Carcass ecology – more than just beetles

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Dead and decaying wood has long been acknowledged for its importance towards insect diversity. The knowledge about carrion ecology, however, is scarce. The lack of studies on carrion ecology in Europe can be explained by strict regulations for handling carcasses. The current paper presents results from observations of large carcasses in Brandenburg state (Germany), elaborating the following orders: Lepidoptera, Hymenoptera, Heteroptera, Orthoptera, and Diptera. Also Collembola, though hardly ever mentioned in association with carcasses, are taken into account. Some final notes are presented about the influence of carcass size, seasonality patterns, competition, and mineral sources as limiting factors.

Introduction

Dead organisms and parts thereof are important elements of temperate ecosystems. In many ecosystems dead and decaying wood forms an important habitat for insects as well as for fungi, lichens, mosses, and even birds. Carrion is another important element, but far less studied for various reasons. Large carcasses of domestic animals are effectively cleaned and the stochastical appearance of larger carcasses of game species adds to the difficulties. In particular our knowledge of the importance of large carcasses for insects, other than Coleoptera and Diptera, and the general food web is limited. Many studies on large carcasses are carried out for forensic purposes. Forensic studies focus on the succession of specific insect groups such as flies and beetles in order to determine the time of death, frequently referred to as the post mortem interval (PMI, Villet 2011). Other insects visiting carcasses such as hymenopterans, butterflies, or grasshoppers are hardly ever registered. Carcasses of domestic pigs are regarded as standard models for human corpses. As domestic animals from conventional farming are usually treated with drugs such as antibiotics and hormones, decomposition processes of these carcasses are disturbed (Brookes 2008, Gennard 2012, Selva pers. comm.). Small carcasses are either soon devoured by scavengers or buried by burying beetles of the genus *Nicrophorus* (e.g. Dekeirsschieter *et al.* 2011).

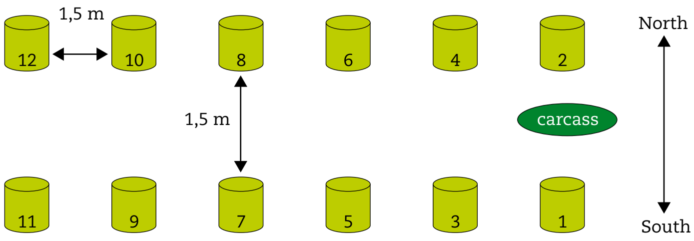
Further reasons for the apparent lack of knowledge on carcass ecology are related to strict regulations for the handling of carcasses or worse, unnecessarily strict interpretation of the existing regulations. In Germany, local authorities can order to remove all kind of carcasses including road kills of game (Krawczynski & Wagner 2008). These strict orders apply especially to carcasses of domestic stock, whereas foresters are generally allowed to hide road kills in thickets. Hiding is important in so far as the mere sight of a carcass can be regarded as 'breach of the peace' as is explicitly stated in 'Tierische Nebenprodukte-Beseitigungsgesetz' (animal by-product law, Gu & Krawczynski 2012a). Some local authorities do not even allow road kills to be left in the landscape. Thus researchers are strongly depending on the willingness of the local veterinary authorities. The legal situation in Belgium is similar to Germany.

The legislation of the European Union has become less strict. Regulation 142/2011 states that in specially protected areas (according to Natura 2000) exposure of large carcasses including cattle is allowed, if feeding of scavenging species of the Birds Directive or FFH Directive is intended. Even though European law should overrule national law, most authorities in Germany insist on the stricter national regulations (Gu & Krawczynski 2012a).

Necros Project

In 2008, Brandenburg University of Technology (Cottbus) started the Necros Project in Brandenburg (East Germany) focusing on carrion ecology by using large carcasses. The local veterinary authorities allowed the use of road kills. Recently, district authorities of Wittenberg (Saxony-Anhalt, Germany) gave permission to carry out research with carcasses of cattle and horses according to regulation 142/2011. The intentions were to collect data like species assemblages and succession and to study the possibilities of restoring food chains with these carcasses (Gu & Krawczynski 2012a).

The purpose of the present paper is to give a brief overview of the insect community associated with large carcasses, based on our own results and a literature review. In the discussion we highlight general aspects of carcass ecology. Our results on beetle assemblages are left out in this paper. This group is dealt with by Colijn (2014), in the current issue.



1. Sampling design in the Necros Project using twelve pitfall traps per carcass.
1. Bemonsteringsmethode in het Necros Project met twaalf bodemvallen per kadaver.

Methods

In the Necros Project the main objects of research were carcasses of the most common game species in Germany, roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). In addition four red deer carcasses (*Cervus elaphus*), one European badger carcass (*Meles meles*), and one mouflon carcass (*Ovis orientalis*) were used.

Insect activity on the carcasses was monitored by means of pitfall traps and direct observations. Two parallel rows of six traps were used, with 1.5 meters distance between traps. All carcasses were placed between traps 1 to 4 (figure 1, 2). Traps were emptied every Monday, Wednesday, and Friday, to get an idea of insect succession. The traps were filled with alcohol (80% ethanol) for killing and preserving arthropods. Soil samples near the carcass were taken and sieved to study maggot density. Automatic cameras were used to monitor vertebrate scavengers. Some interesting insect activity was recorded as well.

The study site is an open area with a mosaic of different vegetational units from grey-hair grass (*Corynephorus canescens*) to wood small reed (*Calamagrostis epigejos*) stands (figure 3). It is a nature reserve on a former military training area in Brandenburg.

Results and discussion

In this section, we present our results of the Necros Project in the first paragraph per group. This is followed by observations or data in literature in one or two paragraphs per group.

Lepidoptera

We found fourteen species of butterflies sucking on carcasses of red deer, roe deer, mouflon, wild boar, or badger: *Aglais io* (Linnaeus), *Apatura ilia* (Denis & Schiffermüller), *Aphantopus hyperantus* (Linnaeus), *Araschnia levana* (Linnaeus), *Argynnis adippe* (Denis & Schiffermüller), *Celastrina argiolus* (Linnaeus), *Coenonympha pamphilus* (Linnaeus), *Hipparchia semele* (Linnaeus), *Nymphalis antiopa* (Linnaeus), *Vanessa atalanta* (Linnaeus), *Vanessa cardui* (Linnaeus), *Polyommatus icarus* (Linnaeus), *Ochlodes sylvanus* (Esper), and *Polygonia c-album* (Linnaeus) (figure 4).

Butterflies have been observed on carrion before (Payne & King 1969, Van Wielink 2004, Burnaz 2007, Gu *et al.* 2011). The sucking behaviour of butterflies on dung and carcasses is called 'puddling' by Downes (1973) and Molleman (2010). Adler & Pearson (1982) and Pivnick & McNeil (2008) suggested that males perform puddling to ingest sodium for higher reproductive success. Boggs & Dau (2004) suggested species or at least family specific 'puddling behaviour'. Such preferential behavior is supported by our observations. Pieridae species were only observed at water puddles and dung, but not at carrion. Most butterfly observations were made in spring and early summer. As our study site lacks flowers at that time of year, butterflies may compensate by sucking on carrion. Moreover, mineral concentration should be higher in carrion than in nectar. This is parallel to observations during the dry season in northern India, where butterflies sucked almost exclusively on dung (Wiegleb unpublished data). Availability of water in carrion and dung might also play a role in puddling. Of the fourteen species we found sucking on carrion, only *Apatura ilia* was known to exhibit this behaviour (Burnaz 2007). Payne & King (1969) quote Klots (1958) who even speculates about the dependency of the genus *Apatura* on carrion.

Hymenoptera

Hornets (*Vespa crabro* Linnaeus) were registered by the automatic video cameras hunting at a boar carcass. We assume that they were hunting blowflies (Calliphoridae), a common behaviour also for *Vespula germanica* (Fabricius) and *Ectemnius* sp. at our carcasses. *Vespula germanica* was also observed feeding directly from the carcass, creating small body sized tunnels. *Bembix rostrata* (Linnaeus), *Ammophila* sp. and an undetermined species of Polistinae also hunted on carcasses, but we could not determine on what species they were feeding. Bees of the genera *Megachile* and *Andrena* frequently visited the carcasses in spring. Likewise in spring we found two representatives of bumblebee genus *Bombus* (family Apidae) sucking on a red deer carcass. *Formica* sp. (Formicidae) have also been observed at larger carcasses. They preyed on maggots, scavenged dead insects of the families Calliphoridae and Geotrupidae and in some cases carried bits of decaying material (figure 5).

Hunting Spheciformes have also been observed by Dudek (2005) on a roe deer carcass. Species that are not carnivorous may suck some juice of carcasses, as we have observed in bees. In Białowieża National Park, honeybees were observed sucking on the carcass of a European bison (*Bison bonasus*). In other parts of the world, some bee species are facultative scavengers (Baumgartner & Roubik 1989, Noll 1997). According to Baumgartner & Roubik (1989), bees search for salt, water, and mineral compounds when visiting carcasses. Hornets hunting blowflies (Calliphoridae) were observed by Bromley (1931).

Braack (1987) found ants feeding directly from a carcass. Van Wielink (2004) found many (>100) *Formica fusca* Linnaeus and *F. rufa* Linnaeus and some specimens of different *Myrmica* species on a roe deer carcass, suggesting that the ants observed are carcass feeders.

Hemiptera

So far, we found three true bug species on carcasses. *Pyrrhocoris apterus* (Linnaeus) and *Coriomeris denticulatus* (Scopoli) were frequently found on carcasses without observing any specific behaviour. *Alydus calcaratus* (Linnaeus), however, is most abundant and was not only sucking on fresh carcasses but also feeds on carcasses during the dry stage after rain.

All species observed are supposed to be phytophagous (Wachmann *et al.* 2007), yet at least one of them regularly feeds on carcasses. There is an old observation from North America (Parshley 1914) of twelve *Corynocoris typhaeus* (Fabricius) specimens at a bird carcass. *Corynocoris typhaeus* is of the same family as *Coriomeris denticulatus* (Coreidae). Schaefer (1980) mentioned several observations of Alydinae on carcasses from American literature where they are associated with carrion or dung. Gu *et al.* (2011) found significantly more cicadas in the pitfall traps closest to the carcass.

2. Pitfall traps around a wild boar carcass with a scavenging red kite, *Milvus milvus* (Linnaeus). The automatic camera is visible in the background. Foto: René Krawczynski
2. Bodemvallen naast een kadaver van een wild zwijn met een aasetende rode wouw, *Milvus milvus* (Linnaeus). De automatische camera is zichtbaar op de achtergrond.

3. Study site on the former military training area in Brandenburg. Foto: René Krawczynski
3. Onderzoeksgebied op het voormalige militaire trainingsveld in Brandenburg.

Collembola

We collected Collembola under and next to a badger carcass one year after decomposition. Significantly positively correlated to the carcass were *Sphaeridia pumilis* (Krausbauer), *Sminthurus nigromaculatus* Tullberg, and *Hypogastrura vernalis* (Carl). 94.6 % of all 7.606 Collembola were *H. vernalis*.

Because springtails are of hardly any importance to forensic science, they are rarely mentioned in the literature. According to Leclerc (1978), Collembola, as well as Diptera and Arachnida, are the opportunists among carrion-associated arthropods. Collembola and other arthropods were reared from soil collected underneath two carcasses in The Netherlands (Van Wielink 2004). Marta *et al*. (2010) only mention that there were Collembola under the studied corpse. We found highest abundance of Collembola one year after decomposition under the carcass, which is contradictory to Carter & Tibbet (2008) who experienced a decrease of Collembola in the latter stages of decomposition. *Hypogastrura vernalis* dominated the carcass community in a similar way as *Isotoma sepulchralis* Folsom, which made up 97% of a grave fauna in Washington, D.C. (Smith 1986).

Orthoptera

We mainly observed species of the suborder Ensifera feeding on deer and boar carcasses. *Decticus verrucivorus* (Linnaeus), *Conocephalus fuscus* (Fabricius), and *Tettigonia viridissima* (Linnaeus) were observed eating from carcasses same as two Caelifera species (figure 6). *Stenobothrus nigromaculatus* (Panzer 1796) was observed eating from a fresh boar carcass and from fly eggs on the carcass. *Calliptamus italicus* (Linnaeus 1758) was seen eating on the dry stage of a roe deer carcass. With the exception of *C. fuscus* the grasshoppers were visibly eating the meat. *Conocephalus*


4. (a) *Araschnia levana* and (b) *Celastrina argiolus* sucking on carcass. Photos: René Krawczynski
4. (a) *Araschnia levana* en (b) *Celastrina argiolus* zuigend op kadaver.


5. (a) *Formica* ants scavenging on a dead blowfly (Calliphoridae) and (b) a *Formica* ant carrying a piece of wild boar carcass. Photos: René Krawczynski
5. (a) *Formica*-mieren ruimen een dode bromvlieg (Calliphoridae) en (b) een *Formica* die een stuk van een kadaver van een wild zwijn draagt.

fuscus seemed to eat the hair but could also have been combing the hair for blood or body fluids.

In three cases *Mantis religiosa* (Linnaeus) was seen; it was at a distance of about 0.5 m, 1.0 m and 5.0 m from a boar carcass. There is no observation that this male specimen was actually preying on the maggots on or near the carcass, but it might be a possibility (Kraczynski & Wagner 2013). Probably due to lack of opportunity, there is only anecdotal evidence for grasshoppers visiting and eating from vertebrate carcasses (Krawczynski & Wagner 2010, Whitman & Richardson 2010).

Diptera

One specific observation rarely described in literature is the mass migration of maggots (Anton *et al.* 2011, Heinrich personal communication). We found evidence of mass movements of maggots into the soil at the carcasses of two red deer and a wild boar. Maggots form a stream of thousands of specimens moving in the same direction. When maggots reach the last larval instar, they leave the carcass to pupate in the surrounding soil far away from predatory insects like Silphidae, Staphylinidae, and Histeridae. In October 2012, we found a 74 kg red deer carcass with hardly any of these predators present. We therefore had the opportunity to study an 'undisturbed' maggot population. We took samples of the surrounding soil at a red deer carcass and sieved it for maggots. The total number of maggots was estimated at 40,000 resulting in about 1.4 kg biomass. However, the maggots in the soil around the carcass did not show any aggregation pattern but were distributed evenly without indication for a certain direction of mass migration. We found only a very low abundance of pupae in the soil, indicating that pupation takes place in spring. On one red deer carcass exposed in May 2012 we observed Tabanidae imagines in large numbers. Most conspicuous was the giant horse fly *Tabanus sudeticus* Zeller (figure 7). Tabanidae imagines fed on the carcass for about one week. We also found *T. sudeticus* at a two-weeks-old carcass of a European bison in Białowieża National Park (Krawczynski unpublished data). On a red deer carcass, a yet undetermined hoverfly (Syrphidae) was found sucking at the horn base.

6. Female *Decticus verrucivorus* on a wild boar carcass with dead maggots. Photo: René Krawczynski
6. Vrouwelijke *Decticus verrucivorus* op een kadaver van een wild zwijn met dode vliegenlarven.

As blowflies (Calliphoridae) are of outmost importance for forensic science, species composition and succession patterns under different circumstances are well studied. Blowfly larvae hibernate as third instar larvae in the soil (Gennard 2012). Other authors give a wide range of maggots or flies on carcasses. Newton & Joosten (2003) counted 12,000 flies for a boar carcass in The Netherlands. Braack (1987) recorded between 115,000 and 210,000 maggots at impala (*Aepyceros melampus*) carcasses in South Africa. However, methods of estimating the numbers are not specified in both cases. As most blowflies lay their eggs at about the same time, pupation and migration also takes place collectively. Sometimes they do not spread evenly in all directions but form a procession. Heinrich (personal communication) suggests that maggots need some moisture for their movement. By moving in procession, they are protected by each other's moisture in a mostly dry environment. Since we did not find an aggregated distribution of maggots in the soil, the stream of maggots probably dissolved when they reached denser vegetation with higher moisture content.

Recently, *Thyreophora cynophila* (Panzer), a piophilid fly species assumed extinct in its former range of central-western Europe, was found again in Spain (Carles-Tora *et al*. 2010). *Thyreophora cynophila* is a highly specialized scavenger. It is active during wintertime and depends on large, broken bones where it deposits the eggs in the marrow. For conservation of this species, exposure of large carcasses alone is not enough. Either the large bones must be opened artificially or the carcasses must be presented in an area where large mammal scavengers like wolf (*Canis lupus*), wolverine (*Gulo gulo*) or bear (*Ursus arctos*) are present. Hence, *Thyreophora cynophila* is not only dependent on large herbivores to provide big bones for breeding, but also on large carnivores to provide access to the bones.

Conclusion

Carcass size

Some species or groups of insects are generally found only on carcasses over a certain size. Braack (1987) found flies of the genus *Sarcophaga* on smaller carcasses only. Piek (2005) mentions the example of *Silpha obscura* Linnaeus, which is found on large carcasses where it scavenges on dead insects. The larger a carcass, the more insects, and especially, the more maggots serving as prey, can be found. Heinrich (personal communication) describes three cases of maggot mass migration from smaller carcasses induced not by the end of larval development, but by finishing the resource before reaching the last instar. In contrast, a large carcass can provide a resource for more than just one generation of insects. This explains why more species can be found in comparison to small carcasses. We found 39 species of Staphylinidae at a single red deer carcass. Some of our observations occurred only at the largest carcasses, such as horse flies, hover flies, hornets and bumblebees. We found *Tabanus sudeticus* for the first seven days on a red deer carcass and an approximately two weeks old carcass of a European bison. *Tabanus sudeticus* is a parasite of larger herbivores such as cattle and horse. This may explain its occurrence on the large carcasses of red deer and bison only in our observations.

Seasonality

At least some insect species found on carcasses show a strong seasonality not only in occurrence but also in the way of utilization of a carcass. *Thyreophora cynophila* (Panzer) is active only in winter (Carles-Tora *et al*. 2010). We observed typically phytophagous species like bees and bumblebees, butterflies, and true bugs such as *Pyrrhocoris apterus* (Linnaeus) mainly in spring. Typical predators that are generally not associated with carcasses, such as wasps, ants, some Ensifera species, and *Mantis religiosa*, were found mainly in late summer. We found some 50 specimens of Spheciformes on and close to a boar carcass hunting *Lucilia* flies in September. Wünsch & Gospodinova (2012) explain untypical hunting behaviour in *Vespula germanica* at the end of the season by a combination of population maximum and food scarcity at that time. As also migrating insectivorous birds such as the European stonechat (*Saxicola rubicola*) visited our carcasses in late summer and early spring, flies and maggots at carcasses seem to be an important food source in late summer/early autumn. Food scarcity may trigger the behaviour to search for food at carcasses.

7. *Tabanus sudeticus* on a red deer carcass. Photo: René Krawczynski
7. *Tabanus sudeticus* op een edelhertkadaver.

Competition

Insects need to detect and colonize ephemeral resources like dung and carrion quickly in order to avoid competition, because these resources are randomly distributed over the landscape. As colonization of seemingly equal carcasses in the same area and the same time can differ considerably, Braack (1987) suggests that there is a strong influence of chance. Gu & Krawczynski (2012b) call this process 'first come, first serve'. Four main groups of organisms compete for the resource, namely microbes (protozoans and bacteria), fungi, insects, and vertebrates. Bacteria may use toxins such as the botulinum toxin to repel some facultative vertebrate scavengers. Insects and fungi can use antibiotics against bacteria, while vertebrates take in both microbes and insects when devouring the carcass. Who takes advantage in the competition is also depending on the species composition. As observed in Brandenburg, wolves open a fresh carcass to eat only the intestines. But as the intestines hold most microbes, their population development is heavily disturbed, resulting in a missing bloating stage.

Mineral resources

Mineral resources are a limiting factor for some insects. *Apatura ilia* is known to search for sodium in dung and carrion. *Ochlodes sylvanus* was often attracted to our sweaty arms during field work, as were *Andrena* sp. Bees are known to exploit tears from different mammals (Bänziger *et al*. 2009). Sodium is an important resource for butterfly reproduction. Krawczynski & Wagner (2010) speculate about higher reproduction success due to mineral resource intake from carcasses by *Calliptamus italicus* females. Of an 80 kg carcass of a red deer we used in 2012, we could collect 3.2 kg of bone material distributed on 100 m^2. Taking these 4% bones as given for any carcass, the yearly harvest of about one million roe deer in Germany (Krawczynski & Wagner 2008) equals some 15 million kg carrion containing about 600 tons of bones. This means the extraction of 600 tons of minerals like calcium without replacement. Under natural conditions, these minerals would stay at the place of decomposition or could be taken in directly by vertebrates, ranging from mice to wild boar, and birds like the bearded vulture (*Gypaetus barbatus*). Large old bones that are high in calcium allow some cryptogams to grow in areas, where acidic soil conditions normally prevent their occurrence (Gu *et al*. 2011). The remains of a carcass have a fertilizing effect on the vegetation (Towne 2000, Danell *et al*. 2002, Gu & Krawczynski 2012a), which may have an effect on phytophagous insects as well. Gu *et al*. (2011) found significantly more cicadas in pitfall traps next to a boar carcass, and this is probably due to the fertilizing effect.

The presence of carcasses in nature is very important and stimulates species richness in all sorts of ways.

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Samenvatting

Kadaverecologie – meer dan alleen kevers
Reeds enkele decennia schatten we dood en rottend hout naar waarde: dood plantaardig materiaal is van groot belang voor de biodiversiteit, die van insecten in het bijzonder. Ook voor dood dierlijk materiaal lijkt dit te gelden, al is de wetenschappelijke kennis omtrent kadavers en hun ecologie schaars. Het gebrek aan kadaverstudies in Europa kan worden verklaard door de strikte reguleringen en wettelijke bepalingen. In het kader van het Necros Project wordt sinds 2008 de ontbinding van kadavers en de activiteiten van insecten gevolgd in Brandenburg (Duitsland). Kadavers van reeën, everzwijnen, enkele edelherten, een Europese das en een moeflon werden gemonitord met behulp van bodemvallen en camera's. Deze bijdrage beschrijft enkele resultaten van dit onderzoek met de nadruk op de volgende insectengroepen: springstaarten (Collembola), vlinders (Lepidoptera), vliesvleugeligen (wespen, bijen, hommels en mieren; Hymenoptera), wantsen (Heteroptera), sprinkhanen (Orthoptera) en vliegen (Diptera). Enkele conclusies worden voorgesteld betreffende de invloed van kadavergrootte, seizoenale variaties, competitie en minerale bronnen als limiterende factor.

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