Note: The intercept represents the abundance on the carrion site in year 2.

Table S6: The optimal negative binomial regression model explaining number of predators caught in pitfall traps (N=120) at Hardangervidda at a site with mass death of reindeer (*Rangifer tarandus*) and a similar control site 300 m away two and three years after the mass death event.

	Estimate	**Std. error**	***p* value**
Intercept	4.830	0.069	<0.001
Site	-0.669	0.099	<0.001
Year	0.299	0.097	0.002
Site:Year	-0.496	0.139	<0.001

Note: The intercept represents the abundance on the carrion site in year 2.

Table S7: The optimal negative binomial regression model explaining number of parasitoids caught in pitfall traps (N=120) at Hardangervidda at a site with mass death of reindeer (*Rangifer tarandus*) and a similar control site 300 m away two and three years after the mass death event.

	Estimate	**Std. error**	***p* value**
Intercept	3.532	0.093	<0.001
Site	-1.059	0.135	<0.001

Note: The intercept represents the abundance on the carrion site.

Table S8: The optimal negative binomial regression model explaining number of detritivores caught in pitfall traps (N=120) at Hardangervidda at a site with mass death of reindeer (*Rangifer tarandus*) and a similar control site 300 m away two and three years after the mass death event.

	Estimate	**Std. error**	***p* value**
Intercept	0.693	0.237	0.003
Site	-1.322	0.397	<0.001
Year	-0.511	0.351	0.145
Site:Year	-1.569	0.874	0.073

Note: The intercept represents the abundance on the carrion site in year 2.

Table S9: The optimal negative binomial regression model explaining number of Diptera caught in pitfall traps (N=120) at Hardangervidda at a site with mass death of reindeer (*Rangifer tarandus*) and a similar control site 300 m away two and three years after the mass death event.

	Estimate	**Std. error**	***p* value**

Intercept	5.814	0.109	<0.001
Site	-1.288	0.126	<0.001
Year	-0.408	0.126	0.001

Note: The intercept represents the abundance on the carrion site in year 2.

Table S10: The optimal negative binomial regression model explaining number of herbivores caught in pitfall traps (N=120) at Hardangervidda at a site with mass death of reindeer (*Rangifer tarandus*) and a similar control site 300 m away two and three years after the mass death event.

	Estimate	**Std. error**	***p* value**
Intercept	2.234	0.094	<0.001
Year	0.707	0.129	<0.001

Note: The intercept represents the abundance in year 2.

Table S11: The optimal negative binomial regression model explaining number of true bugs caught in pitfall traps (N=120) at Hardangervidda at a site with mass death of reindeer (*Rangifer tarandus*) and a similar control site 300 m away two and three years after the mass death event.

	Estimate	**Std. error**	***p* value**
Intercept	0.968	0.199	<0.001
Site	1.001	0.266	<0.001
Year	1.514	0.263	<0.001
Site:Year	-0.646	0.359	0.072

Note: The intercept represents the abundance on the carrion site in year 2.

Table S12: The optimal negative binomial regression model explaining number of herbivorous beetles caught in pitfall traps (N=120) at Hardangervidda at a site with mass death of reindeer (*Rangifer tarandus*) and a similar control site 300 m away two and three years after the mass death event.

	Estimate	**Std. error**	***p* value**
Intercept	1.330	0.149	<0.001
Site	-1.750	0.255	<0.001
Year	-1.266	0.235	<0.001

Note: The intercept represents the abundance on the carrion site in year 2.

Table S13: The optimal negative binomial regression model explaining number of springtails caught in pitfall traps (N=60) at Hardangervidda at a site with mass death of reindeer (*Rangifer tarandus*) and a similar control site 300 m away three years after the mass death event.

	Estimate	**Std. error**	***p* value**
Intercept	6.741	0.138	<0.001
Site	-1.918	0.195	<0.001

Note: The intercept represents the abundance on the carrion site.

Table S14: The optimal negative binomial regression model explaining number of mites caught in pitfall traps (N=60) at Hardangervidda at a site with mass death of reindeer (*Rangifer tarandus*) and a similar control site 300 m away three years after the mass death event.

	Estimate	**Std. error**	***p* value**
Intercept	4.349	0.114	<0.001
Site	-0.950	0.163	<0.001

Note: The intercept represents the abundance on the carrion site.

Table S15: The optimal negative binomial regression model explaining total number of arthropods caught on sticky traps (N=58) at Hardangervidda at a site with mass death of reindeer (*Rangifer tarandus*) and a similar control site 300 m away two and three years after the mass death event.

	Estimate	**Std. error**	***p* value**
Intercept	5.006	0.041	<0.001
Site	-0.498	0.060	<0.001
Year	0.139	0.057	0.015
Site:Year	-0.577	0.089	<0.001

Note: The intercept represents the abundance on the carrion site in year 2.

Table S16: The optimal negative binomial regression model explaining number of individuals of *Parapiophila vulgaris* caught on sticky traps (N=58) at Hardangervidda at a site with mass death of reindeer (*Rangifer tarandus*) and a similar control site 300 m away two and three years after the mass death event.

	Estimate	**Std. error**	***p* value**
Intercept	4.153	0.147	<0.001

Site	-3.474	0.200	<0.001
Year	0.598	0.187	0.001

Note: The intercept represents the abundance on the carrion site in year 2.

Table S17: The optimal negative binomial regression model explaining number of arthropods caught in pitfall traps (N=60) at Hardangervidda at a site with varying carrion density, two and three years after a mass mortality event of reindeer (*Rangifer tarandus*). Springtails and mites excluded.

	Estimate	**Std. error**	***p* value**
Intercept	6.012	0.062	<0.001
Carrion density	0.724	0.197	<0.001

Table S18: The optimal negative binomial regression model explaining number of predators caught in pitfall traps (N=60) at Hardangervidda at a site with varying carrion density, two and three years after a mass mortality event of reindeer (*Rangifer tarandus*).

	Estimate	**Std. error**	***p* value**
Intercept	4.830	0.062	<0.001
Year	0.299	0.087	<0.001

Note: The intercept represents the abundance in year 2.

Table S19: The optimal negative binomial regression model explaining number of parasitoids caught in pitfall traps (N=60) at Hardangervidda at a site with varying carrion density, two and three years after a mass mortality event of reindeer (*Rangifer tarandus*).

	Estimate	**Std. error**	***p* value**
Intercept	3.040	0.091	<0.001
Carrion density	1.947	0.277	<0.001

Table S20: The optimal negative binomial regression models explaining number of detritivores caught in pitfall traps (N=60) at Hardangervidda at a site with varying carrion density, two and three years after a mass mortality event of reindeer (*Rangifer tarandus*).

	Estimate	**Std. error**	***p* value**
Intercept	-0.232	0.204	0.256
Carrion density	2.497	0.500	<0.001

Table S21: The optimal negative binomial regression models explaining number of herbivores caught in pitfall traps (N=60) at Hardangervidda at a site with varying carrion density, two and three years after a mass mortality event of reindeer (*Rangifer tarandus*).

	Estimate	**Std. error**	***p* value**
Intercept	2.267	0.121	<0.001
Carrion density	-0.634	0.296	0.032
Year	0.739	0.152	<0.001

Note: The intercept represents the abundance in year 2.

Table S22: The optimal negative binomial regression models explaining number of true bugs caught in pitfall traps (N=60) at Hardangervidda at a site with varying carrion density, two and three years after a mass mortality event of reindeer (*Rangifer tarandus*).

	Estimate	**Std. error**	***p* value**
Intercept	1.142	0.190	<0.001
Carrion density	-1.258	0.467	0.007
Year	1.504	0.233	<0.001

Note: The intercept represents the abundance in year 2.

Table S23: The optimal negative binomial regression models explaining number of herbivorous beetles caught in pitfall traps (N=60) at Hardangervidda at a site with varying carrion density, two and three years after a mass mortality event of reindeer (*Rangifer tarandus*).

	Estimate	**Std. error**	***p* value**
Intercept	1.204	0.175	<0.001
Carrion density	0.792	0.445	0.075
Year	-1.364	0.268	<0.001

Note: The intercept represents the abundance in year 2.

Table S24: The optimal negative binomial regression models explaining number of Diptera in pitfall traps (N=60) at Hardangervidda at a site with varying carrion density, two and three years after a mass mortality event of reindeer (*Rangifer tarandus*).

	Estimate	**Std. error**	***p* value**
Intercept	5.655	0.126	<0.001

Carrion density	0.431	0.398	0.279
Year	-0.560	0.178	0.002
Carrion density:Year	1.155	0.563	0.040

Note: The intercept represents the abundance in year 2.

Table S25: The optimal negative binomial regression model explaining number of springtails caught in pitfall traps (N=30) at Hardangervidda at a site with varying carrion density, three years after a mass mortality event of reindeer (*Rangifer tarandus*).

	Estimate	**Std. error**	***p* value**
Intercept	6.460	0.145	<0.001
Carrion density	1.320	0.458	0.004

Table S26: The optimal negative binomial regression model explaining number of mites caught in pitfall traps (N=30) at Hardangervidda at a site with varying carrion density, three years after a mass mortality event of reindeer (*Rangifer tarandus*).

	Estimate	**Std. error**	***p* value**
Intercept	4.349	0.085	<0.001

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