Circle of Life

Presence, behaviour and tissue preference of vertebrate scavengers in Dutch protected areas

Student: Ruth van den Herik
Study program: MSc Animal Sciences, Wageningen University and Research
WUR chair group: Resource Ecology Group
Supervisors: Melanie Pekel (ARK Nature), Bart Beekers (ARK Nature) and Patrick Jansen (WUR)
Date: 1 July 2018

Summary

The supply of carrion originating from large wild grazers is very limiting in European ecosystems compared to historic levels. A knowledge gap exists about the importance of large carcasses in nature and the species that might profit from them. The 'Circle of Life' project of ARK Nature aims to restore the scavenger community by increasing the availability of large carcasses in nature areas. During my study the presence, behaviour and tissue preference of vertebrate scavenger species (mammals and birds) at carcasses placed in four nature areas in the Netherlands were studied. Also, an experiment was performed to examine the effects of the initial state of the carcass (closed or opened) on the exploitation by these scavenger species. Furthermore, I assessed which other organisms might profit from the carcasses. European roe deer (*Capreolus capreolus*) carcasses, originating from roadkill, were provided in four nature areas: Kempen~Broek, Landgoed de Hamert, Markiezaat and Valkenhorst. The carcasses were checked for injuries before they were secured in front of a camera trap, to determine if the carcass was initially 'closed' or 'opened'. Every two weeks the camera traps were checked and the video footage was retrieved. The video footage was annotated with the online Agouti application. On two days, the beetle and fly species were actively sampled from the carcasses in Markiezaat & Valkenhorst by employees of EIS Kenniscentrum Insecten. In total 26 different vertebrate animal species were observed on the videos. The five most observed animals where carrion crow, wild boar, red fox, common buzzard and cattle. Most observations showed an animal species belonging to the category of 'waste eater' and indirect scavengers were least observed. The scavenger species that visited the carcasses were different in each nature area. The presence of vertebrate animal species was related to the initial carcass state and presence of wild boar in the area. Also, the primary tissue preference was dissimilar across animal species. Most vertebrate animals had a primary tissue preference for muscle or skin tissue. Furthermore, an association was found between animal species and primary behaviour. Showing interest in the carcasses and eating behaviour were the most prevalent primary behaviours. These behaviours were not consistent across nature areas and were depending on the initial carcass state. Interest was mostly shown by vertebrate scavenger species at closed carcasses and at opened carcasses, eating behaviour was generally observed. During the active sampling of carcasses, 105 beetle species and 18 fly species were found of which most species had a clear relationship with carcasses. The results found in this research show that several vertebrate and invertebrate species profit from the availability of carcasses in Dutch protected areas. My research also contributes with new knowledge on the presence, behaviour and tissue preference of vertebrate scavenger species. Lastly, this research emphasizes the importance of large carcasses in nature areas.

Samenvatting

De aanvoer van aas, afkomstig van grote wilde grazers, is zeer beperkt in Europese ecosystemen in vergelijking met historische niveaus. Een kennishiaat is aanwezig over het belang van grote kadavers in de natuur, en de diersoorten die hiervan zouden kunnen profiteren. Het 'Dood doet Leven' project van ARK Natuurontwikkeling heeft als doel om de aaseter gemeenschap te herstellen door de aanwezigheid van grote kadavers in de natuur te vergroten. Tijdens deze studie is de aanwezigheid, het gedrag en de weefselvoorkeur van gewervelde aaseter soorten (zoogdieren en vogels) op kadavers aanwezig in vier natuurgebieden in Nederland bestudeerd. Verder is er een experiment uitgevoerd om te onderzoeken wat de effecten van de oorspronkelijke kadaver staat (gesloten of geopend) zijn op de exploitatie door deze aaseter soorten. Bovendien heb ik onderzocht welke andere organismen zouden kunnen profiteren van kadavers. Kadavers van reeën (*Capreolus capreolus*) gedood door verkeersaanrijdingen, werden neergelegd in vier natuurgebieden: Kempen~Broek, Landgoed de Hamert, Markiezaat en Valkenhorst. De kadavers werden onderzocht op verwondingen voordat zij voor een cameraval werden bevestigd, om te bepalen of het kadaver gesloten of geopend was. Elke twee weken werden de cameravallen gecontroleerd en de videobeelden verzameld. De video's werden vervolgens geannoteerd met de online applicatie Agouti. Op twee dagen zijn de aanwezige kever- en vliegsoorten actief verzamelend van de kadavers in Markiezaat en Valkenhorst door medewerkers van EIS Kenniscentrum Insecten. In totaal zijn 26 gewervelde diersoorten waargenomen op de camerabeelden. De vijf meest waargenomen soorten waren zwarte kraai, wild zwijn, vos, buizerd en koe. De meeste observaties lieten een diersoort zien van de categorie 'afvaleters' en indirecte aaseters werden het minst waargenomen. De aaseter soorten die de kadavers bezochten waren verschillend in elke natuurgebied. De aanwezigheid van gewervelde diersoorten was gerelateerd aan de oorspronkelijke kadaver staat en de aanwezigheid van wild zwijn in het gebied. De primaire weefselvoorkeur was verschillend per diersoort. De meeste gewervelde aaseters hadden een primaire weefselvoorkeur voor spierweefsel of huidweefsel. Bovendien, was er een verband gevonden tussen de aanwezige diersoorten en het primaire gedrag. De meest waargenomen primaire gedragingen waren interesse tonen in de kadavers en eet gedrag. Deze gedragingen waren verschillend in alle natuurgebieden en afhankelijk van de staat van het kadaver. Interesse werd voornamelijk getoond door gewervelde aaseters soorten bij gesloten kadavers, en bij geopende kadavers werd voornamelijk eet gedrag geobserveerd. Tijdens het actief bemonsteren van de kadavers zijn er 105 kever soorten en 18 vlieg soorten gevonden, waarvan de meeste soorten een duidelijke binding hadden met kadavers. De resultaten die gevonden zijn in dit onderzoek laten zien dat veel verschillende gewervelde en ongewervelde diersoorten profiteren van de aanwezigheid van kadavers in Nederlandse natuurgebieden. Mijn onderzoek draagt ook bij met nieuwe kennis over de aanwezigheid, gedrag en weefselvoorkeur van gewervelde aaseters. Ten slotte benadrukt dit onderzoek het belang van grote kadavers in de natuur.

Content

1. Introduction

Large carcasses in European ecosystems have disappeared and are rare nowadays. Reasons for this are the conversion of wilderness areas to agricultural land; the disappearance and replacement of large wild grazers such as aurochs and wild horses by livestock; managing remaining wild herbivores at low population densities (population management) and the destruction of carcasses of road kills (Beekers et al., 2017; Fielding et al., 2014). In Europe the regulation 1069/2009 applies, which obligates that owners of captive farm animals remove dead animals, including the carcasses of cattle and horses that graze in nature areas. This regulation does not include wild animals, and therefore these carcasses may remain in nature (Colijn & Beekers, 2013; EUR-Lex, 2009). However, the most recent regulation states that carcasses of captive farm animals living in nature, may be used for feeding of endangered or protected species stated in the Habitats and Birds Directives (Colijn & Beekers, 2013; EUR-Lex, 2011). In conclusion, the supply of carrion originating from large wild grazers is very limiting in European countries compared to historic levels (Beekers et al., 2017; Fielding et al., 2014).

An increase in the natural supply of large carcasses is required to restore the food chain and the scavenger community in European landscapes. Large herbivore carcasses provide a large amount of energy, water and minerals for a relative long period, compared to small carcasses (Barton et al., 2013; Cortés-Avizandra et al., 2016). A large variety of scavenger species can benefit from a large carcass. Scavenger species can be divided into 4 categories: 1) obligate scavengers; 2) facultative scavengers; 3) indirect scavengers and 4) waste eaters. Obligate scavengers rely on carrion for their survival and reproduction, which are only vulture species (*Accipitridae* and *Cathartidae*). On the other hand, facultative scavengers are not solely dependent on carrion but are observed near carcasses, for example red kite (*Milvus milvus*) and beech marten (*Martes foina*) (Beasley et al., 2015; Wenting & Beekers, 2015). Common ravens are classified as obligate scavengers during the winter months and as waste eaters during the summer months. Scavengers that eat insects and their larvae that are present on carcasses, are called indirect scavengers and an example is the little owl (*Athene noctua*). The last category, the waste eaters, consists of animal species that forage on all types of rotting waste, such as the common buzzard (*Buteo buteo*) and carrion crow (*Corvus corone*) (Wenting & Beekers, 2015).

Not only mammal and bird species benefit from the availability of large carcasses. A large carcass offers nourishment to over a thousand species of insects, including 750 beetle species and 150 fly species. In summer, carrion is an important food source for the developmental stage of insects which reproduce inside or underneath the carcass (Beekers et al., 2017; Colijn & Beekers, 2013). A cadaver serves as a highly concentrated island of fertility or cadaver decomposition island (CDI), and contributes to landscape heterogeneity (Barton et al., 2013; Carter et al., 2007). The carcasses provide local concentrations of nutrients which can have a positive effect on the soil and vegetation. For example, the bones of a dead animal can provide lime-deficient soils with minerals for decades. Carrion can therefore contribute to many parts of the ecological community and nutrient cycle, in direct and indirect ways (Barton et al., 2013; Beekers et al., 2017; Carter et al., 2007).

1.1. The Circle of Life Project

The 'Circle of Life' project of ARK Nature aims to restore the scavenger community by increasing the availability of large carcasses in nature areas in the Netherlands. The Circle of Life approach is also used by the organisation Rewilding Europe in its rewilding areas. Four species of vultures where once abundant in central and southern Europe, but they disappeared from most European countries due to the low number of large carcasses. In the 1960s only 2,000 pairs of griffon vultures and 200 pairs of black vultures (*Coragyps atratus*) were left in Spain. Since then vulture populations are recovering due to reintroduction of herbivores and vultures, species protection and establishment of supplementary feeding stations to supply carrion (ARK Nature, n.d.; Beekers et al., 2017). Due to the lack of carrion, the population size of some birds of prey species has decreased in the Netherlands, for example of red kite (*Milvus milvus*), black kite (*Milvus migrans*) and common raven (*Corvus corax*). This might also be the reason that the cinereous vulture (*Aegypius monachus*) is not breeding in the Netherlands anymore (ARK Nature, n.d.). In the Circle of Life project, pilot areas were developed with partners like project Necros in Germany, Belgium and the Netherlands to study the species that benefit from the presence of carcasses, originating from road kill. Over the last six years, 95 species of mammals and birds have been observed around the carcasses in these countries, including rare species such as ravens, red and black kites, white-tailed eagles (*Haliaeetus albicilla*), griffon vultures (*Gyps fulvus*), wildcats (*Felis silvestris*) and grey wolves (*Canis lupus*) (Beekers et al., 2017; Brandenburgische Technische Universität, 2017). From 2012 to 2015 ARK Nature has worked on restoring the scavenger community in the province of Limburg in the Netherlands, as part of the Circle of Life project. The pilot areas were located in the nature areas Kempen~Broek, De Meinweg, De Maasduinen and Drielandenpark. During the winter of 2013/2014 common ravens were frequently observed at carcasses at De Maasduinen (Landgoed de Hamert). In 2014, these birds have successfully bred in the province of Limburg, for the first time since 1870. The supply of carcasses may have contributed to the breeding success of common raven and it was suggested that other (seasonal) obligatory scavengers also benefit from the presence of carrion (Wenting & Beekers, 2015). From the pilot areas it also became clear that it was important to vary the location where the carrion was made available, to prevent monopolizing by dominant individuals or species (Cortés-Avizandra et al., 2012). Moreover, the peak in the supply of carrion should match the natural peak in mortality among large herbivores, which is near the end of winter, and overlaps the reproductive season of many scavengers (Beekers et al., 2017).

From February 2017 until January 2018, no active research was conducted for the Circle of Life project by ARK Nature. This study will on one hand be a follow-up of the research on profiting scavengers conducted in the province of Limburg, but on the other hand will be scaled up with new research questions and to pilot areas in the province of Noord-Brabant. For example, the behaviour of scavenger species around carcasses has not been studied extensively, and factors influencing this behaviour are not completely known. In addition, it is not quite known what the effect is of an initially closed versus an opened carcass on the profiting scavenger species. An opened carcass may mimic the visitation of for example wild boar, grey wolf and Eurasian lynx (*Lynx lynx*) and might facilitate for other (smaller) scavenger species, because the meat is faster and easily accessible (Olson et al., 2016; Selva, 2004). This experiment would be particularly interesting to conduct in areas where wild boar is absent, to observe if visitation of smaller vertebrate scavenger species is facilitated by opened carcasses. It is also not clear if scavengers prefer certain types of tissue they consume and thus it remains unknown how and which vertebrate scavenger species contribute to the consumption and dispersion of nutrients present in carrion.

2. Aim & Research Questions

The supply of carrion originating from large wild grazers is very limiting in European ecosystems compared to historic levels. This resulted in a knowledge gap about the importance of large carcasses in nature and the species that might profit from them. The aim of this internship research is to gain more insight in the scavenger species that benefit from carcasses in Dutch protected areas. The presence, behaviour and tissue preference of vertebrate scavenger species (birds and mammals) at carcasses placed in four nature areas in the Netherlands will therefore be studied. Also, an experiment was performed to examine the effects of the initial state of the carcass (closed or opened) on the exploitation by these scavenger species. Furthermore, I assessed which other organisms might profit from the carcasses. With this research the following research questions will be answered:

1. Which vertebrate scavenger species visit the carcasses and is there a difference in the presence of these species between the different areas?
    1.1. What is the effect of initially closed or opened carcasses on the presence of these scavenger species?
    1.2. Which tissues are eaten by which scavenger species and do they have a preference?
2. What is the behaviour of the vertebrate scavenger species around the carcasses and is there a difference in this behaviour between the different areas?
    2.1. What is the effect of initially closed or opened carcasses on the behaviour of the scavenger species?
3. Are there other organisms that benefit from the carcasses, and in which manner?

2.1. Predictions

1. Which vertebrate scavenger species visit the carcasses and is there is there a difference in the presence of these species between the different areas?

Expected is that red fox (*Vulpus vulpus*), common buzzard and wild boar (*Sus scrofa*) will be the most frequently observed vertebrate scavenger species, because these species consume carrion as part of their diet and were often observed at carcasses in previous studies (Selva et al., 2005; Wenting, 2014; Wenting & Beekers, 2015). Red fox and common buzzard are also widely distributed species in the Netherlands (NDFF, 2018a; Sovon Vogelonderzoek Nederland, 2016a) Furthermore, wild boar is responsible for a large amount of scavenging in the Netherlands and has established populations in the provinces of Noord-Brabant and Limburg (NDFF, 2018b; Poelarends et al., 2012). Taking their distribution into account, it is expected that wild boar will be the most frequent scavenger at Valkenhorst and Kempen~Broek. Other scavenger species that are expected to visit the carcasses frequently are carrion crow, European polecat (*Mustela putorius*) and beech marten (*Martes foina*) (Poelarends et al., 2012; Wenting, 2014; Wenting & Beekers, 2015).

In the areas where wild boar is present (Valkenhorst and Kempen~Broek), I predict that wild boar will be the dominant scavenger species visiting the carcasses. In areas without wild boar (Landgoed de Hamert and Markiezaat) the red fox is expected to be predominantly present at the carcasses (Poelarends et al., 2012; Wenting, 2014). Furthermore, I expect that common raven, red kite and black kite will also be observed at carcasses in Landgoed de Hamert, Kempen~Broek and Valkenhorst, even though their population sizes are quite low in the Netherlands (Sovon Vogelonderzoek Nederland, 2014a; Sovon Vogelonderzoek Nederland, 2014b; Sovon Vogelonderzoek Nederland, 2016b). These species all consume carrion as part of their diet (Poelarends et al., 2012; Rösner et al., 2005; Zawadzka, 1999). Furthermore, it was found that the community of scavengers is highly nested and that rare scavengers are likely to be present at carcasses which are also visited by the common scavengers (Selva & Fortuna, 2007).

1.1. What is the effect of initially closed or opened carcasses on the presence of these scavenger species?

The ability of scavengers to locate and exploit carcasses is determined by their foraging behaviour, their visual and olfactory abilities and their capability to open carcasses (Selva et al., 2005). Intact carcasses might be hard to open for some scavenger species. Grey wolf and wild boar can open a carcass and therefore they could facilitate for other smaller scavengers (Poelarends et al., 2012; Selva et al., 2005). In the areas where wild boar is absent (Landgoed de Hamert and Markiezaat), a difference in profiting scavengers is expected between opened and closed carcasses, with smaller scavenger species as carrion crow and beech marten visiting opened carcasses more frequently. In the areas where wild boar is present (Valkenhorst and Kempen~Broek), it is expected that these animals will predominantly scavenge from both opened and closed carcass and therefore no difference in visiting scavenger species between the two carcass states is expected.

1.2. Which tissues are eaten by which scavenger species and do they have a preference?

The hypothesis is that scavenger species prefer the type of tissue they eat and/or take from the carcasses. Wild boar is physiologically able to open carcasses, and it is known that wild boar families can consume a whole carcass in just a few days scavengers (Poelarends et al., 2012; Selva et al., 2005). Therefore, it is expected that wild boar does not have a tissue preference and will consume all tissue types, including bones. By opening the carcasses, wild boar could improve the accessibility of internal tissues by smaller vertebrate scavengers. It is therefore expected that smaller scavengers will mostly eat the softer tissues (e.g. nose, ears, eyes and anus) from closed carcasses and internal tissues (e.g. muscle tissue and organs) from opened carcasses (Poelarends et al., 2012). Bones are expected to be gnaw on by wild boar, red fox and wood mouse for calcium. Secondary scavenger species that are known to eat insects and their larvae present on carcasses are wild boar, common raven, red fox, European hedgehog (*Erinaceus europaeus*), carrion crow, European badger (*Meles meles*), little owl (*Athene noctua*), European jackdaw (*Coloeus monedula*), Eurasian magpie (*Pica pica*), European robin (*Erithacus rubecula*), common starling (*Sturnus vulgaris*), great tit (*Parus major*) and wood mouse (*Apodemus sylvaticus*). Hairs could be taken by for example European jackdaw, European robin, common starling and great tit (ARK Nature, 2013; Lardinois, 2005; Poelarends et al., 2012).

2. What is the behaviour of the vertebrate scavenger species around the carcasses and is there a difference in this behaviour between the different areas?

It is expected that the scavenger species will mostly show eating behaviour or interest towards the carcasses. In earlier research it was found that the primary behaviour of red fox, wild boar and common buzzard around carcasses was eating behaviour (Bos et al., 2013; Wenting, 2014). Showing interest towards the carcass was the second most observed behaviour of these species. Because wild boar commonly visits the carcasses in family groups, intraspecific behaviour is expected to be frequently observed for this species (Poelarends et al., 2012; Wenting, 2014). Scavenger-specific differences in carrion consumption and behaviour around carcasses probably exist among carcass types. Also, it has been shown that mammalian carnivores avoid the consumption of carnivore carcasses (e.g. fox and badger), however exceptions might exist during winter conditions (Moleón et al., 2017; Olsen et al., 2016, Wenting, 2014). Because of these reasons only one type of herbivore carcasses will be used in this research. Therefore, the effects of type of carcass on the visiting scavenger species will be eliminated and no behavioural differences of scavengers are expected between the different areas.

2.1. What is the effect of initially closed or opened carcasses on the behaviour of the scavenger species?

A difference in the behaviour of profiting scavengers is expected between initially closed and opened carcasses, with smaller scavenger species showing eating behaviour more frequently at opened carcasses compared to closed carcasses. When carcasses are opened, the smaller scavengers can easily access the muscle tissues and internal organs. However, when carcasses are closed it might be harder for these smaller scavenger species to eat from it. In that case it is expected that smaller scavengers

will show more interest behaviour (e.g. sniffing) than eating behaviour at closed carcasses. No behavioural differences of red fox and wild boar are expected between opened and closed carcass, because these species can easily open closed herbivore carcasses and show eating behaviour (Poelarends et al., 2012; Selva et al., 2005; Wenting, 2014).

3. Are there other organisms that benefit from the carcasses, and in which manner?

Mammal and bird species are not the only organisms that will profit from the availability of large carcasses and it is expected that several insect species and plant species will also profit. It was found that large carcasses offer nourishment to over a thousand species of insects, including 750 beetle species, 150 fly species and numerous species of snails, earthworms, spiders, harvestmen, mites, wood lice, centipedes and springtails. Beetle species of the family Silphidae are dependent on carcasses for their reproduction, because their larvae solely consume carrion (Beekers et al., 2017; Colijn, 2014; Colijn & Beekers, 2013). Therefore, it is expected that besides Silphidae species, several other insect species will be observed at the carcasses. Furthermore, temperature and moisture are found to strongly influence the carcass decomposition rate and nutrient cycling rates through microbial decomposers. Nitrogen and phosphorus will become available for uptake by plants during the mineralisation process of microbes (Barton et al., 2013). These nutrients will promote local primary production near the carcasses (Olsen et al., 2016).

3. Materials

For conducting this research, 9 Bushnell Trophy Cam Aggressor camera traps are needed in total, preferably from 2017. These cameras have a Low-Glow hardly visible infrared flash; a detection distance of around 30 meters; a 1080p Full HD video resolution; a reaction time of 0.73 seconds and a recovery time of 1.5 seconds for video triggers (Wildlife Monitoring Solutions, 2017). These specifications ensure a high-quality video result and a low chance of missing a passing animal. To prevent destruction or theft of the cameras, metal housings in combination with a chain and lock were used for securing the cameras. On each camera housing a plasticized 'Circle of Life' label (Dutch: 'Dood doet Leven') was attached with duct tape to inform visitors and to provide an e-mail address which they could contact if they have questions about the project (Figure 1). Furthermore, Eneloop rechargeable AA batteries and Sandisk SDHC memory cards were used for running the cameras. It is advised to have some extra memory cards, because so memory cards can be changed in the field, without the need of a laptop to firstly retrieve the video material from the memory cards. General fieldwork supplies such as disposable gloves, hand sanitizer gel, a knife and scissors were also needed. All the video material was stored on an external hard drive especially designated for the Circle of Life project and in the online Agouti application (Table 1) (Wageningen University & Research Centre, n.d.).

Figure 1. Labelling of the cameras.

Table 1. The materials that are needed in total for the camera trapping experiment.

Quantity	Description
9	Bushnell Trophy Cam Aggressor 2015 or 2017 camera trap
9	Bushnell Trophy Cam 2015 or 2017 metal housing with lock
9	Cable or chain to secure carcass to wooden pole
9	Chains to secure camera to a tree or pole
1	Disposable gloves
1	Duct tape
18	Eneloop Rechargeable batteries (8xAA)
1	External hard drive 2 TB
1	GPS device or mobile phone with GPS function
1	Hand sanitizer gel
1	Japcall 16-bank battery charger
1	Knife
1	Laptop
1	Measuring tape
1	Photo camera or mobile phone with camera function
9	Plasticized 'Doet doet Leven' camera labels
9*	Sandisk SDHC 16GB or 32GB memory card
1	Scissors
9	Wooden poles

* Minimum number

4. Methods

4.1. Field Study

For this research, European roe deer (*Capreolus capreolus*) carcasses were provided in four nature areas in the Netherlands: Kempen~Broek, Landgoed de Hamert (part of National park de Maasduinen), Markiezaat and Valkenhorst from February 2018 until May 2018 (Figure 2; Annex 1).

Figure 2. Locations of the nature areas where the experiment will be performed.

In each of these areas, two camera traps were placed, except for Kempen~Broek where three cameras were placed. If possible at the locations, the camera traps were facing north to prevent overexposure caused by sunlight. The camera traps were secured to a sturdy pole or tree at approximately 1 meter high if possible, slightly facing the ground, and at about 2 meters distance to the carcass (Figure 3). If needed, vegetation in front of the camera trap was cut or removed to avoid false triggers. The length of the videos was 60 seconds, with one second delay. The highest resolution, medium LED control and medium sensor levels were used. Before placing the carcass, a test run was performed to check the camera trap placing and video settings. If false triggers occurred regularly, the sensory level was set to low (ARK Nature, 2016). The roe deer carcasses, originating from roadkill, were collected and brought to the manager of the different nature areas by SAMF (i.e. Dutch organisation for dealing with and monitoring road kill; Stichting Afhandeling & Monitoring Fauna-aanrijdingen, n.d.) in the province of Noord-Brabant. In the province of Limburg, the carcasses were provided by the municipality of Leudal and managers of Stichting het Limburgs Landschap.

Figure 3. Placement of a roe deer carcass in front of the camera trap at Loozerheide, Kempen~Broek.

Only roe deer carcasses were used to eliminate the effects of type of carcass on the visiting scavenger species and their behaviour (Moleón et al., 2017; Olsen et al., 2016, Wenting, 2014). The carcasses were checked for injuries before they were placed in front of a camera trap, to determine if the carcass was initially 'closed' or 'opened' (Table 2). The information on when a roe deer carcass was placed in front of a camera trap, at which location and the state of the carcass was stored in an Excel file (in Dutch), which was send to the managers of the nature areas to be filled in (Annex 2).

Table 2. Criteria for distinguishing between opened and closed deer carcasses.

Closed carcass	Opened carcass
No or minor injuries (e.g. abrasions, broken bones)	Major injuries (e.g. large wounds)
Closed abdomen	Opened abdomen: internal organs visible.

Ideally, the sample size of opened and closed carcasses would be roughly the same. During the research, some carcasses were opened manually when opened carcasses were lacking. The carcasses were placed in front of the camera traps, and secured with a chain or cable to avoid them being dragged out of the scope of the camera by scavengers (ARK Nature, 2016). In case the supply of roe deer carcasses at one location was higher than the available camera trapping locations, the carcasses were frozen if storage was present or otherwise placed at other sites inside the nature area (i.e. not included in this study). Every two weeks the camera traps were checked and the captured videos were copied from the SD-card to a laptop and external hard drive. If needed, the batteries were replaced. The area around the carcasses was searched for animal tracks (paw prints, faecal matter, feathers etc.), which were photographed (ARK Nature, 2016).

To investigate which insect species might benefit from the availability of carcasses during this study, Ed Colijn, Hans Huijbregts and Oscar Vorst from EIS Kenniscentrum Insecten (European Invertebrate Survey Netherlands) once visited and actively sampled the carcasses present at Markiezaat and Valkenswaard. Beetles and flies were collected and later identified to species level (EIS Kenniscentrum Insecten, 2018).

4.2. Annotation Video Footage

The video footage was annotated with the Agouti application (Wageningen University & Research Centre, n.d.). Each video of one minute was analysed as a separate observation. For describing the primary and secondary behaviour of the scavengers, an ethogram with 8 behaviours was used (Table 3; Wenting & Beekers, 2015). The primary and secondary type of tissue that is preferred by the scavenger, was also classified (Table 4).

Table 3. Ethogram for describing the behaviour of the visiting scavenger species, with behaviours in alphabetical order (Wenting & Beekers, 2015).

Behaviour	Abbreviation	Description
Collecting material (carcass)	CMC	Collecting meat and/or hairs from the carcass.
Collecting material (environment)	CME	Collecting leaves and/or plants from the environment of the carcass.
Eating	EAT	The animal touches the carcass with their mouth/beak and eats from it (swallowing of carcass tissue).
Interest	INT	The animal moves in the direction of the carcass.
Interspecific interaction	INTER	Physical and non-physical contact between animals of different species.
Intraspecific interaction	INTRA	Physical and non-physical contact between animals of the same species.
Passing	PAS	The animal passes the carcass but does not walk towards it or react to it.
Standing on top of carcass	STA	The animal touches the carcass with their paws only.

Table 4. Classification of the type of tissue that a scavenger might eat or take from the carcass.

	Type of tissue
1	Bones, hooves
2	Hairs
3	Nose, ears, eyes, anus, skin (armpits, abdomen).
4	Skin on other parts of the body
5	Muscle tissue
6	Organs
7	Insects and larvae that are present on the carcass (indirect).

4.3. Data Analysis

After finalizing annotating all the videos, an export of the data was created. This CSV file was converted to an Excel file by using the 'text to columns' option. To this file some extra information was added per observation. Firstly, the animal species category was specified. The scavenger species were divided into 4 categories: 1) obligate scavenger; 2) facultative scavenger; 3) secondary scavenger and 4) waste eater, which was already explained in the introduction of this report (Chapter 1; Wenting & Beekers, 2015). The last category 'carcass visitor' consists of animal species that are not considered a scavenger species and incidentally passed the camera or visited the carcasses. Secondly, the column containing both observed behaviours and tissue preference was split into four separate variables: primary behaviour; secondary behaviour; primary tissue preference and secondary tissue preference. Next, the begin state (closed or opened) of the carcass at which an animal was observed was added to the observations, by comparing the timestamp of the video with the information on the supply and state of roe deer carcass provided by the managers of the nature areas. Lastly, the variables 'nature area'

and 'presence wild boar' (absent or present) were added so that later in the statistical analyses the results could be compared between all nature areas and between areas where wild boar is present or absent. Multiple Pivot tables were created in Excel to sort and summarize the associated data before each statistical analysis, to get an overview of the grouping of the data.

The variables 'animal species, 'animal species category', 'carcass state', 'nature area', 'presence wild boar', 'primary behaviour', 'secondary behaviour', 'primary tissue preference' and 'secondary tissue preference' were all measured on the nominal level (i.e. categorical data) and consisted of two or more categorical groups. For the following research questions significant associations between variables were tested by performing the Pearson's Chi-square test in IBM SPSS Statistics 24 (IBM Corp., 2016):

1. Which vertebrate scavenger species visit the carcasses and is there a difference in the presence of these species between the different areas?
- Animal species * nature area
- Animal species category * nature area

1.1. What is the effect of opening carcasses on the presence of these scavenger species?
- Animal species * carcass state
- Carcass state * presence wild boar + for each species separately

1.2. Which tissues are eaten by which scavenger species and do they have a preference?
- Primary tissue preference * secondary tissue preference
- Animal species category * primary tissue preference
- Animal species * primary tissue preference + for each animal species category separately

2. What is the behaviour of the vertebrate scavenger species around the carcasses and is there a difference in this behaviour between the different areas?
- Animal species * primary behaviour
- Animal species * secondary behaviour
- Nature area * primary behaviour + for each species separately

2.1. What is the effect of opening carcasses on the behaviour of the scavenger species?
- Carcass state * primary behaviour + for each species separately

The Pearson's Chi-square test evaluates if a relationship exists between two categorical variables. The null hypothesis is that no relationship exists on the categorical variables; they are independent. In IBM SPSS Statistics, the Pearson's Chi-square test is part of the 'Crosstabs' procedure, where contingency tables are constructed of the data. The p-values of this test are only trustworthy when the sample sizes of the used variables are large enough, which is indicated by 20% or less of the contingency cells having expected values below five. When this was not the case, the p-values from the Fisher's Exact test (2x2 contingency tables) or Monte Carlo Exact test (larger contingency tables) were retrieved which do not rely on the sample size assumption. Furthermore, the value of Cramer's V were checked, which is a value between zero and one and indicates the strength of the association between two categorical variables: 0.00 to 0.20 (weak); 0.2 to 0.6 (moderate) and over 0.6 (strong).

5. Results

In the period of February 2018 until May 2018, the camera traps were set-up in the different nature areas and the videos were collected. The supply of roe deer carcasses varied during these months and was different for each sampling location. Therefore, the start date when the first roe deer carcass was placed, the end date when the sampling locations where visited last and the supply of opened or closed carcasses also varied between sampling locations. The video footage resulting of these cameras was annotated until the end of April 2018 with a total of 1827 observations. These observations only included the videos where at least one vertebrate animal species was visible, the videos made when checking the cameras were not included. A large variation existed in the total number of observations per sampling location. The number of observations of 'Bosrand' at Landgoed de Hamert and 'Stramproy' at Kempen~Broek could have been higher because at both sampling locations once a SDHC memory card appeared to be defective while checking the camera traps and therefore observations could have been lost (Table 5).

Table 5. Per sampling location, the start and end date of the camera trapping experiment, the total supply of roe deer carcasses and the number of observations that were annotated.

Sampling location	Start date	End date	Total supply of roe deer carcasses (closed/opened)	Number of observations[1]
Kempen~Broek			7 (4/3)	1051
De Graus	1 March 2018	30 May 2018	2 (1/1)	480
Loozerheide	27 February 2018	30 May 2018	3 (1/2)	89
Stramproy	22 February 2018	30 May 2018	2 (2/0)	482
Landgoed de Hamert			3 (1/2)	7
Bosrand	12 April 2018	23 May 2018	1 (1/0)	0
Westmeerven	26 March 2018	23 May 2018	2 (0/2)	7
Markiezaat			8 (5/3)	508
De Duintjes	19 February 2018	25 May 2018	5 (4/1)	507
Hogerwaard	6 April 2018	25 May 2018	3 (1/2)	1
Valkenhorst			5 (5/0)	261
Grevenschutven	28 March 2018	30 May 2018	2 (2/0)	171
Oude Baan	26 March 2018	30 May 2018	3 (3/0)	90
Total			23 (15/8)	1827

[1]The number of observations annotated until the end of April 2018.

5.1. Scavenger Species

1. Which vertebrate scavenger species visit the carcasses and is there a difference in the presence of these species between the different areas?

In total 26 different vertebrate animal species were observed on the videos, including domestic animals (e.g. cat, cattle, dog and horses) and humans who were walking in the nature areas. The top-5 most observed animals where carrion crow (26.3%), wild boar (20.1%), red fox (12%), common buzzard (11.2%) and cattle (7.6%) (Table 6).

Table 6. Overview of the vertebrate animal species that where observed on the video footage of the camera traps, including their scientific species name, species category (determined beforehand), the total number of times the animal was observed and the relative number of observations (%).

Species name (*Scientific name*)	Category	Number of observations	Relative number of observations (%)
Beech marten (*Martes foina*)	Facultative scavenger	37	2.0
Brown rat (*Rattus norvegicus*)	Waste eater	1	0.1
Carrion crow (*Corvus corone*)	Waste eater	481	26.3
Cattle (*Bos taurus*)	Carcass visitor	138	7.6
Common blackbird (*Turdus merula*)	Indirect scavenger	2	0.1
Common buzzard (*Buteo buteo*)	Waste eater	204	11.2
Common pheasant (*Phasianus colchicus*)	Carcass visitor	3	0.2
Common wood pigeon (*Columba palumbus*)	Carcass visitor	4	0.2
Domestic cat (*Felis catus*)	Facultative scavenger	118	6.5
Domestic dog (*Canis lupus familiaris*)	Carcass visitor	10	0.6
Eurasian jay (*Garrulus glandarius*)	Carcass visitor	1	0.1
European hare (*Lepus europaeus*)	Carcass visitor	6	0.3
European robin (*Erithacus rubecula*)	Indirect scavenger	1	0.1
European roe deer (*Capreolus capreolus*)	Carcass visitor	35	1.9
European stonechat (*Saxicola rubicola*)	Carcass visitor	1	0.1
Grey heron (*Ardea cinerea*)	Carcass visitor	1	0.1
Great tit (*Parus major*)	Indirect scavenger	31	1.7
Horse (*Equus caballus*)	Carcass visitor	112	6.1
Human (*Homo sapiens*)	Carcass visitor	22	1.2
Meadow pipit (*Anthus pratensis*)	Indirect scavenger	1	0.1
Red fox (*Vulpes vulpes*)	Waste eater	220	12.0
Song thrush (*Turdus philomelos*)	Indirect scavenger	4	0.2
Western jackdaw (*Coloeus monedula*)	Waste eater	1	0.1
Western yellow wagtail (*Motacilla flava*)	Indirect scavenger	6	0.3
Wild boar (*Sus scrofa*)	Waste eater	368	20.1
Wood mouse (*Apodemus sylvaticus*)	Indirect scavenger	19	1.0
Total		1827	100

Most observations showed an animal species belonging to the category of 'waste eater' (70%) and indirect scavengers were least observed (4%) (Figure 4).

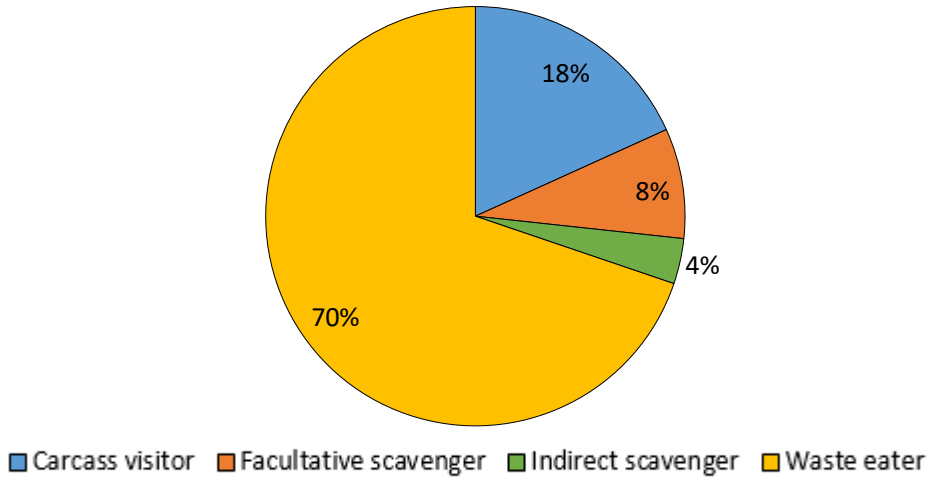
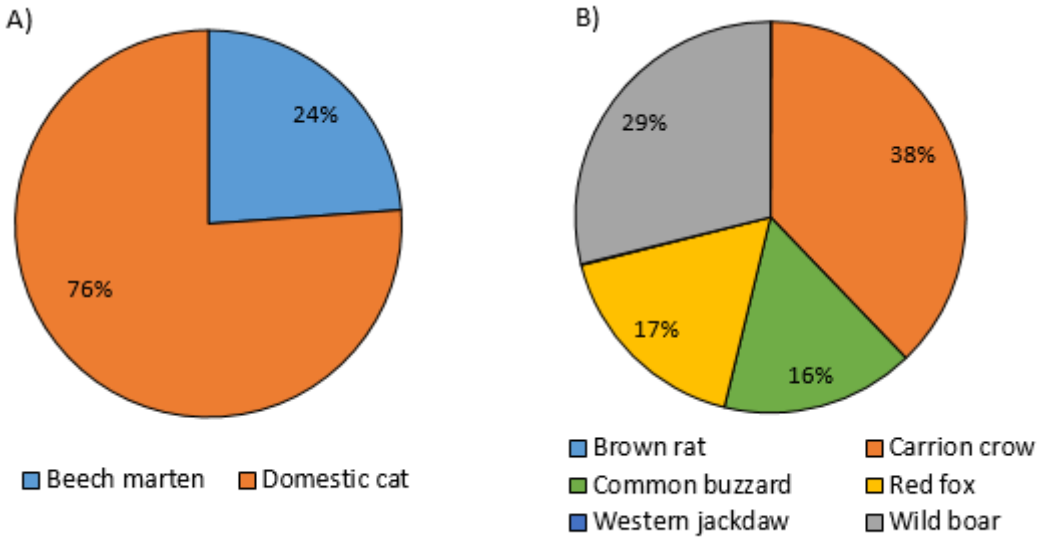


Figure 4. Observed vertebrate animal species per category.

Of the two observed facultative scavenger species, the domestic cat was observed more often (76%) than the beech marten (24%). The carrion crow was the most observed waste eater species (38%), followed by wild boar (29%). Great tit (48%) and wood mouse (30%) were the most observed indirect scavengers. Cattle (41%) and horse (34%) were frequently observed carcass visitors (Figure 5).



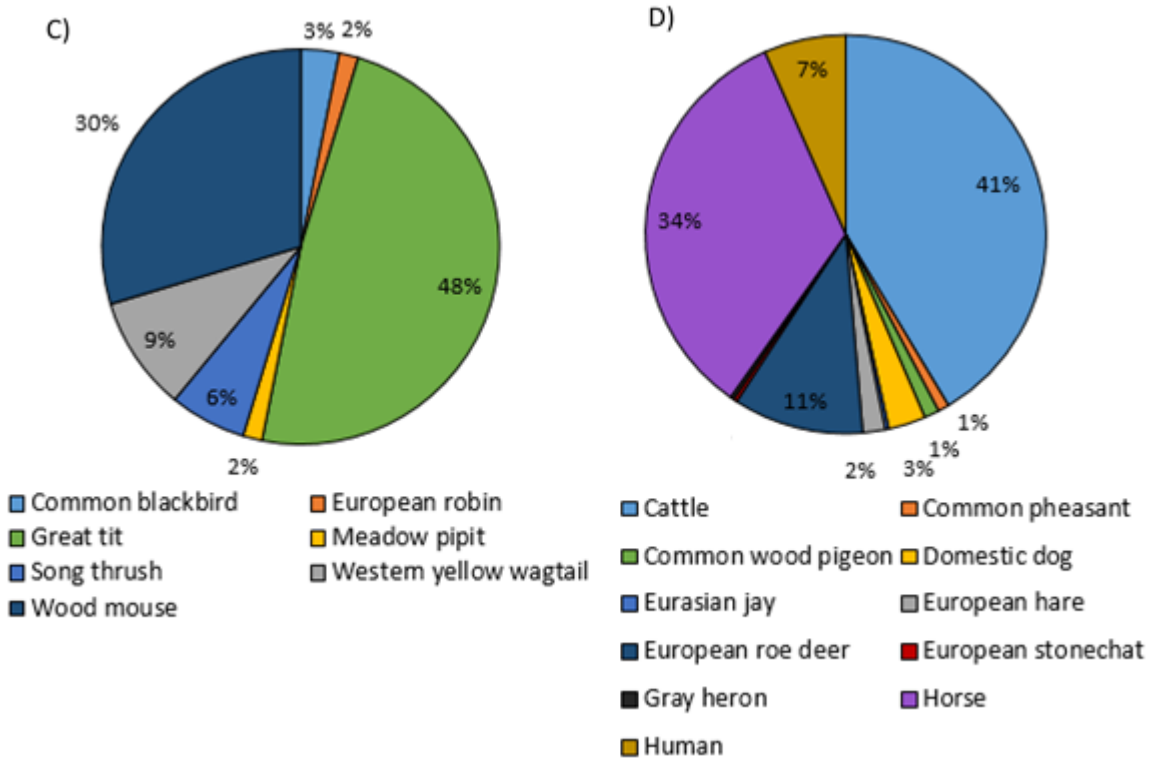
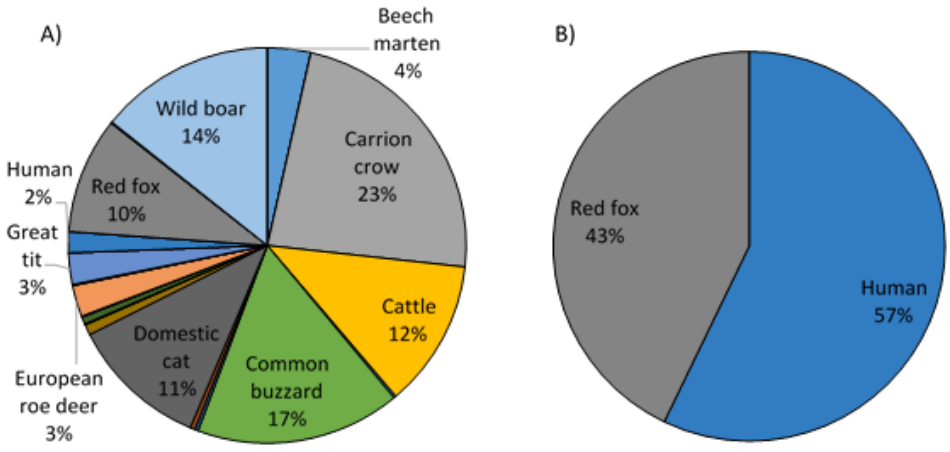


Figure 5. Observed vertebrate animal species per category; A) facultative scavengers, B) waste eaters, C) indirect scavengers and D) carcass visitors.

Nineteen different animal species were observed at Kempen~Broek. Of these species carrion crow (23%), common buzzard (17%) and wild boar (14%) were most frequently observed. At Landgoed de Hamert only humans (57%) and red foxes (43%) were seen on the video footage. Out of the nine observed animal species at Markiezaat, carrion crow (46%), red fox (22%) and horses (22%) were most often seen. Ten animal species were observed at Valkenhorst and wild boar (84%) was most frequently observed (Figure 6).



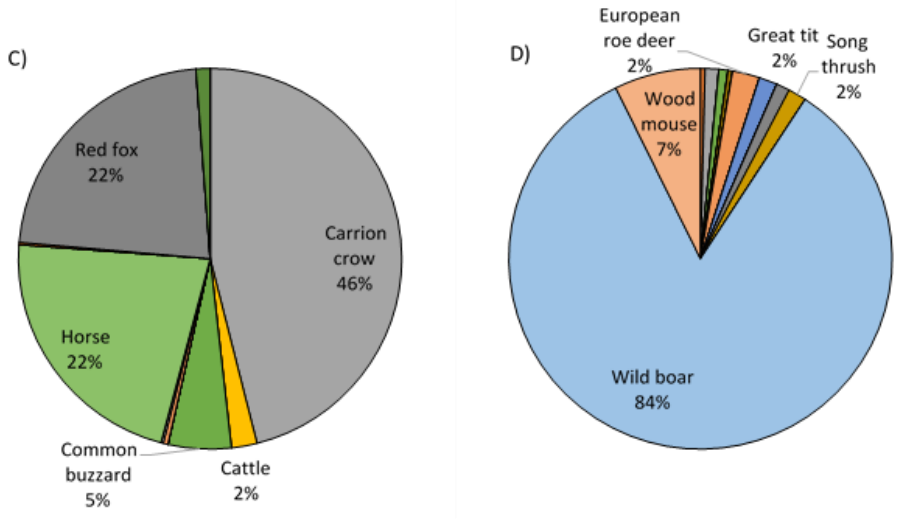


Figure 6. Observed vertebrate animal species per nature area: A) Kempen~Broek, B) Landgoed de Hamert, C) Markiezaat and D) Valkenhorst. The labels and percentages of species observed less than 1% are not shown.

A significant moderate association was found between the observed vertebrate animal species and the four nature areas, meaning that the observed species were dissimilar in each nature area (Monte Carlo Exact test: $p < 0.001$; Cramer's V: 0.575). Also, a significant moderate association was found between the animal category and the four nature areas (Monte Carlo Exact test: $p < 0.001$; Cramer's V: 0.204). At three of the four nature areas waste eaters were the most observed animal species category (64-87%). At Landgoed de Hamert carcass visitors (57%) were more often observed than waste eaters (43%). Facultative scavengers were only observed at Kempen~Broek (15%). Indirect scavengers were rarely seen at Kempen~Broek (3%), Markiezaat (1%) and Valkenhorst (10%) (Figure 7).

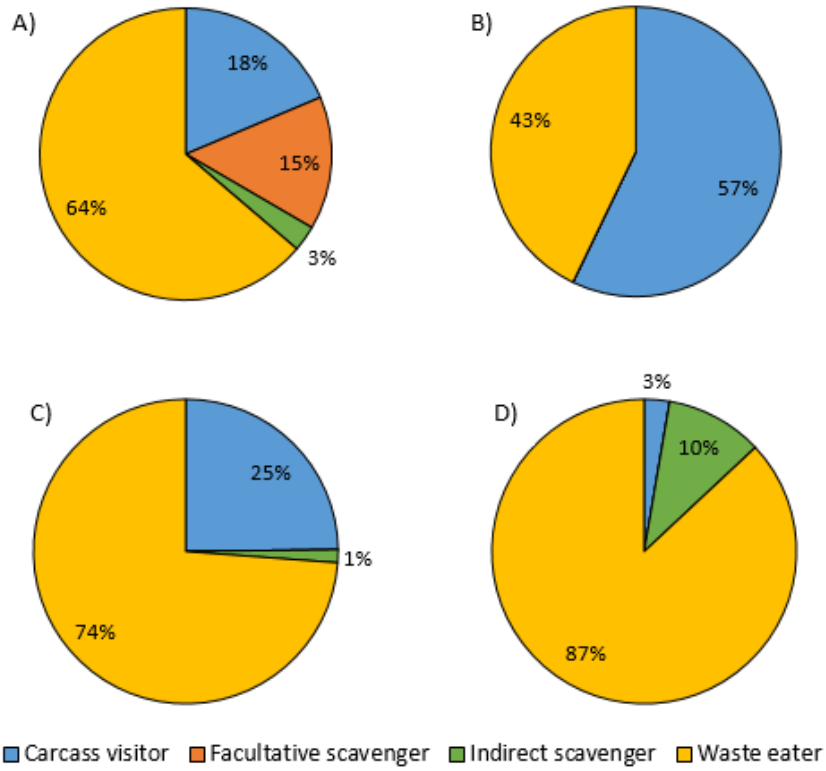


Figure 7. Observed vertebrate animal species per category at the different nature areas: A) Kempen~Broek, B) Landgoed de Hamert, C) Markiezaat and D) Valkenhorst.

5.1.1. Closed vs. Opened Carcasses

1.1. What is the effect of initially closed or opened carcasses on the presence of these scavenger species?

In 1418 observations a vertebrate animal species was observed at an initially closed carcass and in 409 observations at an initially opened carcass. In the nature areas where wild boar was absent (Landgoed de Hamert and Markiezaat) a total of 515 observations was analysed compared to 1312 observations in nature areas where wild boar was present (Kempen~Broek and Valkenhorst) (Table 7). Overall a significant moderate association was found between the presence of a certain species and carcass state (Monte Carlo Exact test: $p < 0.001$; Cramer's V: 0.473) and a significant strong association between the presence of a certain species and the presence of wild boar (Monte Carlo Exact test: $p < 0.001$; Cramer's V: 0.650), meaning that the observed animal species were different for each carcass state and presence of wild boar. On species level, only significant moderate associations were found between carcass state, wild boar presence and the presence of carrion crow (Pearson's Chi-square test: $X^2_1 = 82.301$, $p < 0.001$; Cramer's V: 0.414), cattle (Pearson's Chi-square test: $X^2_1 = 13.424$, $p < 0.001$ Cramer's V: 0.312) and common buzzard (Pearson's Chi-square test: $X^2_1 = 24.567$, $p < 0.001$; Cramer's V: 0.347). Carrion crow was mostly present on closed carcasses especially in the areas where wild boar was absent. Common buzzard was only observed at closed carcasses when wild boar was not present, whereas in areas where wild boar was present this species was almost equally present at closed (49%) and opened (51%) carcasses. Cattle was observed around both initial carcass states (Figure 8).

Non-significant associations were found for European roe deer, human and red fox (Fisher's Exact test: $p > 0.05$). Wild boar was mostly observed at closed carcasses. For all the other observed species no associations could be determined because they were only observed at one carcass state or at nature areas with the same wild boar presence (Table 7).

Table 7. Number of observations of vertebrate animal species at closed and opened carcasses in nature areas where wild boar was absent and present.

	Number of observations					
	Wild boar absent		Wild boar present		Total	
Species	Closed	Opened	Closed	Opened	Closed	Opened
Beech marten			30	7	30	7
Brown rat			1		1	0
Carrion crow	229	5	162	85	391	90
Cattle		11	73	54	73	65
Common blackbird			1	1	1	1
Common buzzard	27		87	90	114	90
Common pheasant			3		3	0
Common wood pigeon			3	1	3	1
Domestic cat			53	65	53	65
Domestic dog			3	7	3	7
Eurasian jay				1	0	1
European hare			5	1	5	1
European robin				1	0	1
European roe deer	1	1	24	9	25	10
European stonechat	1				1	0
Grey heron			1		1	0

Great tit			24	7	24	7
Horse	110	2			110	2
Human		4	1	17	1	21
Meadow pipit	1				1	0
Red fox	113	4	100	3	213	7
Song thrush			4		4	0
Western jackdaw				1	0	1
Western yellow wagtail	2	4			2	4
Wild boar			340	28	340	28
Wood mouse			19		19	0
Total	484	31	934	378	1418	409

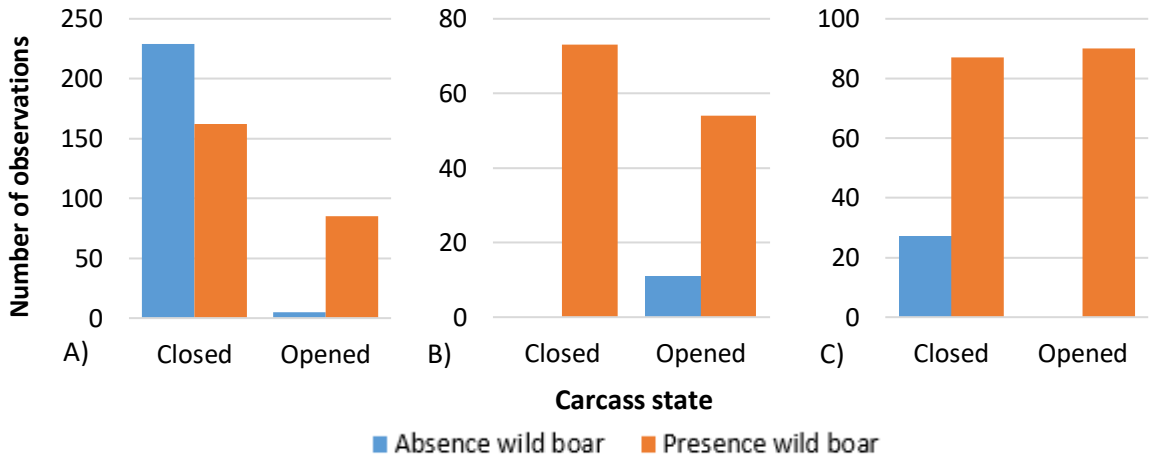


Figure 8. Number of observations of A) carrion crow, B) cattle and C) common buzzard at closed and opened carcasses and in nature areas where wild boar was absent and present.

5.1.2. Tissue Preference

1.2. Which tissues are eaten by which scavenger species and do they have a preference?

In 647 out of 1827 observations a primary tissue preference could be determined and in 215 observations a secondary tissue preference was observed. Most vertebrate animals had a primary or secondary tissue preference for muscle tissue (35% and 37%) or skin on other parts of the body (35% and 34%). Bones, hairs and insects and larvae present on the carcasses were least chosen (Figure 9).

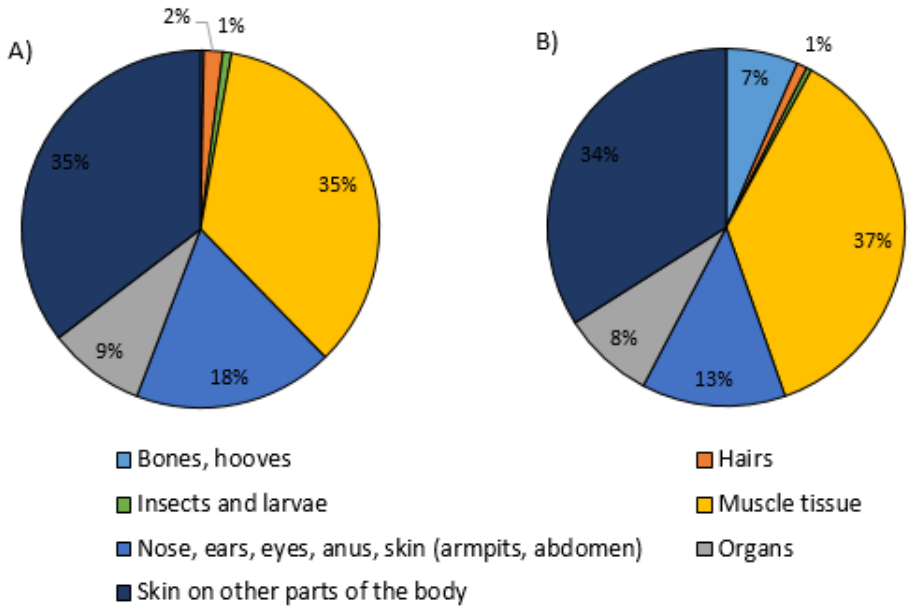


Figure 9. Primary (A) and secondary (B) tissue preference of the vertebrate animal species observed eating around the carcasses.

In 47 cases (64%) the skin of the carcass was the secondary tissue preference when the primary tissue preference was muscle tissue. The other way around, in 65 cases (74%) muscle tissue was the second most preferred tissue when species mostly preferred to eat the skin of the carcass body. The skin of the carcass body was also observed to be the most selected secondary tissue, when species primary preferred soft tissues (40%) and organs (54%). No indirect tissue preferences were observed when species preferred to take hairs or eat insects and larvae that were present on the carcass (Table 8).

Table 8. The number of observations where a secondary tissue preference was observed in combination with a primary tissue preference.

	Secondary tissue preference							
Primary tissue preference	Bones & hooves	Hairs	Insects & larvae	Muscle tissue	Soft tissues[1]	Organs	Skin[2]	Total
Bones & hooves							1	1
Hairs								0
Insects & larvae								0
Muscle tissue	3	1		1	15	6	47	73
Soft tissues[1]	1		1	9		4	10	25
Organs	1			4	8		15	28
Skin[2]	9	1		65	5	8		88
Total	14	2	1	79	28	18	73	215

[1] Nose, ears, eyes, anus, skin (armpits, abdomen)
[2] Skin on other parts of the carcass

Furthermore, a moderate significant association was found between animal species category and primary tissue preference, meaning that the primary tissue preference was dissimilar across animal species categories (Monte Carlo Exact test: $p < 0.001$; Cramer's V: 0.500). Facultative scavengers had a preference for skin tissue on other parts of the body (63%) and also regularly preferred muscle tissue (35%). Indirect scavengers evenly preferred insects and larvae present on the carcass and hairs (both 50%). Waste eaters had a preference for muscle tissue (35%) and skin tissue on other parts of the body (32%). Softer tissues (nose, ears, eyes, anus and skin from armpits and abdomen) were mostly eaten

by waste eaters (21%) and in a lesser extent by facultative scavengers (2%). Organs were only consumed by waste eaters (10%). The carcass visitors never consumed or took tissue from the carcasses and therefore they did not have a preference (Figure 10).

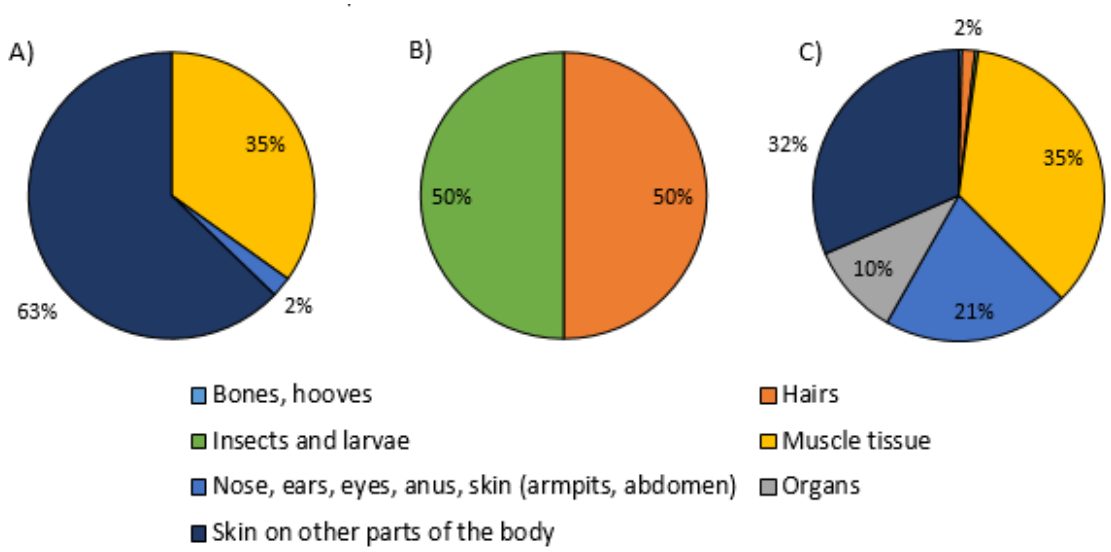


Figure 10. Primary tissue preference of the vertebrate animal species per category: A) facultative scavenger, B) indirect scavenger and C) waste eater. Carcass visitors never showed a tissue preference.

Overall, a moderate significant association was found between animal species and primary tissue preference, meaning that the primary tissue preference was dissimilar across animal species (Monte Carlo Exact test, $p < 0.001$; Cramer's V: 0.455). However, by grouping the species into categories, only a moderate significant association between animal species and primary tissue preference was found for the waste eaters (Monte Carlo Exact test: $p < 0.01$, Cramer's V: 0.302). No significant associations were found for the facultative scavengers (Monte Carlo Exact test: $p > 0.05$; $N = 86$) and indirect scavengers (Monte Carlo Exact test: $p > 0.05$) between animal species and primary tissue preference. Within the waste eaters, it was observed that carrion crow and common buzzard mostly ate muscle tissue (47% and 54% respectively) and regularly ate soft tissues (28% and 24% respectively). Red fox and wild boar on the other hand preferred skin tissue on other parts of the carcass (53% and 67% respectively). Wild boar was the only species that was observed breaking bones by biting on them. Organs were only eaten by waste eaters. Within the facultative scavengers, beech marten once ate muscle tissue whereas domestic cat mostly ate skin on other parts of the carcass. Of the indirect scavengers, great tit only took hairs and song thrush and western yellow wagtail were observed eating insects and larvae present on the carcasses (Table 9).

Table 9. Counts of the primary tissue preference of the vertebrate animal species per animal category.

Category & Species	Bones & hooves	Hairs	Insects & larvae	Muscle tissue	Soft tissues[1]	Organs	Skin[2]	Total
Facultative scavenger				30	2		54	86
Beech marten				1				1
Domestic cat				29	2		54	85
Indirect scavenger		3	3					6
Great tit		3						3
Song thrush			1					1
Western yellow wagtail			2					2
Waste eater	2	8	2	196	115	57	175	555
Carrion crow		7	2	112	67	24	25	237
Common buzzard				56	25	2	21	104
Red fox		1		16	17	11	50	95
Western jackdaw				1				1
Wild boar	2			11	6	20	79	118
Total	2	11	5	226	117	57	229	647

[1] Nose, ears, eyes, anus, skin (armpits, abdomen)
[2] Skin on other parts of the carcass

5.2. Animal Behaviour

2. What is the behaviour of the vertebrate scavenger species around the carcasses and is there a difference in this behaviour between the different areas?

Of 1808 observations the behaviour of the vertebrate animal species could be determined. Interest in the carcass (34%), eating (32%) and passing the carcass (24%) were the most prevalent primary behaviours. Of the secondary behaviours, eating (35%) and interest in the carcass (30%) were the most observed behaviours (Figure 11).

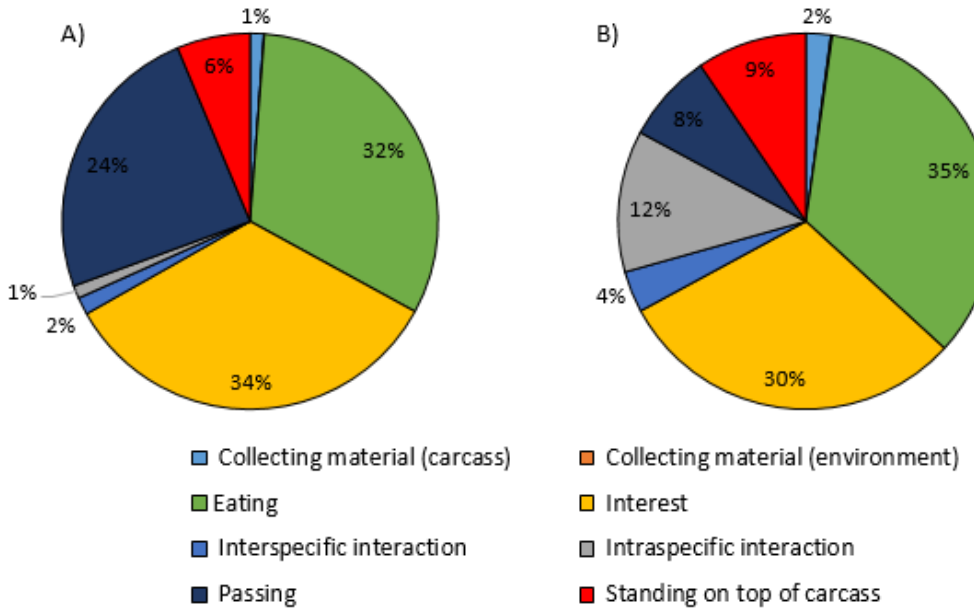


Figure 11. Primary (A) and secondary behaviours (B) of the vertebrate animal species observed around the carcasses.

A moderate significant association was found between animal species and primary behaviour, meaning that each species showed different (combinations of) primary behaviours around the carcasses (Monte Carlo Exact test, p <0.01; Cramer's V: 0.331). 'Eating' was the most often observed primary behaviour of carrion crow, domestic cat and wild boar. Beech marten, horse, human, red fox and wood mouse primary showed interest in the carcasses. The collection of material from the carcasses was observed several times as primary behaviour for carrion crow, great tit and red fox. Interspecific interactions were observed between carrion crow and common buzzard. The common buzzard was the only species that mostly showed 'standing on top of carcass' as primary behaviour. Cattle, roe deer and great tit primary passed the carcasses without reacting to it (Table 10).

Table 10. Counts of the primary behaviour that the vertebrate animal species showed around the carcasses by using the abbreviations of the different behaviours as described in the methods (Chapter 4).

	Primary behaviour								
Species	CMC	CME	EAT	INT	INTER	INTRA	PAS	STA	Total
Beech marten	1			26			10		37
Brown rat				1					1
Carrion crow	11	1	199	131	21	6	84	25	478
Cattle				33			102		135
Common blackbird							2		2
Common buzzard			44	41	4	1	19	89	198
Common pheasant							3		3
Common wood pigeon							4		4
Domestic cat			76	29			13		118
Domestic dog			1	5			4		10
Eurasian jay							1		1
European hare							6		6
European robin							1		1
European roe deer				14			21		35
European stonechat							1		1
Grey heron							1		1
Great tit	3						26		31
Horse				54		4	52		110
Human				13			8		21
Meadow pipit							1		1
Red fox	6		61	123		2	27		219
Song thrush			1				3		4
Western jackdaw			1						1
Western yellow wagtail							6		6
Wild boar			191	129		7	38		365
Wood mouse				13			6		19
Total	21	1	574	612	27	20	439	114	1808

Secondary behaviours were observed for 15 of the 26 vertebrate animal species. A moderate significant association was found between animal species and secondary behaviour, meaning that each species showed different (combinations of) secondary behaviours around the carcasses (Monte Carlo Exact test, p <0.01; Cramer's V: 0.282). Eating behaviour was the most observed secondary behaviour of beech marten, common buzzard, domestic cat and red fox. Carrion crow, cattle and wild boar mostly

showed interest in the carcasses as secondary behaviour. Intraspecific behaviour was often observed for horse and wild boar. 'Standing on top of the carcass' was quite often observed as secondary behaviour for carrion crow (Table 11).

Table 11. Counts of the secondary behaviour that the vertebrate animal species showed around the carcasses by using the abbreviations of the different behaviours as described in the methods (Chapter 4).

	Secondary behaviour								
Species	CMC	CME	EAT	INT	INTER	INTRA	PAS	STA	Total
Beech marten			5	2			1		8
Carrion crow	8	1	85	94	18	20	19	54	299
Cattle				15		2	10		27
Common buzzard			94	10	9	2		13	128
Domestic cat			20	10			1	6	37
Domestic dog			1						1
European hare				1					1
European roe deer				1			1		2
Great tit				2			3		5
Horse				22		27	17	3	69
Human				1					1
Red fox	8		41	32	1	1	8		91
Western jackdaw				1					1
Western yellow wagtail			2		1				3
Wild boar	2		44	65	1	51	5	4	172
Total	18	1	292	256	30	103	65	80	845

By combining the observation data of all animal species, a significant but weak association was found between nature area and primary behaviour, meaning that the primary behaviours shown were not similar across nature areas (Monte Carlo Exact test, $p < 0.01$; Cramer's v: 0.175). Thereafter these test statistics were calculated for each species separately. Because most of the species were only observed in one nature area and/or were observed showing one type of primary behaviour, the test statistic could not be calculated for each species.

A moderate significant association between nature area and primary behaviour was found for carrion crow (Monte Carlo Exact test, $p < 0.01$; Cramer's v: 0.400), cattle (Monte Carlo Exact test, $p < 0.001$; Cramer's v: 0.398), European roe deer (Monte Carlo Exact test, $p < 0.01$; Cramer's v: 0.568), great tit (Monte Carlo Exact test, $p < 0.01=5$; Cramer's v: 0.528) and wild boar (Monte Carlo Exact test, $p < 0.001$; Cramer's v: 0.318). Carrion crow mostly showed eating behaviour in Kempen~Broek (43%) and Markiezaat (41%), but only showed collecting material from the carcasses at Valkenhorst. At Kempen~Broek cattle mostly passed the carcasses (81%) but at Markiezaat they mostly showed interest (82%). European roe deer frequently passed the carcasses at Kempen~Broek (74%), showed interest behaviour as much as passing behaviour at Markiezaat (both 50%) and at Valkenhorst only interest behaviour was observed. Great tit mostly showed no interest in the carcasses at Kempen~Broek (84%), but evenly collected material from the carcasses (hairs) and passed the carcasses at Valkenhorst (both 50%). Lastly, wild boar frequently showed eating behaviour at Kempen~Broek (53%) and Valkenhorst (52%). However, at Kempen~Broek they also regularly passed the carcasses (21%) (Table 12).

Non-significant associations between nature area and primary behaviour were found for common buzzard, domestic dog, human and red fox (Monte Carlo Exact test, $p > 0.05$). Common buzzard was mostly observed standing on top of a carcass at Kempen~Broek (46%) and Markiezaat (41%). At Valkenhorst common buzzard was only observed showing interest. Domestic dogs and humans frequently showed interest and passed the carcasses frequently at the nature areas they were observed. Red fox was mostly observed showing interest in the carcasses at all four nature areas (55.6-66.7%) (Table 12).

Table 12. The number of primary behaviour observations that animals species showed around the carcasses in at least two nature areas, by using the abbreviations of the behaviours as described in the methods (Chapter 4).

	Primary behaviour								
Species & Nature area	CMC	CME	EAT	INT	INTER	INTRA	PAS	STA	Total
Carrion crow	11	1	199	131	21	6	84	25	478
Kempen~Broek	5		104	68	6		37	21	241
Markiezaat	3	1	95	63	15	6	47	4	234
Valkenhorst	3								3
Cattle				33			102		135
Kempen~Broek				24			100		124
Markiezaat				9			2		11
Common buzzard			44	41	4	1	19	89	198
Kempen~Broek			41	32	3	1	14	78	169
Markiezaat			3	7	1		5	11	27
Valkenhorst				2					2
Domestic dog			1	5			4		10
Kempen~Broek			1	4			4		9
Valkenhorst				1					1
European roe deer				14			21		35
Kempen~Broek				7			20		27
Markiezaat				1			1		2
Valkenhorst				6					6
Great tit	3				2		26		31
Kempen~Broek	1				2		24		27
Valkenhorst	2						2		4
Human				13			8		21
Kempen~Broek				9			8		17
Landgoed de Hamert				4					4
Red fox	6		61	123		2	27		219
Kempen~Broek	3		23	55		1	17		99
Landgoed de Hamert				2			1		3
Markiezaat	3		38	64		1	8		114
Valkenhorst				2			1		3
Wild boar			191	129		7	38		365
Kempen~Broek			78	39			31		148
Valkenhorst			113	90		7	7		217
Total	20	1	496	489	27	16	329	114	1492

5.2.1. Closed vs. Opened Carcasses

2.1. What is the effect of initially closed or opened carcasses on the behaviour of the scavenger species?

Behaviours were recorded of the vertebrate animal species around closed (n = 1413) and opened carcasses (n = 395). By combining the observation data of all animal species, a significant but weak association was found between carcass state and primary behaviour, meaning that the observed primary behaviours were different at both carcass states (Monte Carlo Exact test, $p < 0.001$; Cramer's V: 0.148). The primary behaviours that were mostly observed at closed carcasses were showing interest (37%) and eating behaviour (30%). At opened carcasses, eating behaviour (40%) was generally observed (Figure 12).

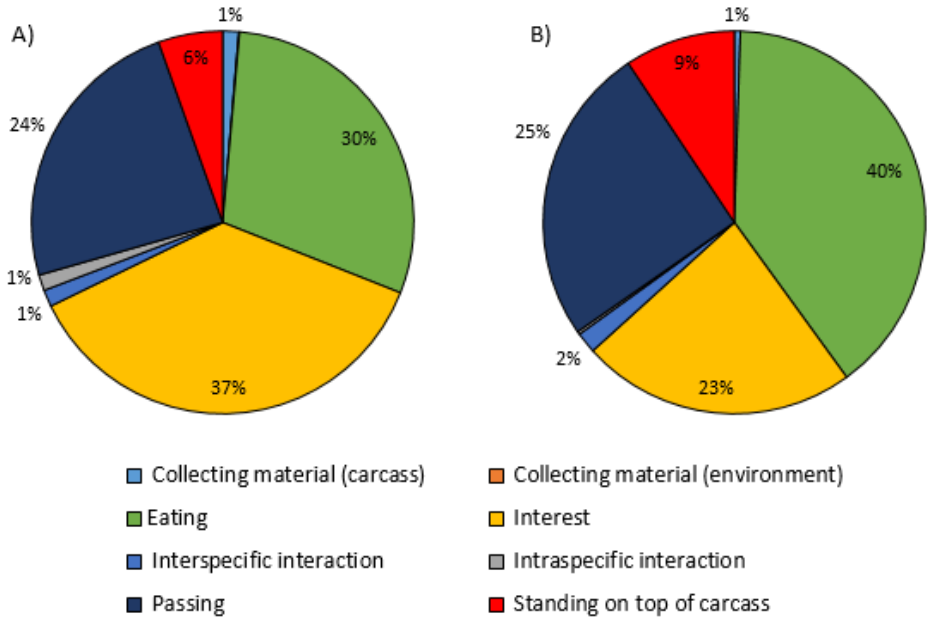


Figure 12. Primary behaviours of vertebrate animal species observed at A) closed and B) opened carcasses.

Because the majority of the species were only observed at one carcass state and/or were observed showing one type of primary behaviour, the test statistics could not be calculated for each species. Significant associations between carcass state and primary behaviour were found for the animal species cattle, common buzzard, domestic cat, great tit and wild boar. Cattle was mostly passing the carcasses independently of the state. Common buzzard was mostly standing on top of closed and opened carcasses but showed more interest at closed carcasses and eating behaviour at opened carcasses. The domestic cats showed frequently interest and eating behaviour at closed carcasses and at opened carcasses mostly eating behaviour. Great tits were generally passing the carcasses independently of the state. Lastly, wild boar showed frequently eating behaviour at both closed and opened carcasses. Non-significant associations between carcass state and primary behaviour were found for beech marten, carrion crow, domestic dog, European roe deer, horse, human and red fox (Table 13; Annex 3).

Table 13. Results of the statistical analyses used to test the association between carcass state and primary behaviour for the species for which enough data was present; statistical test used, significance level, Cramer's V value and the primary behaviours that were mostly shown at closed and opened carcasses.

Species	Statistical test	p-value	Cramer's V	Most observed behaviour closed carcasses	Most observed behaviour opened carcasses
Beech marten	Monte Carlo Exact	$p > 0.05$	-	Interest (77%)	Passing (57%)
Carrion crow	Monte Carlo Exact	$p > 0.05$	-	Eating (39%)	Eating (54%)
Cattle	Pearson's Exact test	$p < 0.01$	0.228	Passing (85%)	Passing (65%)
Common buzzard	Monte Carlo Exact	$p < 0.001$	0.328	Standing on top of carcass (51%)	Standing on top of carcass (37%)
Domestic cat	Pearson's Exact test	$p < 0.001$	0.467	Interest (42%)	Eating (85%)
Domestic dog	Monte Carlo Exact	$p > 0.05$	-	Interest 100%)	Passing (57%)
European roe deer	Fisher's Exact test	$p > 0.05$	-	Passing (60%)	Passing (60%)
Great tit	Monte Carlo Exact	$p < 0.05$	0.505	Passing (88%)	Passing (71%)
Horse	Monte Carlo Exact	$p > 0.05$	-	Interest (50%)	Passing (100%)
Human	Fisher's Exact test	$p > 0.05$	-	Passing (100%)	Interest (65%)
Red fox	Monte Carlo Exact	$p > 0.05$	-	Interest (56%)	Interest (67%)
Wild boar	Monte Carlo Exact	$p < 0.01$	0.197	Eating (50%),	Eating (81%)

5.3. Other Profiting Organisms

3. Are there other organisms that benefit from the carcasses, and in which manner?

The carcasses present at Valkenhorst and Markiezaat were actively sampled at 3 and 9 May 2018 respectively to investigate the presence of beetle and fly species. At that moment carcasses were present at all camera locations (Greveschutven, Oude Baan, Hogerwaard and De Duintjes). In total, 105 beetle species and 18 fly species were identified by Ed Colijn, Hans Huijbregts, Frank van Nunen and Oscar Vorst. Beetle species were found from the following 17 families: Carabidae, Chrysomelidae, Clambidae, Cleridae, Cryptophagidae, Curculionidae, Dermestidae, Histeridae, Hydraenidae, Hydrophilidae, Monotomidae, Nitidulidae, Ptiliidae, Pyrochroidae, Scarabaeidae, Silphidae and Staphylinidae. Flies species were identified of the families: Calliphoridae, Fanniidae, Muscidae, Piophilidae, Sarcophagidae and Sepsidae (Annex 4).

6. Discussion

6.1. Scavenger species

1. Which vertebrate scavenger species visit the carcasses and is there a difference in the presence of these species between the different areas?

It was predicted that red fox, wild boar and common buzzard would be the most frequently observed scavenger species at the carcasses (Poelarends et al., 2012; Selva et al., 20115; Wenting & Beekers, 2015). These species were indeed regularly observed, however carrion crow was seen more often. This could be explained by the fact that carrion crow eats carrion as part of their diet and is also a widely observed species in the Netherlands, with an estimated 70.000 to 100.000 breeding pairs in 2000 (Holyoak, 1968; Sovon Vogelonderzoek Nederland, 2002). Domesticated cattle and horses were also regularly observed at Markiezaat and Kempen~Broek because these species are grazing in the areas as part of the nature management (Brabants Landschap, 2018a; RLKM, 2015). A European polecat was once observed at Landgoed de Hamert, however at that time no carcass was present and therefore this observation was not included in this study. It was expected that this species would be frequently observed at carcasses in the different nature areas, however it could be that the supply of the roe carcasses was not near a European polecat territory at some locations and therefore was not discovered by this species (Lodé, 1996; Zoogdiervereniging, n.d.-a).

A difference in the presence of scavenger species was expected between the different areas and indeed a significant association was found between observed animal species and the four nature areas. Also, a significant association was found between animal species category and nature area. Wild boar was the most observed scavenger species at Valkenhorst, which was in line with the hypothesis (Poelarends et al., 2012; Wenting, 2014). However, at Kempen~Broek this species was relatively less observed. Wild boar was only captured by the camera traps at 'Stramproy' and 'De Graus'. It could be that wild boar populations are more established in Valkenhorst, because during the checking of the camera traps more wild boar rooting places were seen there compared to Kempen~Broek.

Wild boar is not present at Markiezaat and Landgoed de Hamert and for these areas was expected that red fox would be predominantly present at the carcasses (Poelarends et al., 2012; Wenting, 2014). Red foxes were visiting the carcasses at Markiezaat regularly, but carrion crow was observed more than twice as often. At Landgoed de Hamert too few observations of animal species visiting the carcasses were made to get a good idea of the scavenger species community in that area. The 'Westmeerven' and 'Bosrand' camera trapping locations were new, and these locations were probably not yet discovered by the scavenger species. Red fox was observed a couple of times, thus if the 'Circle of Life' research continues at Landgoed de Hamert it might become clear if this species is the dominant scavenger species.

During this study no common ravens, black kites or red kites were observed at the carcasses in the different nature areas. The prediction was that these species would be observed at the carcasses, because they all consume carrion as part of their diet (Poelarends et al., 2012; Rösner et al., 2005; Zawadzka, 1999). However, these species are rare scavenger species in the Netherlands and it could be that during this research very low numbers of these birds were present close to the nature areas (Sovon Vogelonderzoek Nederland, 2014a; Sovon Vogelonderzoek Nederland, 2014b; Sovon Vogelonderzoek Nederland, 2016b). For example, Bernd-Jan Bulsink, nature manager at Landgoed de Hamert, reported that two red kites were once seen in the area and that black kite was only spotted flying over. The low number of observations of these birds around the nature areas in combination with the new camera trapping locations could explain why red and black kites were not observed at the carcasses. However, common ravens were several times heard and seen around the Valkenhorst, but were never observed at the carcasses. In addition it was reported that a pair had successfully bred at Leenderbos (located south of Valkenhorst) and that two young ravens had fledged (Staatsbosbeheer, 2018). These young ravens have not been fed with carrion originating from the

carcasses provided in this research. Breeding common ravens are reported to forage within a defended area during the nesting season, close to the nest (Liebezeit & George, 2002). It could be that enough food was present at Leenderbos and that foraging on carcasses at Valkenhorst was not needed or that these carcasses were located to far from the nest.

6.1.1. Closed vs. opened Carcasses

1.1. What is the effect of initially closed or opened carcasses on the presence of these scavenger species?

In the areas where wild boar was absent (Landgoed de Hamert and Markiezaat), a difference in profiting scavengers was expected between opened and closed carcasses, with smaller scavenger species as carrion crow and beech marten visiting opened carcasses more frequently. This is because opened carcasses would probably imitate the visit of wild boar (Poelarends et al., 2012; Selva et al., 2005). In the areas where wild boar was present (Valkenhorst and Kempen~Broek) on the other hand, it was expected that these animals would scavenge from all carcasses and hereby would open closed carcasses. Therefore, no difference in visiting scavenger species at carcasses with the opened or closed initial state was expected in these areas. Indeed, a significant association was found between the presence of a certain species and carcass state and between the presence of a certain species and the presence of wild boar. On species level, significant associations were found between carcass state, wild boar presence and the presence of carrion crow, cattle and common buzzard. As expected, carrion crow and common buzzard were both observed at initially closed and opened carcasses in areas where wild boar was present. However, in areas where wild boar was absent, these scavenger species were more often observed at closed carcasses, which was not expected. During the analysis of tissue preferences of these species became clear that both species regularly ate from softer tissues (i.e. eyes, ears, nose, anus, skin of the armpits and abdomen) which were always accessible independently of carcass initial state and that muscle tissue could be quite easily accessed if a small wound was present on a closed carcass. Cattle was only present at Kempen~Broek (wild boar present) and Markiezaat (wild boar absent) and in the last area they were only observed around an opened carcass, explaining the found significant association (Bakker & Caspers, 2007; RLKM, 2015. Red fox was more often observed at closed carcasses, independently of wild boar presence, which could be explained by the fact that like wild boar red fox had the ability to open roe deer carcasses. However, most animal species were either observed at carcasses with the same initial state or in areas with the same presence of wild boar. For these species it was therefore not possible to determine if there was an association between their presence, initial carcass state and presence of wild boar. To investigate this, more observations of species as beech marten are needed in further research.

6.1.2. Tissue Preference

1.2. Which tissues are eaten by which scavenger species and do they have a preference?

Furthermore, the hypothesis was that scavenger species would have a tissue preference and indeed a significant association was found between animal species and primary tissue preference. By grouping the species into categories, it was shown that the waste eaters significantly preferred the same type of tissues. Wild boar was mostly observed eating skin on other parts of the roe deer body but was also regularly observed eating organs and muscle tissue. In a few cases, wild boar also ate soft tissues (i.e. eyes, ears, nose, anus, skin of the armpits and abdomen) and was observed breaking bones. From these observations it did not become clear if wild boar had a tissue preference or just ate all parts of the roe deer carcasses. It was easier to determine from the videos that they were eating skin than for instance when they were eating muscle or organ tissue. These last tissues are located deeper inside the carcass and therefore harder to see from the videos. But these results do show that wild boars can eat almost the whole carcass, which was in line with the hypothesis. Furthermore, it was expected that smaller scavenger species would prefer soft tissues and internal tissues (e.g. muscle tissue and organs) if they were accessible (Poelarends et al., 2012). Of the facultative scavengers, beech marten was only observed once eating muscle tissue which is too less to determine if this really is a tissue preference.

Domestic cat had a clear preference for muscle tissue. No significant association was found between animal species and primary tissue preference for the indirect scavengers. This can be explained by the fact that great tit only preferred hairs and song thrush and western yellow wagtail tail only preferred insects and larvae present on the carcasses. But due to the low total number of observations in this species category the overall tissue preference for indirect scavengers was not significant.

6.2. Animal Behaviour

2. What is the behaviour of the vertebrate scavenger species around the carcasses and is there a difference in this behaviour between the different areas?

It was expected that the scavenger species would mostly show eating behaviour or interest towards the carcasses (Bos et al., 2013; Wenting, 2014). This was the case in this research, where the most observed primary and secondary behaviours were both eating behaviour and showing interest. Also, a significant association was found between animal species and primary behaviour. Eating behaviour was mostly observed as primary behaviour of carrion crow, domestic cat and wild boar. Meanwhile, red fox was primary showing interest behaviour and common buzzard was most often observed standing on the carcass. The behaviour of red fox could be explained by the fact that they seem to notice the camera traps, especially at night when the low glow LEDs are on. It was often seen that red foxes were looking straight into the camera and maybe because of that were carefully approaching the carcasses and showing interest behaviour instead of eating behaviour. It has been shown that white flash cameras affect animal behaviour, causing them to flee. Infrared illumination may reduce this flight response, but it was suggested that foxes could still detect this (Meek et al., 2014). 'Standing on top of the carcasses' was only observed as primary behaviour of carrion crow and common buzzard. This might be a bird-specific behaviour. By standing on top of the carcass, it might be easier for them to access the internal tissues. Interspecific behaviours were observed for carrion crow and common buzzard because they regularly were both at the same time present at the carcass locations. Intraspecific interactions were mostly observed between individuals of the species wild boar and carrion crow, because they frequently visited the carcasses in pairs (carrion crow) or in families with juveniles (wild boar) which has also been reported before (Poelarends et al., 2012; Wenting, 2014).

No behavioural differences of scavengers were expected between nature areas. Because only roe deer carcasses are used in this research, scavenger-specific differences in behaviour among carcass types would be eliminated (Moleón et al., 2017; Olsen et al., 2016, Wenting, 2014). However, over all animal species a significant but weak association was found between nature area and primary behaviour, which was not expected. When the same analysis was conducted for each species separately it became clear that this association was found for carrion crow, cattle, European roe deer, great tit and wild boar. This could partly be explained by the lower number of observations of cattle, European roe deer and great tit. Also, these species were mostly present at one area and were only very few times observed in in another area. Carrion crow mostly showed eating behaviour at Kempen~Broek and Markiezaat but was during all the three visits to Valkenhorst observed collecting material from the carcasses. Due to the very low number of observations at one specific sampling location, the results could easily lead to significant differences in primary behaviours across the different nature areas for these species. The behaviour of wild boar was indeed a bit different at Kempen~Broek and Valkenhorst. At both nature areas they mostly showed eating behaviour, but at Kempen~Broek they also regularly passed the carcasses without reacting to it. This was not expected for this species. In addition, wild boar was also less observed at the camera trapping locations at Kempen~Broek. These both results could indicate that the supply of roe deer carcasses was not where most wild boar was present or where wild boar regularly searched for food in Kempen~Broek. At Valkenhorst, several ponds and a large fen (Greveschutven) can be found, close to both camera traps. Of wild boar it is known that they prefer to live in forests close to marshes where they can take mud baths (Zoogdiervereniging, n.d.-b). Maybe because of this characteristic at Valkenhorst more wild boars were observed at carcasses there.

6.2.1. Closed vs. Opened Carcasses

2.1. What is the effect of initially closed or opened carcasses on the behaviour of the scavenger species?

A difference in the behaviour of scavengers was expected between opened and closed carcasses, with smaller scavenger species showing eating behaviour more frequently at opened carcasses compared to closed carcasses. At closed carcasses it was expected that these species would mostly show interest behaviour (Poelarends et al., 2012; Wenting, 2014). A significant but weak association was found between carcass state and primary behaviour when the data for all species was combined. Of the smaller scavenger species, a significant association between carcass state and primary behaviour was only found for domestic cat. This species almost evenly showed interest and eating behaviour at closed carcasses and predominantly eating behaviour at opened carcasses. This is in line with the hypothesis. Unfortunately, because beech marten was only observed a few times, no significant association between carcass state and primary behaviour could been found. The primary behaviour of carrion crow was eating at both initially closed and opened carcasses, however across all observed primary behaviours no significant association was found with carcass state. The same was found for red fox which mostly showed interest behaviour independently of initial carcass state, and also for this species no significant association was found. These results could be explained by the fact that these species showed a broad range of behaviours at carcasses in general. Furthermore, these results could indicate that the initial carcass state does not affect primary behaviour, but that the state of the carcass at the time when the species is observed is more important. Because at that moment the scavenger will probably react differently if the carcass is closed or opened. For example, if a closed carcass is brought to the nature area and a larger scavenger species opens it, the next time a smaller scavenger species is visiting it is reacting to an opened carcass instead of the initial closed carcass. For further research it is therefore advised to note the carcass state at each observation individually instead of only at the beginning. No behavioural differences of wild boar was expected between opened and closed carcasses. Eating behaviour was mostly observed at initially opened and closed carcasses, showing that indeed this species can open closed carcasses.

6.3. Other Profiting Organisms

3. Are there other organisms that benefit from the carcasses, and in which manner?

It was expected that several insects would profit from the presence of large carcasses, including beetles and flies. Especially the species that are dependent on carcasses for their reproduction are expected to be found (Colijn & Beekers, 2013). During the active sampling of insects at the carcasses at Markiezaat and Valkenhorst, 108 beetle species and 18 fly species were identified. Also, numerous larvae of several insect species were observed at the carcasses. Some of the observed beetle species are dependent on carrion for their survival and were expected to be found. For example, larvae of the beetle family Silphidae are strictly necrophage, which means that they solely consume carrion (Colijn, 2014; von Hoermann et al., 2018). Burying beetles (genus *Nicrophorus*) bury small vertebrates in the soil as food for their larvae, but they also colonize larger vertebrate carcasses (von Hoermann et al., 2018). Furthermore, species of the beetle family Nitidulidae (genus *Omosita*) which feed on keratine and/or skin, the rove beetle *Creophilus maxillosus* and the three *Necrobia*-species which are specialized in eating carrion, were also present at the carcasses. Other observed species have an opportunistic relationship with carcasses, for example dung beetles of the *Scarabaeinae* family and rove beetles of the family *Staphylinidae*, which are both found on carrion and manure. Hister beetles (*Histeridae*) are carnivorous and predominantly live from larvae and fly pupae present on carcasses and manure. The larvae of skin beetles (*Dermestidae*) consume skin, hair and feathers. Minute beetles (*Clambidae*), silken fungus beetles (*Cryptophagidae*), featherwing beetles (*Ptiliidae*) and *Monotomidae* species are mycophages and likely survive from the fungi that forms on decomposing parts found on carrion, but are also found on various other substrates (Colijn, 2014). However, some species were found which did not have any known relationship with carcasses: a water beetle (*Ochthebius minimus*), a fire-coloured beetle (*Pyrochroidae serraticornis*), a tortoise beetle (*Cassida nebulosi*) (Nagasawa &

Matsuda, 2005) and true weevils (*Curculionidae*). These beetle species were accidentally found on and around the carcasses. The fly species *Lucilia Caesar*, *Phormia regina* and *Calliphora vomitoria* (Calliphoridae), *Hydrotaea* spp. (Muscidae), *Stearibia nigriceps* and *Parapiophilia vulgaris* (Piophilidae) that were found, were also collected in earlier research on pig carcasses in in Central Europe (Matuszewski et al., 2008).

7. Conclusion & Recommendations

The supply of carrion originating from large wild grazers is very limiting in European ecosystems compared to historic levels and therefore a knowledge gap exists about the importance of large carcasses in nature and the species that might profit from them. My research contributes with new knowledge on the presence, behaviour and tissue preference of vertebrate scavenger species at carcasses in Dutch protected areas. Also, the effects of the initial carcass state (closed or opened) on the exploitation by these scavenger species was studied for the first time. Lastly, I assessed which invertebrate organisms might profit from the availability of carcasses. My results show that several vertebrate and invertebrate animal species benefit from carcasses. Also, the initial carcass state had an significant effect on the presence, primary behaviour and primary tissue preference of vertebrate scavenger species. During the active sampling of carcasses, 105 beetle species and 18 fly species were found. Most of these species had a clear relationship with carcasses and profit from the availability of them in nature areas. In conclusion, this research emphasizes the importance of large carcasses in nature areas. The practice of distributing wildlife carcasses originating from roadkill in nearby nature areas, should be part of the Dutch and European nature management to support several scavenger species.

In future research the effects of carcass state on the presence, behaviour and tissue preference of scavenger species could be further studied to gain more knowledge on these relationships. In my research it became clear that the state of a carcass changes in time, and that the carcass state during the observation might be more important than the initial carcass state which was scored on beforehand. Also, it was sometimes hard to differentiate between tissue types on the video footage. A cafeteria-style experiment could be performed, where the scavengers have the choice between for example 1) an closed carcass, 2) an opened carcass without internal organs, 3) an opened carcass with internal organs and 4) internal organs only. In this way it can be determined if carcass state is the most important factor affecting the presence, behaviour and tissue preference of scavengers or that the accessibility of specific tissues is more important. In addition, the tissue preference of the different scavengers can be more thorough researched.

References

ARK Nature. (n.d.). Dood doet Leven. Retrieved 5 January 2018 from https://www.ark.eu/Nature/natuurlijke-processen/dood-doet-leven

ARK Nature. (2013). Werkblad dood dier: Tabel lijkenpikkers [PDF-file]. Retrieved 15 January 2018 from https://www.ark.eu/sites/default/files/media/Dood_doet_Leven/werkbladen-en-tabel.pdf

ARK Nature. (2014). Nieuwe natuur, sterke landbouw: Europa ondersteunt gebiedsontwikkeling in het Kempen~Broek en het Drielandenpark [PDF file].

ARK Nature. (2016). Protocol onderzoek kadavers met fotovallen [Word file].

Bakker, V., & Caspers, T. (2007). *Brabant in de Ban van Buiten: Gids van de natuurgebieden van Brabants Landschap*. Haaren: Brabants Landschap.

Barton, P. S., Cunningham, S. A., Lindenmayer, D. B., & Manning, A. D. (2013). The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia*, 171(4), 761-772.

Beasley, J. C., Olson, Z. H., & DeVault, T. L. (2015). Ecological role of vertebrate scavengers. *Carrion ecology, evolution and their applications*, 107-27.

Beekers, B. (2017). The Circle of Life project: Supporting Europe's scavengers. Retrieved 5 January 2018 from https://www.rewildingeurope.com/blog/the-circle-of-life-project-supporting-europes-scavengers/

Beekers, B., Meertens, H., Reiniers, K. & Helmer, H. (2017). Circle of Life: A new way to support Europe's scavengers [PDF file]. Retrieved 5 January 2018 from https://www.ark.eu/sites/default/files/media/Dood_doet_Leven/Brochure_Circle_of_Life.pdf

Bos, N., Leliveld, K., Beekers, B. & Meertens, H. (2013). Aandacht voor kadavers in de natuur. *Zoogdier*, 24(1), 1-4.

Brabants Landschap. (2018a). Markiezaatsmeer. Retrieved 22 January 2018 from http://www.brabantslandschap.nl/ontdek-de-natuur/natuurgebieden/brabantse-wal/markiezaatsmeer/

Brabants Landschap. (2018b). Valkenhorst. Retrieved 12 January 2018 from http://www.brabantslandschap.nl/ontdek-de-natuur/natuurgebieden/eindhoven/valkenhorst/?gclid=CjwKCAiA1uHSBRBUEiwAkBCtzeX-A2GB2XgJZ__KDkMCay3vsyd3nNPcYTaoNkcJg-BBKPU5JWjNwBoCxlMQAvD_BwE

Brandenburgische Technische Universität. (2017). Necros – Project: Tierkadaver und Biodiversität. Retrieved 19 January from https://www.b-tu.de/fg-oekologie/forschung/projekte/abgeschlossene-projekte/necros-projekt

Carter, D. O., Yellowlees, D., Tibbett, M. (2007). Cadaver decomposition in terrestrial ecosystems. *Faculty Publications: Department of Entomology*. Paper 251.

Colijn, E. (2014). Kevers op kadavers in Nederland, de stand van zaken. *Entomologische Berichten* 74 (1-2), 60-67.

Colijn, E. & Beekers, B. (2013). Zonder dood, minder leven: Ruimte voor aas(fauna) in het natuurbeheer. *De Levende Natuur* 114 (5).

Cortés-Avizanda, A., Jovani, R., Carrete, M., & Donázar, J. A. (2012). Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. *Ecology*, *93*(12), 2570-2579.

Cortés-Avizanda, A., Blanco, G., DeVault, T. L., Markandya, A., Virani, M. Z., Brandt, J., & Donázar, J. A. (2016). Supplementary feeding and endangered avian scavengers: benefits, caveats, and controversies. *Frontiers in Ecology and the Environment*, *14*(4), 191-199.

EIS Kenniscentrum Insecten. (2018). EIS Kenniscentrum insecten en andere ongewervelden. Retrieved 22 June 2018 from http://www.eis-nederland.nl/home

EUR-Lex. (2009). Regulation (EC) No. 1069/2009 of European Parliament and of the Council of 21 October 2009 laying down health rules as regards animal by-products and derived products not intended for human consumption and repealing Regulation (EC) No 1774/2002 (Animal by-products Regulation).

EUR-Lex. (2011). Commission Regulation (EU) No. 142/2011 of the Commission of 25 February 2011. Implementing Regulation (EC) No. 1069/2009 of the European Parliament and of the Council laying down health rules as regards animal by-products and derived products not intended for human consumption and implementing Council Directive 97/78/EC as regards certain samples and items exempt from veterinary checks at the border under that Directive.

Fielding, D., Newey, S., van der Wal, R., Irvine, R. J. (2014). Carcass provisioning to support scavengers: Evaluating a controversial nature conservation practice. *Ambio*, 43(6), 810-819.

von Hoermann, C., Jauch, D., Kubotsch, C., Reichel-Jung, K., Steiger, S., & Ayasse, M. (2018). Effects of abiotic environmental factors and land use on the diversity of carrion-visiting silphid beetles (Coleoptera: Silphidae): A large scale carrion study. *PloS one*, *13*(5), e0196839.

Holyoak, D. (1968). A comparative study of the food of some British Corvidae. *Bird Study*, *15*(3), 147-153.

IBM Corp. (2016). IBM SPSS Statistics for Windows, Version 24.0. Armonk, NY: IBM Corp.

Lardinois, R. (2005). *Dood doet leven: de natuur van dode dieren*. Dieren, Utrecht: KNNV Uitgeverij i.s.m. Stichting Kritisch Bosbeheer.

Liebezeit, J. R., & George, T. L. (2002). *A Summary of Predation by Corvids on Threatened and Endangered Species in California and Management Recommendations to Reduce Corvid Predation: Final Report to California Department of Fish and Game, Species Conservation and Recovery Program*. State of California, the Resources Agency, Department of Fish and Game, Habitat Conservation Planning Branch.

Lodé, T. (1996). Conspecific tolerance and sexual segregation in the use of space and habitats in the European polecat. *Acta theriologica*, *41*(2), 171-176.

Matuszewski, S., Bajerlein, D., Konwerski, S., & 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.

Meek, P. D., Ballard, G. A., Fleming, P. J., Schaefer, M., Williams, W., & Falzon, G. (2014). Camera traps can be heard and seen by animals. *PloS one*, *9*(10), e110832.

Moleón, M., Martínez-Carrasco, C., Muellerklein, O. C., Getz, W. M., Muñoz-Lozano, C., & Sánchez-Zapata, J. A. (2017). Carnivore carcasses are avoided by carnivores. *Journal of Animal Ecology,* 86, 1179-1191.

Nagasawa, A., & Matsuda, K. (2005). Effects of feeding experience on feeding responses to spinach in Cassida nebulosa L.(Coleoptera: Chrysomelidae). *Applied Entomology and Zoology*, *40*(1), 83-89.

NDFF. (2018a). NDFF Verspreidingsatlas Zoogdieren: Vos (*Vulpes vulpes*). Retrieved 5 June 2018 from https://www.verspreidingsatlas.nl/8496252

NDFF. (2018b). NDFF Verspreidingsatlas Zoogdieren: Wild zwijn (*Sus scrofa*). Retrieved 5 June 2018 from https://www.verspreidingsatlas.nl/8496237

Olson, Z. H., Beasley, J. C., & Rhodes Jr, O. E. (2016). Carcass type affects local scavenger guilds more than habitat connectivity. *PloS one*, *11*(2), e0147798.

Poelarends, P., De Baat, P., Van Dalen, D., Gremmen, P. & Oldenburg, C. (2012). Academic Consultancy Training, Wageningen University.

RLKM. (2015). Welkom bij grenspark Kempen~Broek. Retrieved 5 March 2018 from https://www.kempenbroek.eu/nl

Rösner, S., Selva, N., Müller, T., Pugacewicz, E., & Laudet, F. (2005). Raven Corvus corax ecology in a primeval temperate forest. *Corvids of Poland. Bogucki Wyd, Nuak, Poznan*, 385-405.

Selva, N. (2004). The role of scavenging in the predator community of Bialowieza Primeval Forest. *PhD thesis, University of Sevilla*.

Selva, N. & Fortuna, M. A. (2007). The nested structure of a scavenger community. *Proceedings: Biological Sciences*, 274(1613), 1101-1108.

Selva, N., Jędrzejewska, B., Jędrzejewski, W., & Wajrak, A. (2005). Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Canadian Journal of Zoology*, *83*(12), 1590-1601.

Sovon Vogelonderzoek Nederland. (2002). Zwarte kraai: verspreiding broedvogels 1998-2000. Retrieved 22 June 2018 from https://www.sovon.nl/nl/soort/15671

Sovon Vogelonderzoek Nederland. (2014a). Rode wouw: verspreiding niet broedvogels 1989-2014. Retrieved 5 June 2018 from https://www.sovon.nl/nl/soort/2390

Sovon Vogelonderzoek Nederland. (2014b). Zwarte wouw: verspreiding niet broedvogels 1989-2014. Retrieved 5 June 2018 from https://www.sovon.nl/nl/soort/2380

Sovon Vogelonderzoek Nederland. (2016a). Buizerd: verspreiding broedvogels 1998-2000 en niet broedvogels 2012-2016. Retrieved 5 June 2018 from https://www.sovon.nl/nl/soort/2870

Sovon Vogelonderzoek Nederland. (2016b). Raaf: verspreiding broedvogels 2014-2016 en niet broedvogels 1989-2014. Retrieved 29 June 2016 from https://www.sovon.nl/nl/soort/15720

Staatsbosbeheer. (2018). Raaf na ruim een eeuw terug in Leenderbos. Retrieved 29 June 2018 from https://www.staatsbosbeheer.nl/Over-Staatsbosbeheer/Nieuws/2018/06/raaf-terug-in-leenderbos

Stichting Afhandeling & Monitoring Fauna-aanrijdingen. (n.d.). Aanrijding met wild. Retrieved 11 January 2018 from http://www.fauna-aanrijding.nl/aanrijding-met-wild/

Stichting het Limburgs Landschap. (n.d.). Landgoed de Hamert. Retrieved 12 January 2018 from http://www.limburgs-landschap.nl/gebieden/landgoed-de-hamert

Wageningen University & Research Centre. (n.d.). Agouti. Retrieved 19 January 2018 from https://www.agouti.eu/

Wenting, E. (2014). Kadavers in de Limburgse voorbeeldgebieden: Profiterende aaseters in de periode van november 2013 tot en met januari 2014. HAS Hogeschool, 's-Hertogenbosch.

Wenting, E. & Beekers, B. (2015). Mogelijke bijdrage van kadavers aan het broedsucces van Raven in Nationaal Park De Maasduinen. *Natuurhistorisch maandblad* 104 (5).

Wildlife Monitoring Solutions. (2017). Bushnell Trophy Cam Aggressor 2017 – Bruin (119874). Retrieved 6 June 2018 from https://www.wildlifemonitoringsolutions.nl/bushnell-trophy-cam-aggressor-2017-zichtbare-infrarood-flits-bruin.html

Zawadzka, D. (1999). Feeding habits of the black kite Milvus migrans, red kite Milvus milvus, white-tailed eagle Haliaeetus albicilla and lesser spotted eagle Aquila pomarina in Wigry National Park (NE Poland). *Acta ornithologica*, *34*(1), 65-75.

Zoogdiervereniging. (n.d.-a). Bunzing (Mustela putorius). Retrieved 22 June 2018 from http://www.zoogdiervereniging.nl/bunzing-mustela-putorius

Zoogdiervereniging. (n.d.-b). Het Wild zwijn (Sus scrofa). Retrieved 22 June 2018 from http://www.zoogdiervereniging.nl/het-wild-zwijn-sus-scrofa

Annex

Annex 1 – Description of nature areas

Landgoed de Hamert
Contact person(s): Bernd-Jan Bulsink & Ralph Vossen (Stichting het Limburgs Landschap).

Landgoed de Hamert is a 1084-hectare nature area located between the cities of Wellerlooi and Arcen in the province of Limburg and is part of the Maasduinen National Park (Figure 13). Many different types of landscape are present in the area: grasslands, dry deciduous and coniferous forests, heathland, high moor, agricultural fields and wet forests. Various fens are present in the open parts of the nature area. The Westmeerven is the most westerly located fen, and to the east of it lies Heerenven, which is clearly visible from the observation post on the Dikkenberg. Cattle and sheep are grazing in the area and wild boar is not present (Stichting het Limburgs Landschap, n.d.). In 2014, a pair of common ravens was breeding in the Maasduinen National Park (Wenting & Beekers, 2015) .

Figure 13. Location of the camera traps (red stars) Bosrand and Westmeerven at Landgoed de Hamert.

Kempen~Broek
Contact person(s): Huub Verlinden (Municipality Leudal).

On the border of the Dutch and Belgian province of Limburg, lies the nature reserve Kempen~Broek, which extends over the municipalities of Cranendonck, Weert, Nederweert, Bocholt, Bree, Kinrooi and Maaseik (Figure 14). Kempen~Broek is characterized by the concatenation of nature areas, e.g. Laurabossen, Loozerheide, Weerterbos and Wijffelterbroek. This 25,000-hectare nature area consists of both wet and dry landscapes. Marshes, open water, streams, heather, hayland and agricultural fields are present. Previously, the zinc factory Nyrstar and ARK Nature were the owners of the Loozerheide area, and in 2017 it was transferred to the Dutch nature conservation organization Natuurmonumenten. Tauros cattle is grazing at the Loozerheide and Highland cattle at De Graus and Stramproy. Also wild boar is present (ARK Nature, 2014; RLKM, 2015).

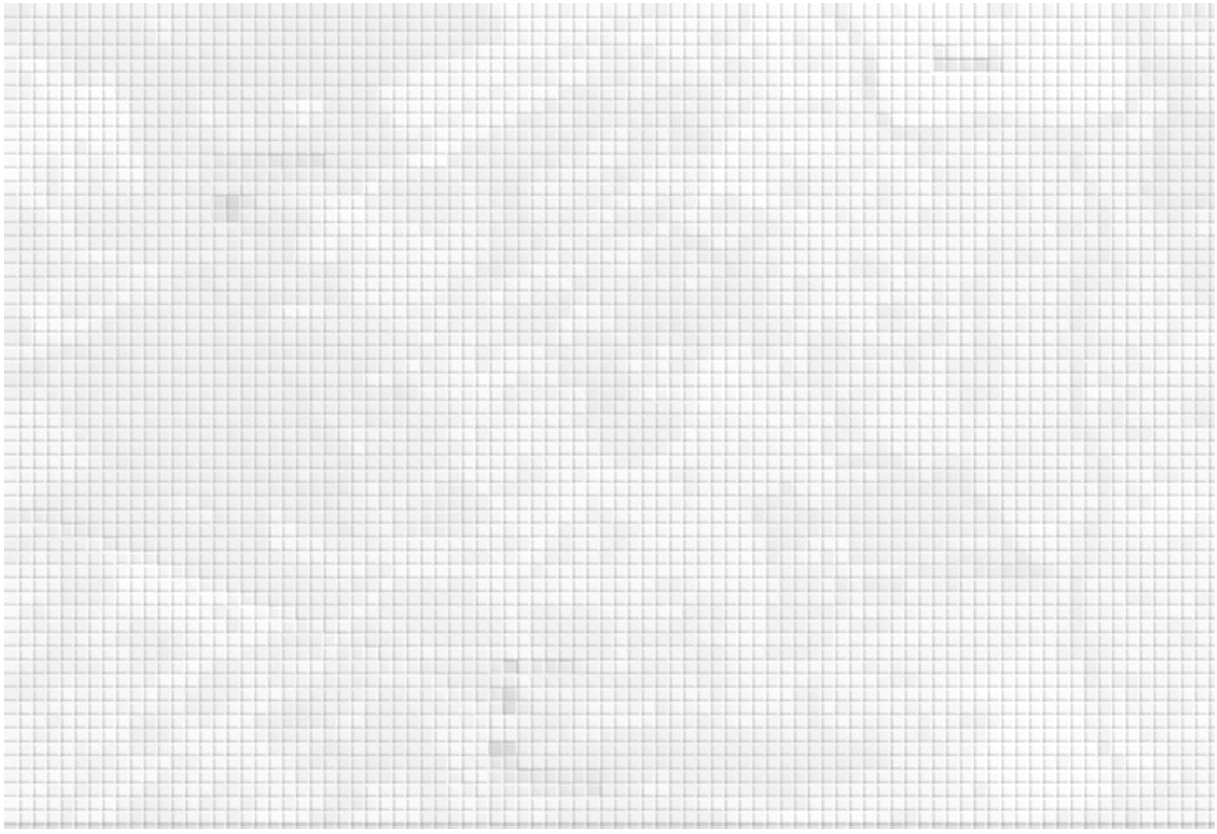


Figure 14. Location of the camera traps (red stars) at Kempen~Broek; De Graus, Loozerheide and Stramproy.

Markiezaat
Contact person(s): Erik de Jonge (Brabants Landschap).

Markiezaat is 1971-hectare nature area located southern to the city of Bergen op Zoom (Figure 15). Due to the construction of dams and the Schelde-Rijnkanaal canal in 1984, part of the Oosterschelde estuary was closed off from the open sea, and Markiezaat was created. Over time, this salt marsh area changed into a freshwater marsh and lake (Markiezaatsmeer) with an island called 'Spuitkop'. A variety of landscapes is present: (reed) marsh, grassland, thickets and forest. This area is known for its large population of 125 breeding birds, of which the Eurasian spoonbill (*Platalea leucorodia*) is an example. Every autumn and winter, white-tailed eagles hunt at Markiezaat. Icelandic horses and cattle are grazing in the area. Wild boar is not present, however many foxes are. The vast majority of this area is not open to the public: one walking path is present which leads to a watchtower and bird-watching hut (Bakker & Caspers, 2007; Brabants Landschap, 2018a).

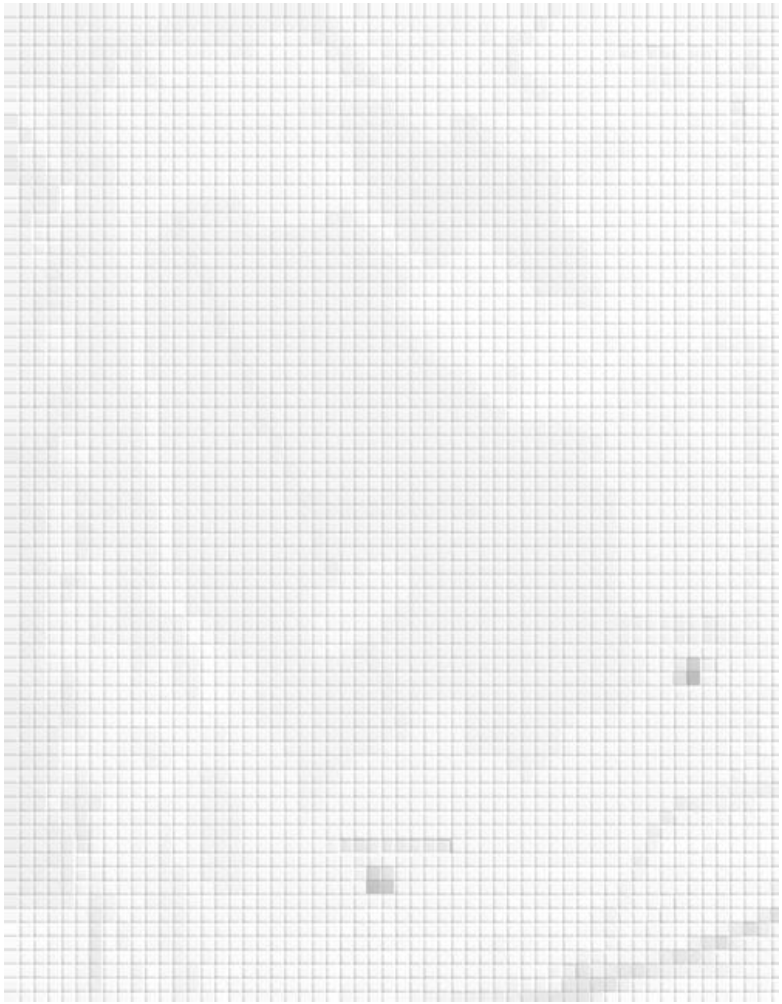


Figure 15. Location of the camera traps (red star) at Markiezaat; De Duintjes and Hogerwaard.

Valkenhorst

Contact person(s): Mari de Bijl & Nick Jeurisse (Brabants Landschap).

Valkenhorst is a 798-hectare nature area located eastern to the city of Valkenswaard in the province of Noord Brabant (Figure 16). Both dry and wet landscapes are present. Typical for the area are the former fish ponds, which are now part of a bird reserve, and are therefore not accessible to the public. Also, several fens are present in the area. Various waterfowl species are breeding in Valkenhorst, and special is the breeding of the bird species Eurasian bittern (*Botaurus stellaris*) and European jackdaw bittern (*Ixobrychus minutus*). The European nightjar (*Caprimulgus europaeus*) and black kite (*Milvus migrans*) are also present, and in 2017 common ravens (*Corvus corax*) were regularly observed. Scottish highlanders and ponies graze in a fenced 100-hectare area in Valkenhorst, close to the Spinsterberg. Estimated is that more than 100 wild boars are present in Valkenhorst (Bakker & Caspers, 2007; Brabants Landschap, 2018b).

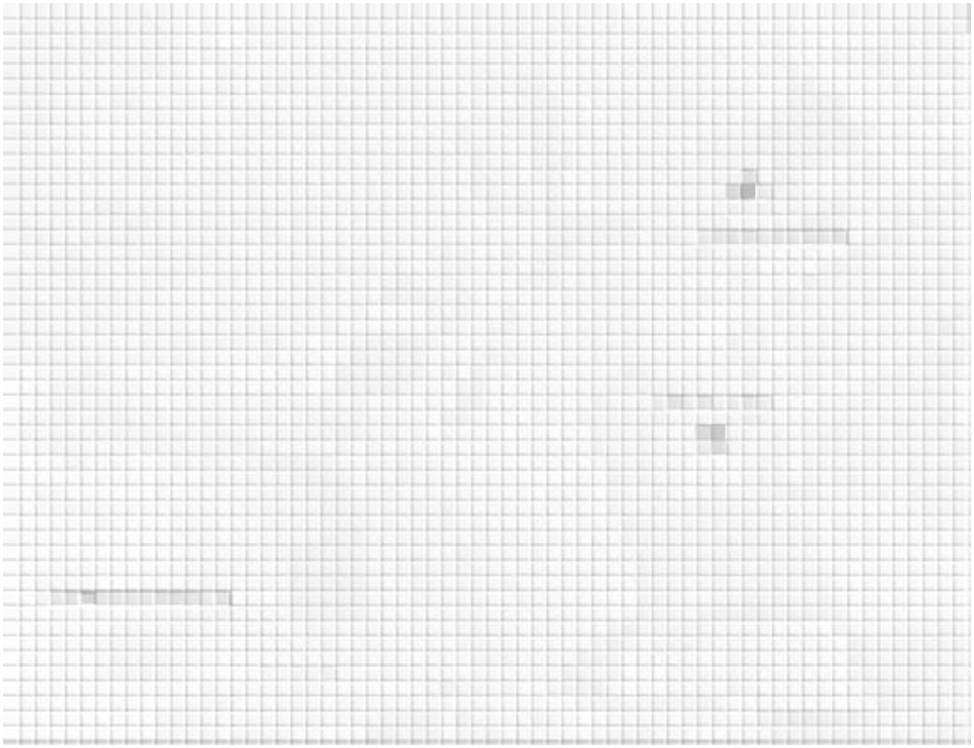


Figure 16. Location of the camera traps (red star) and fish ponds at Valkenhorst: Greveschutven and Oude Baan.

Annex 2 – Form supply roe deer cadavers (Dutch)

	A	B	C	D	E	F	G
1	**Aanvoer ree kadavers**						
2	**Naam (voornaam + achternaam)**	Ruth van den Herik					
3							
4	**Datum neerleggen (dd-mm-jjjj)**	**Natuurgebied**	**Voor wildcamera? (ja/nee)**	**Zo ja: locatie wildcamera**	**Staat karkas (open/gesloten)**	**Beschrijving verwondingen**	**Overige opmerkingen**
5	19-2-2018	Markiezaat	Ja	De Duintjes	Gesloten	Geen zichtbare verwondingen.	In ochtend reebok neergelegd. Paarden kwamen snuffelen. Door koude weer bevroren.
6	22-2-2018	Kempen-Broek	Ja	Stramproy	Gesloten	Gat bij schouder.	Afschot. Bevroren jaarling reebok.
7	27-2-2018	Kempen-Broek	Ja	Loozerheide	Gesloten	Geen zichtbare verwondingen.	Bevroren oude reegeit.
8	1-3-2018	Kempen-Broek	Ja	De Graus	Open	Gat in buikholte.	Open door aanrijding. Smalree.
9	20-3-2018	Kempen-Broek	Ja	Loozerheide	Open	Open bij achterpoten/billen.	Open door aanrijding. Bok 4 jaar oud. Versleept naar sloot (bij weghalen camera?)
10	20-3-2018	Kempen-Broek	Ja	Stramproy	Gesloten	Poten gebroken.	Lag zeker al 14 dagen. Geit.
11	26-3-2018	Valkenhorst	Ja	Oude Baan	Gesloten	Schaafwonden.	Geit
12	26-3-2018	De Hamert	Ja	Westmeerven	Open	Darmen eruit.	
13	28-3-2018	Valkenhorst	Ja	Greveschutven	Gesloten		
14	5-4-2018	Markiezaat	Ja	De Duintjes	Gesloten	Huid weg achterpoten, gat in bovenbeen achterpoot.	Dood door afrastering.
15	6-4-2018	Markiezaat	Ja	Hogerwaard	Open	Open bij spiermassa rond kruis.	Ree met gezwel op schouder. Dood door aanrijding. Heel veel insecten ter plaatse!
16	9-4-2018	Valkenhorst	Ja	Greveschutven	Gesloten	Achterpoten gebroken. Schaafplekken.	Bok. Gewei eraf gehaald.
17	12-4-2018	Kempen-Broek	Ja	De Graus	Gesloten		
18	12-4-2018	Markiezaat	Ja	Bosrand			
19	19-4-2018	Markiezaat	Ja	De Duintjes	Open	Zij open	Neergelegd samen met slachtafval tweede ree (organen etc.)
20	20-4-2018	Valkenhorst	Ja	Oude Baan	Gesloten		
21	4-5-2018	De Hamert	Ja	Westmeerven	Open	Buik open gemaakt.	2 embryo's
22	7-5-2018	Markiezaat	Ja	De Duintjes	Gesloten	Geen zichtbare verwondingen.	Resten vorige 2 kadavers nog aanwezig (botten en haren).
23	7-5-2018	Markiezaat	Ja	Hogerwaard	Gesloten		
24	9-5-2018	De Hamert	Ja	3e locatie	Gesloten	Kop eraf voor onderzoek, schotwond	Geschoten. Zeer vermagerd (14.5 kg), keelhorzels
25	9-5-2018	Kempen-Broek	Ja	Loozerheide	Open		
26	24-5-2018	Markiezaat	Ja	De Duintjes	Gesloten		
27	24-5-2018	Markiezaat	Ja	Hogerwaard	Open		
28	24-5-2018	Valkenhorst	Ja	Oude Baan	Gesloten		
29							

Figure 17. Form where the supply of roe deer carcasses was filled in by the nature managers.

Annex 3 – Primary Behaviour and Carcass State

	Primary behaviour																		
	Closed carcass									Opened carcass									
Species	CMC	CME	EAT	INT	INTER	INTRA	PAS	STA	Total	CMC	CME	EAT	INT	INTER	INTRA	PAS	STA	Total	Total
Beech marten	1			23			6		30				3			4		7	37
Brown rat				1					1										1
Carrion crow	9	1	152	110	19	6	75	19	391	2		47	21	2		9	6	87	478
Cattle				11			61		72				22			41		63	135
Common blackbird							1		1							1		1	2
Common buzzard			14	26	1		15	58	114			30	15	3	1	4	31	84	198
Common pheasant							3		3										3
Common wood pigeon							3		3							1		1	4
Domestic cat			21	22			10		53			55	7			3		65	118
Domestic dog				3					3			1	2			4		7	10
Eurasian jay																1		1	1
European hare							5		5							1		1	6
European robin																1		1	1
European roe deer				10			15		25				4			6		10	35
European stonechat							1		1										1
Gray heron							1		1										1
Great tit	3						21		24					2		5		7	31
Horse				54		4	50		108							2		2	110
Human							1		1				13			7		20	21
Meadow pipit							1		1										1
Red fox	6		61	119		2	25		213				4			2		6	219
Song thrush			1				3		4										4
Western jackdaw												1						1	1
Western yellow wagtail							2		2							4		4	6
Wild boar			169	128		7	34		338			22	1			4		27	365
Wood mouse				13			6		19										19
Total	19	1	418	520	20	19	339	77	1413	2		156	92	7	1	100	37	395	1808

Figure 18. Number of primary behaviours observed at closed and opened carcasses, for each animal species.

Annex 4 – Present Beetle and Fly Species

Table 14. Observed beetle families and species at the carcasses at Markiezaat and Valkenhorst.

Scientific family name	Species
Carabidae	*Dyschirius globosus* *Acupalpus parvulus* *Agonum marginatum*
Chrysomelidae	*Cassida nebulosa*
Clambidae	*Clambus armadillo*
Cleridae	*Necrobia ruficollis* *Necrobia violacea* *Necrobia rufipes*
Cryptophagidae	*Atomaria testacea*
Curculionidae	*Phyllobius pomaceus* *Nedyus quadrimaculatus* *Gymnetron antirrhini* *Rhinusa linariae*
Dermestidae	*Dermestes maculatus* *Dermestes undulatus*
Histeridae	*Saprinus semistriatus* *Saprinus virescens* *Margarinotus ventralis* *Margarinotus carbonarius* *Margarinotus ignobilis* *Margarinotus brunneus* *Hister unicolor*
Hydraenidae	*Ochthebius minimus*
Hydrophilidae	*Sphaeridium bipustulatum* *Sphaeridium lunatum* *Cercyon lateralis* *Cercyon unipunctatus* *Cercyon pygmaeus* *Cryptopleurum minutum* *Cryptopleurum crenatum*
Monotomidae	*Monotoma brevicollis*
Nitidulidae	*Omosita discoidea* *Omosita colon*
Ptiliidae	*Ptenidium pusillum* *Ptenidium nitidum* *Ptiliola kunzei* *Ptiliolum fuscum* *Acrotrichis grandicollis* *Acrotrichis sericans* *Acrotrichis dispar* *Acrotrichis cf atomaria* *Acrotrichis fascicularis*
Pyrochroidae	*Pyrochroa serraticornis*
Scarabaeidae	*Onthophagus ovatus* *Onthophagus similis* *Onthophagus coenobita*

	Aphodius pusillus *Aphodius granarius*
Silphidae	*Nicrophorus humator* *Nicrophorus vespilloides* *Nicrophorus vespillo* *Necrodes littoralis* *Thanatophilus rugosus* *Thanatophilus sinuatus* *Oiceoptoma thoracicum*
Staphylinidae	*Megarthrus prosseni* *Megarthrus denticollis* *Omalium rivulare* *Omalium oxyacanthae* *Carpelimus elongatulus* *Oxytelus laqueatus* *Anotylus sculpturatus* *Anotylus tetracarinatus* *Paederus fuscipes* *Paederidus ruficollis* *Philonthus intermedius* *Philonthus laminatus* *Philonthus tenuicornis* *Philonthus succicola* *Philonthus cruentatus* *Philonthus jurgans* *Philonthus varians* *Philonthus splendens* *Philonthus sanguinolentus* *Philonthus parvicornis* *Bisnius cephalotes* *Bisnius sordidus* *Bisnius parcus* *Bisnius fimetarius* *Gabrius piliger* *Creophilus maxillosus* *Ontholestes murinus* *Autalia rivularis* *Philhygra palustris* *Atheta divisa* *Atheta harwoodi* *Atheta amicula* *Atheta zosterae* *Atheta canescens* *Atheta sordidula* *Atheta celata* *Atheta nigripes* *Atheta atramentaria* *Atheta longicornis* *Acrotona pseudotenera* *Acrotona muscorum* *Acrotona aterrima*

	Acrotona benicki *Meotica filiformis* *Oxypoda opaca* *Tinotus morion* *Aleochara curtula* *Aleochara lata* *Aleochara intricata* *Aleochara tristis*

Table 15. Observed fly families and species at the carcasses at Markiezaat and Valkenhorst.

Scientific family name	Species
Calliphoridae	*Calliphora vicina* *Calliphora vomitoria* *Lucilia caesar* *Lucilia illustris* *Lucilia sericata* *Phormia regina*
Fanniidae	spp.
Muscidae	*Graphomya maculata* *Hydrotaea aenescens* *Hydrotaea albipuncta* *Hydrotaea armipes* *Hydrotaea dentipes* *Hydrotaea ignava* *Morellia aenescens* *Morellia hortorum* *Musca autumnalis*
Piophilidae	*Parapiophila vulgaris* *Stearibia nigriceps*
Sarcophagidae	*Ravinia pernix*
Sepsidae	spp.