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Animal biodiversity and food web restoration based on large vertebrate carcasses

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in Environmental Sciences.

By

**Master of Science
Xiaoying Gu**

from

Liaoning, China

Supervisor: Prof. Dr. rer. nat. habil. Gerhard Wiegand

Supervisor: PD Dr. rer. nat. habil. Udo Bröring

Date of oral examination: 16.07.2014

Affidavit

I hereby declare that this thesis entitled “Animal biodiversity and food web restoration based on large vertebrate carcasses” submitted to the Brandenburg University of Technology Cottbus - Senftenberg, is an original research undertaken by me under the supervision of Prof. Dr. rer. nat. habil. Gerhard Wiegand and PD Dr. rer. nat. habil. Udo Bröring, at the Chair of General Ecology, Faculty of Environmental Sciences and Process Engineering. The results contained in this thesis have not been submitted to any other university or institutions for the award of any degree or diploma.

Xiaoying Gu, M.Sc.

Signature.....

Date.....

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Abstract (English)

Carcasses of large vertebrate animals are integral elements in the natural environment. The aim of the present study is to clarify the relation between large carcasses and local ecosystems. It has been investigated which and how many animals are directly or indirectly involved into the carcass decomposition process, and whether there is a succession of community pattern during different carcass decomposition stages. A special focus was on the question how the temporal and the spatial distribution of arthropods are influenced by the carcass and its properties. A new classification of decomposition stages is proposed based on a new openness index for a carcass. Three carcass food web models for the research area were composed dependent on different seasons in the course of the year: Carcass exposed in spring, summer, and winter, respectively. Subsequently, the feasibility of using carcasses as a tool for food web restoration on a regional scale has been discussed.

From 2009 to 2011, in total, nine different carcasses from *Meles meles*, *Capreolus capreolus*, *Cervus elaphus*, and *Sus scrofa* were exposed in the research area, a former military training area situated in Eastern Germany. Pitfall traps were used to collect arthropods visiting the carcasses. Bird's and Mammal's attendance have been detected by automatic cameras and direct observation. In total, more than 112,000 arthropods from 25 taxa were identified. For Coleoptera Silphidae, Geotrupidae, Trogidae, Staphylinidae (partly) and Heteroptera the investigation could be carried out on species level. The existence of carcasses in the research area significantly increased arthropod diversity and abundance. Long term exposed carcasses significantly influenced vertebrates occurrence, vegetation and the surrounding soil as to diversity and various environmental conditions, respectively. The main consumers of carcasses in summer were various arthropods, *Corvus corax* and *Haliaeetus albicilla*. Besides the already well-known carrion arthropods, Orthoptera, Lepidoptera, and Apocrita were observed

using carcasses directly. In winter, the main consumers of carcasses were *Sus scrofa*, *Vulpes vulpes*, *Canis lupus*, *Corvus corax*, and *Haliaeetus albicilla*. By multivariate analysis it could be shown that the main factors influencing the occurrences of arthropods are the weight and the degree of openness of the carcass, and the main factor for the carcasses decomposition process is the openness index of the carcass. Carcass exposition is a cheap and efficient method to use large wild games which did not die from disease for the food web restoration in the research area.

Keywords: Large vertebrate animal carcasses, decomposition process, stages of succession, arthropods, food web restoration, former military training area, Germany

Abstract (German)

Kadaver größerer Wirbeltiere sind integraler Bestandteile einer naturnahen Landschaft. Das Ziel der vorliegenden Arbeit ist es, die Bedeutung größerer Kadaver für das lokale Ökosystem weitergehend zu klären. Dazu wurde untersucht, welche und wie viele Tiere direkt oder indirekt am Dekompositionsprozess beteiligt sind und ob es eine bestimmte Abfolge bestimmter Lebensgemeinschaften im Verlauf verschiedener Abbaustadien gibt. Insbesondere wurde die Frage nach der zeitlichen und räumlichen Verteilung verschiedener Tiergruppen am Aas untersucht. Eine neue Klassifikation verschiedener Dekompositionsstadien auf Grundlage eines neu eingeführten „openness index“ für Kadaver wird vorgeschlagen. Drei verschiedene Modelle für die Sukzession der Lebensgemeinschaften am Kadaver werden entwickelt, je nachdem, ob das Aas im Frühling, Sommer oder Winter exponiert ist. Des Weiteren wird die Möglichkeit diskutiert, Kadaver als Mittel zur Wiederherstellung natürlicher Nahrungsnetze auf regionaler Ebene einzusetzen.

Zwischen 2009 und 2011 wurden insgesamt neun Kadaver der Säugetierarten *Meles meles*, *Capreolus capreolus*, *Cervus elaphus* und *Sus scrofa* im Untersuchungsgebiet Lieberoser Heide, einem ehemaligen Truppenübungsplatz in Ostdeutschland, exponiert. Die Erfassung der Arthropoden am Aas erfolgte mit Bodenfallen. Die Präsenz von Vögeln und Säugetieren am Aas wurde mit automatischen Kameras und direkter Beobachtung ermittelt. Insgesamt wurden ca. 112.000 Arthropoden aus 25 Taxa identifiziert. Für die Coleoptera Silphidae, Geotrupidae, Trogidae, Staphylinidae (zum Teil) und Heteroptera konnten die Untersuchungen auf Artebene erfolgen. Die Präsenz von Kadavern führte zur deutlichen Erhöhung der lokalen Biodiversität und Abundanz der Arthropoden. Über eine längere Zeitdauer exponierte Kadaver führten zu vermehrtem Auftreten von Wirbeltieren und beeinflussten Vegetation und Bodenparameter der unmittelbaren Umgebung deutlich. Die wichtigsten Konsumenten

am Aas im Sommer waren diverse Arthropoden, *Corvus corax* und *Haliaeetus albicilla*. Neben den bereits bekannten aasfressenden Arthropoden wurden auch Orthopteren, Lepidopteren und Apocrita als direkte Nutzer am Aas beobachtet. Im Winter waren die wichtigsten Konsumenten *Sus scrofa*, *Vulpes vulpes*, *Canis lupus*, *Corvus corax*, und *Haliaeetus albicilla*. Durch die Anwendung multivariater Statistik konnte gezeigt werden, dass die wichtigsten Faktoren, die das Auftreten von Arthropoden beeinflussen, das Gewicht und der Öffnungsgrad (openness index) des Kadavers sind, der wichtigste Faktor für den konkreten Ablauf der Dekomposition wiederum der Öffnungsgrad. Die Exposition von Kadavern größerer, nicht krankheitsbedingt verendeter Wildtiere ist eine günstige und effektive Methode zur Etablierung natürlicher Nahrungsnetze.

Keywords: Größere Vertebraten, Tierkadaver, Dekomposition, Sukzession, Sukzessionsstadien, Arthropoda, Wiederherstellung natürlicher Nahrungsnetze, ehemalige Truppenübungsplätze, Deutschland

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1 Introduction

Many scientists have pointed out the importance of carcasses at various aspects: releasing energy and nutrients to the wider ecosystem, affecting movements and spatial distribution of species, influencing ecosystem diversity and function (Cortés-Avizanda et al. 2009, Carter et al. 2007). For scientific ecology, two aspects are of special interest: which and how many species are directly or indirectly involved into the carcass decomposition process, and what about the succession of community pattern during the carcass decomposition.

Related investigations are far too few especially in Germany. The strict regulations concerning the handling of carcasses are an important reason, which put not only livestock, but also wild animal carcasses under strict management. EU Directive 1774/2002 required that all animal products meeting certain criteria were to be disposed of through controlled methods, including burial and incineration. In recent years, the legislation of the European Union has become less strict. Regulation 142/2011 states that in specially protected areas (according to Natura 2000) exposures of large carcasses including cattle should be allowed, when feeding of scavenging species of the Birds Directive or FFH Directive is intended. Even though European laws should overrule national law, most authorities in Germany insist on stricter national regulations (Gu & Krawczynski 2012). The strict order causes lack of livestock carcasses in the landscape. In addition, hunting removes high quantities of potential game carcasses as well. In the hunting season 2007/2008, in total 145,000 tons of animal carcass were removed from landscape in Germany (Krawczynski & Wagner 2008).

In Germany there are many former military training areas which are now used as nature conservation areas with unoptimistic environment. Therefore, the need for a cheap, effective, and environmental friendly method to restore the landscape is urgent. Such former military areas are not open to the public because of the residual explosives. We assume that carcasses are capable to increase animal diversity and abundance in a given area, carcasses will bring positive influences on the surrounding environment (soil and vegetation). Furthermore, we assume also that exposing large carcasses in nature brings

benefit to the local animal community and restore the local food web, even the local ecosystem.

However, most researches related to carrion decomposition and animal community successions have focused on forensic entomology and the association with criminal events. Recent research in Germany on dead animals carried out in Jena between 2007 and 2008 was about to analyze the decomposition processes and insect succession on domestic pig carcasses. Its main objective was to establish a forensic entomological database (Anton et al. 2011). Forensic researches prefer using carcasses of domestic pigs, however, domestic animals from conventional farming are usually treated with drugs such as anti-biotic and hormones, therefore, decomposition process of these carcasses are affected (Gu et al. 2014). Prior to the Necros Project, long time research on wild animals without drug treatment exposed in nature conservation areas have never been done before in Germany.

At the Brandenburg University of Technology in Cottbus - Senftenberg, the Necros Project (2008 - 2014) started focusing on carrion ecology by using large wild animal carcasses in Brandenburg (East Germany). The local veterinary authorities allowed the use of road kills. The intentions were to collect data like species assemblages and succession and to study the possibilities of restoring food chains with these carcasses (Gu et al. 2014). The present study covers the years 2009 to 2011, and focuses on the temporal and spatial aspects of the carrion arthropods and carcass decompositions in the research area. Vertebrate scavengers and soil content around carcasses have been investigated through study projects, bachelor theses, and master theses in the Necros project. By these studies the following questions are addressed:

1. Does the decomposition of all carcasses follow the same process? What are the main factors influencing the decomposition process?
2. Are there certain assemblages of carrion arthropods? What are the factors influencing the occurrence of arthropods?
3. How does the carcass influence the surrounding environment?
4. How does the carcass influence the local food web?

5. Can carcasses be used as a restoration method? If yes, what kind of carcass should be exposed, when and where?

We hypothesized that the decomposition process of a carcass is influenced by the species of the dead animals, seasonality, and the local consumers' community. There is a certain succession within the carrion community and this succession is influenced by the decomposition stage of carcasses and the seasonality. Carcasses bring positive influences to the surrounding environment, e.g. to fertilize the soil and the vegetation. Sufficient carcass resources increase the diversity of the community (both arthropods and vertebrates), strengthen and restore the local food web.

2 Materials and methods

2.1 Research area

The research area Lieberoser Heide is located in eastern Brandenburg (Germany) (51°55' N, 14°18' E, Figures 2.1.1). The size of the whole area is about 28,000 hectares. Lieberoser Heide was used as military training area from 1945 to 1994. Afterwards this area was transferred to the Forest Department of Brandenburg (Landesbetrieb Forst Brandenburg) as a natural conservation area (Brunk et al. 2004). In the center of Lieberose Heide there is an open area surrounded by a belt of pine forest which is around 9.8 hectares (Figure 2.1.2). This open area was used to bury all the garbage when the Russian army left. This area contains no dangerous explosives in the soil.

Commonly observed habitat types of this open landscape include species rich psammophytic grassland, tall grass prairies, high forbes communities with ruderal and forest margin communities, dwarf shrub heathland, open forest and scrubland (Brunk et al. 2004). Dominant species in this area include *Calamagrostis*, *Agrostis*, *Echium*, *Tanacetum*, as well as dwarf shrubs, mosses, and lichens (Figure 2.1.3). In Lieberoser Heide large vertebrate scavengers such as wolf (*Canis lupus*), fox (*Vulpes vulpes*), wild boar (*Sus scrofa*), raccoon dog (*Nyctereutes procyonoides*), pine marten (*Martes*

martes), raven (*Corvus corax*), red kite (*Milvus milvus*), and white tailed eagle (*Haliaeetus albicilla*) are abundant. The public is not allowed to enter this area for the reason of safety and nature conservation. Therefore, the carcasses used in experiments did not disturb the public.



Figure 2.1.1 Location of the research area in Germany, it is indicated by the green point (source: Google map).



Figure 2.1.2 Study area, the yellow circle indicates the location of the sampling sites (source: Google map).



Figure 2.1.3 Landscape around the sampling sites in Lieberoser Heide (photo was taken on 08.08.2011).

Field work was carried out from 2009 to 2011. Meteorological information of the three years was taken from the nearest weather station in Cottbus. Spring 2010 (mean temperature was 8.8 °C) and winter 2010 (mean temperature was - 1.8 °C) were the coldest among all three years. Precipitation in summer and autumn 2010 were extremely high reached 292.1 mm and 284.6 mm. In chapter 3, the minimal temperature of every sampling day was used for the statistical analysis, and the data were taken from the weather station of Cottbus on the website: <http://www.wetteronline.de/rueckblick>.

2.2 Carcasses exposed

The carcasses which were used in this study were provided by the Forest Department of Brandenburg (Landesbetrieb Forst Brandenburg). From 2009 to 2011 in total nine carcasses were exposed in the research area: one European badger (*Meles meles*) carcass weight 6 kg, six roe deer (*Capreolus capreolus*) carcasses weight from 9 kg to 17 kg, one red deer (*Cervus elaphus*) carcass weight 75 kg, and one wild boar (*Sus scrofa*) carcass weight 30 kg (Table 2.2.1).

Table 2.2.1 Carcasses exposed in the research area.

No.	Scientific name	Weight (kg)	Sampling start	Sampling end	Duration (days)	Habitat	Open wound
1	<i>Meles meles</i>	6	22.06.2009	31.07.2009	40	Grassland	No
2	<i>Capreolus capreolus</i>	9	21.07.2009	21.09.2009	63	Grassland	Yes
3	<i>Capreolus capreolus</i>	12	05.08.2009	23.09.2009	50	Grassland	Yes
4	<i>Capreolus capreolus</i>	13	03.09.2010	29.09.2010	21	Grassland	Yes
5	<i>Capreolus capreolus</i>	8	08.09.2010	18.10.2010	41	Forest	No
6	<i>Capreolus capreolus</i>	17	16.03.2011	10.08.2011	148	Grassland	Yes
7	<i>Capreolus capreolus</i>	15	06.04.2011	02.11.2011	211	Grassland	Yes
8	<i>Cervus elaphus</i>	75	18.05.2011	02.11.2011	169	Grassland	No
9	<i>Sus scrofa</i>	30	01.06.2011	02.11.2011	155	Grassland	Yes

The animals were killed by car accidents or hunting. They were tested before being exposed in the research area to ensure that they did not carry any infectious diseases. All carcasses were exposed in open grass land, except carcass no. 5, which was deposited in a pine forest in 2010 for habitat comparison. All carcasses were monitored by automatic cameras. Additional photo shooting and direct observations have been done on every sampling day. The times of starting the sampling depended on the availability of carcasses. The exposing time of carcass no. 4 was the shortest (only 21 days); while at carcass no. 7, it was the longest which lasted in total 211 days.

2.3 Sampling design

2.3.1 Pitfall trapping

Pitfall traps were used in this study to collect ground dwelling communities. Pitfall trapping is a sampling technique which is widely used in studies of seasonal fluctuations, spatial distribution patterns, relative abundance in different micro-habitats, daily activity rhythms, and in community surveys. It is most commonly used to monitor biodiversity of ground dwelling organisms. Pitfall traps are cost- and time effective (Paulson 2005).

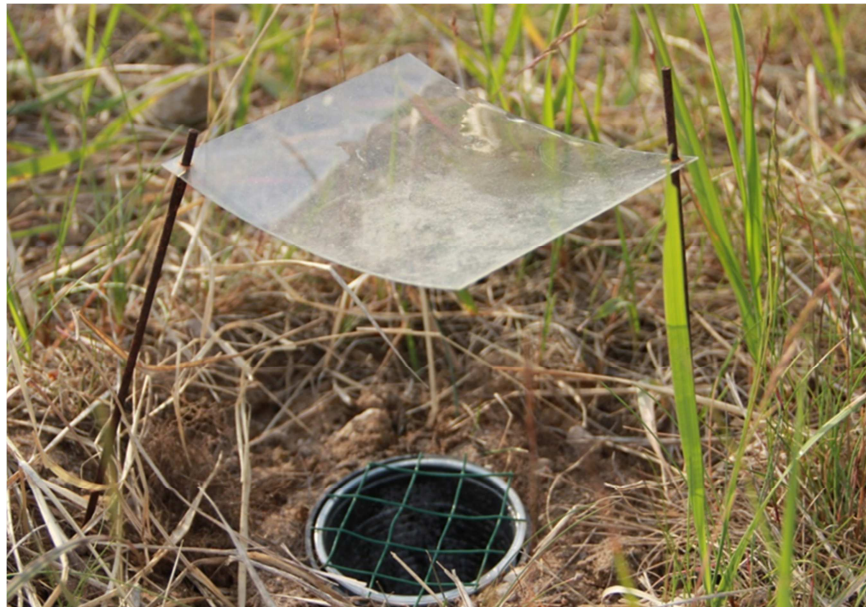


Figure 2.3.1 A single pitfall trap.

Pitfall traps which were used in this study were made up by three parts: plastic containers with 70 % ethanol for collecting and storing the animals; green grids for avoiding small mammals from falling into the pitfall traps; and plastic covers as protection from the rainfall (Figure 2.3.1).

2.3.2 Sampling design

Twelve pitfall traps were installed around each carcass (Figure 2.3.2). The carcass was put in the middle of the first four pitfall traps. The distance between each two pitfall traps was 1.5 meter. The results of trap no. 1 to no. 4 reflected the community which was influenced by the carcass micro-habitat; the results were influenced by both seasonality and the decomposition process of the carcass. The results of trap no. 9 to no. 12 were considered as the normal community in the research area, the results were only influenced by seasonality, but not the carcass.

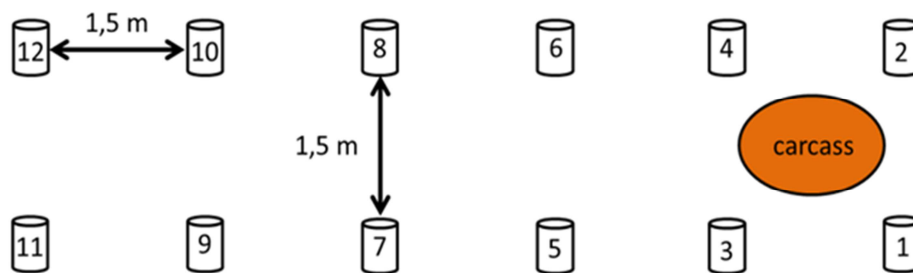


Figure 2.3.2 Sampling design of twelve pitfall traps (Gu et al. 2014).

The animals collected by the pitfall traps were restored in glasses with 80 % ethanol solution and identified in the laboratory. For carcass no. 8 and no. 9, in total five taxa (Silphidae, Geotrupidae, Staphylinidae, Trogidae, and Heteroptera) were identified into the species level. Table 2.3.1 gives an overview of the participants who have involved in the study and their tasks.

Table 2.3.1 Overview of participants involved in the study.

Carcass	Field work	Laboratory work	
		Taxa of arthropods	Species identification
No. 1 No. 2 No. 3	Robert Hering Rene Krawczynski Hans-Georg Wagner Xiaoying Gu	Xiaoying Gu Li Li Carolyn Lutze and others	Silphidae: Xiaoying Gu Geotrupidae: Bartosz Lysakowski, Xiaoying Gu Staphylinidae: Armin Rose Trogidae: David Bautze Heteroptera: Dortje Knoop
No. 4 No. 5	Xiaoying Gu Bendix Klarczyk	Xiaoying Gu Viola Strutzberg	
No. 6 No. 7	Xiaoying Gu, David Kschenka	Xiaoying Gu	
No. 8 No. 9	Xiaoying Gu David Smyth and others	Xiaoying Gu Gisa Schröder David Smyth and others	

2.4 Determination and nomenclature of species

Determination of Geotrupidae species is according to Machatschke (1969) and Bunalski (1999). Nomenclature of Geotrupidae species is according to Machatschke (1969). Determination and nomenclature of Silphidae species is according to Freude (1971). Determination and nomenclature of Trogidae species is according to Machatschke (1969). Determination of Heteroptera species is according to Wagner (1952, 1966, 1967), and nomenclature of Heteroptera species is according to Fauna Europaea. Determination and nomenclature of Staphylinidae species is according to Köhler & Kausnizer (1998) and Assing & Schülke (1999, 2001, 2006).

2.5 Statistical analysis

2.5.1 Spatial distribution

According to the Kolmogorov-Smirnov-Lilliefors test, the results of pitfall traps were not normally distributed; therefore, the Mann-Whitney U test and the Kruskal-Wallis

test were used to analyze the spatial distribution of arthropods. IBM SPSS Statistics 21 has been used for these tests (IBM Deutschland, Ehningen).

The Mann-Whitney U test is a non-parametric test for the null hypothesis that two groups are from the same totality. Twelve pitfall traps were divided into two groups according to the distance between the pitfall trap to the carcass (blue frame of Figure 2.5.1). Group 1 (trap no. 1 to no. 4) was close to the carcass. Group 2 (trap no. 5 to no. 12) was further away from the carcass. When the results of the Mann-Whitney U test are significant ($p < 0.05$), group 1 and group 2 have significant differences.

As to the Kruskal-Wallis test, twelve pitfall traps were divided into three groups (green frame of Figure 2-5-1). Group 1 (trap no. 1 to no. 4) was close to the carcass. Group 2 (trap no. 5 to no. 8) was relatively close to the carcass. Group 3 (trap no. 9 to no. 12) was far away from the carcass. When the results of the Kruskal-Wallis test are significant ($p < 0.05$), at least one group has significant difference from the others.

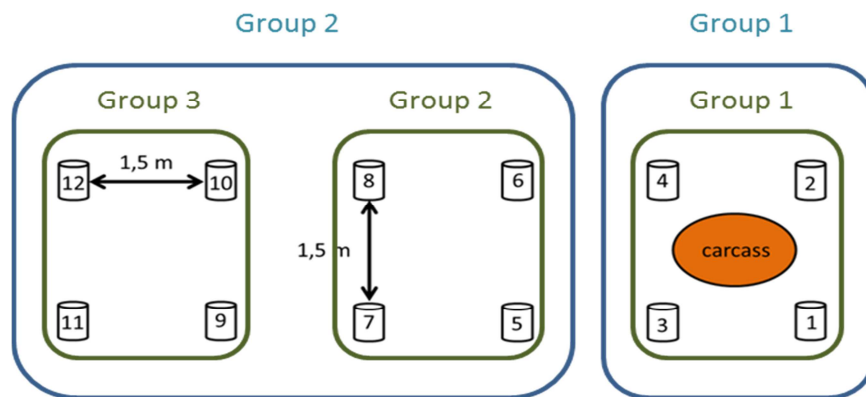


Figure 2.5.1 The classification of the Mann-Whitney U test (two groups in blue frame) and the Kruskal-Wallis test (three groups in green frame).

The taxa or species which showed significant relations with the carcass according to the statistical analysis were rechecked by the bar charts, in order to ensure whether the significant relation was a positive significant correlation. Because it was also possible that in group 1 much fewer arthropods were collected compared to other groups, then it was a negative significant correlation.

2.5.2 Temporal distribution

The temporal (inter-annual) species turnover S_τ was calculated according to Tokeshi (1990):

$$S_\tau = 0.5 \sum_{i=1}^n |P_i(t) - P_i(t+1)| \quad (1)$$

where $P_i(t)$ and $P_i(t+1)$ are the proportional abundance of taxon i in sample t and $t+1$ respectively, and n is the total number of taxa occurring on the two occasions. The abundance data are log transformed prior to calculations.

Spearman's rank correlation test was used to test the relationship between the number of arthropods and the minimal temperature. IBM SPSS Statistics 21 has been used for this test (IBM Deutschland, Ehningen).

2.5.3 Diversity index

Shannon-Wiener diversity index (H') was used to calculate the diversity:

$$H' = - \sum_{i=1}^S P_i \times \ln P_i \quad (2)$$

Where P_i is the proportion of the i^{th} taxon, \ln is the natural logarithm of P_i , and S is the number of taxa in the community (Molles & Cahill 1999).

2.5.4 Correspondence analysis

Detrended correspondence analysis (DCA) was used to find out the possible factors which ordinate the carcasses according to the occurrence of arthropods. Canonical correspondence analysis (CCA) was applied to elucidate the relationships among biological assemblages of arthropods, carcass parameters and environmental parameters. Both tests were carried out with the software of Canoco 4.5.1 (ter Braak & Verdonshot 1995, Jongman et al. 1995, ter Braak 1996, ter Braak & Šmilauer 1998, ter Braak & Šmilauer 2002)

3 Results

3.1 Overview

A total of 112,004 arthropods of 25 taxa were identified (Table 3.1.1). The numbers of following five taxa were extremely high: Formicidae (14,817 individuals, 13.2 %), Coleoptera-larvae (14,386 individuals, 12.8 %), Diptera (13,913 individuals, 12 %), Histeridae (13,430 individuals, 12 %), Silphidae (9,006 individuals, 8 %). The numbers of following eight taxa were relatively high: Brachycera-larvae (6,533 individuals, 5.8 %), Auchenorrhyncha (6,153 individuals, 5.5 %), Saltatoria (5,703 individuals, 5.1 %), Carabidae (5,434 individuals, 4.9 %), Staphylinidae (5,232 individuals, 4.7 %), Araneae (5,175 individuals, 4.6 %), Dermestidae (4,643 individuals, 4.1 %), and Geotrupidae (4,546 individuals, 4 %).

At carcass no. 8 in total 6,298 individuals and at carcass no. 9 in total 1,766 individuals were identified into species level. For both carcasses, the most abundant species of Silphidae were *Thanatophilus rugosus*, *Thanatophilus sinuatus*, and *Necrodes littoralis*. The most abundant species of Geotrupidae was *Trypocopris vernalis*. The abundant species of Trogidae and Heteroptera were different. At carcass no. 8 the most abundant species of Trogidae was *Trox cadaverinus*. At carcass no. 9 the most abundant species of Trogidae were *Trox cadaverinus* and *Trox hispidius*, and the most abundant species of Heteroptera was *Alydus calcaratus* (Table 3.1.2).

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Table 3.1.1 Overview of arthropods which were identified (“C” is the abbreviation of carcass).

Taxa		C 1	C 2	C 3	C 4	C 5	C 6	C 7	C 8	C 9
1	Cleridae	42	0	0	0	0	14	8	318	4
2	Coccinellidae	52	0	1	0	0	1	5	6	0
3	Curculionidae	10	5	0	5	1	14	19	42	3
4	Carabidae	477	827	447	158	31	77	1,091	1,200	1,126
5	Dermestidae	54	0	60	1	0	47	291	3,154	1,036
6	Elateridae	28	0	5	0	0	3	7	34	0
7	Histeridae	1,190	565	139	49	1	18	83	9,442	1,943
8	Silphidae	588	213	22	40	5	1,339	1,645	3,731	1,423
9	Staphylinidae	487	165	279	182	83	60	375	2,638	963
10	Scarabidae	772	429	215	400	104	255	508	1768	619
11	Trogidae	7	0	1	0	0	1	30	207	61
12	Coleoptera-larvae	3,037	516	41	5	2	807	1,393	7,385	1,200
13	Brachycera	1,853	308	81	0	0	10	197	56	609
14	Nematocera	364	78	11	0	0	0	23	157	2
15	Other Diptera	123	0	164	490	1,873	193	611	5,299	1,411
16	Brachycera-larvae	30	17	77	11	1,502	1	9	660	4,226
17	Apiformes	23	0	0	3	0	3	3	22	1
18	Formicidae	991	149	67	155	69	861	2,435	6,028	4,062
19	Other Hymenoptera	247	167	67	5	4	6	63	97	7
20	Auchenorrhyncha	1,180	287	432	116	2	311	948	1,533	1,344
21	Dermaptera	51	12	1	0	0	1	0	24	0
22	Heteroptera	346	8	5	1	0	13	21	93	92
23	Saltatoria	1,895	776	299	47	1	318	816	333	1,223
24	Araneae	682	390	254	103	76	613	832	1,690	535
25	Isopoda	141	10	2	0	1	0	0	24	6
Sum		14,670	4,922	2,670	1,771	3,755	4,966	11,413	45,941	21,896

Table 3.1.2 Species of four taxa at carcass no. 8 and no. 9.

Species	Carcass no. 8	Carcass no. 9
Silphidae	3,650 (11 species)	1,017 (5 species)
<i>Thanatophilus rugosus</i> (Linnaeus, 1758)	383 (10 %)	265 (26 %)
<i>Thanatophilus sinuatus</i> (Fabricius, 1775)	2,407 (66 %)	732 (72 %)
<i>Necrodes littoralis</i> (Linnaeus, 1758)	838 (23 %)	17 (2 %)
<i>Necrophorus humator</i> (Fabricius, 1775)	2 (< 1 %)	0
<i>Necrophorus vestigator</i> (Herschel, 1807)	6 (< 1 %)	2 (< 1 %)
<i>Necrophorus fossor</i> (Erichson, 1837)	1 (< 1 %)	0
<i>Necrophorus sepultor</i> (Gyllenhal, 1827)	7 (< 1 %)	0
<i>Necrophorus investigator</i> (Fabricius, 1775)	3 (< 1 %)	1 (< 1 %)
<i>Necrophorus vespilloides</i> (Herbst, 1783)	2 (< 1 %)	0
<i>Oiceoptoma thoracica</i> (Linnaeus, 1758)	1 (< 1 %)	0
Geotrupidae	1,546 (3 species)	484 (3 species)
<i>Trypocopris vernalis</i> (Linnaeus, 1758)	1416 (91 %)	456 (94 %)
<i>Typhaeus typhoeus</i> (Linnaeus, 1758)	9 (< 1 %)	7 (2 %)
<i>Anoplotrupes stercurosus</i> (Scriba, 1791)	121 (8 %)	21 (4 %)
Trogidae (identified by David Bautze)	347 (4 species)	55 (2 species)
<i>Trox cadaverinus</i> (Illiger, 1802)	318 (92 %)	26 (47 %)
<i>Trox sabulosus</i> (Linnaeus, 1758)	8 (2 %)	0
<i>Trox hispidius</i> (Pontoppidan, 1763)	20 (5 %)	29 (53 %)
<i>Trox scaber</i> (Linnaeus, 1767)	1 (< 1 %)	0
Heteroptera (identified by Dortje Knoop)	84 (16 species)	79 (8 species)
<i>Acalypta gracilis</i> (Fieber, 1844)	2 (2 %)	0
<i>Aradus cinnamomeus</i> (Spinola, 1837)	1 (1 %)	0
<i>Alydus calcaratus</i> (Linnaeus, 1758)	0	52 (66 %)
<i>Beosus maritimus</i> (Scopoli, 1763)	2 (2 %)	1 (1 %)
<i>Coriomeris scabricornis</i> (Panzer, 1806)	1 (1 %)	8 (10 %)
<i>Coriomeris denticulatus</i> (Scopoli, 1763)	1 (1 %)	0
<i>Drymus sylvaticus</i> (Panzer, 1809)	4 (5 %)	0
<i>Geocoris grylloides</i> (Linnaeus, 1761)	1 (1 %)	8 (10 %)
<i>Graptopeltus lynceus</i> (Fabricius, 1775)	1 (1 %)	1 (1 %)

Species	Carcass no. 8	Carcass no. 9
Larvae of Heteroptera	23 (27 %)	6 (8 %)
<i>Kalama tricornis</i> (Schrank, 1801)	6 (7 %)	0
<i>Lygus rugulipennis</i> (Poppius, 1911)	1 (1 %)	0
<i>Lytocoris campestris</i> (Poppius, 1911)	16 (19 %)	0
<i>Myrmus miriformis</i> (Fallen 1807)	1 (1 %)	0
<i>Rhynocoris iracundus</i> (Poda, 1761)	0	1 (1 %)
<i>Rhyparochromus pini</i> (Linnaeus, 1761)	5 (6 %)	0
<i>Saldula saltatoria</i> (Linnaeus, 1758)	1 (1 %)	0
<i>Xanthochilus quadratus</i> (Fabricius, 1798)	0	8 (10 %)

Because of the limitation of time, not all Staphylinidae individuals were identified into species level. The abundant species of the identified individuals at carcass no. 8 were *Creophilus maxillosus*, *Aleochara bipustulata*, and *Ontholestes murinus*. At carcass no. 9 the most abundant species was *Aleochara bipustulata* (Table 3.1.3).

Table 3.1.3 Species of Staphylinidae at carcass no. 8 and no. 9 (identified by Armin Rose).

Species	Carcass no. 8	Carcass no. 9
Staphylinidae	671 (59 species)	131 (22 species)
<i>Acrotona aterrima</i> (Gravenhorst, 1802)	8	0
<i>Aleochara bilineata</i> (Gravenhorst, 1802)	0	5
<i>Acrotona exigua</i> (Erichson, 1837)	1	0
<i>Acrotona muscorum</i> (Briout, 1860)	3	0
<i>Acrotona parvula</i> (Mannerheim, 1831)	7	0
<i>Acrotona sylvicola</i> (Kraatz, 1856)	2	0
<i>Aleochara bipustulata</i> (Linnaeus, 1761)	64	52
<i>Aleochara curtula</i> (Goeze, 1777)	2	0
<i>Aleochara intricata</i> (Mannerheim, 1830)	5	0
<i>Anotylus hamatus</i> (Fairmaire & Laboulb, 1856)	11	0
<i>Anotylus tetracarınatus</i> (Block, 1799)	1	0
<i>Atheta crassicornis</i> (Fabricius, 1792)	1	0
<i>Atheta divisa</i> (Märkel, 1844)	4	0

Species	Carcass no. 8	Carcass no. 9
<i>Atheta gagatina</i> (Baudi, 1848)	8	1
<i>Atheta fungi</i> (Gravenhorst, 1806)	0	1
<i>Atheta inquinula</i> (Gravenhorst, 1802)	2	0
<i>Atheta laticollis</i> (Stephens, 1832)	1	0
<i>Atheta longicornis</i> (Gravenhorst, 1802)	2	0
<i>Atheta nigra</i> (Kraatz, 1856)	1	0
<i>Atheta orbata</i> (Erichson, 1837)	0	9
<i>Atheta oblita</i> (Erichson, 1839)	2	0
<i>Atheta palustris</i> (Kiesenwetter, 1844)	5	0
<i>Atheta pseudoelongatula</i> (Bernhauer, 1907)	9	0
<i>Atheta sordidula</i> (Erichson, 1837)	2	0
<i>Bisnius cephalotes</i> (Gravenhorst, 1802)	2	0
<i>Bisnius nitidulus</i> (Gravenhorst, 1802)	3	0
<i>Bisnius parvus</i> (Sharp, 1874)	4	0
<i>Creophilus maxillosus</i> (Linnaeus, 1758)	241	6
<i>Dinaraea angustula</i> (Gyllenhal, 1810)	0	17
<i>Emus hirtus</i> (Linnaeus, 1758)	1	0
<i>Gyrophypnus fracticornis</i> (Müller, 1776)	1	0
<i>Leptacinus formicetorum</i> (Märkel, 1841)	0	1
<i>Leptacinus intermedius</i> (Donisthorpe, 1936)	0	2
<i>Leptacinus pusillus</i> (Stephens, 1832)	1	0
<i>Nehemitropia lividipennis</i> (Mannh., 1830)	10	0
<i>Ocypus olens</i> (Müller, 1764)	24	12
<i>Ocypus picipennis</i> (Fabricius, 1793)	2	5
<i>Oligota parva</i> (Kraatz, 1862)	5	0
<i>Oligota pumilio</i> (Kiesenwetter, 1858)	2	0
<i>Oligota pusillima</i> (Gravenhorst, 1806)	1	0
<i>Omalius rivulare</i> (Paykull, 1879)	1	0
<i>Ontholestes murinus</i> (Linnaeus, 1758)	120	1
<i>Ontholestes tessellatus</i> (Geoffroy, 1785)	2	0
<i>Oxypoda haemorrhoea</i> (Mannerheim, 1830)	1	3
<i>Oxypoda opaca</i> (Gravenhorst, 1802)	8	0

Species	Carcass no. 8	Carcass no. 9
<i>Oxytelus piceus</i> (Linnaeus, 1767)	1	0
<i>Philonthus albipes</i> (Gravenhorst, 1802)	3	1
<i>Philonthus carbonarius</i> (Gravenhorst, 1802)	5	0
<i>Philonthus concinnus</i> (Gravenhorst, 1802)	27	0
<i>Philonthus cruentatus</i> (Gmelin, 1790)	1	0
<i>Philonthus debilis</i> (Gravenhorst, 1802)	1	0
<i>Philonthus discoideus</i> (Gravenhorst, 1802)	1	0
<i>Philonthus intermedius</i> (Lacordaire, 1835)	1	0
<i>Philonthus jurgans</i> (Tottenham, 1937)	1	0
<i>Philonthus lepidus</i> (Gravenhorst, 1802)	2	3
<i>Philonthus longicornis</i> (Stephens, 1832)	1	0
<i>Philonthus marginatus</i> (Müller, 1764)	1	0
<i>Philonthus punctus</i> (Gravenhorst, 1802)	0	1
<i>Philonthus politus</i> (Linnaeus, 1758)	32	0
<i>Philonthus rectangulus</i> (Sharp, 1874)	1	0
<i>Philonthus spinipes</i> (Sharp, 1874)	2	0
<i>Philonthus varians</i> (Paykull, 1879)	8	4
<i>Placusa tachyporoides</i> (Waltl, 1838)	7	0
<i>Platydracus latebricola</i> (Gravenhorst, 1806)	0	1
<i>Platydracus stercorarius</i> (Olivier, 1795)	0	3
<i>Quedius levicollis</i> (Brullé, 1832)	4	1
<i>Quedius molochinus</i> (Gravenhorst, 1806)	1	0
<i>Quedius picipes</i> (Mannerheim, 1830)	1	0
<i>Tachinus lignorum</i> (Linnaeus, 1758)	0	1

3.2 Spatial distribution of Arthropoda

3.2.1 Overview

Table 3.2.1 shows the results of the Mann-Whitney U test and the Kruskal-Wallis test. Geotrupidae, Silphidae, Staphylinidae, Histeridae, Coleoptera-larvae, and Diptera showed significant spatial relations with more than six carcasses. Dermestidae and

Brachycera-larvae showed significant spatial relations with five carcasses. Trogidae and Saltatoria showed significant spatial relations with four carcasses.

In order to compare the results, nine carcasses were divided into four classes according to the weight: small carcasses (around 6 kg), medium sized carcasses (around 12 kg), large carcasses (around 30 kg), and very large carcasses (around 70 kg).

3.2.2 Distribution of arthropods around a small carcass (*Meles meles*)

Table 3.2.1 shows that nine taxa: Silphidae, Dermestidae, Trogidae, Histeridae, Geotrupidae, Coleoptera-larvae, Isopoda, Heteroptera, and Brachycera had significant spatial relations with carcass no. 1. Large number of Saltatoria (1,895 individuals), Auchenorrhyncha (1,180 individuals), and Formicidae (991 individuals) were collected; however, none of them showed significant spatial relation with carcass no. 1.

At carcass no. 1, in total 52 % of the arthropods (7,891 individuals) were collected by the first four traps (Figure 3.2.1). 86 % of Silphidae (505 individuals, Figure 3.2.2), 85 % of Dermestidae (46 individuals, Figure 3.2.3), 89 % of Histeridae (1,054 individuals, Figure 3.2.6), 86 % of Trogidae (6 individuals, Figure 3.2.5), 84 % of Geotrupidae (507 individuals, Figure 3.2.8), 71 % of Coleoptera-larvae (2,146 individuals, Figure 3.2.4), and 58 % of Brachycera (1,069 individuals, Figure 3.2.7) were collected by the first four pitfall traps.

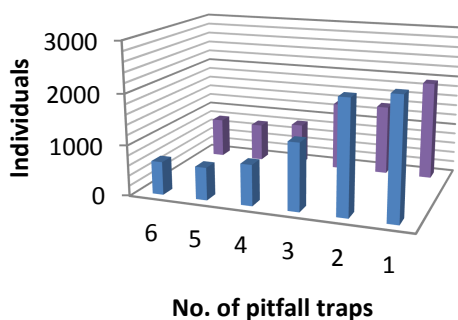


Figure 3.2.1 Distribution of all individuals at carcass no. 1.

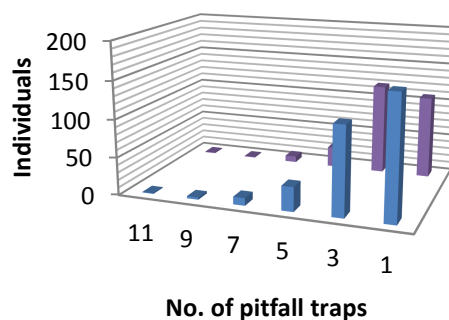


Figure 3.2.2 Distribution of Silphidae at carcass no. 1.

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Table 3.2.1 Overview of the results of the Mann-Whitney U test (MWU) and the Kruskal-Wallis test (KW) of nine carcasses (“p < 0.05” is indicated by grey color, “N” indicates that no individual was collected).

Taxa	Carcass no. 1		Carcass no. 2		Carcass no. 3		Carcass no. 4		Carcass no. 5		Carcass no. 6		Carcass no. 7		Carcass no. 8		Carcass no. 9	
	MWU	KW	MWU	KW	MWU	KW	MWU	KW	MWU	KW	MWU	KW	MWU	KW	MWU	KW	MWU	KW
Silphidae	0.004	0.007	0.004	0.015	0.004	0.005	0.109	0.162	0.016	0.017	0.730	0.031	0.004	0.010	0.004	0.007	0.004	0.015
Dermestidae	0.048	0.114	N	N	0.004	0.005	N	N	N	N	0.109	0.200	0.004	0.024	0.004	0.016	0.004	0.015
Trogidae	0.048	0.055	N	N	0.570	0.368	N	N	N	N	0.570	0.368	0.004	0.018	0.004	0.010	0.004	0.008
Staphylinidae	0.368	0.058	0.008	0.036	0.028	0.049	0.028	0.063	0.154	0.263	0.028	0.070	0.004	0.018	0.004	0.007	0.004	0.012
Cleridae	0.683	0.895	N	N	N	N	N	N	N	N	0.073	0.070	0.073	0.070	0.004	0.013	0.017	0.032
Histeridae	0.016	0.012	0.016	0.012	0.004	0.013	0.048	0.028	0.570	0.368	0.073	0.103	0.004	0.012	0.004	0.007	0.004	0.020
Carabidae	0.368	0.469	0.154	0.341	0.016	0.055	0.283	0.432	0.368	0.584	0.570	0.787	0.154	0.065	0.241	0.292	0.214	0.292
Geotrupidae	0.004	0.015	0.004	0.015	0.004	0.018	0.004	0.014	0.008	0.032	0.004	0.007	0.004	0.023	0.004	0.010	0.004	0.012
Coleoptera-larvae	0.008	0.010	0.028	0.015	0.006	0.020	0.808	0.915	0.808	0.577	0.004	0.009	0.004	0.007	0.004	0.007	0.004	0.018
Brachycera	0.004	0.023	0.283	0.087	0.016	0.053	N	N	N	N	N	N	0.109	0.102	0.808	0.351	0.004	0.025
Nematocera	0.933	0.054	0.808	0.745	0.283	0.431	N	N	N	N	N	N	0.008	0.035	0.048	0.108	N	N
Other Diptera	0.109	0.238	0.570	0.232	0.028	0.073	0.004	0.022	0.016	0.012	0.028	0.048	0.004	0.007	0.004	0.015	1.000	1.000
Brachycera-larvae	0.461	0.445	0.576	0.512	0.016	0.023	0.570	0.368	0.109	0.023	0.570	0.368	0.283	0.387	0.016	0.043	0.048	0.063
Saltatoria	0.109	0.234	0.048	0.027	0.016	0.012	0.368	0.404	0.570	0.368	0.368	0.466	0.214	0.058	0.008	0.031	0.016	0.050
Formicidae	0.368	0.526	0.461	0.097	0.648	0.289	0.073	0.138	N	N	0.028	0.043	0.283	0.542	0.008	0.037	0.933	0.246
Heteroptera	0.004	0.018	0.154	0.256	1.000	0.239	N	N	N	N	0.048	0.085	0.214	0.249	0.368	0.373	0.004	0.022
Auchenorrhyncha	0.368	0.584	1.000	0.143	0.461	0.436	0.461	0.644	0.570	0.577	0.283	0.086	1.000	0.943	0.028	0.085	0.570	0.491
Isopoda	0.004	0.019	0.154	0.034	0.570	0.368	N	N	0.570	0.368	1.000	1.000	1.000	1.000	0.283	0.473	0.214	0.267
Araneae	1.000	0.734	0.570	0.393	0.154	0.215	0.570	0.733	0.154	0.302	0.680	0.696	0.368	0.298	0.028	0.038	0.368	0.513

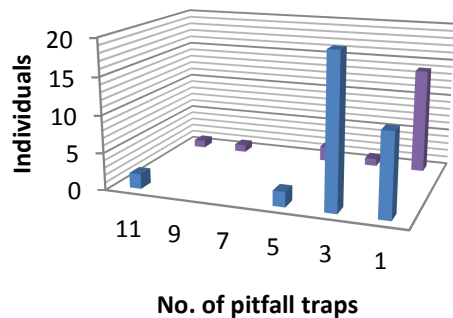


Figure 3.2.3 Distribution of Dermestidae at carcass no. 1.

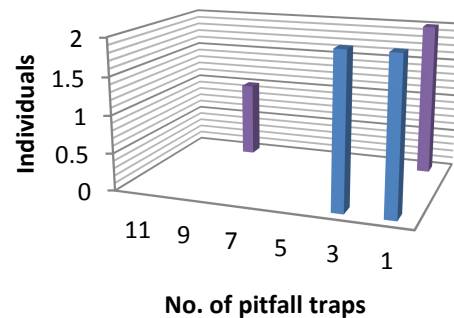


Figure 3.2.4 Distribution of Coleoptera-larvae at carcass no. 1.

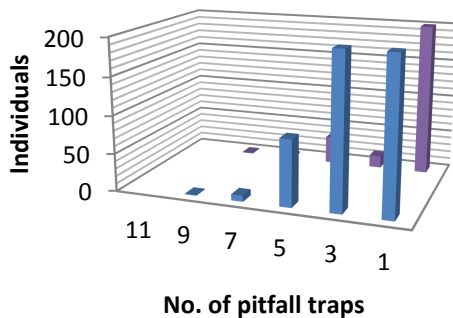


Figure 3.2.5 Distribution of Trogidae at carcass no. 1.

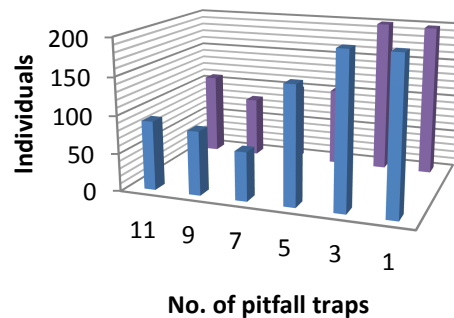


Figure 3.2.6 Distribution of Histeridae at carcass no. 1.

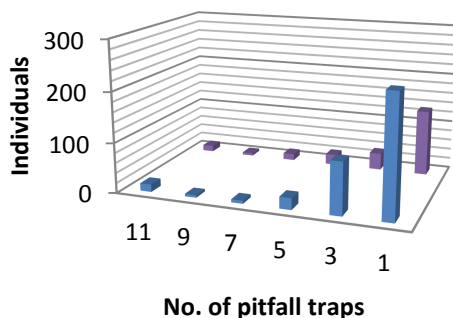


Figure 3.2.7 Distribution of Brachycera at carcass no. 1.

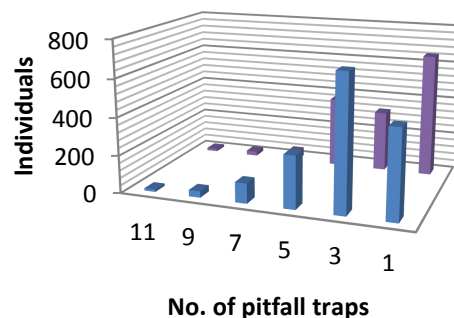


Figure 3.2.8 Distribution of Geotrupidae at carcass no. 1.

3.2.3 Distribution of arthropods around medium sized carcasses (*Capreolus capreolus*)

Six medium sized carcasses were investigated: carcass no. 2, no. 3, no. 4, no. 5, no. 6, and no. 7. Arthropods at carcass no. 4 and no. 5 were mainly collected by the first four pitfall traps: 70 % of arthropods at carcass no. 4 (1,247 individuals, Figure 3.2.11), and 69 % of arthropods at carcass no. 5 (2,603 individuals, Figure 3.2.12). However, around other medium sized carcasses, arthropods collected by the first four traps were less than 60 %. In total, 55 % of arthropods at carcass no. 2 (2,737 individuals, Figure 3.2.9), 58 % of arthropods at carcass no. 3 (2,748 individuals, Figure 3.2.10), 56 % of arthropods at carcass no. 6 (2,799 individuals, Figure 3.2.13), and 51 % of arthropods at carcass no. 7 (11, 568 individuals, Figure 3.2.14) were collected by the first four traps.

Table 3.2.2 shows the percentages and the number of the individuals of nine taxa which were collected by the first four pitfall traps. More than 80 % of Silphidae, Histeridae, and Brachycera-larvae were collected by the first four traps. 78 % of Geotrupidae, around 60 % of Staphylinidae and Diptera were collected by the first four traps.

Table 3.2.2 Percentage and number of individuals of nine taxa distributed in the first four pitfall traps at medium sized carcass (Silp: Silphidae, Hist: Histeridae, Stap: Staphylinidae, Geot: Geotrupidae, Dipt: Diptera, C-lar: Coleoptera-larvae, B-lar: Brachycera-larvae).

	Carcass no. 2		Carcass no. 3		Carcass no. 4		Carcass no. 5		Carcass no. 6		Carcass no. 7		Median
Hist	100 %	564	94 %	131	100 %	49	100 %	1	56 %	10	84 %	70	97 %
Silp	94 %	200	100 %	22	88 %	35	80 %	4	66 %	1,339	78 %	1,654	84 %
B-lar	18 %	3	91 %	70	100 %	11	72 %	1,085	100 %	1	44 %	9	82 %
Geot	83 %	354	78 %	166	77 %	298	57 %	53	81 %	208	62 %	313	78 %
C-lar	83 %	429	73 %	30	60 %	3	50 %	1	82 %	658	84 %	1,170	78 %
Dipt	46 %	179	72 %	118	84 %	410	73 %	1,368	42 %	64	53 %	437	63 %
Stap	65 %	108	56 %	153	76 %	138	49 %	41	57 %	34	60 %	226	59 %

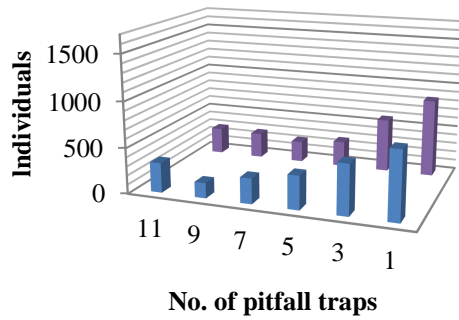


Figure 3.2.9 Distribution of all individuals at carcass no. 2.

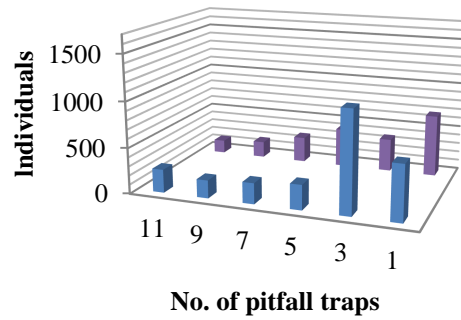


Figure 3.2.10 Distribution of all individuals at carcass no. 3.

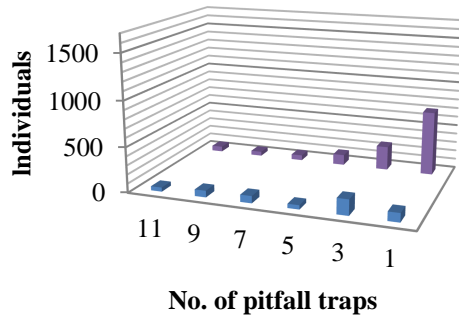


Figure 3.2.11 Distribution of all individuals at carcass no. 4.

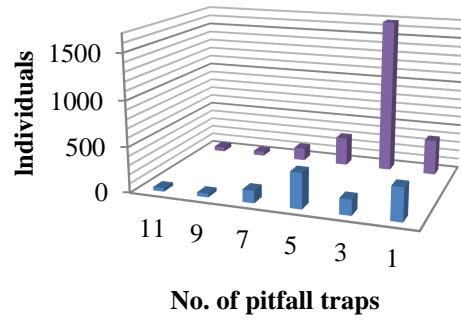


Figure 3.2.12 Distribution of all individuals at carcass no. 5.

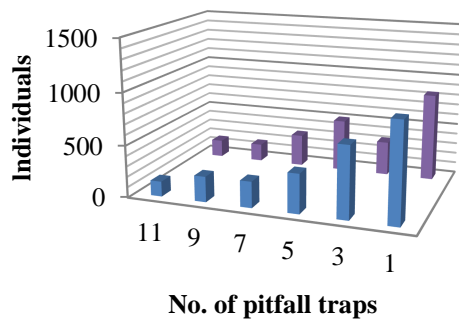


Figure 3.2.13 Distribution of all individuals at carcass no. 6.

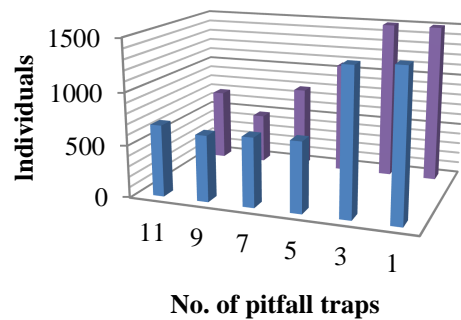


Figure 3.2.14 Distribution of all individuals at carcass no. 7.

3.2.4 Distribution of arthropods around a large carcass (*Sus scrofa*) and a very large carcass (*Cervus elaphus*)

At carcass no. 8, in total 81 % of arthropods were collected by the first four pitfall traps (Figure 3.2.15), and at carcass no. 9 the number was 60 % (Figure 3.2.16). Table 3.2.1 shows that 15 taxa had significant spatial relations with carcass no. 8 (Silphidae, Dermestidae, Trogidae, Staphylinidae, Cleridae, Histeridae, Geotrupidae, Coleoptera-larvae, Diptera, Brachycera-larvae, Saltatoria, Formicidae, Auchenorrhyncha, and Araneae), and 12 taxa had significant spatial relations with carcass no. 9 (Silphidae, Dermestidae, Trogidae, Staphylinidae, Cleridae, Histeridae, Geotrupidae, Coleoptera-larvae, Brachycera, Brachycera-larvae, Saltatoria, and Heteroptera).

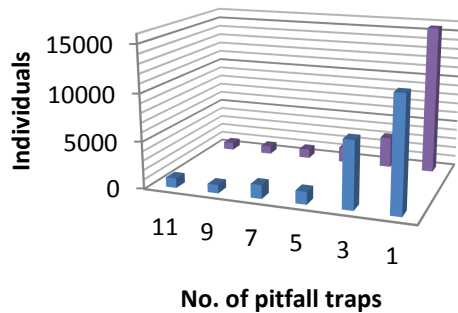


Figure 3.2.15 Distribution of all individuals at carcass no. 8.

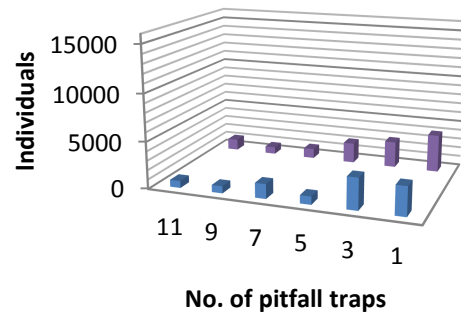


Figure 3.2.16 Distribution of all individuals at carcass no. 9.

Table 3.2.3 shows that more than 80 % of Silphidae, Dermestidae, Trogidae, Histeridae, and Coleoptera-larvae were distributed in the first four pitfall traps at both carcass no. 8 and no. 9. At carcass no. 8, 99 % of Brachycera-larvae were collected by the first four pitfall traps (660 individuals, Figure 3.2.17); however, at carcass no. 9, the percentage was only 49 % (2,079 individuals, Figure 3.2.18). At carcass no. 9, in total 1,068 Brachycera-larvae were collected by pitfall trap no. 5.

Table 3.2.3 Percentage and number of individuals of nine taxa distributed in the first four pitfall traps at carcass no. 8 and no. 9.

Taxa	Carcass no. 8		Carcass no. 9	
Brachycera-larvae	99 %	660	49 %	2,079
Cleridae	97 %	318	88 %	7
Coleoptera-larvae	91 %	7,358	81 %	978
Diptera	79 %	5,355	64 %	437
Dermestidae	98 %	3,154	94 %	978
Histeridae	99 %	9,442	92 %	1,799
Geotrupidae	92 %	1,605	73 %	403
Silphidae	82 %	3,731	94 %	1,342
Staphylinidae	89 %	2,638	64 %	982
Trogidae	97 %	207	95 %	57

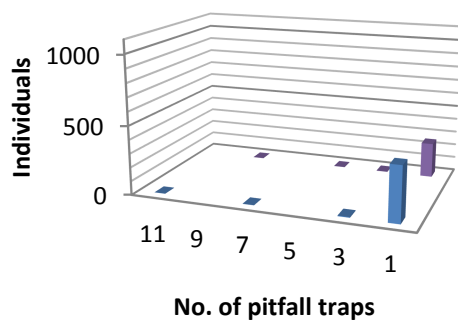


Figure 3.2.17 Distribution of Brachycera-larvae at carcass no. 8.

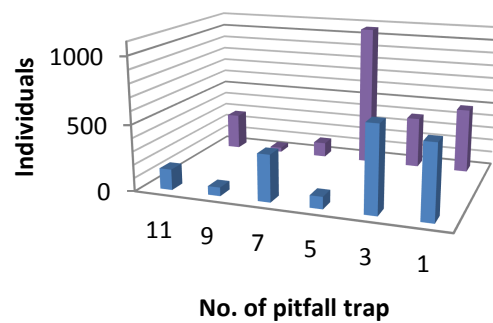


Figure 3.2.18 Distribution of Brachycera-larvae at carcass no. 9.

Table 3.2.1 shows that Saltatoria and Auchenorrhyncha had significant spatial relations with carcass no. 8, however, according to Figure 3.2.19 and Figure 3.2.20 these two taxa had no positive significant relations with carcass no. 8. Araneae (Figure 3.2.21) and Formicidae (Figure 3.2.22) had significant spatial relations with carcass no. 8. Saltatoria (Figure 3.2.23) and Heteroptera (Figure 3.3.24) had significant spatial relations with carcass no. 9.

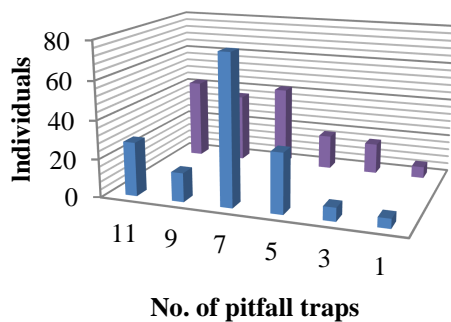


Figure 3.2.19 Distribution of *Saltatoria* at carcass no. 8.

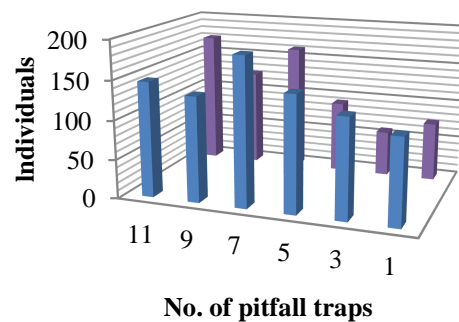


Figure 3.2.20 Distribution of *Auchenorrhyncha* at carcass no. 8.

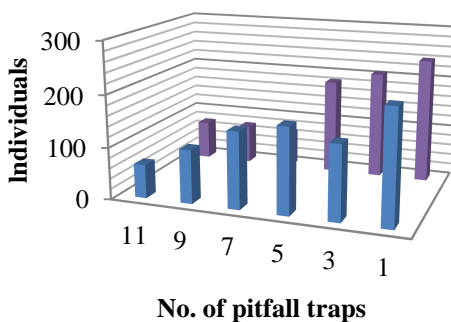


Figure 3.2.21 Distribution of *Araneae* at carcass no. 8.

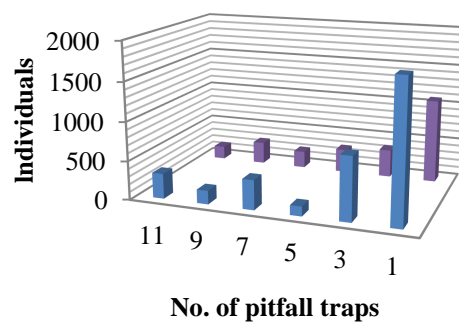


Figure 3.2.22 Distribution of *Formicidae* at carcass no. 8.

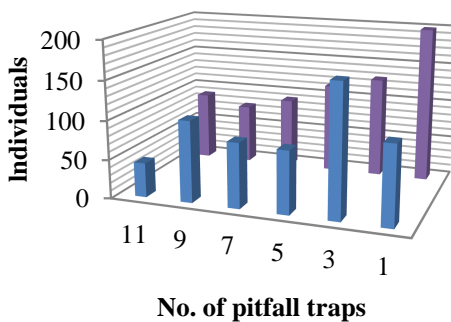


Figure 3.2.23 Distribution of *Saltatoria* at carcass no. 9.

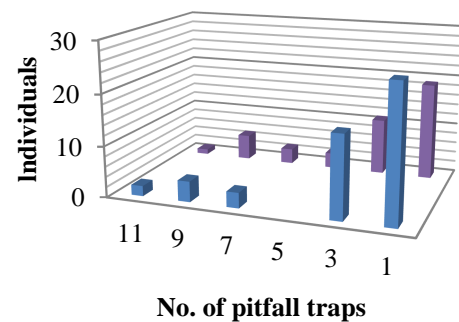


Figure 3.2.24 Distribution of *Heteroptera* at carcass no. 9.

3.2.5 Distribution of arthropods in species level at carcass no. 8 and no. 9

Thanatophilus rugosus, *Thanatophilus sinuatus*, *Necrodes littoralis*, *Trox cadaverinus*, and *Trox hispidius* showed significant relations with carcass no. 8 and carcass no. 9. *Lyctocoris campestris* showed significant relation with carcass no. 8. *Alydus calcaratus* showed significant relation with carcass no. 9 (Table 3.2.4).

Table 3.2.4 Overview of the results of the Mann-Whitney U test (MWU) and the Kruskal-Wallis test (KW) in species level at carcass no. 8 and no. 9, ($p < 0.05$ is indicated by grey color, and “N” indicates that this species was not found).

Family	Species	Carcass no. 8		Carcass no. 9	
		MWU	KW	MMU	KW
Silphidae	<i>Thanatophilus rugosus</i>	0.004	0.007	0.004	0.009
	<i>Thanatophilus sinuatus</i>	0.004	0.010	0.004	0.011
	<i>Necrodes littoralis</i>	0.004	0.012	0.008	0.012
Geotrupidae	<i>Trypocopris vernalis</i>	0.004	0.023	0.004	0.019
	<i>Anoplotrupes stercuosus</i>	0.004	0.022	0.004	0.020
Trogidae	<i>Trox cadaverinus</i>	0.048	0.106	0.004	0.010
	<i>Trox hispidius</i>	0.008	0.015	0.004	0.009
Heteroptera	<i>Alydus calcaratus</i>	N	N	0.004	0.010
	<i>Lyctocoris campestris</i>	0.048	0.100	N	N

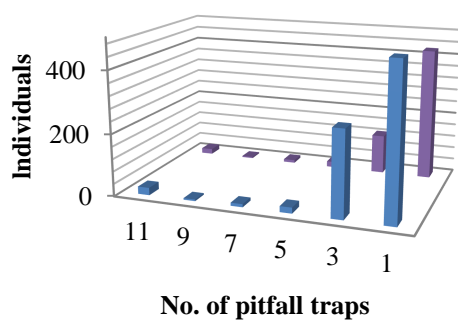


Figure 3.2.25 Distribution of *Trypocopris vernalis* (Geotrupidae) at carcass no. 8.

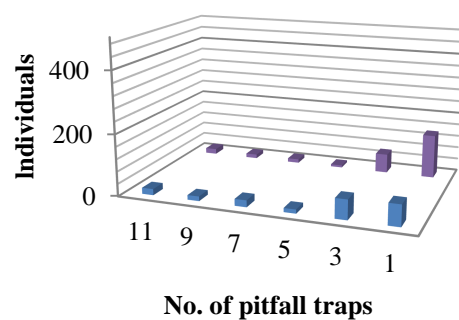


Figure 3.2.26 Distribution of *Trypocopris vernalis* (Geotrupidae) at carcass no. 9.

Table 3.2.5 shows that 93 % of *Trypocopris vernalis* were collected by the first four pitfall traps at carcass no. 8 (Figure 3.2.25), and at carcass no. 9 the percentage was 74 % (Figure 3.2.26).

Table 3.2.5 Percentage and number of individuals distributed in the first four pitfall traps at carcass no. 8 and no. 9.

Species	Carcass no. 8		Carcass no. 9	
<i>Thanatophilus rugosus</i>	84 %	320	95 %	253
<i>Thanatophilus sinuatus</i>	82 %	1,966	90 %	659
<i>Necrodes littoralis</i>	77 %	643	76 %	13
<i>Trypocopris vernalis</i>	93 %	1,416	74 %	337
<i>Anoplotrupes stercurosus</i>	92 %	111	81 %	17
<i>Trox cadaverinus</i>	89 %	142	92 %	24
<i>Trox hispidius</i>	90 %	18	97 %	28

As to the identified Staphylinidae individuals, following species showed significant spatial relations with carcass no. 8: *Acrotona aterrima*, *Aleochara bipustulata*, *Aleochara intricata*, *Anotylus hamatus*, *Atheta pseudoelongatula*, *Creophilus maxillosus*, *Nehemitropia lividipennis*, *Oligota parva*, *Ontholestes murinus*, *Oxypoda opaca*, *Philonthus concinnus*, and *Philonthus politus*. Only *Creophilus maxillosus* showed significant spatial relation with carcass no. 9.

3.3 Temporal distribution and succession of carcass-related arthropods

3.3.1 Temporal distribution of carcass-related arthropods in 2009

Figure 3.3.1 shows that at carcass no. 1 the number of arthropods first reached a small peak on the 6th exposure day (26.06.2009) with 1,479 individuals, the abundant taxa on this day included Silphidae (176 individuals), Histeridae (276 individuals), and Diptera (733 individuals). On the 13th exposure day (03.07.2009) the number of arthropods

reached the highest point, in total 3,353 individuals were collected, and the most abundant group on this day was Coleoptera-larvae (2,017 individuals). After the 17th exposure day (07.07.2009), the number of arthropods decreased sharply.

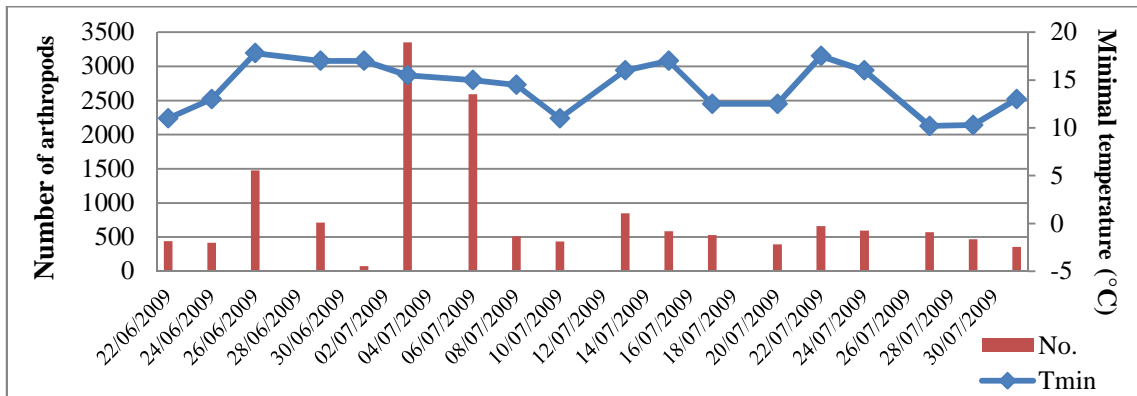


Figure 3.3.1 Distribution of arthropods at carcass no. 1.

Figure 3.3.2 shows that at carcass no. 1 there were two significant assemblage changes of arthropods: the first one was from 26.06.2009 to 07.07.2009, the turnover index increased from 0.22 to 0.63, and the second one was from 03.07.2009 to 06.07.2009, the turnover index decreased from 0.53 to 0.16. The diversity of arthropod taxa reached the highest value on 24.06.2009 ($H' = 2.50$). The lowest diversity occurred on 03.07.2009 ($H' = 1.44$), on the same day, the number of arthropods reached the highest peak. Another low diversity value occurred on 26.06.2009 ($H' = 1.71$).

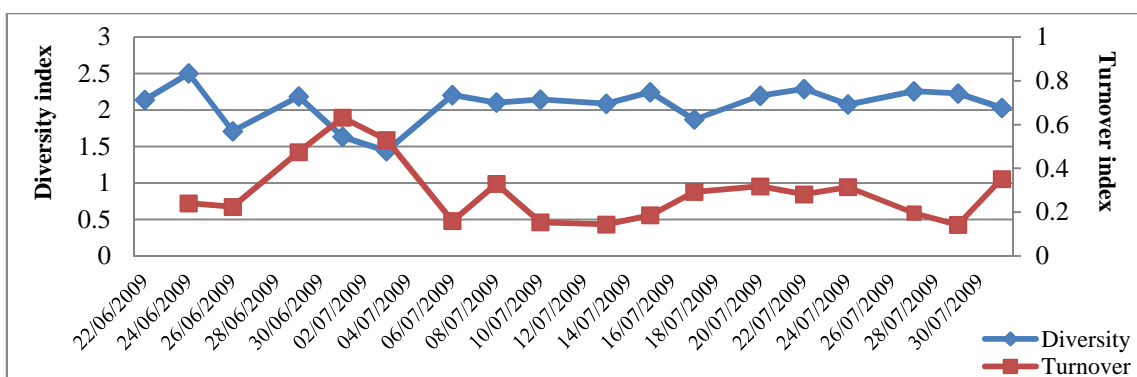


Figure 3.3.2 Diversity index and turnover index of arthropods at carcass no. 1.

Figure 3.3.3 shows that the number of arthropods reached the unique peak on the 8th exposure day (29.07.2009) with 1,032 individuals. The most abundant taxa on this day included: Silphidae (111 individuals), Histeridae (474 individuals), Carabidae (122 individuals), and Geotrupidae (136 individuals). At carcass no. 2, the data were missing from 31.07.2009 to 05.08.2009; therefore, there is a bias in Figure 3.3.3 and Figure 3.3.4

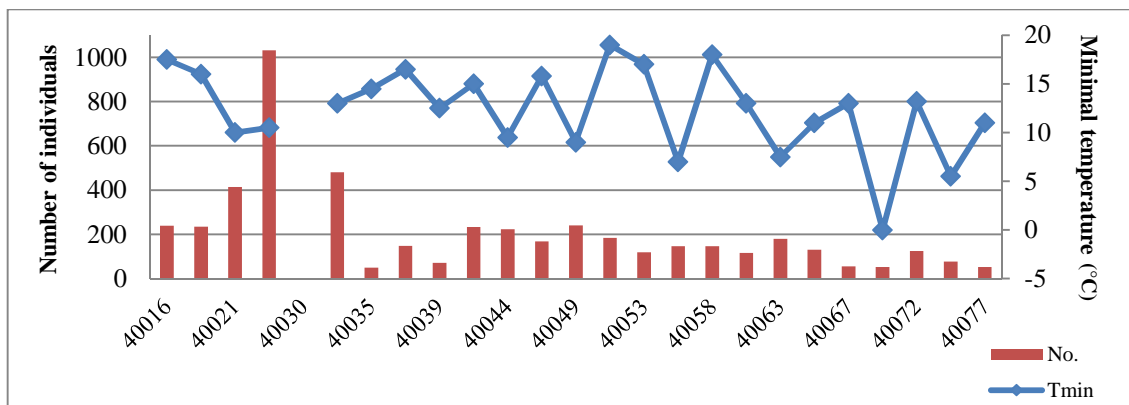


Figure 3.3.3 Distribution of arthropods at carcass no. 2 (data between 31.07.2009 and 05.08.2009 were missing).

Figure 3.3.4 shows that at carcass no. 2 a remarkable change of the arthropods assemblage occurred between 29.07.2009 and 10.08.2009, the Tokeshi turnover index increased from 0.17 to 0.47. Two highest diversity values occurred on 27.07.2009 ($H' = 2.41$) and 19.08.2009 ($H' = 2.33$). The lowest value of diversity occurred on 10.08.2009 ($H' = 1.57$).

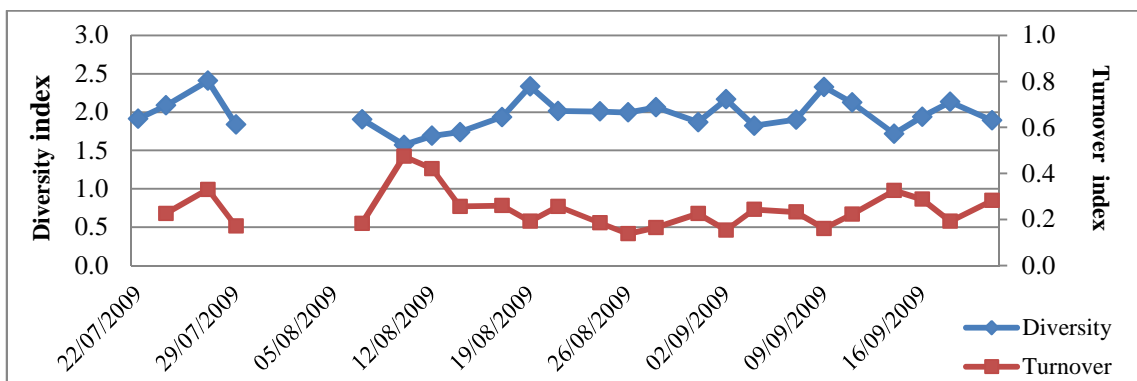


Figure 3.3.4 Diversity index and turnover index of arthropods at carcass no. 2 (data between 31.07.2009 and 05.08.2009 were missing).

Figure 3.3.5 shows that at carcass no. 3, the number of arthropods reached the highest peak on the 5th exposing day (10.08.2009) with 498 individuals. The most abundant group on this day was Histeridae (183 individuals). On 26.08.2009 (the 21st exposure day) a smaller peak with 334 individuals occurred. On 18.09.2009 (the 44th exposure day) the last peak with 310 individuals occurred. At carcass no. 3, the data of 14.09.2009 were missing; therefore, there is a gap in Figure 3.3.5 and Figure 3.3.6.

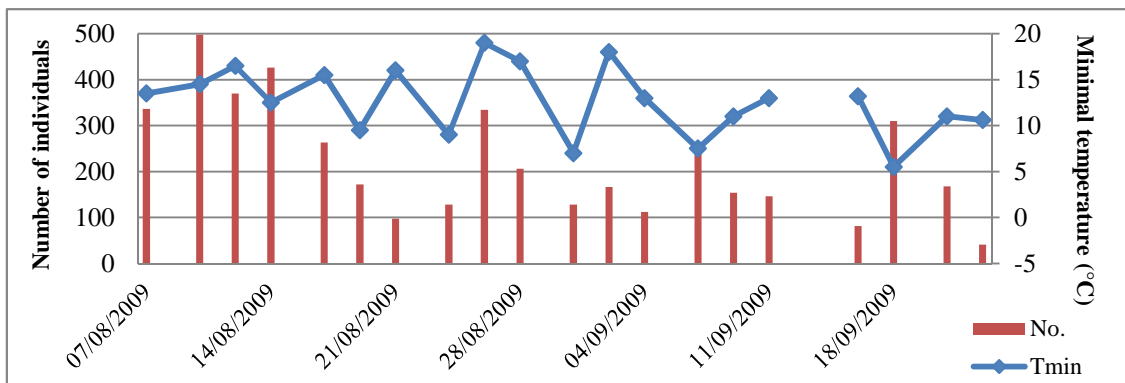


Figure 3.3.5 Distribution of arthropods at carcass no. 3 (data of 14.09.2009 were missing).

Figure 3.3.6 shows that at carcass no. 3, a conspicuous change of arthropod assemblage occurred between 18.09.2009 and 21.09.2009, the Tokeshi turnover index decreased from 0.44 to 0.19. The diversity index was the lowest on 12.08.2009 ($H' = 1.60$). The diversity index kept in a high level between 14.08.2009 and 24.08.2009 ($H' > 2$).

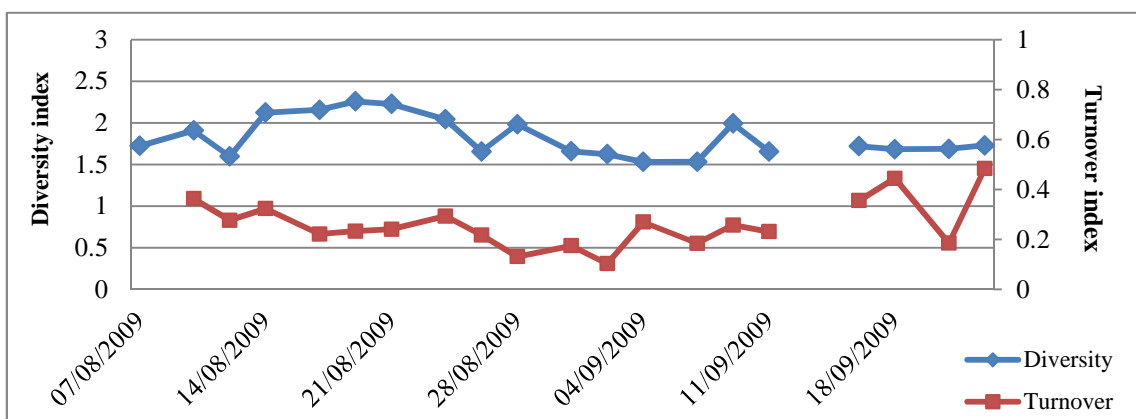


Figure 3.3.6 Diversity index and turnover index of arthropods at carcass no. 3 (data for 14.09.2009 were missing).

Figure 3.3.7 shows the temporal distribution of Silphidae in the summer of 2009 at carcass no. 1, no. 2 and no. 3. At the three carcasses, Silphidae occurred as soon as the carcasses were exposed. At all three carcasses, the number of Silphidae reached the peak between the 5th and 8th exposure days, and a small peak occurred between the 13th and the 17th exposure days. At carcass no. 1, the number of Silphidae reached the highest peak on the 6th exposure day with 176 individuals, the second peak occurred on the 13th exposure day with 120 individuals. At carcass no. 2, the number of Silphidae first showed a small peak on the 6th exposure day with 71 individuals, followed by a bigger one on the 8th exposure day with 111 individuals. At carcass no. 3, the number of Silphidae reached the peak on the 5th exposure day (10.08.2009) with 60 individuals.

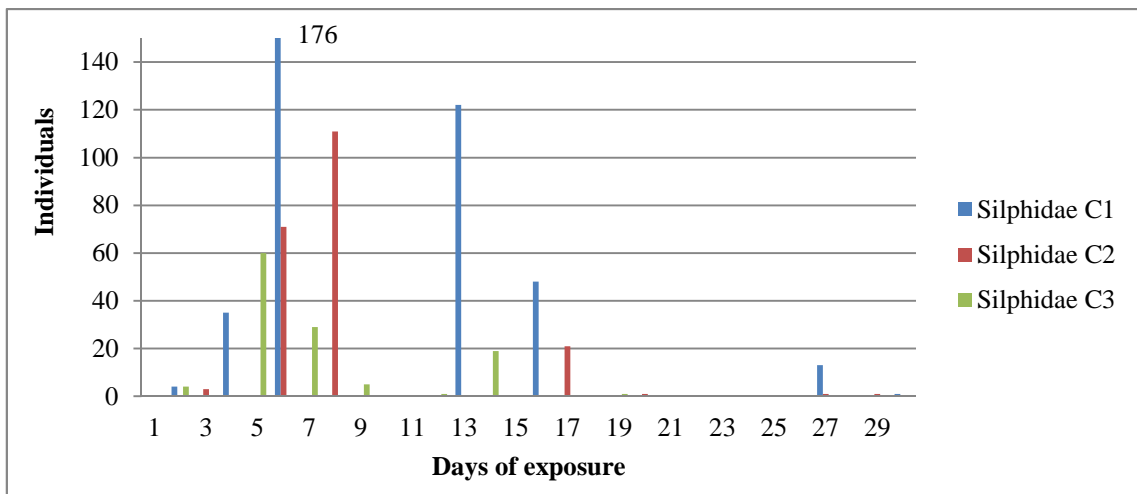


Figure 3.3.7 Distribution of Silphidae at carcass no. 1, no. 2, and no. 3 in 2009.

Figure 3.3.8 shows the temporal distribution of Histeridae in the summer of 2009. At carcass no. 1, Histeridae occurred as soon as the carcass was exposed. At carcass no. 2, Histeridae first occurred on the 6th exposure day. At carcass no. 3, Histeridae first occurred on the 5th exposure day. The number of Histeridae at carcass no.1 showed one conspicuous peak on the 13th exposure day with 637 individuals. At carcass no. 2 the number of Histeridae showed one unique peak on the 8th exposure day with 474 individuals. At carcass no. 3, the number of Histeridae showed two conspicuous peaks, the first one was on the 5th exposure day with 183 individuals, and the second one was on the 7th exposure day with 188 individuals.

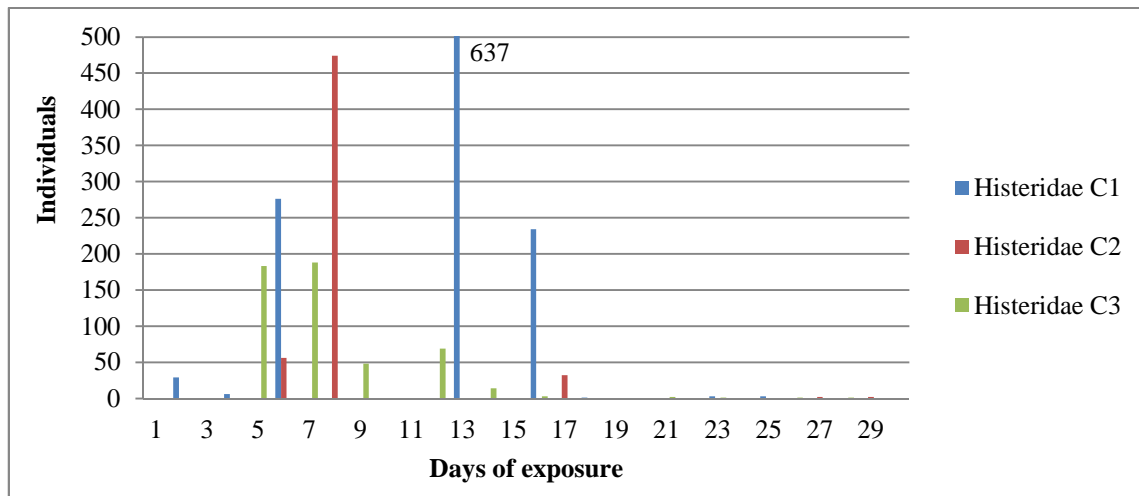


Figure 3.3.8 Distributions of Histeridae at carcass no. 1, no. 2, and no. 3 in 2009.

Figure 3.3.9 shows the temporal distribution of Staphylinidae in the summer of 2009 at carcass no. 1, no. 2, and no. 3. Staphylinidae occurred as soon as the three carcasses were exposed. At carcass no. 1, the number of Staphylinidae kept increasing since the 2nd exposure day, and reached the unique peak on the 16th exposure day (06.07.2009) with 253 individuals. At carcass no. 2, the highest peak was on the 57th exposure day with 42 individuals. At carcass no. 3, the number of Staphylinidae showed four similar peaks, the first peak occurred on the 14th exposure day with 28 individuals, the second peak occurred on the 23rd exposure day with 30 individuals; the third peak was on 33rd exposure day with 36 individuals, and the fourth peak was on the 44th exposure day with 32 individuals.

Figure 3.3.10 shows the temporal distribution of Geotrupidae at carcass no. 1, no. 2 and no. 3 in the summer of 2009. At carcass no. 1, Geotrupidae were first collected on the 4th exposure day. The number of Geotrupidae reached the highest peak on the 16th exposure day with 152 individuals. At carcass no. 2, Geotrupidae were first collected on the 2nd exposure day. The number of Geotrupidae reached the peak on the 8th exposure day with 136 individuals. After that the number decreased sharply. At carcass no. 3, the number of Geotrupidae fluctuated, no apparent peaks occurred.

Figure 3.3.11 shows the temporal distribution of Diptera at carcass no. 1, no. 2 and no. 3 in the summer of 2009. Diptera occurred at as soon as the carcasses were exposed. At carcass no. 1, the number of Diptera showed a conspicuous peak on the 6th exposure day with 733 individuals, and followed by two small peaks on the 16th exposure day with 259 individuals, and on the 34th exposure day with 236 individuals. At carcass no. 2, the number of Diptera showed two small peaks; the first one was on the 6th exposure day with 36 individuals, the second one was on the 34th exposure day with 58 individuals. At carcass no. 3, the number of Diptera had a unique peak on the 9th exposure day with 123 individuals.

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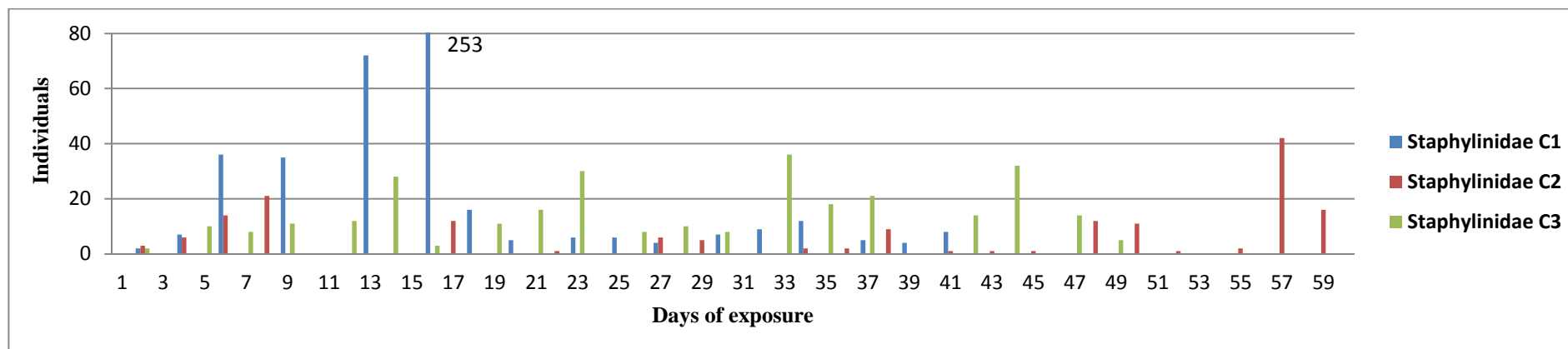


Figure 3.3.9 Distribution of Staphylinidae at carcass no. 1, no. 2, and no. 3 in 2009.

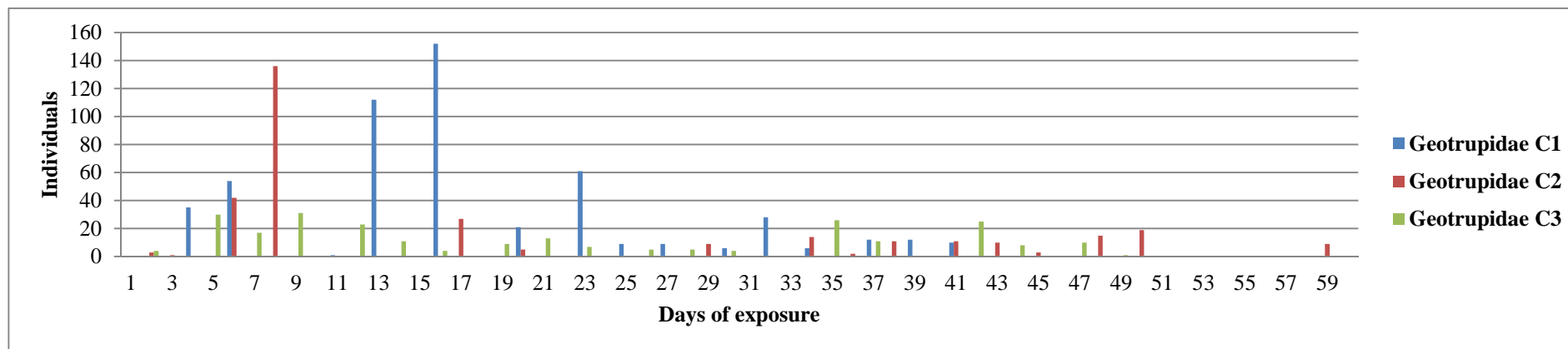


Figure 3.3.10 Distribution of Geotrupidae at carcass no. 1, no. 2, and no. 3 in 2009.

Animal biodiversity and food web restoration based on large vertebrate carcasses

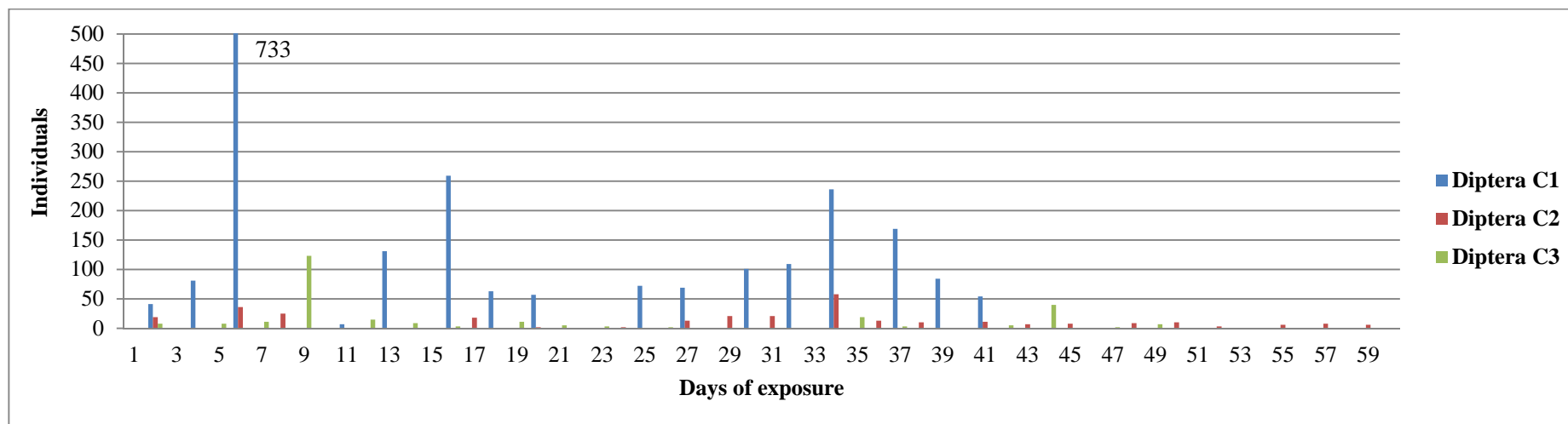


Figure 3.3.11 Distributions of Diptera at carcass no. 1, no. 2, and no. 3 in 2009.

3.3.2 Temporal distribution of carcass-related arthropods in 2010

At carcass no. 4, the peak of arthropods occurred on the 10th exposure day (13.09.2010) with 508 individual (Figure 3.3.12). The abundant taxa on this day included Geotrupidae (132 individuals), Diptera (132 individuals), Staphylinidae (60 individuals), Carabidae (32 individuals), Histeridae (31 individuals), and Silphidae (26 individuals).

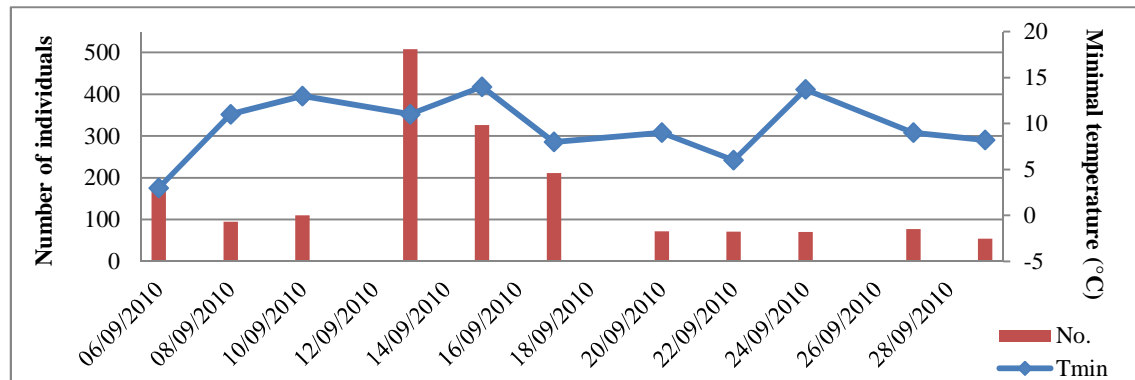


Figure 3.3.12 Distribution of arthropods at carcass no. 4.

Figure 3.3.13 shows that at carcass no. 4, a conspicuous change of arthropod assemblage occurred between 10.09.2010 and 13.09.2010, the Tokeshi turnover index increased from 0.13 to 0.29. The diversity index had no apparent change between the first exposure day ($H' = 0.86$) and the last exposure day ($H' = 0.85$). On 15.09.2010, the diversity index was the lowest ($H' = 0.52$).

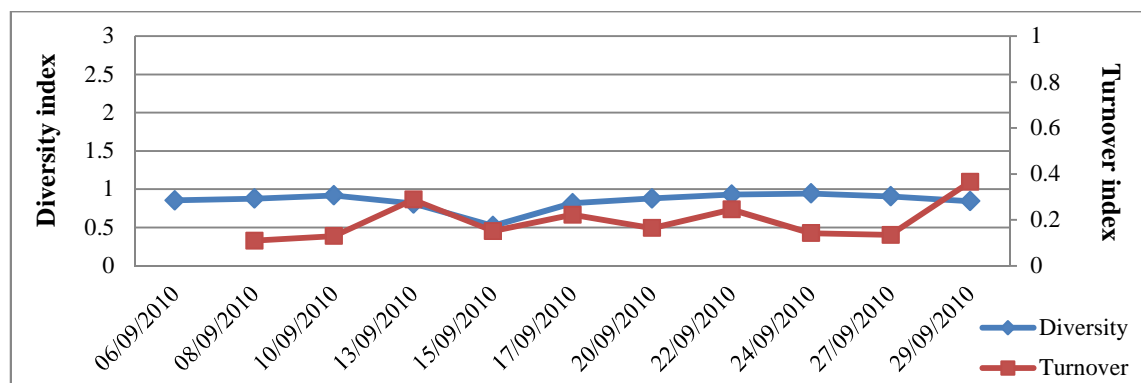


Figure 3.3.13 Diversity index and turnover index of arthropods at carcass no. 4.

Figure 3.3.14 shows that the number of arthropods at carcass no. 5 was very low until the 18th exposure day (26.09.2010), a huge amount of maggots leaked out from the anus of carcass no. 5. The number of arthropods reached the unique peak on 27.09.2010 with 3,089 individuals. The abundant taxa on this day included Diptera (1,585 individuals) and Brachycera-larvae (1,455 individuals).

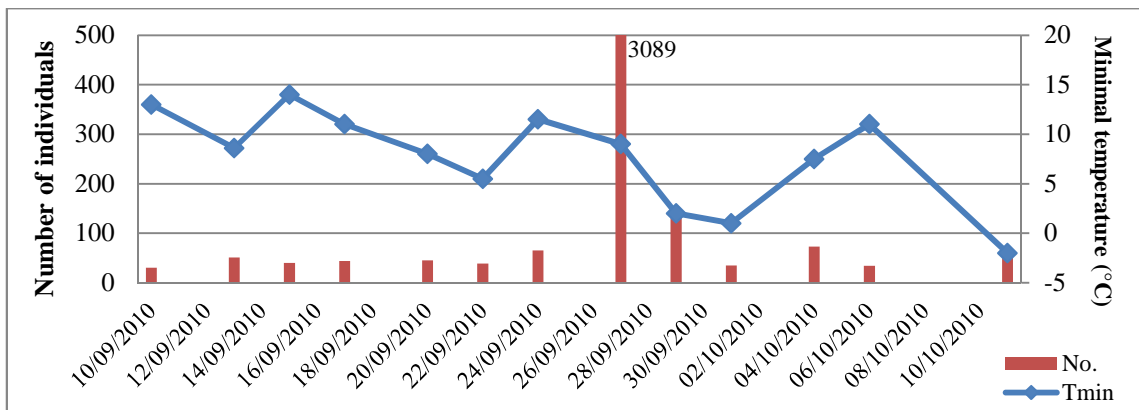


Figure 3.3.14 Distribution of arthropods at carcass no. 5.

Figure 3.3.15 shows that at carcass no. 5, the lowest diversity index occurred on 27.09.2010 ($H' = 0.79$), and the highest diversity index occurred on 06.10.2010 ($H' = 2.03$). The biggest change of arthropod assemblage occurred between 06.10.2010 and 11.10.2010, the turnover index decreased from 0.34 to 0.15.

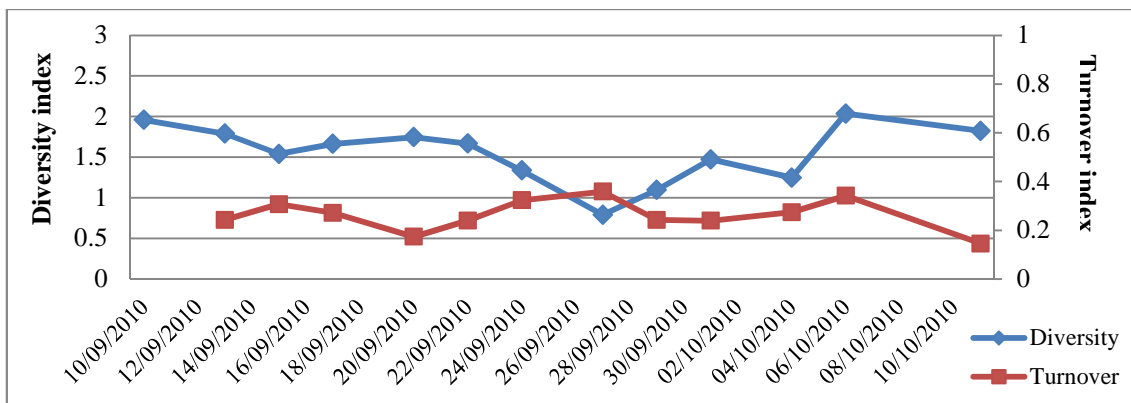


Figure 3.3.15 Diversity index and turnover index of arthropods at carcass no. 5.

Figure 3.3.16 shows the distribution of Silphidae in the autumn of 2010. At carcass no. 4, Silphidae were first collected on the 5th exposure day (08.09.2010), and the number of individuals reached the highest peak on the 10th exposure day with 26 individuals. At carcass no. 5, Silphidae were first collected on the 16th exposure day (24.09.2010), and in total only five Silphidae individuals were collected.

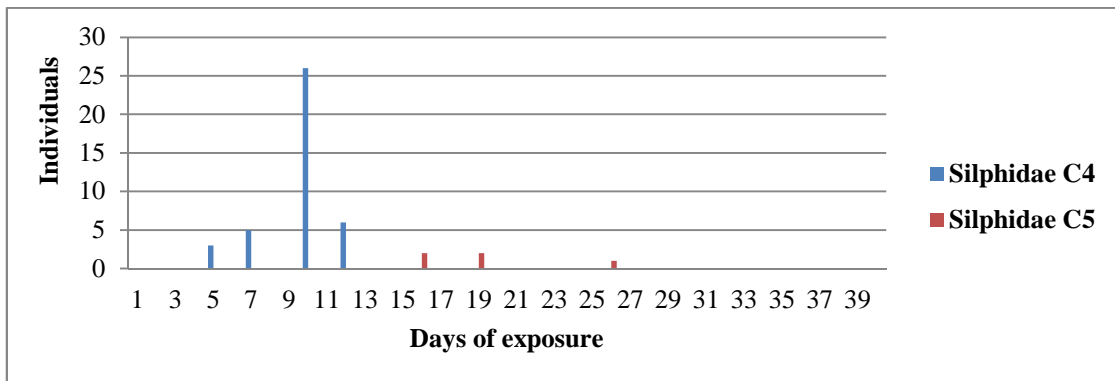


Figure 3.3.16 Distribution of Silphidae at carcass no. 4 and no. 5 in 2010.

Figure 3.3.17 shows the distribution of Histeridae in the autumn of 2010. At carcass no. 4, Histeridae were first collected on the 10th exposure day with 31 individuals, after that the number of individuals decreased. No Histeridae were collected after the 19th exposure day. At carcass no. 5, only one Histeridae was collected on the 19th exposure day (27.09.2009).

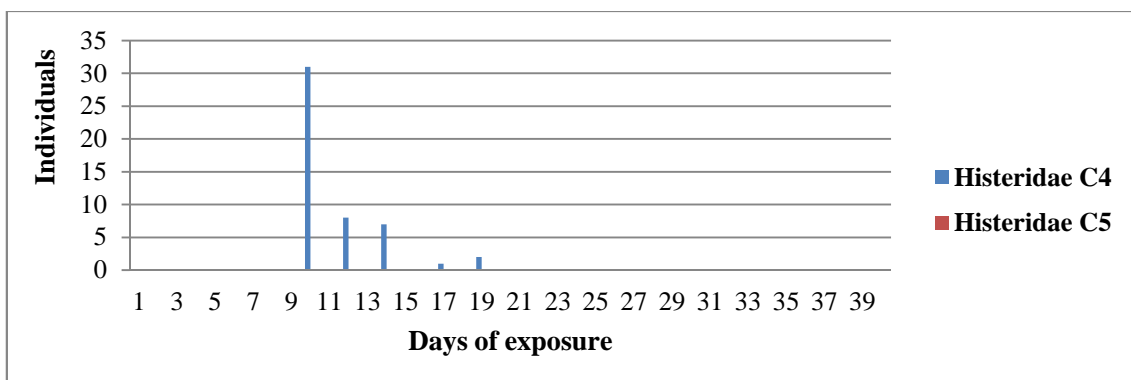


Figure 3.3.17 Distribution of Histeridae at carcass no. 4 in 2010, no Histeridae were collected at carcass no. 5.

Figure 3.3.18 shows the distribution of Staphylinidae in the autumn of 2010. At carcass no. 4, Staphylinidae were first collected on the 3rd exposure day. The number of individuals showed two peaks, the first one was on the 10th exposure day with 51 individuals, and the second one was on the 14th exposure day with 43 individuals. At carcass no. 5, Staphylinidae were first collected on the 2nd exposure day. There was a small peak of on the 19th exposure day with 20 individuals.

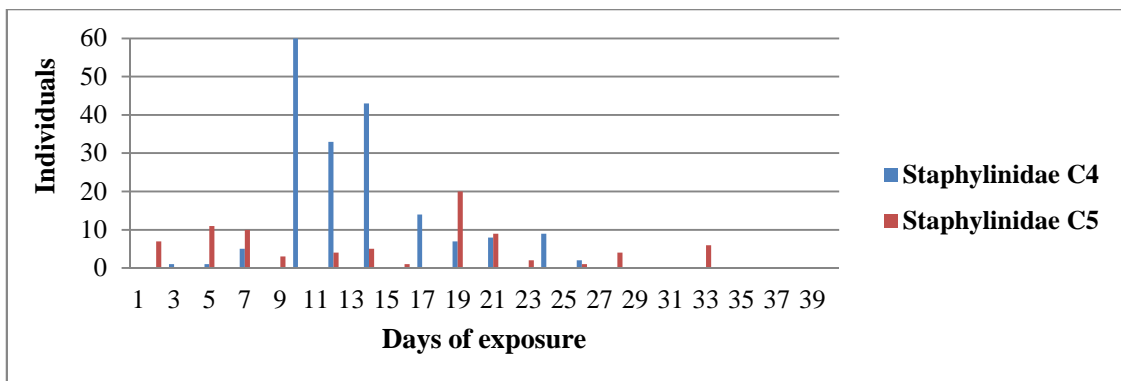


Figure 3.3.18 Distribution of Staphylinidae at carcass no. 4 and no. 5 in 2010.

Figure 3.3.19 shows the temporal distributions of Geotrupidae in the autumn of 2010. At carcass no. 4, Geotrupidae were first collected on the 3rd exposure day, and the number reached a conspicuous peak on the 10th exposure day with 132 individuals. On the 14th exposure day there was a small peak with 51 individuals, after that the number decreased. At carcass no. 5, Geotrupidae were first collected on the 2nd exposure day, and no apparent peak occurred.

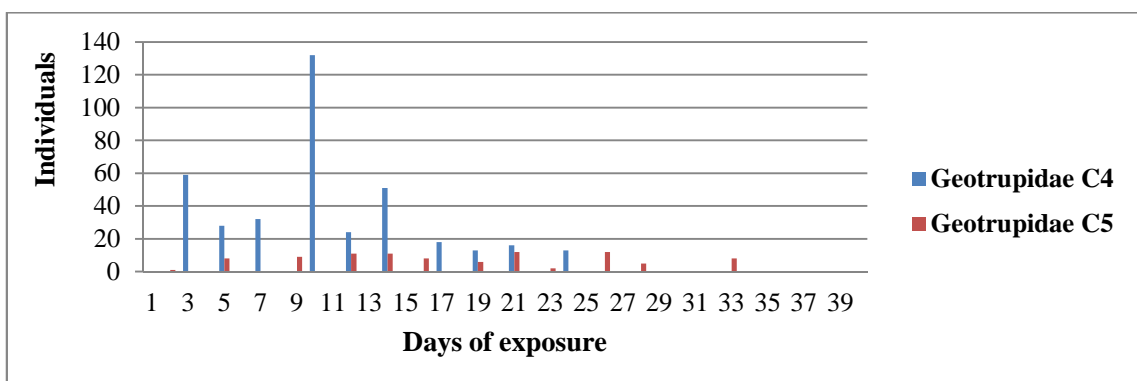


Figure 3.3.19 Distribution of Geotrupidae at carcass no. 4 and no. 5 in 2010.

Figure 3.3.20 shows the distributions of Diptera in the autumn of 2010. At carcass no. 4, Diptera were first collected on the 3rd exposure day, and the number of Diptera reached the highest peak on the 12th exposure day with 221 individuals. No Diptera were collected after the 26th exposure day. At carcass no. 5, Diptera were first collected on the 2nd exposure day. The number of individuals showed a conspicuous peak on the 19th exposure day with 1,585 individuals. After the 34th exposure day, no Diptera were collected.

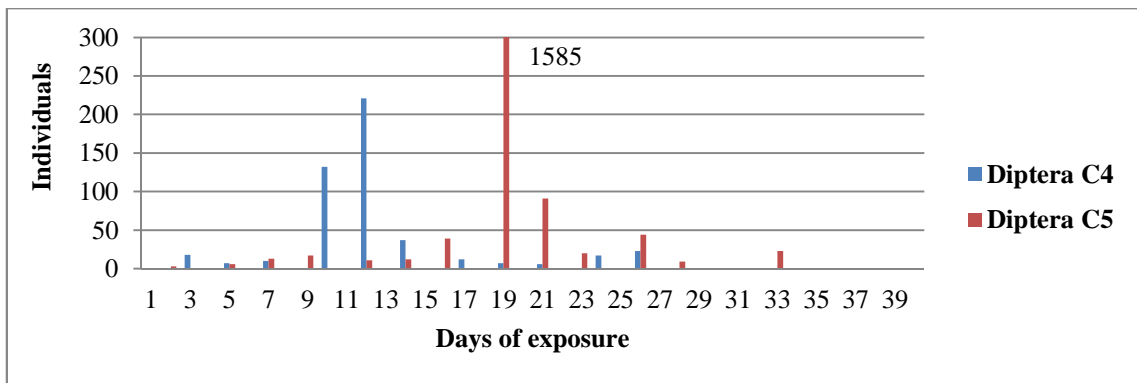


Figure 3.3.20 Distribution of Diptera at carcass no. 4 and no. 5 in 2010.

3.3.3 Temporal distribution of carcass-related arthropods in 2011

At carcass no. 6, the number of arthropods showed a small peak on 18.04.2011 with 266 individuals, and on 20.05.2011 the number reached the highest peak (the 66th exposure day) with 788 individuals (Figure 3.3.21). The abundant taxon on this day was Silphidae (474 individuals).

At carcass no. 6, on 29.04.2011 the diversity index was the highest ($H' = 2.32$), and on 11.07.2011 the diversity index was the lowest ($H' = 0.63$). A conspicuous change of arthropod assemblage occurred between 13.07.2011 and 15.07.2011, the turnover index decreased from 0.69 to 0.22 (Figure 3.3.22). The data from 20.05.2011 to 06.06.2011 were missed; therefore, there were two gaps in Figure 3.3.21 and Figure 3.3.22.

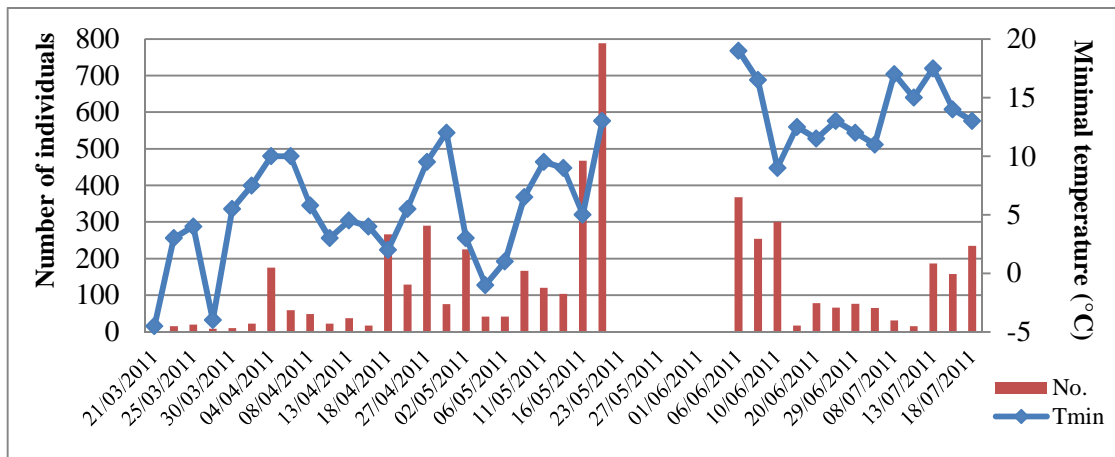


Figure 3.3.21 Distribution of arthropods at carcass no. 6 (data from 20.05.2011 to 06.06.2011 were missing).

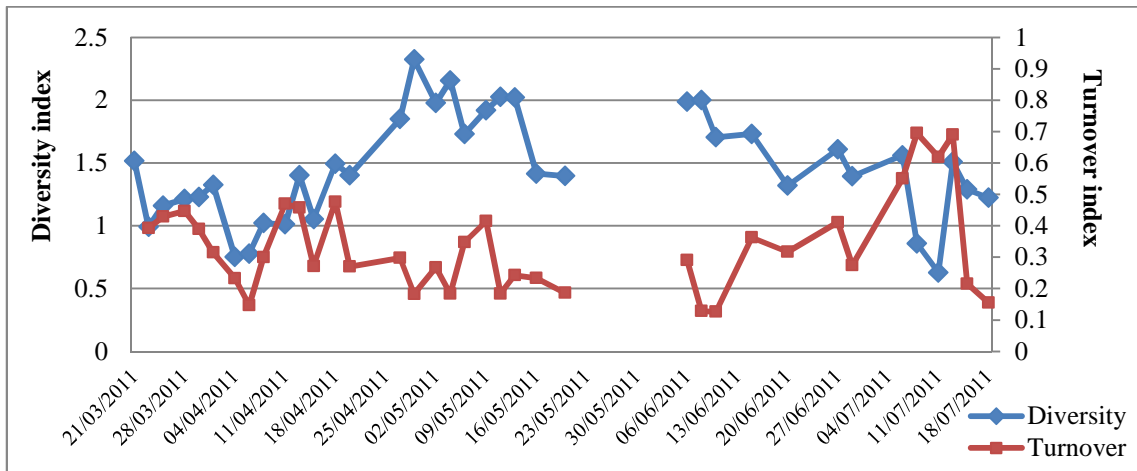


Figure 3.3.22 Diversity index and turnover index of arthropods at carcass no. 6 (data from 20.05.2011 to 06.06.2011 were missing).

Figure 3.3.23 shows that at carcass no. 7, the number of arthropods had two conspicuous peaks, the first one was on the 21st exposure day (on 27.04.2011) with 1,069 individuals, the most abundant taxa on this day included Silphidae (385 individuals) and Formicidae (499 individuals). The second peak occurred on the 47th exposure day (on 23.05.2011) with 1,465 individuals, the most abundant taxa on this day included Silphidae (470 individuals) and Coleoptera-larvae (499 individuals). The temperature was the lowest on 04.05.2011 (- 1 °C), on this day only 41 individuals were collected.

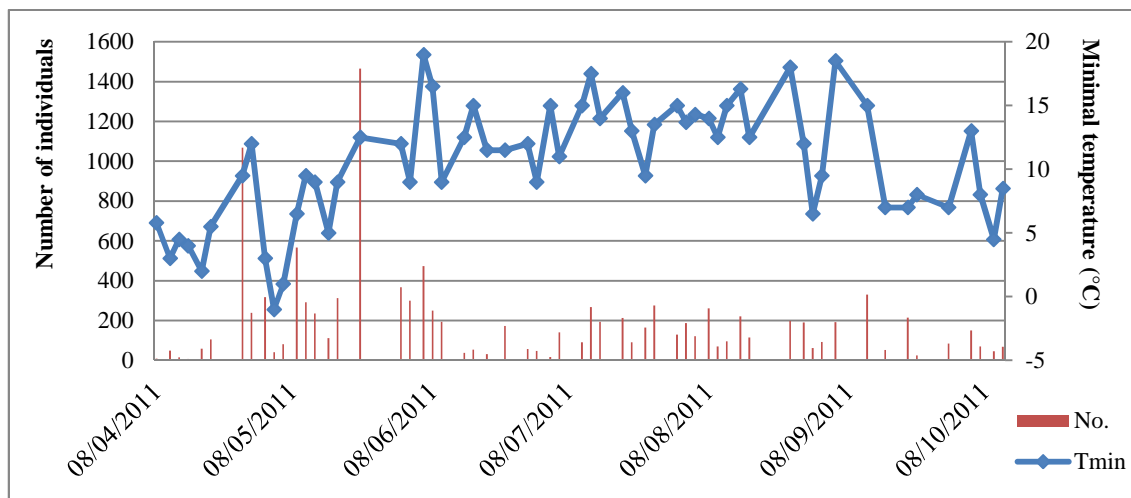


Figure 3.3.23 Distribution of arthropods at carcass no. 7.

Figure 3.3.24 shows that at carcass no. 7, two conspicuous changes of arthropods assemblage occurred from 18.04.2011 to 29.04.2011. The Tokeshi turnover index decreased from 0.67 to 0.25 between 27.04.2011 and 29.04.2011. From 18.04.2011 to 20.04.2011, the Tokeshi index increased from 0.21 to 0.66. From 10.06.2011 to 15.07.2011, the Tokeshi index had again strong fluctuations. The diversity index was extremely low on 20.04.2011 ($H' = 0.57$), and on 01.07.2011 ($H' = 0.39$).

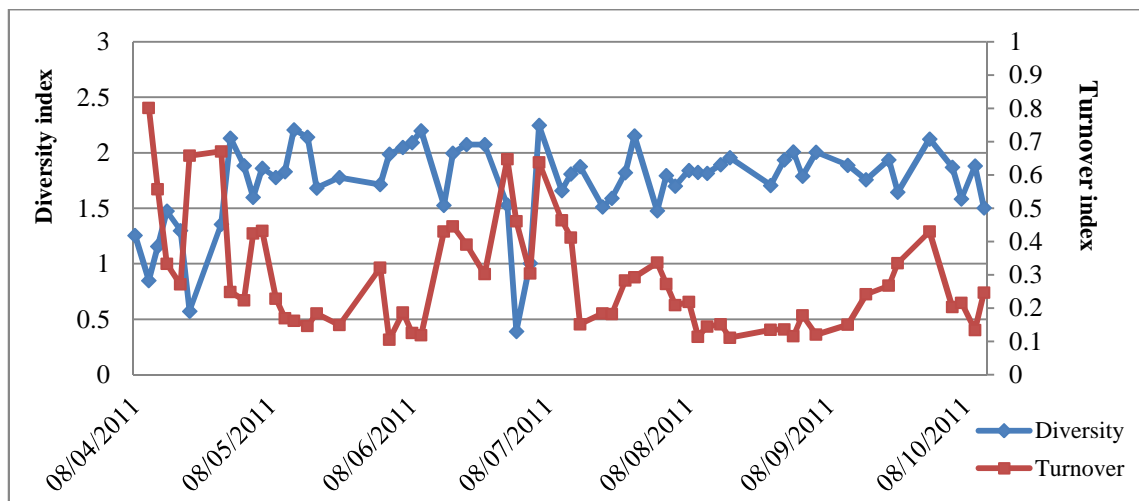


Figure 3.3.24 Diversity index and turnover index of arthropods at carcass no. 7.

Figure 3.3.25 shows the distribution of Silphidae from the spring to the autumn in 2011. At carcass no. 6, Silphidae were first collected on the 9th exposure day, and the number of Silphidae reached highest peak on the 66th exposure days with 474 individuals. After the 66th exposure day, no Silphidae were collected. At carcass no. 7, Silphidae were first collected on the 5th exposure day. The number of Silphidae had two peaks, the first one was on the 21st day with 385 individuals, and the second one was on the 47th exposure day with 470 individuals. After the 56th exposure day, no Silphidae were collected.

Figure 3.3.26 shows the distribution of Histeridae from the spring to the autumn in 2011. At carcass no. 6, Histeridae were first collected on the 43rd exposure day. The number of Histeridae reached the unique peak on the 66th exposure day with only seven individuals. At carcass no. 7, Histeridae were first collected on the 21st exposure day. The number of Histeridae reached the peak on the 47th exposure day with 21 individuals.

Figure 3.3.27 shows the distribution of Staphylinidae from the spring to the autumn in 2011. At carcass no. 6, Staphylinidae were first collected on the 5th exposure day. The number of Staphylinidae reached the peak on the 45th exposure day with ten individuals. At carcass no. 7, Staphylinidae were first collected on the 14th exposure day. The number of Staphylinidae reached the highest peak on the 23rd exposure day with 22 individuals.

Figure 3.3.28 shows the distribution of Geotrupidae from the spring to the autumn in 2011. At carcass no. 6, Geotrupidae were first collected on the 24th exposure day. The number of Geotrupidae reached the peak on the 43rd exposure day with 28 individuals. After that, the number decreased. At carcass no. 7, Geotrupidae were first collected on the 14th exposure day. The number of Geotrupidae reached the peak on the 21st exposure day with 34 individuals. After that the number decreased.

Figure 3.3.29 shows the distribution of Coleoptera-larvae from the spring to the autumn in 2011. At carcass no. 6, Coleoptera-larvae were first collected on the 29th exposure day. The number of Coleoptera-larvae showed three peaks, the first peak was on the 34th exposure days with 101 individuals, the second one was on the 43rd exposure day with 130 individuals, and the third one was on the 80th exposure day with 137 individuals. At

carcass no. 7, Coleoptera-larvae were first collected on the 21st exposure day. The highest peak occurred on the 47th exposure day with 499 individuals. After that, the number decreased.

Figure 3.3.30 shows the distribution of Diptera from the spring to the autumn in 2011. At carcass no. 6, Diptera were first collected on the 5th exposure day. The number of Diptera reached the highest peak on the 76th exposure day with 24 individuals. At carcass no. 7, Diptera were first collected on the 2nd exposure day. The number of Diptera reached the first peak on the 21st exposure day with 70 individuals, and the second peak occurred on the 47th exposure day with 47 individuals.

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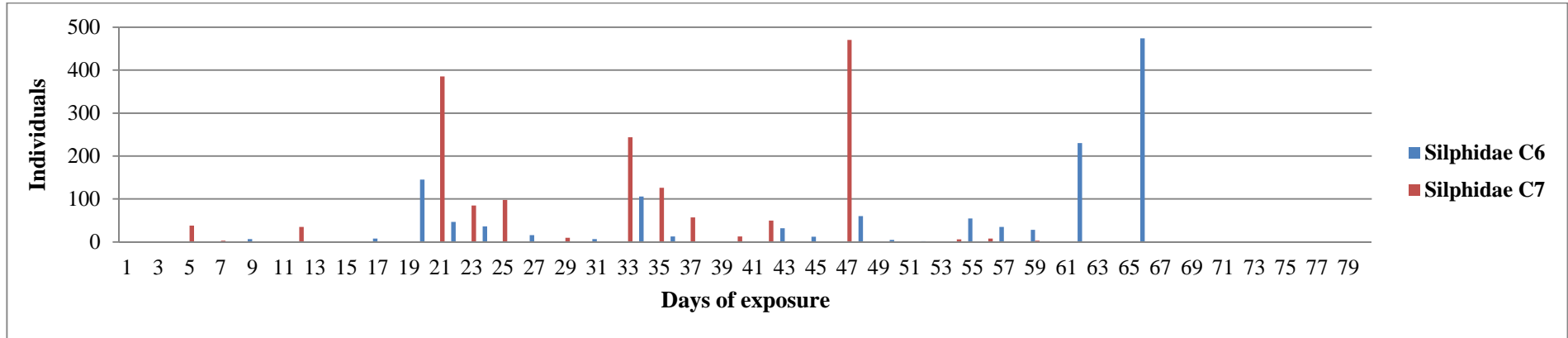


Figure 3.3.25 Distribution of Silphidae at carcass no. 6 and no. 7 in 2011.

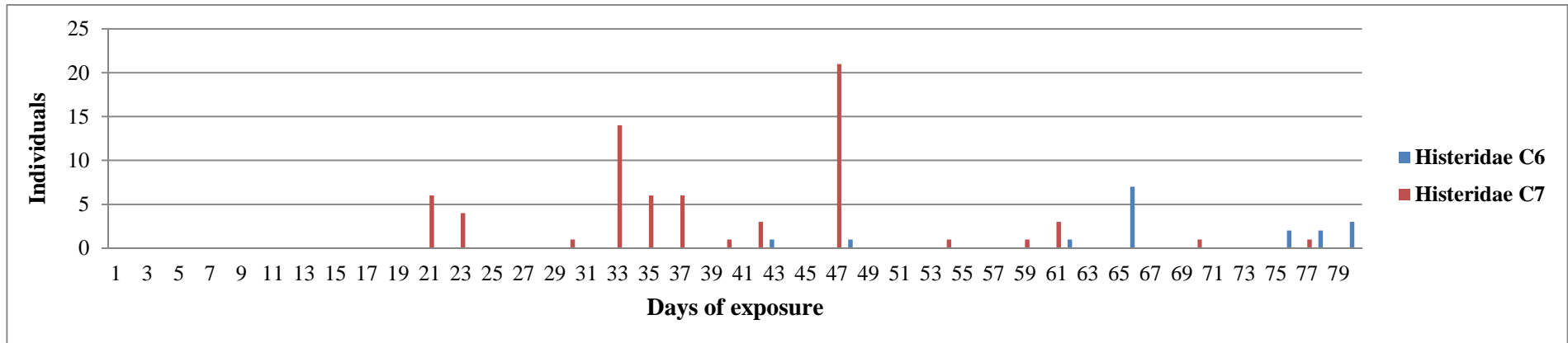


Figure 3.3.26 Distribution of Histeridae at carcass no. 6 and no. 7 in 2011.

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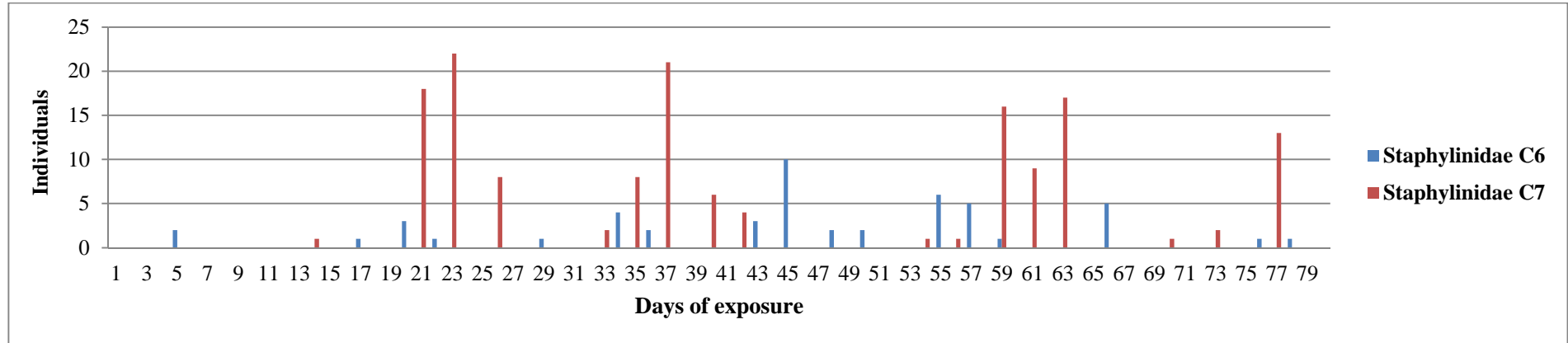


Figure 3.3.27 Distribution of Staphylinidae at carcass no. 6 and no. 7 in 2011.

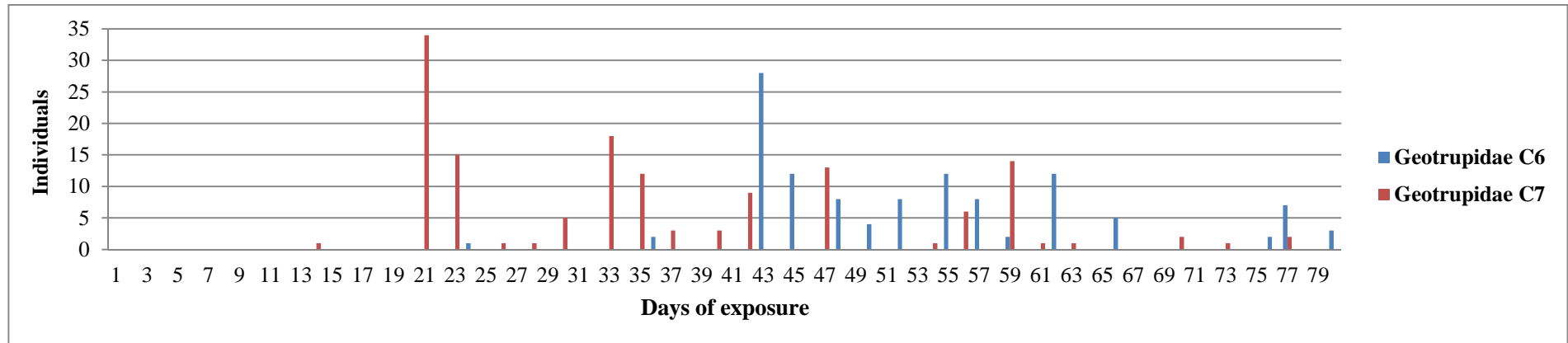


Figure 3.3.28 Distribution of Geotrupidae at carcass no. 6 and no. 7 in 2011.

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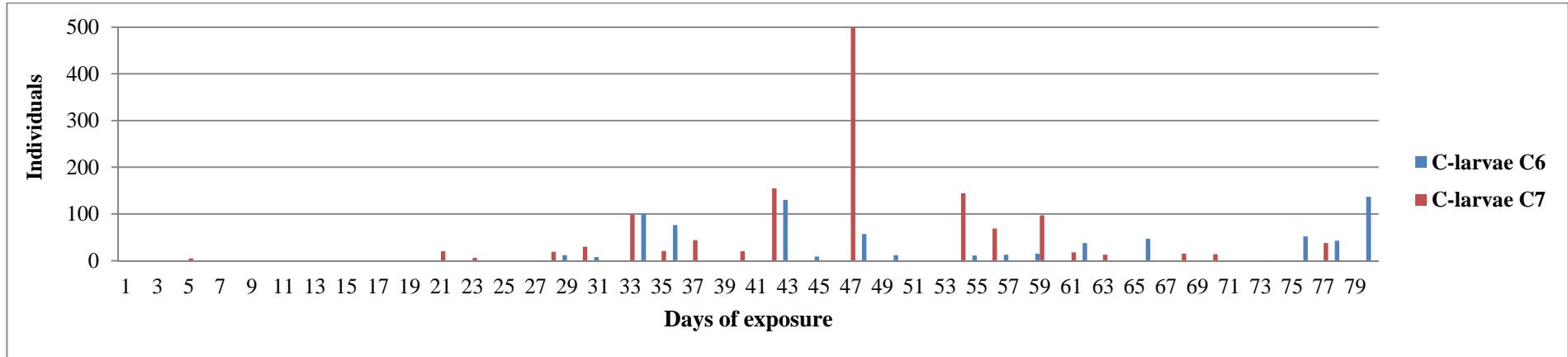


Figure 3.3.29 Distribution of Coleoptera-larvae at carcass no. 6 and no. 7 in 2011.

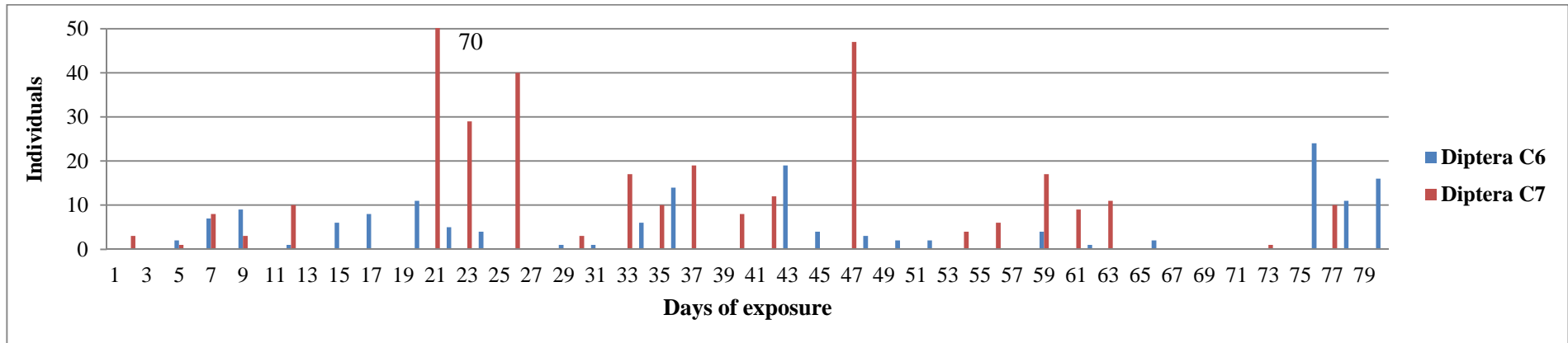


Figure 3.3.30 Distribution of Diptera at carcass no. 6 and no. 7 in 2011.

Figure 3.3.31 shows that at carcass no. 8, the number of arthropods reached the first peak on the 5th exposure day (23.05.2011) with 2,499 individuals. The abundant taxa on this day included Silphidae (823 individuals), and Histeridae (725 individuals). The second peak occurred on the 19th exposure day (06.06.2011) with 2,948 individuals, the abundant taxa on this day included Histeridae (801 individuals), Coleoptera-larvae (581 individuals), and Formicidae (600 individuals). After that, the number of arthropods decreased sharply, until the 42nd exposure day (29.06.2011) the number increased to 1,432. After 03.08.2011, the number started to decrease.

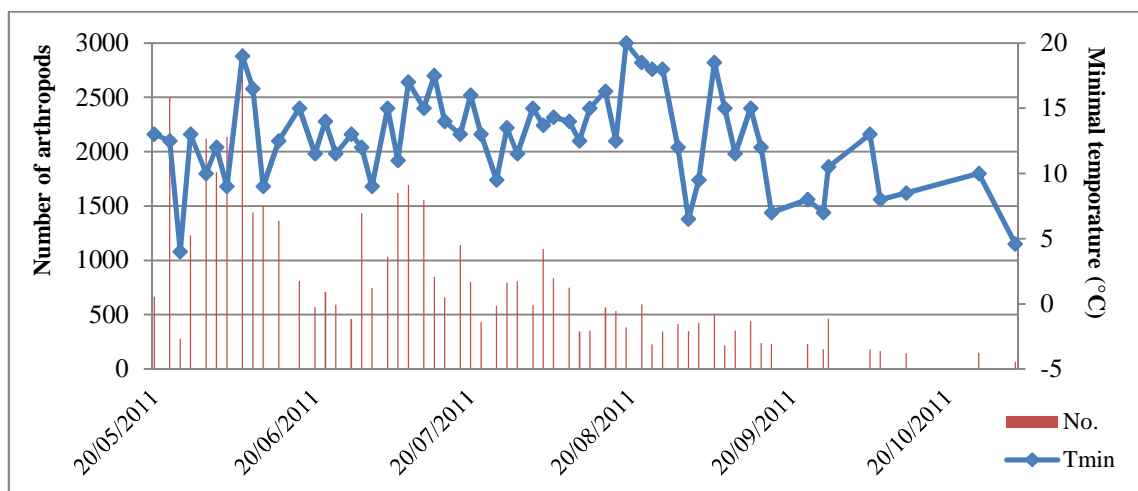


Figure 3.3.31 Distribution of arthropods at carcass no. 8.

Figure 3.3.32 shows that there were two conspicuous changes of the arthropods assemblage at carcass no. 8. The first one was between 23.05.2011 and 25.05.2011, the Tokeshi turnover index increased from 0.16 to 0.43. The second one was between 27.05.2011 and 30.05.2011, the turnover index decreased from 0.37 to 0.10. From 01.06.2011 to 22.06.2011, the Tokeshi turnover index was stable. From 24.06.2011 to the end, the Tokeshi turnover index kept fluctuating. On 09.09.2011 ($H' = 0.96$) and on 12.10.2011 ($H' = 0.84$), the diversity indexes were extremely low. The highest diversity index ($H' = 2.47$) occurred on 25.07.2011. At carcass no. 8, when the diversity index decreased, the turnover index decreased too, for example, on 23.05.2011, 24.06.2011, 04.07.2011, 22.07.2011, and 26.09.2011.

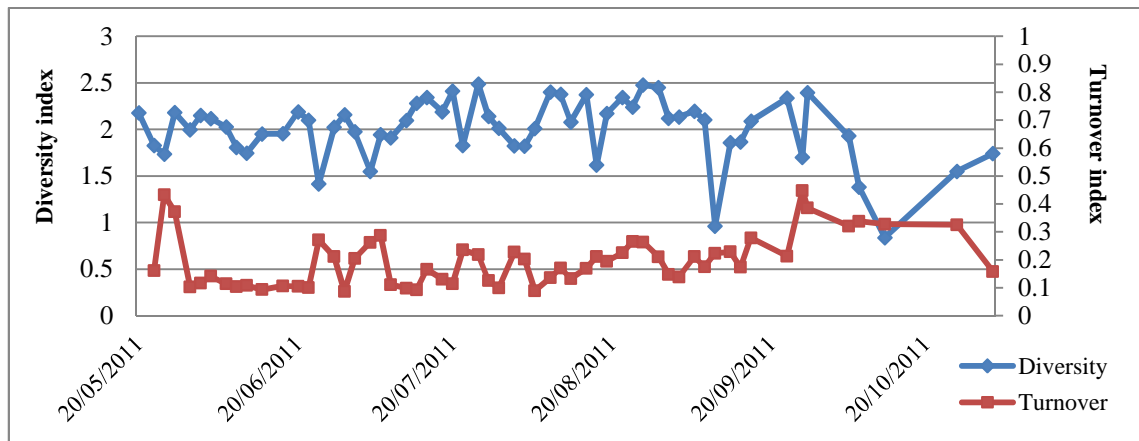


Figure 3.3.32 Diversity index and turnover index of arthropods at carcass no. 8.

Figure 3.3.33 shows that at carcass no. 9, the number of arthropods reached the first peak on the 6th exposure day (06.06.2011) with 2,468 individuals, the most abundant taxa included Histeridae (955 individuals) and Silphidae (603 individuals). The highest peak occurred on the 10th exposure day (10.06.2011) with 2,807 individuals, the most abundant taxon was Brachycera-larvae with 2,144 individuals. From 13.06.2011 to 15.06.2011, the number of arthropods decreased sharply from 2,144 to 733.

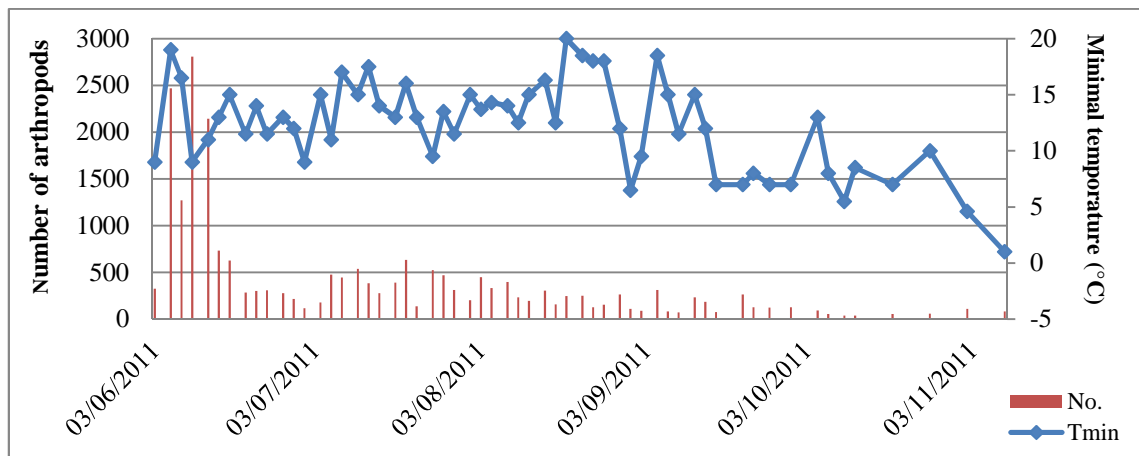


Figure 3.3.33 Distribution of arthropods at carcass no. 9.

Figure 3.3.34 shows that at carcass no. 9, the lowest diversity index ($H' = 1.03$) occurred on 10.06.2011. The Tokeshi turnover index showed there was an apparent change of arthropods assemblage between 06.06.2011 and 08.06.2011, the Tokeshi turnover index decreased from 0.33 to 0.18. At carcass no. 9, the relation between the

diversity index and the turnover index were different from that at carcass no. 8. For example, on 08.06.2011, 25.07.2011, 12.09.2011, and 21.09.2011, when the diversity index increased, the Tokeshi turnover index increased too, however, on 04.07.2011 when the Tokeshi turnover index increased, the diversity index decreased. Therefore, there was no relation between the diversity index and the Tokeshi turnover index.

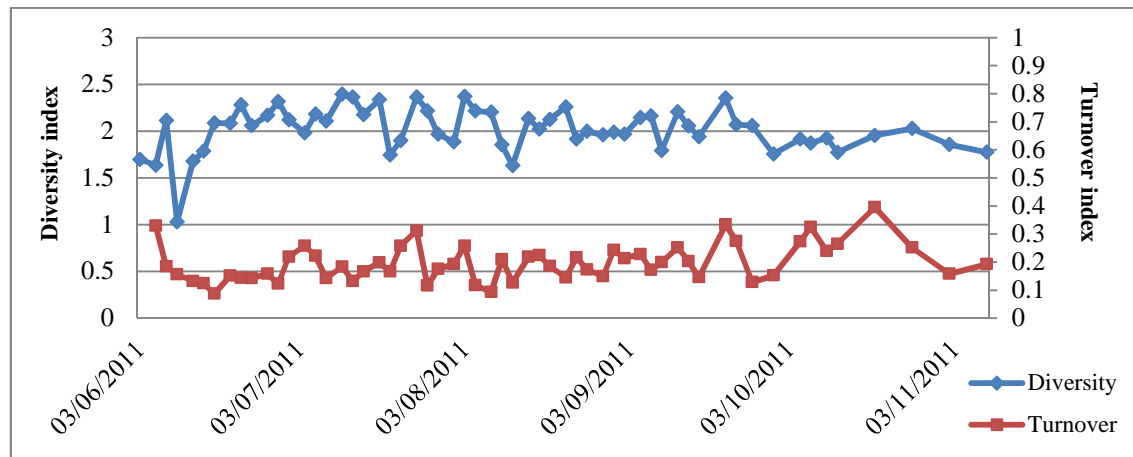


Figure 3.3.34 Diversity index and turnover index of arthropods at carcass no. 9.

Figure 3.3.35 shows the distribution of Silphidae from the summer to the winter in 2011. At carcass no. 8, Silphidae were first collected on the 2nd exposure day. The number of individuals showed only one conspicuous peak on the 5th exposure day with 823 individuals. At carcass no. 9, Silphidae were first collected on the 6th exposure day, the number of individuals showed one apparent peak on the 6th exposure day with 603 individuals. On the 38rd exposure day there was a small peak with 163 individuals.

Figure 3.3.36 shows the distribution of Histeridae from the summer to the winter in 2011. At carcass no. 8, Histeridae were first collected on the 2nd exposure day. The number of individuals showed four peaks, the first one was on the 5th exposure day with 725 individuals, the second one was on the 19th exposure day with 801 individuals, the third one was on the 51st exposure day with 736 individuals, and the last one occurred on the 76th exposure day with 565 individuals. At carcass no. 9, Histeridae were first collected on the 4th exposure day. The number of Histeridae showed one conspicuous

peak on the 4th exposure day with 955 individuals. On the 64th exposure day there was a small peak with 300 individuals.

Figure 3.3.37 shows the distribution of Staphylinidae from the summer to the winter in 2011. At carcass no. 8, Staphylinidae were first collected on the 2nd exposure day. The number increased until the 26th exposure day (89 individuals), after that the number decreased. After the 49th exposure day, the number of Staphylinidae started to increase and reached the highest peak on the 76th exposure day with 148 individuals. At carcass no. 9, Staphylinidae were first collected on the 8th exposure day. The number of Staphylinidae showed two peaks, the first one occurred on the 13th exposure day with 111 individuals, and the second one occurred on the 64th exposure day with 68 individuals.

Figure 3.3.38 shows the distribution of Geotrupidae from the summer to the winter in 2011. At carcass no. 8, Geotrupidae were first collected on the 2nd exposure day. The number of Geotrupidae showed three apparent peaks, the first one was on the 2nd exposure day with 103 individuals, and the second one was on the 19th exposure day with 131 individuals, after that the number decreased. The third peak occurred on the 51st exposure day with 111 individuals. At the carcass no. 9, Geotrupidae were first collected on the 3rd exposure day. The number of Geotrupidae showed two conspicuous peaks. The first one was on the 6th exposure day with 44 individuals. The second one was on the 39th exposure day with 38 individuals.

Figure 3.3.39 shows the distribution of Dermestidae from the summer to the winter in 2011. At carcass no. 8, Dermestidae were first collected on the 5th exposure day. On the 16th exposure day, there was a small peak with 155 individuals. The number of Dermestidae increased to 339 on the 42nd exposure day. The highest peak occurred on the 49th exposure day with 415 individuals. At carcass no. 9, Dermestidae were first collected on the 6th exposure day. The conspicuous peak occurred on the 36th exposure day with 129 individuals.

Figure 3.3.40 shows the distribution of Diptera from the summer to the winter in 2011. At carcass no. 8, Diptera were collected on the 2nd exposure day. The highest peak

occurred on the 12th exposure day with 347 individuals. On the 74th exposure day, there was a small peak with 215 individuals. At carcass no. 9, Diptera were first collected on the 3rd exposure day. The number of Diptera showed only one peak on the 13th exposure day with 342 individuals.

Figure 3.3.41 shows the distribution of Coleoptera-larvae from the summer to the winter in 2011. At carcass no. 8, Coleoptera-larvae were first collected on the 2nd exposure day. The number of Coleoptera-larvae reached the first peak on the 12th exposure day with 672 individuals. After the 23rd exposure day, the number decreased. On the 54th exposure day, there was a small peak with 297 individuals. The highest peak occurred on the 72nd exposure day with 886 individuals. At carcass no. 9, Coleoptera-larvae were first collected on the 8th exposure day. The number had two conspicuous peaks, the first one was on the 13th exposure day with 167 individuals, and the second one was on the 17th exposure day with 177 individuals.

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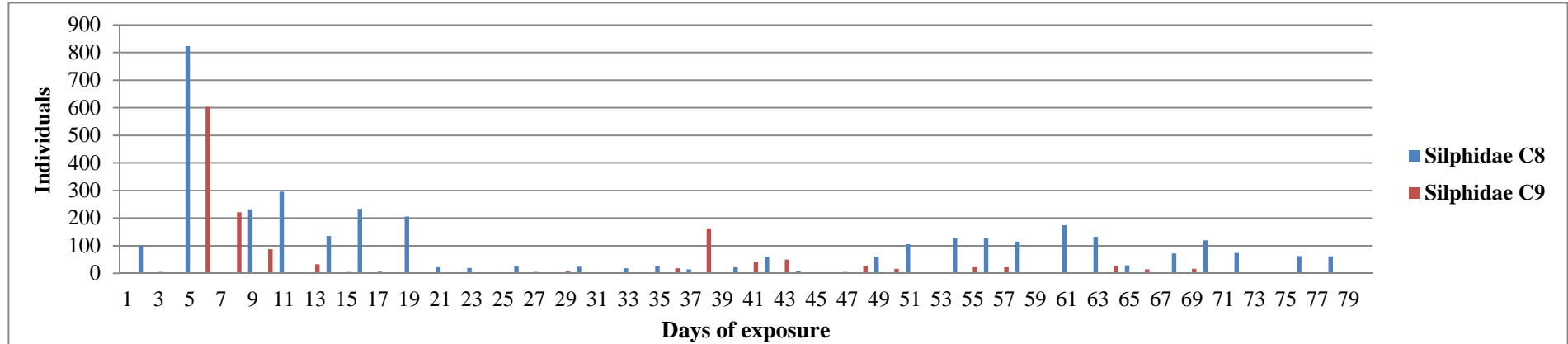


Figure 3.3.35 Distribution of Silphidae at carcass no. 8 and no. 9 in 2011.

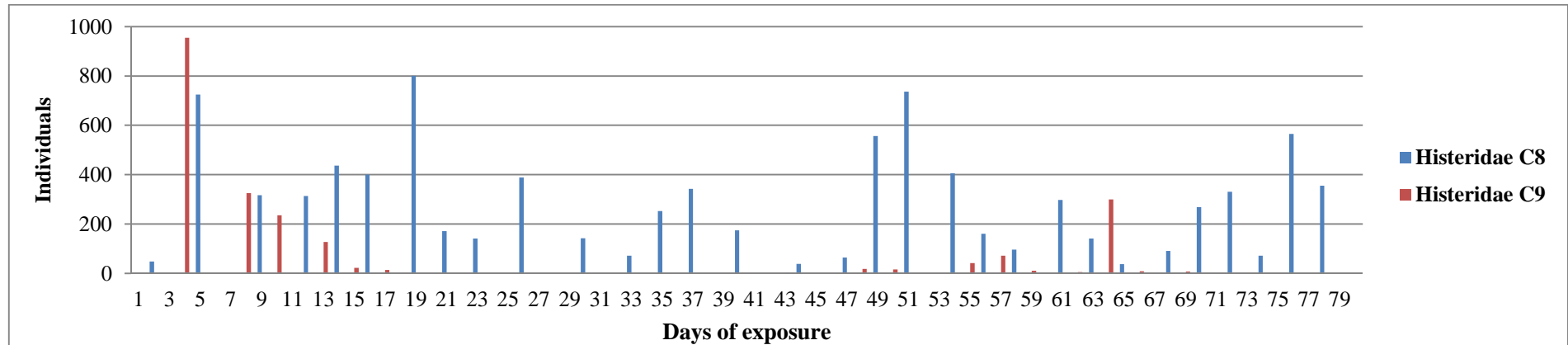


Figure 3.3.36 Distribution of Histeridae at carcass no. 8 and no. 9 in 2011.

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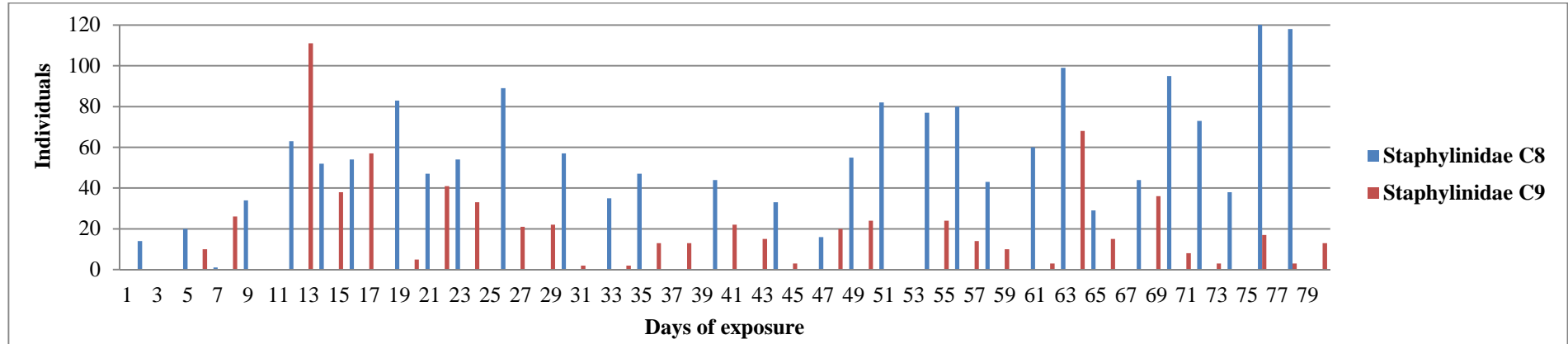


Figure 3.3.37 Distribution of Staphylinidae at carcass no. 8 and no. 9 in 2011.

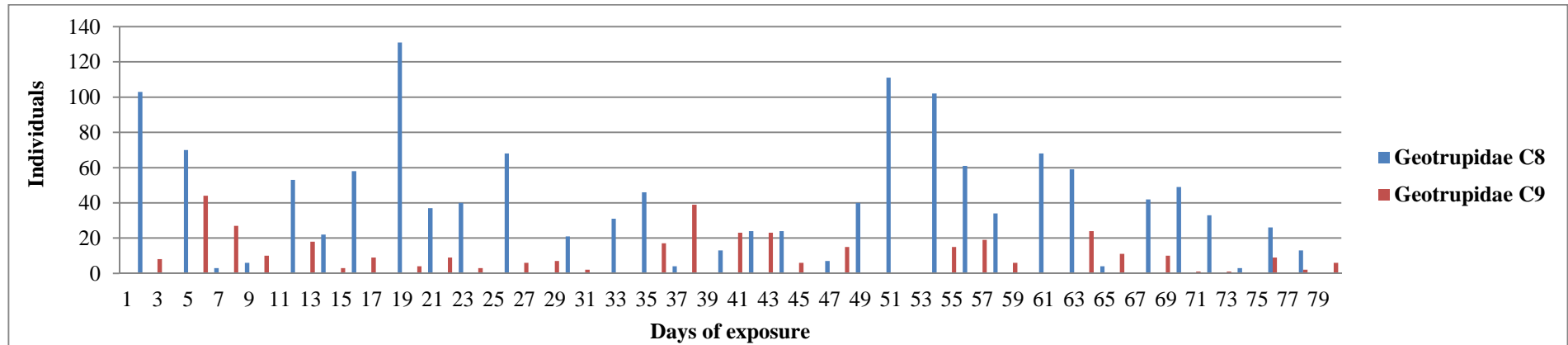


Figure 3.3.38 Distribution of Geotrupidae at carcass no. 8 and no. 9 in 2011.

Animal biodiversity and food web restoration based on large vertebrate carcasses

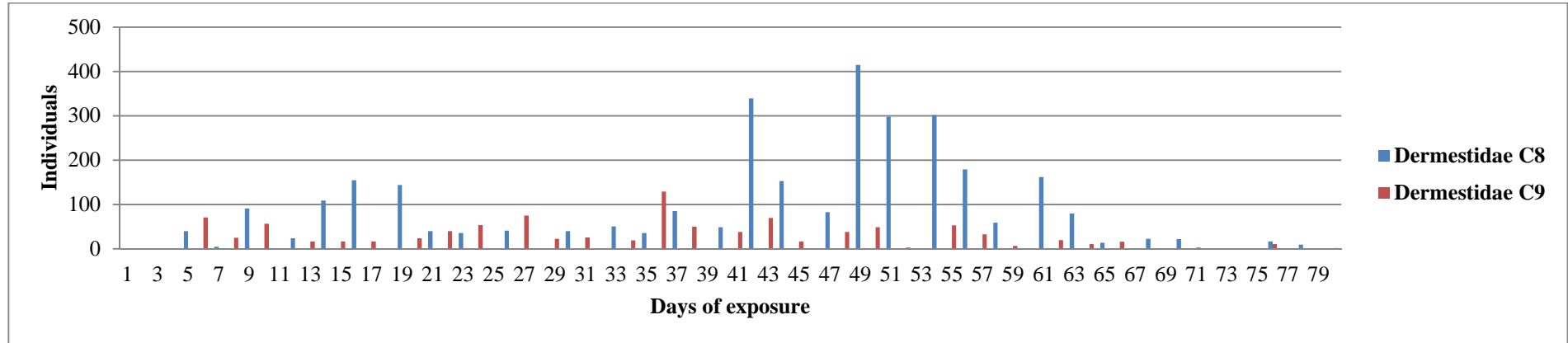


Figure 3.3.39 Distribution of Dermestidae at carcass no. 8 and no. 9 in 2011.

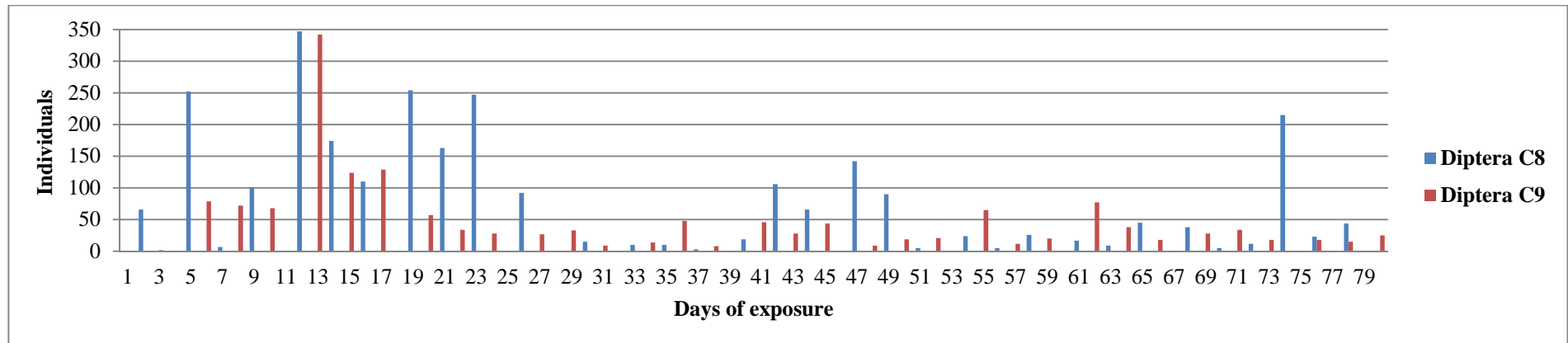


Figure 3.3.40 Distribution of Diptera at carcass no. 8 and no. 9 in 2011.

Animal biodiversity and food web restoration based on large vertebrate carcasses

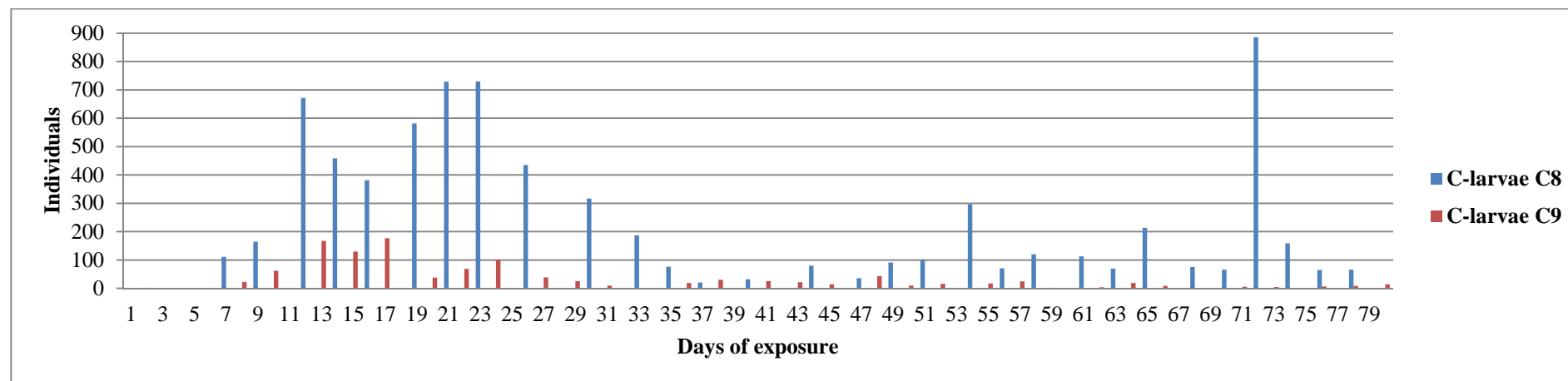


Figure 3.3.41 Distribution of Coleoptera-larvae at carcass no. 8 and no. 9 in 2011.

3.4 Succession of Silphidae and Geotrupidae species in 2011

3.4.1 Succession of Silphidae species

In total, ten species of Silphidae were recorded in 2011. At carcass no. 8 all ten species were recorded. Five species at carcass no. 9, four species at carcass no. 7, and three species and at carcass no. 6 were recorded (Table 3.4.1).

Table 3.4.1 Number of Silphidae species collected in 2011.

Species of Silphidae	Carcass no. 6	Carcass no. 7	Carcass no. 8	Carcass no. 9
<i>Thanatophilus rugosus</i>	84	304	383	265
<i>Thanatophilus sinuatus</i>	1,340	1,152	2,407	733
<i>Necrodes littoralis</i>	28	107	838	17
<i>Necrophorus humator</i>	0	0	2	0
<i>Necrophorus vestigator</i>	0	1	6	2
<i>Necrophorus fossor</i>	0	0	1	0
<i>Necrophorus sepultor</i>	0	0	7	0
<i>Necrophorus investigator</i>	0	0	3	1
<i>Necrophorus vespilloides</i>	0	0	2	0
<i>Oeceoptana thoracica</i>	0	0	1	0
Sum	1,452	1,564	3,650	1,018

Figure 3.4.1 shows that *Thanatophilus rugosus* (13 %), *Thanatophilus sinuatus* (74 %) and *Necrodes littoralis* (13 %) were the most abundant species of Silphidae in 2011. Figure 3.4.2 shows that the second abundant species at carcass no. 6, no. 7, and no. 9 was *Thanatophilus rugosus*. At carcass no. 8, the second abundant species was *Necrodes littoralis*.

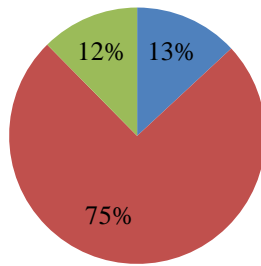


Figure 3.4.1 Composition of Silphidae species in 2011.

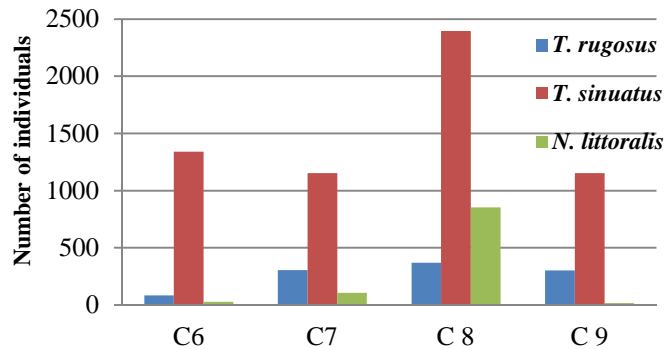


Figure 3.4.2 Abundant species of Silphidae in 2011 (“C” is the abbreviation of the carcass).

At carcass no. 6, *Thanatophilus rugosus* and *Thanatophilus sinuatus* were first collected on the 9th exposure day. *Necrodes littoralis* was first collected on the 28th exposure day. The first peak of *Thanatophilus sinuatus* was on the 19th exposure day with 140 individuals, and the second peak was on the 58th exposure day with 243 individuals (Figure 3.4.3).

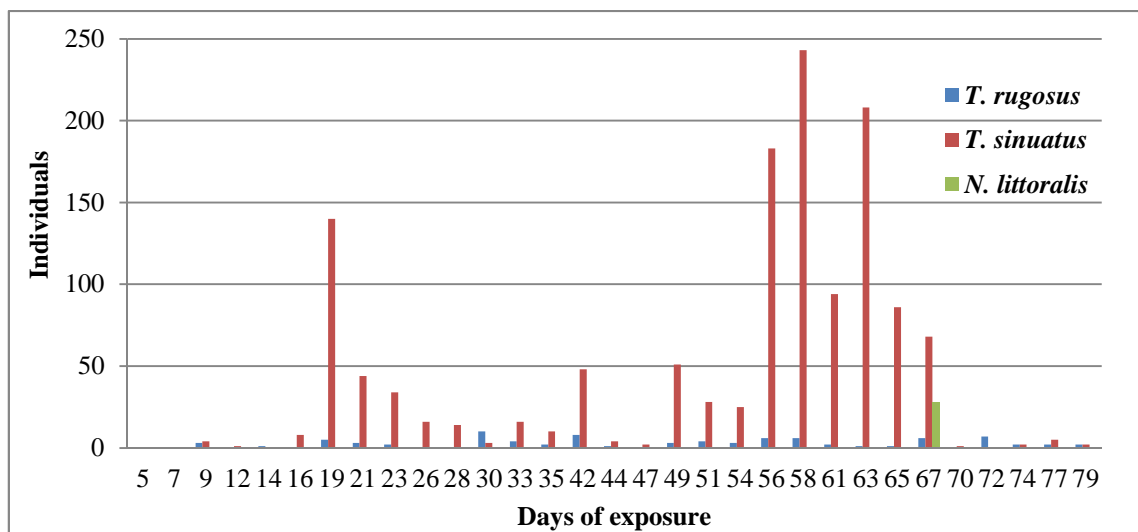


Figure 3.4.3 Distribution of Silphidae species at carcass no. 6.

At carcass no. 7, *Thanatophilus rugosus*, *Thanatophilus sinuatus* and *Necrodes littoralis* were first collected on the 5th exposure day. The number of *Thanatophilus sinuatus* reached the first peak on the 21st exposure day with 251 individuals, the highest peak

occurred on the 33rd exposure day with 280 individuals, and the last peak occurred on 44th exposure day with 177 individuals. The number of *Thanatophilus rugosus* showed only one conspicuous peak on the 21st exposure day with 118 individuals. The number of *Necrodes littoralis* showed one peak on 21st exposure day with 66 individuals (Figure 3.4.4).

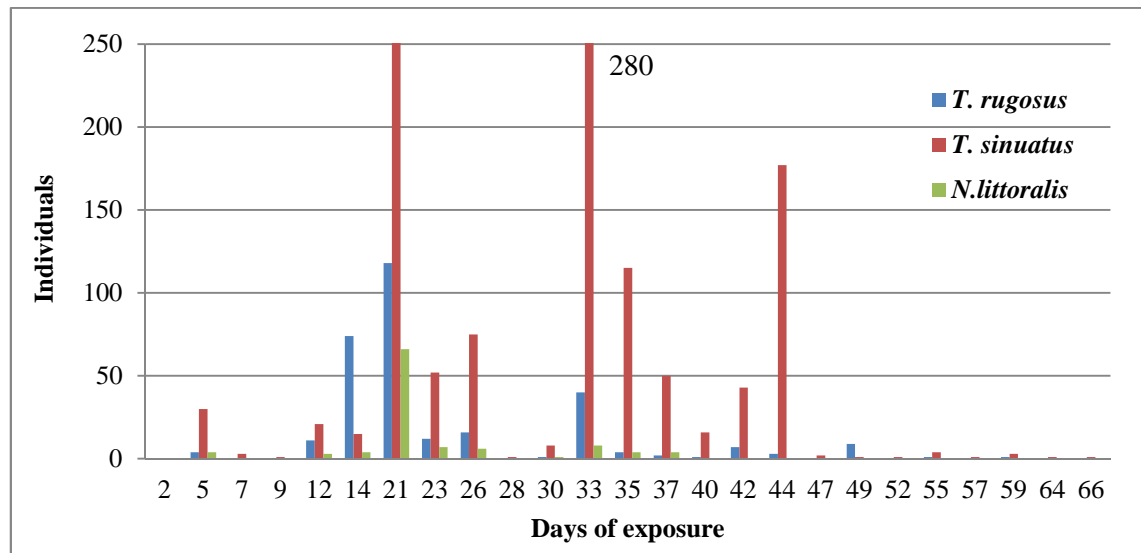


Figure 3.4.4 Distribution of Silphidae species at carcass no. 7.

Figure 3.4.5 shows that at carcass no. 8, *Thanatophilus sinuatus*, *Thanatophilus rugosus* and *Necrodes littoralis* were first collected on the 2nd exposure day. *Thanatophilus sinuatus* was mainly collected from the 5th and 16th exposure day and from the 50th to the 62nd exposure day. The number of *Thanatophilus sinuatus* reached the highest peak on the 5th exposure day with 614 individuals. The number of *Thanatophilus rugosus* showed two peaks, the first one was on the 5th exposure day with 79 individuals, and the second one was on the 19th exposure day with 83 individuals. The number of *Necrodes littoralis* showed one peak on the 5th exposure day with 142 individuals.

Figure 3.4.6 shows that at carcass no. 9, *Thanatophilus sinuatus* was first collected on the 2nd exposure day. The number of *Thanatophilus sinuatus* showed two peaks, the first one was on the 5th exposure day with 235 individuals, and the second one was on the 37th exposure day with 146 individuals. *Thanatophilus rugosus* and *Necrodes littoralis*

were first collected on the 5th exposure day. The number of *Thanatophilus rugosus* had only one conspicuous peak on the 5th exposure day with 235 individuals (Figure 3.4.6).

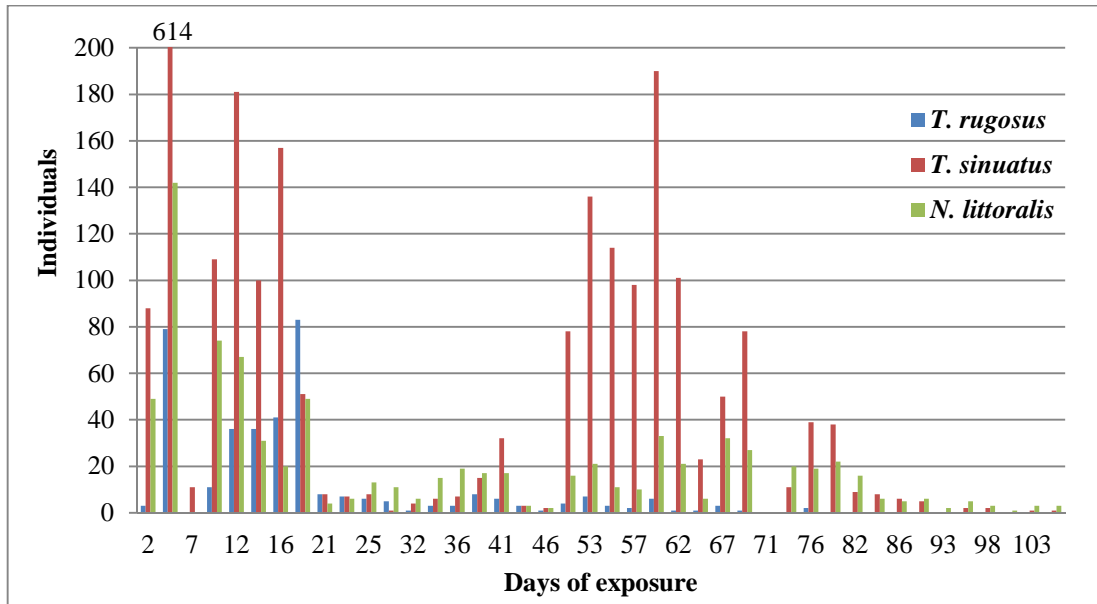


Figure 3.4.5 Distribution of Silphidae species at carcass no. 8.

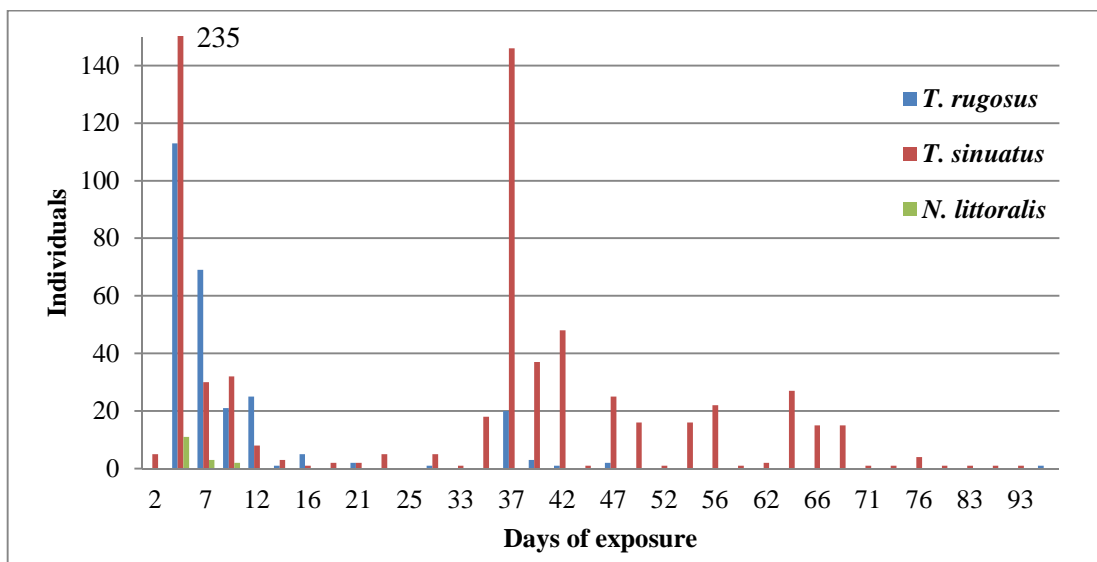


Figure 3.4.6 Distribution of Silphidae species at carcass no. 9.

3.4.2 Succession of Geotrupidae species

In total, three species of Geotrupidae were collected in the research area in 2011: *Trypocopris vernalis*, *Typhaeus typhoeus*, and *Anoplotrupes stercurosus*. Figure 3.4.7 shows that at all four carcasses in 2011 the most abundant Geotrupidae species was *Trypocopris vernalis*. Table 3.4.2 shows that at carcass no. 8, the number of Geotrupidae was the highest (1,545 individuals), the number at carcass no. 6 was the lowest (147 individuals).

Table 3.4.2 Number of Geotrupidae species collected in 2011.

Species of Geotrupidae	Carcass no. 6	Carcass no. 7	Carcass no. 8	Carcass no. 9
<i>Trypocopris vernalis</i>	144	338	1,414	432
<i>Typhaeus typhoeus</i>	0	22	9	7
<i>Anoplotrupes stercurosus</i>	3	6	122	16
Sum	147	366	1,545	455

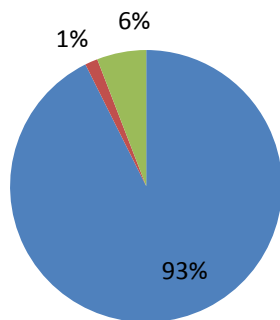


Figure 3.4.7 Composition of Geotrupidae species in 2011.

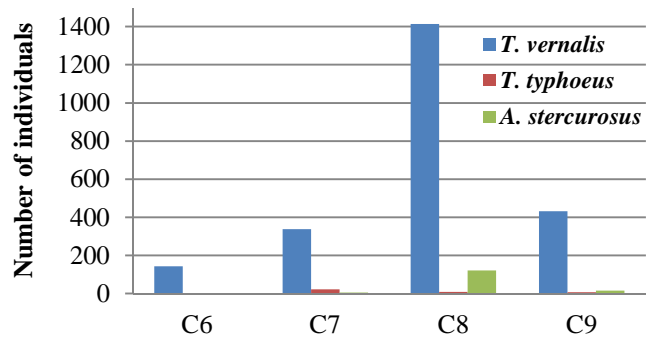


Figure 3.4.8 Comparison of abundant species of Geotrupidae species in 2011 (“C” is the abbreviation of carcass).

At carcass no. 6, *Trypocopris vernalis* was first collected at the 23rd exposure day (08.04.2011). *Anoplotrupes stercurosus* was first collected on the 47th exposure day (Figure 3.4.9). No *Typhaeus typhoeus* was found at carcass no. 6.

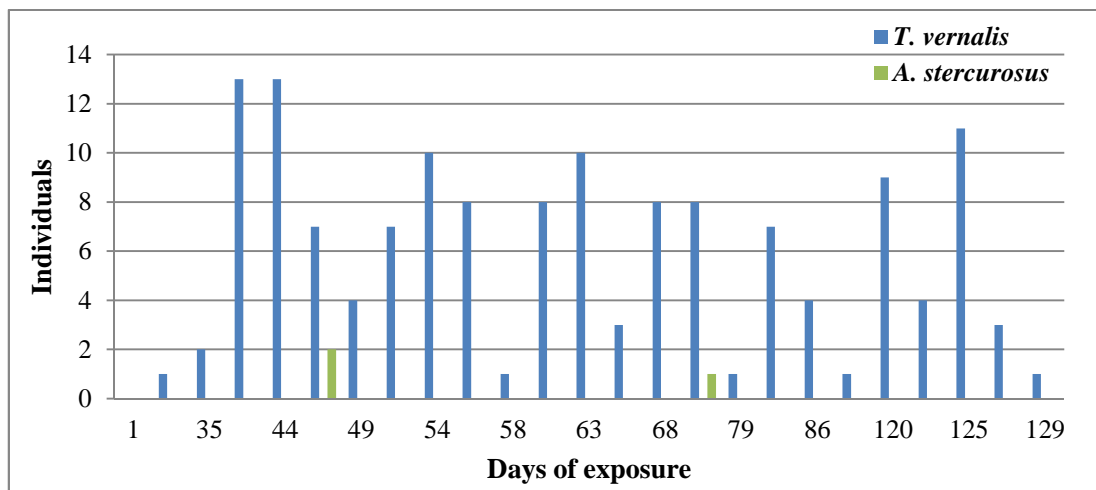


Figure 3.4.9 Distribution of Geotrupidae species at carcass no. 6.

At carcass no. 7, *Trypocopris vernalis* was first collected on the 12th exposure day (18.04.2011) and the number of *Trypocopris vernalis* showed three peaks, the first one was on the 21st exposure day with 26 individuals, the highest one was on the 96th exposure day with 31 individuals, and the last one was on the 167th exposure day with 24 individuals. *Typhaeus typhoeus* was first collected on the 164th exposure day. *Anoplotrupes stercuosus* was first collected on the 160th exposure day (Figure 3.4.10).

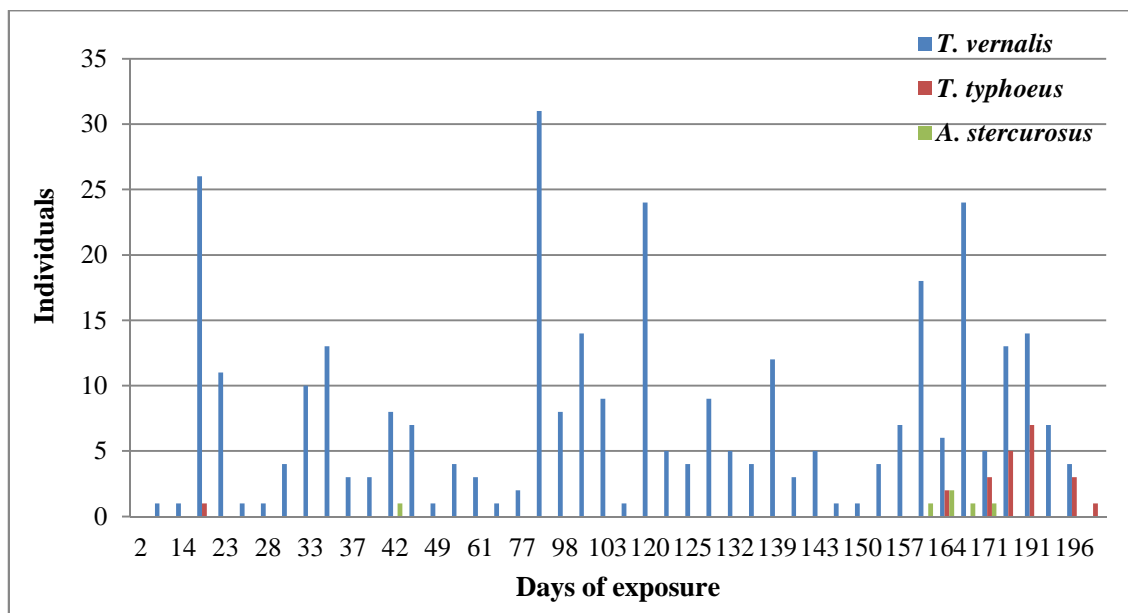


Figure 3.4.10 Distribution of Geotrupidae species at carcass no. 7.

At carcass no. 8, *Trypocoprís vernalis* was first collected on the 2nd exposure day (20.05.2011), and the number of *Trypocoprís vernalis* increased with fluctuations and reached the highest peak on 54th exposure day with 87 individuals. *Typhaeus typhoeus* was first collected on the 2nd exposure day. *Anoplotrupes stercurosus* was first collected on the 2nd exposure day, and the number reached the peak on the 19th exposure day with 9 individuals (Figure 3.4.11).

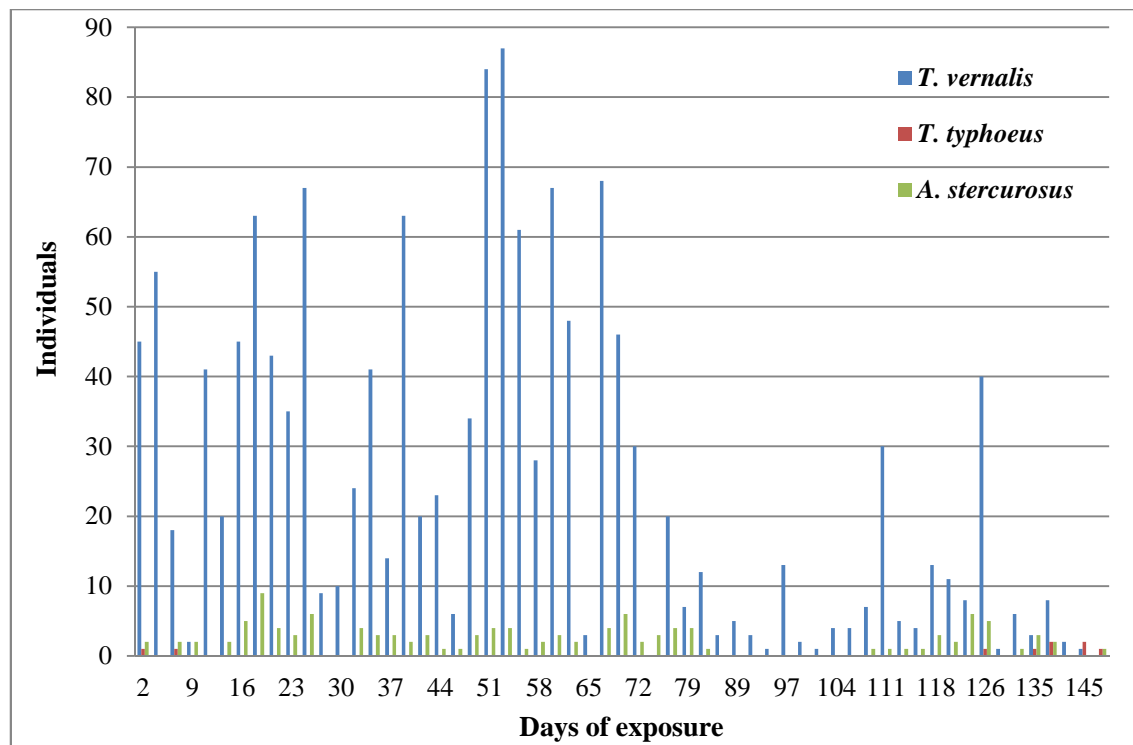


Figure 3.4.11 Distribution of Geotrupidae species at carcass no. 8.

At carcass no. 9, *Trypocoprís vernalis* was first collected on the 2nd exposure day (03.06.2011), and the number of *Trypocoprís vernalis* reached the highest peak on the 37th exposure day with 38 individuals. *Anoplotrupes stercurosus* was first collected on the 5th exposure day with four individuals. *Typhaeus typhoeus* was first collected since the 126th exposure day (Figure 3.4.12).

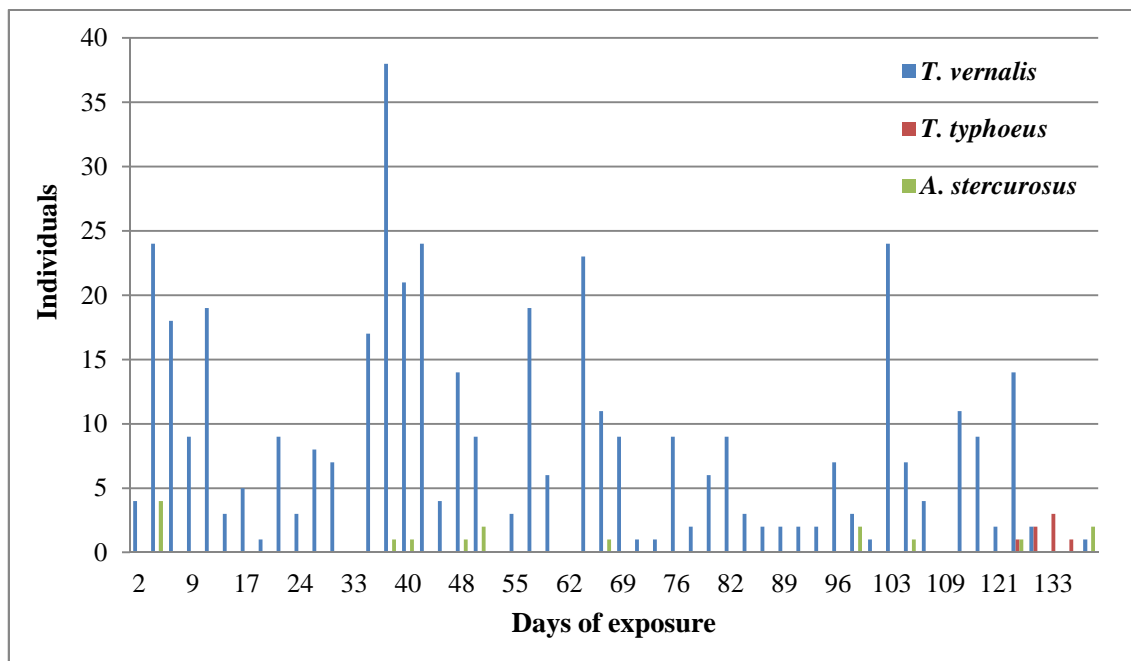


Figure 3.4.12 Distribution of Geotrupidae species at carcass no. 9.

4 Discussion

4.1 Methods

4.1.1 Pitfall traps

Pitfall traps are cheap and efficient method for arthropod collection (Luff 1975); however, there are four imperfections which can be improved for further study. Firstly, in this research, pitfall traps were not installed directly under the carcass but around the carcass. The arthropods fell into pitfall traps when they came to or left the carcass. Therefore, the actual number of arthropods living on carcasses was higher than the number showed by pitfall traps. However, the design of pitfall traps fulfilled the object of checking the occurrence and assemblage of arthropod community around carcasses.

Secondly, when Coleoptera-larvae and Brachycera-larvae complete their developments on carcasses, they migrate in different directions and pupate in the surrounding soil

(Goff 2009 a). The pitfall traps in this study were installed on the same level of the soil surface, so the number of larvae collected by pitfall traps was much lower than the actual number. In order to resolve this problem, an additional investigation on larvae around carcasses has been done in 2012, 150 mm deep soil samples were taken in eight directions, and the larvae in the soil were counted to adjust the results.

Thirdly, extreme climate conditions influenced the performance of the pitfall traps. High temperature and longtime sunlight in summer caused ethanol evaporation in short time. Storm and heavy rain filled the traps with water, and arthropods in the traps were washed away.

At last, sometimes wild boars in the research area destroyed the pitfall traps and overturned the carcass to feed on the arthropods. Figure 4.1.1 shows a sampling area which destroyed by wild boar. In order to avoid the bias, for modeling, one week (sum of three times sampling) was used as one unit to calculate the number of arthropods. The last two imperfections caused the bias of the temporal distribution of the arthropods at carcass no. 2, no. 3 and no. 6 in chapter 3.3.



Figure 4.1.1 Sampling area of carcass no. 9 destroyed by wild boars (photos were taken on 16.09.2011).

4.2 Biology of abundant taxa in the research area

Staphylinidae are the largest beetle family in central Europe with almost 2,000 species (Harde & Severa 1998). Most of the species in this family are predatory species (Koch 1989). Histeridae species are all carnivore; in general they feed on larvae of small insects in decaying plant and animal matters (Harde & Severa 1998). *Dermestes* species of Dermestidae feed on the carcasses of vertebrates (Peacock 1993).

Trogidae and Cleridae were not abundant at the carcass in this study but they used the carcasses for the longest time. Cleridae adults and larvae are predacious. Some species occur on flowers or wood, while species of *Necrobia* can be found on old bones and carrion (Harde & Severa 1998). Trogidae species live on dry material of animal origin such as skins, hooves, feathers, bones and cadavers (Harde & Severa 1998).

Table 4.2.1 Biology of abundant beetle taxa in the research area (Harde & Severa 1998, Koch 1989), (“No. of individuals” is the sum of the number which were collected in the research area at all nine carcasses, and “No. of species” is the number of species in central Europe).

Family	Habitat and Ecological niche	Food	No. of species	No. of individuals
Dermestidae	On matter of animal origin, on flowers	Carcass of vertebrates	48	4,643
Geotrupidae	On dung, carrion, rotting fungi	Dung, fungi, carcasses	8	4,546
Histeridae	On carrion, dung, rotting fungi, and under bark	Larvae of small insects in decaying plant and carcasses	94	13,430
Silphidae	On carrion, on decaying plant and living plant tissue	Carcasses, maggots, other small arthropods visit carrion, plant tissues	30	9,006
Staphylinidae	Depends on different genera	Predatory, fungi, algae, decaying plant matter, parasitoid on other insects	2,000	5,232

In central Europe, eight species of Geotrupidae have been recorded. In the research area, three species were found (Table 4.2.2). *Trypocopris vernalis* is present from March to

November and prefers living in open land (Rößner 2012), and it was the most abundant species in our research area. *Anoplotrupes stercurosus* is present from February to December mostly, and prefers living in forest (Rößner 2012). However, in the research area, in total 147 individuals of *Anoplotrupes stercurosus* were collected in 2011 at open landscape (122 individuals were collected at carcass no. 8).

Table 4.2.2 Biology of Geotrupidae species in the research area (Rößner 2012, Hard & Severa 1998), (“No. of individuals” is the sum of individuals collected in the research area in 2011).

Species	Habitat	Active period in the year	Ecological niche	Food	No. of individuals
<i>Trypocopris vernalis</i>	Open to semi open sandy area	March to November	On dung	Dung	2,328
<i>Typhaeus typhoeus</i>	Heath plains, light pine forest, open and semi-open landscape	All over the year	On dung	Dung	38
<i>Anoplotrupes stercurosus</i>	Forest	February to December	On carcasses, on dung, and fungi	Carcasses, dung, and human feces	147

In central Europe, Silphidae include 12 genera with 30 species. Most species of genera *Necrophorus*, *Necrodes*, *Oeceoptoma*, and *Silpha* are necrophagous (Hard & Severa 1998, Ruzicka 1994). In the research area, ten species of Silphidae were recorded (Table 4.2.3). *Thanatophilus sinuatus* was the most abundant species. In total 838 individuals of *Necrodes littoralis* were collected at carcass no. 8, since *Necrodes littoralis* prefers living on large carcasses (Erbeling 1990), and the weight of carcass no. 8 was the heaviest (75 kg). *Necrophorus* species were not often collected, since they prefer living on small vertebrates, e.g. birds and rats. Only one individual of *Oeceoptana thoracica* was collected at carcass no. 8, this species prefers living in the forest (Erbeling 1990).

Table 4.2.3 Biology of Silphidae species in the research area (Erbeling 1990, Koch 1989, Ruzicka 1994), (“No. of individuals” is the sum of individuals collected in the research area in 2011).

Species	Habitat	Active period in the year	Ecological niche	Food	No. of individuals
<i>Thanatophilus rugosus</i>	Open land, light forest, forest edges	April to September	On carcasses, bones, skin	Carcasses, maggots, dead insects	1,036
<i>Thanatophilus sinuatus</i>	Open land, light forest, forest edges	April to September	On carcasses, bones, skin	Carcasses, maggots, dead insects	5,632
<i>Necrodes littoralis</i>	Dry forest edges, meadows, floodplains, heath land	April to September	On large carcasses, bones, skin	Carcasses, maggots	990
<i>Necrophorus humator</i>	Moist forest, forest edge, flood plain, garden, meadow	April to October	On carcasses, bones, in dung, in rotting fungi	Carcasses, maggots, small <i>Necrophilous</i> arthropods	2
<i>Necrophorus vestigator</i>	Large open area with enough sun exposed field, heath land	April to September	On carcasses, in dung, in rotting fungi	Carcasses; maggots; small <i>Necrophilous</i> arthropods	9
<i>Necrophorus fossor</i>	Forest, forest edge, dry area, field, meadow, fallow	June to November	On carcasses, in dung of carnivores	Carcasses; maggots; small <i>Necrophilous</i> arthropods	1
<i>Necrophorus sepultor</i>	Especially in forests, agaricol, otherwise mostly in large-scale field landscape	April to September	On carcasses, in dung of carnivore and omnivore, in rotting fungi	Carcasses; maggots; small <i>Necrophilous</i> arthropods	7
<i>Necrophorus investigator</i>	Especially in forest, heather land, moist meadow	June to October	On small carcasses, fresh bone, in rotting fungi	Carcasses, maggots, small <i>Necrophilous</i> arthropods	4
<i>Necrophorus vespilloides</i>	Forest especially dry conifer forest; forest edge	April to November	On small carcasses, in dung, in rotting fungi	Carcasses, maggots, small <i>Necrophilous</i> arthropods	2
<i>Oeceoptana thoracica</i>	Forest, woods, garden, grassland, prefer forest area	April to August	On carcasses, in dung, in rotting fungi	Carcasses, dung, rotting fungi	1

In the research area, Geotrupidae used the carcass significantly longer than Silphidae. Geotrupidae species were collected by the pitfall traps until the 200th exposure day; however, after the 70th exposure day no Silphidae species were collected any more.

4.3 Decomposition process of carcasses

4.3.1 Decomposition stages

Decomposition stages are often used in forensic science to describe the decomposition process of carcasses. The most common definition of decomposition stages in the forensic science includes the fresh stage, the bloated stage, the decay stage, the post decay stage, and the skeletal stage. The five stages are divided as follows: fresh stage starts at the moment of death and continues until the bloated stage starts. Calliphoridae and Sarcophagidae arrive first at the fresh stage, and female flies will deposit eggs in the openings of the head. The bloated stage is caused by the metabolic process of the anaerobic bacteria, during the bloated stage the body is a distinct habitat, and masses of maggots are observed. The decay stage begins when the body deflates. Diptera-larvae are present during this stage. By the end of this stage, the flies will have completed their development and pupate in the surrounding soil. Subsequently, post decay stage starts when the body is reduced to skin, cartilage, and bone. Coleoptera replace Diptera as dominant taxa. In forensic science, besides the physical appearance, Diptera is the main taxon to distinguish the different decomposition stages. The skeletal stage is when only bones and hair remain, and no obviously carrion - frequenting taxa are observed (Goff 2009 a). However, in our research, at the skeletal stage, Geotrupidae, Dermestidae, Trogidae, and Cleridae were often found on bones.

The definitions of decomposition stages in scientific ecology are different; the decomposition stages are often connected with arthropod successions. Schoenly and Reid (1987) summarized the arthropod succession and the decomposition stages boundary of eleven published carrion studies, each author of the eleven cases has used their own explanations to describe the decomposition stages, and the length of decomposition stages of each case is different. For example, Bornemissza (1957)

described the decay stages of a guinea pig with initial decay, putrefaction, black putrefaction, butyric fermentation, and dry decay. Jirón and Cartín (1981) described the decay stages of a dog with discoloration stage, emphysematic stage, liquefactive stage, and mummification. In fact, decomposition stages with clear boundaries do not exist in the nature. The succession of arthropods which live on carrion is a continuum change, and hardly any carrion study completely supported a staged-based view of faunal succession (Schoenly & Reid 1987).

The assemblages of arthropods are influenced by many factors and are different in different seasons and habitats, so in this study, the decomposition stages were defined according to the change of physical features of carcasses, not the assemblages of arthropods. When a carcass is not open, clearly a bloated stage exists, in total four stages can be distinguished: the fresh stage, the bloated stage, the black purification stage (starts when the body deflates and the main feature is the carcass starts to turn black), and the mummification stage. Figure 4.3.1 shows that the bloated stage of carcass no. 5 started after five days exposure, the black purification stage started after 14 days exposure, and the decomposition process ended by the mummification stage.

When a carcass is open, no bloated stage occurs, and the decomposition stages include the fresh stage, the decay stage, and the skeletal stage. The decay stage is further divided into wet decay stage and dry decay stage according to the physical appearance of the carcass. During the wet decay stage the body is wet, when the dry decay takes place the body turns dry and most flesh are consumed. Figure 4.3.2 shows the decomposition stages of carcass no. 6. On 16.03.2011, as soon as the carcass was exposed, the fresh stage started. On 28.03.2011, carcass no. 6 was in the wet decay stage, on 13.05.2011 carcass no. 6 was in the dry decay stage, and on 10.06.2011 it was in the skeletal stage.

Braack (1981) mentioned that the species richness and the diversity of the community is the highest around the transition from the wet to dry decay stage. However, according to the results of our research, the diversity index (H') fluctuated permanently around 2.0 (most often from 1.3 to 2.3), except carcass no. 4, the diversity index at carcass no. 4

was lower than 1.0 during the whole decomposition process, and the lowest value was $H' = 0.52$. The highest diversity index at different carcasses occurred on different days. Table 4.3.1 shows that when the number of arthropods reached the highest peak, the diversity index was relatively low, and no significant relation was found between the diversity index and the Tokeshi index. The diversity index in this study was calculated in taxon level, not in species level, that could be a possible reason caused different results with Braack (1981).



Figure 4.3.1 Decomposition process of carcass no. 5.



Figure 4.3.2 Decomposition process of carcass no. 6.

Table 4.3.1 Comparison of the diversity index (“C” is the abbreviation of carcass, “No.” is the number of the arthropods, “No. max” indicates the maximal number of arthropods during the whole decomposition process, “H” indicates the diversity index, “T” indicates the turnover index, “H’ max” indicates the maximal value of the diversity index during the whole decomposition process).

Carcass	Exposure day	No. max	H’	T	Exposure day	No.	H’ max	T
No. 1	13	3,353	1.44	0.53	16	2,593	2.21	0.16
No. 2	8	1,032	1.84	0.17	6	414	2.41	0.33
No. 3	5	498	1.91	0.36	14	172	2.26	0.23
No. 4	10	508	0.81	0.28	21	70	0.95	0.14
No. 5	19	3,089	0.79	0.36	28	34	2.03	0.34
No. 6	67	788	1.39	0.19	44	76	2.32	0.18
No. 7	47	1,465	1.78	0.15	90	141	2.25	0.64
No. 8	19	2,948	2.02	0.11	101	344	2.48	0.26
No. 9	23	2,807	1.03	0.16	54	537	2.39	0.18

4.3.2 Factors influencing decomposition process

In forensic research carcasses are mostly put into cages and covered by wires to protect them from vertebrate scavengers. When the influences of large scavengers are excluded, the duration and specificity of different decomposition stages are dependent on the weight of carcasses, season, biotic and abiotic conditions of the habitat, for example, the ambient temperature, the degree of humidity as well as the quality and quantity of insect colonization (Anton et al. 2011, Matuszewski et al. 2008).

However, in nature when large scavengers exist, they are the main factor to determine how long the carcasses will maintain. In terrestrial ecosystems, where large scavengers exist, carcasses are mainly consumed by scavengers, in summer 35 % to 75 % of the carcasses, and in winter 100 % (Carter et al. 2007). The investigation about European bison carcasses in Bialowieza primeval forest shows that the time of carcass depletion does not depend on body mass or activity of ravens, but it is affected by carcass openness and wolf visits (Selva et al. 2003).

Figure 4.3.3 shows that an opened deer carcass was consumed completely in three days in the research area. It is assumed the scavengers were wolves. In the sand area of Lieberoser Heide on 19.10.2013, six wolves depleted a whole wild boar carcass in several hours (Andre 2014, in prep). When large vertebrate scavengers exist in the research area, carcasses were consumed very fast, and no decomposition stages were observed.



Figure 4.3.3 A roe deer carcass was consumed in three days.

4.4 Interactions between the carcass and the ecosystem

The studies in forensic science mainly focus on how to use the succession pattern of arthropods, and the change of surrounding environment to estimate the minimum post-mortem interval (Archer 2003, Villet 2011). The present study has considered a reverse direction: how the carcasses influence the arthropod community and the surrounding environment?

Barton et al. (2012) illustrated the concept “Ephemeral Resource Patch”, which considered carcasses as a unique resource pool, and affected the ecological communities by the dynamic temporal decomposition and patchy spatial occurrence. Carter et al. (2007) illustrated the concept “Cadaver Decomposition Island”: cadaveric materials are rapidly introduced to below-ground floral and faunal communities, which results in the formation of a highly concentrated island of fertility. Each cadaver decomposition island is an ephemeral nature disturbance which can contribute to landscape heterogeneity, and they are a specialized habitat for a number of flies, beetles, and pioneer vegetation, which enhanced biodiversity in terrestrial ecosystems (Carter et al. 2007).

4.4.1 Arthropods live on carcasses

In the research area besides well-known necrophagous species (Staphylinidae, Silphidae, Geotrupidae, Histeridae, Dermestidae, Diptera, and Brachycera-larvae, Figure 4.4.1), bees, butterflies, wasps, Heteroptera, and Saltatoria were also observed using the carcasses directly.

Table 4.4.1 shows the guilds classification of functional communities in the research area. In forensic entomology, animals on carrion are divided to four guilds according to their dietary preferences, which include necrophages, omnivores, predators, and parasitoids (Villet 2001, Goff 2009 b). Compared to the original table from Goff (2009 b), Araneae, Lepidoptera, and Saltatoria are added. And it is the first time that Saltatoria were recorded using carcasses directly in Germany (Figure 4.4.3).

Table 4.4.1 Guilds classification of functional communities living on carcasses in the research area of Lieberoser Heide (modified according to Goff 2009 b).

Guild	Necrophagous species	Predators and Parasites	Omnivorous species
Dietary preferences	Obligate carrion-feeding	Prey on necrophagous species	Feed on carrion opportunistically, prey on necrophagous species
Members	Diptera, Maggots, Silphidae, Dermestidae, and Trogidae	Larvae and adults of Histeridae, Staphylinidae, Adults of Silphidae, Diptera, Hymenoptera, and Mesostigmata	Aranea, Lepidoptera, Saltatoria, Hymenoptera (Formicidae, Apiformes), and scavenging vertebrates

Fourteen species of butterflies were found 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 and Schiffermüller), *Celastrina argiolus* (Linnaeus), *Coenonympha pamphilus* (Linnaeus), *Hipparchia semele* (Linnaeus), *Nymphalis antiopa* (Linnaeus), (Figure 4.4.3), *Vanessa atalanta* (Linnaeus), *Vannesa cardui* (Linnaeus), *Polyommatus icarus* (Linnaeus), *Ochlodes sylvanus* (Esper), and *Polygonia calbum* (Linnaeus) (Gu et al. 2014).



Figure 4.4.1 Necrophagous species occurred in 30 minutes when carcass no. 5 was exposed (photo was taken on 18.05.2011).



Figure 4.4.2 *Nymphalis antiopa* on carcass.



Figure 4.4.3 Diptera and Saltatoria on bones.

The presence of carcasses increased the abundance of arthropods in the research area. Table 4.4.2 shows that at carcass no. 8, in total 37,818 individuals were collected by the first four traps and only 3,540 individuals were collected by the last four traps.

Table 4.4.2 Comparison of spatial distributions of arthropods.

Carcass	Number of arthropods		Number of taxa	
	First four traps	Last four traps	First four traps	Last four traps
No. 1	7,891	2,844	26	26
No. 2	3,076	1,517	23	18
No. 3	2,748	777	22	15
No. 4	1,247	225	18	11
No. 5	2,603	177	15	9
No. 6	2,799	729	26	16
No. 7	5,095	2,480	27	24
No. 8	37,818	3,540	28	28
No. 9	13,241	3,467	27	27

Table 4.4.2 shows that there is a remarkable difference of the numbers of arthropods collected at different carcasses, therefore, detrended correspondence analysis (DCA) was used to analyze the similarity of occurrence of arthropods at different carcasses. The first axis explains 44.7 % of the taxa abundance variance, and the first two axes

explain 56.4 % of the variance. Three hypotheses are drawn from Figure 4.4.4. Firstly, carcasses with similar weights locate near to each other, therefore, carcass no. 8, and no. 9 are away from other carcasses. Secondly, carcasses exposed in same habitat locate near to each other. Carcass no. 5 was the only one which was exposed in forest; therefore, it locates far away from others. Thirdly, carcasses exposed in the same season locate near to each other; therefore, carcass no. 3 and no. 4 are near to each other.

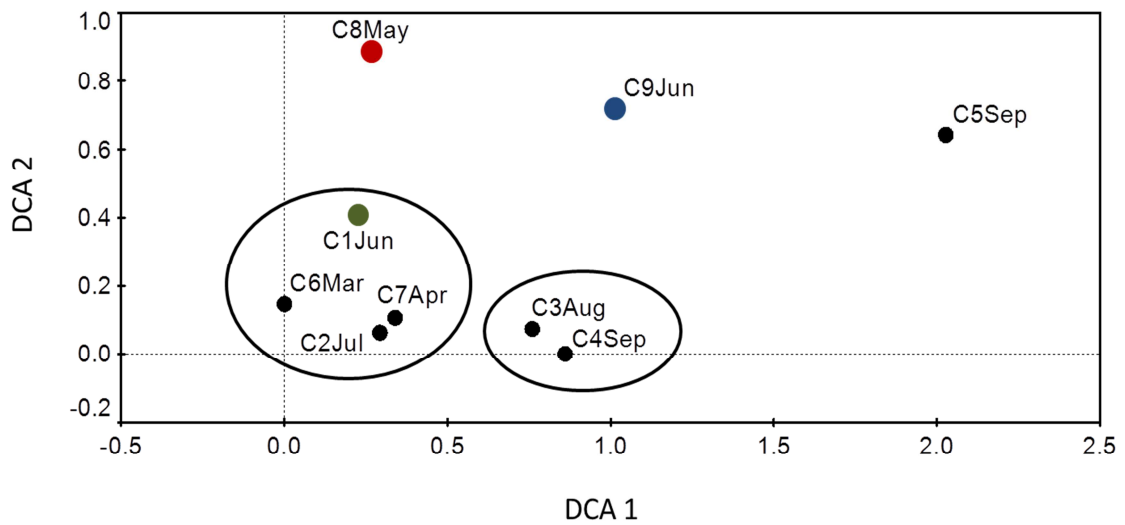


Figure 4.4.4 Ordination of the detrended correspondence analysis based on the occurrence of arthropod taxa (DCA), (Black: *Capreolus capreolus*; green: *Meles meles*, red: *Cervus elaphus*, blue: *Sus scrofa*. Abbreviation of “C1Jun” means carcass no. 1 was exposed in June).

In order to prove these hypotheses, canonical correspondence analysis (CCA) was used to analyze the related parameters. Environmental parameters include the mean temperature and the precipitation of the first month when a carcass was exposed (Table 4.4.3). Carcass parameters include the weight and the openness index of the carcasses, the openness indexes are defined in three different levels (Table 4.4.4).

Table 4.4.3 Environmental parameters (source: <http://www.wetterkontor.de>, weather station: Cottbus).

Carcass	First month of exposing	Average temperature (°C)	Precipitation (mm)
No. 1	Jun. 2009	15.3	93.8
No. 2	Jul. 2009	17.4	108.8
No. 3	Aug. 2009	18.5	48.9
No. 4	Sep. 2010	11.4	69.8
No. 5	Sep. 2010	11.4	69.8
No. 6	Mar. 2011	4.7	34.5
No. 7	Apr. 2011	10.9	23.1
No. 8	May. 2011	14.9	46.1
No. 9	Jun. 2011	16.5	54.6

Table 4.4.4 Definition of openness index.

Openness index	Definition and characteristic	Carcass
1	Carcass is with no open wound, during decomposition there is a significant bloated stage	No. 1, No. 5
2	Carcass is with open wound, but all inside tissues are still in the carcass	No. 8
3	Carcass is completely open at abdomen and no inside tissues is left	No. 2, No. 3, No. 4, No. 6, No. 7, No. 9

Figure 4.4.5 shows the results of CCA, the first axis explained 20.6 % of the variance of the occurrence of arthropods, and the first two axes explained 35.2 % of the variance. Carcass no. 1 and no. 5 locate near to each other. The openness index of both carcasses is 1. Carcass no. 2, no. 3, no. 4, no. 6, no. 7 and no. 9 locate near to each other. The openness index of all these carcasses is 3. Carcass no. 8 is far away from others. The weight of carcass no. 8 is the heaviest, and its openness index is 2.

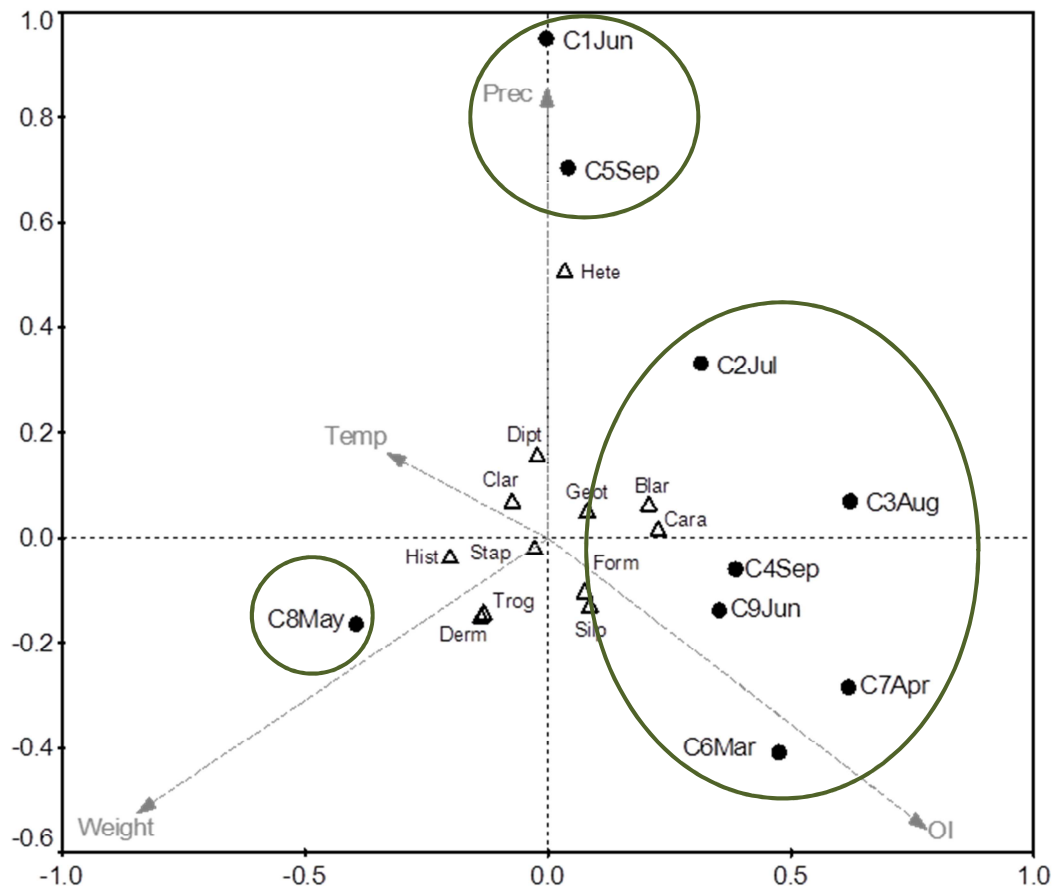


Figure 4.4.5 Ordination based on canonical correspondence analysis (CCA). Abbreviations of arthropod groups: Heteroptera (Hete), Diptera (Dipt), Coleoptera-larvae (Clar), Staphylinidae (Stap), Histeridae (Hist), Dermestidae (Derm), Trogidae (Trog), Geotrupidae (Geot), Brachycera-larvae (Blar), Carabidae (Cara), Formicidae (Form), Silphidae (Silp); abbreviations of environmental parameters: temperature (Temp), precipitation (Prec); abbreviations of carcass parameters: weight (Weight), openness index (OI), duration of exposing (Dur). “C1Jun” is the abbreviation of carcass no. 1 exposed in June.

Table 4.4.5 shows the marginal effects and the conditional effects of the CCA analysis. According to the conditional effects, none of the parameters have significant relation with the occurrence of arthropods around carcasses. However, the marginal effects show that the weight of carcasses is the most important parameter, and the openness index is the second important one. Compared to environment parameters, carcasses parameters have stronger influence on the occurrence of arthropods.

Table 4.4.5 Marginal effects and conditional effects of canonical correspondence analysis (see Figure 4.4.5).

Var. No.	Marginal Effects		Conditional Effects			
	Variable	Lambda 1	Variable	Lambda A	P	F
1	Weight	0.09	Weight	0.09	0.206	1.61
2	OI	0.09	OI	0.08	0.260	1.40
4	Prec	0.06	Temp	0.06	0.388	0.95
3	Temp	0.06	Prec	0.01	0.854	0.21

Table 4.4.5 shows that the average temperature is not a main factor of influencing the occurrence of arthropods. However, the temporal distributions of arthropods have differences in different seasons. When the temperature is below 6 °C, most arthropod activity ceases (Goff 2009 b). According to the results of the present research, in spring and autumn, the number of arthropods reached the first peak mostly after the 10th exposure day (e.g. carcass no. 4, carcass no. 6, and no. 7), and the first peak of arthropods at carcass no. 7 even occurred on the 66th exposure day. In summer, the number of arthropods reached the first peak earlier, mostly between the 4th and the 6th exposure day (e.g. carcass no. 1, carcass no. 3, carcass no. 8, and carcass no. 9). Therefore, a specific rank correlation analysis between the number of arthropods and the minimal temperature has been done.

Spearman Rho test was used to check the relation between the temperature and the number of arthropods. The null hypothesis is that there is no significant relation between the number of arthropods and the minimal temperature on certain sampling day. Table 4.4.6 shows that there are significant relations between the number of arthropods and the minimal temperature at carcass no. 6, no. 7, no. 8 and no. 9 ($p < 0.05$). However, the Spearman's Rho values (r_s) are quite low, which means there is a significant relation but not strong.

Table 4.4.6 Results of Spearman Rho test (r_s), “C” is the abbreviation of carcass, “No. 1” is the abbreviation carcass no. 1, “ $p < 0.05$ ” is indicated by the grey color.

C	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9
r_s	0.467	- 0.390	0.242	0.174	- 0.303	0.380	0.375	0.271	0.458
p	0.051	0.900	0.305	0.610	0.314	0.021	0.003	0.038	0.000

4.4.2 Vertebrate scavengers

Obligate scavengers, for example the old and new world vultures, will become extinct if there are not sufficient carcasses, and nearly all carnivore vertebrates consume fresh carrion (DeVault et al. 2003). Large long - lasting carcasses may play an important role by providing food to facultative and obligate vertebrate scavengers for long periods especially under severe winter conditions (Selva et al. 2003). In total, 70 species of vertebrates were observed using carcasses in Europe (Beekers et al. 2014, in prep). Endangered species such as wolf, black vulture, and griffon vulture were found near carcasses. In the research area of Lieberoser Heide in total 22 species of vertebrate scavengers were recorded (Table 4.4.7).

Ravens and raptors were observed in high abundance as diurnal visitors, they came to the carcass during the morning hours, however, wild boar, red fox and wolf were observed at the carcass during the night (Lepaleni et al. 2013). Ravens did not only feed directly on carcass, but also fed on maggots and Coleoptera-larvae which migrated away from the carcass and pupated in surrounding soil.

White - tailed eagle and red fox were mainly solitary feeders. Foxes mostly came alone, unless a mother fox came with young foxes. Adult red fox sometimes showed up together with several young foxes. Young foxes were mainly observed feeding on the insects on the carcass. Wild boars always came in a group.

Ravens were observed solitarily, in pairs or in groups. The largest group of ravens feeding at the same time one on carcass included 25 individuals. Ravens were feeding, playing, mobbing, and grooming on the carcass (Kielon 2009, Lova 2009). According

to the photo documentations in 2010 and 2011, in winter more vertebrate scavengers visited the carcasses and fierce fights happened sometimes because of the lack of other food resource.

Table 4.4.7 List of vertebrate scavengers in Lieberoser Heide (Krawczynski et al. 2009, Südbeck et al. 2009, Meinig et al. 2009, FFH list is according to <http://www.fauna-flora-habitatrichtlinie.de/>).

No.	Animal species	Scientific name	EU Status, RL D
1	Wolf	<i>Canis lupus</i>	FFH* II; 1
2	Fox	<i>Vulpes vulpes</i>	
3	Raccoon dog	<i>Nyctereutes procyonoides</i>	
4	European badger	<i>Meles meles</i>	
5	Wild boar	<i>Sus scrofa</i>	
6	Domestic cat	<i>Felis silvestris catus</i>	
7	Sea eagle	<i>Haliaeetus albicilla</i>	VS RL I
8	Red kite	<i>Milvus milvus</i>	VS RL I
9	Marsh harrier	<i>Circus aeruginosus</i>	VS RL I
10	Common buzzard	<i>Buteo buteo</i>	
11	Hoopoe	<i>Upupa epops</i>	RL 2
12	Common raven	<i>Corvus corax</i>	
13	Hooded crow	<i>Corvus corone cornix</i>	
14	Magpie	<i>Pica pica</i>	
15	Eurasian jay	<i>Garrulus glandarius</i>	
16	Great tit	<i>Parus major</i>	
17	Blue tit	<i>Parus caeruleus</i>	
18	Common blackbird	<i>Turdus merula</i>	
19	European stonechat	<i>Saxicola rubicola</i>	V
20	Whinchat	<i>Saxicola rubetra</i>	3
21	European robin	<i>Erithacus rubecula</i>	
22	Great grey shrike	<i>Lanius excubitor</i>	2

4.4.3 Soil and vegetation

After two months of exposure, a vegetation ring occurred around carcass no. 8, with the time going on, the ring developed to a vegetation island (Figure 4.4.6). In order to check how the carcass influenced the soil content, 60 soil samples from the center of carcass no. 8 were collected after one year (on 20.07.2012). The result of the soil parameters shows that the soil samples nearer to carcass no. 8 contained higher content of water, ammonium, nitrate and phosphate (Laaser & Lutze 2013). Soil samples at carcass no. 7 were collected after 203 days of exposure, at carcass no. 9 after 147 days of exposure. The results of the soil parameters from these two carcasses show that the samples near to the carcasses contained more ammonium, nitrate and phosphate (Mrosk 2012).



Figure 4.4.6 Cadaver Decomposition Island (CDI) around carcass no. 8.

Soil samples at carcass no. 1 were collected one year after the decomposition in June 2010. At carcass no. 1, Collembola in the soil has been also investigated. The number of Collembola was higher in the soil samples near to the carcass (Klonowski & Rößler 2013). *Sphaeridia pumilis* (Krausbauer), *Sminthurus nigromaculatus* (Tullberg), and

Hypogastrura vernalis (Carl) showed significantly positive relation to the carcass, and 94.6 % of all 7,606 Collembola were *Hypogastrura vernalis* (Gu et al. 2014).

4.5 Food webs based on carcasses

4.5.1 The importance of carcasses for the food web

Carcasses are relatively easy to handle since they cannot defend themselves, thus scavenging allows access to excellent food resources with no additional prey death and without the consumer exerting energy to chase or subdue its prey (Wilson & Wolkovich 2011). The carrion consuming behaviors of scavengers cause serious consequences for the pattern and stability of food webs (Beasley 2012). As a high-quality form of detritus, carcasses regulate the population of carcass consumers which can be analyzed by a bottom - up model. Furthermore it influences the potential prey of facultative scavengers which can be analyzed by a top - down model (Wilson & Wolkovich 2011, Cortés-Avizanda et al. 2009). It has been proved by the research carried out in Bialowieza forest in 2008 that carrion permeated into apparently distant trophic levels: in the proximities to carcass sites, the number of facultative scavengers (red fox, common ravens, and jays) increased significantly, conversely their potential prey (brown hares and squirrels) showed the opposite trend (Cortés-Avizanda et al. 2009).

4.5.2 Carcass food webs in the research area

Figure 4.5.1, Figure 4.5.3 and Figure 4.5.5, respectively, describe the main carrion consumers during the decomposition in spring, summer, and winter in 2011. The grey boxes represent the carcass, the height of the grey box roughly represents the weight of the carcass, and the length of the grey box indicates how long the carcass remains in a similar physical appearance which could be considered as the length of one decomposition stage. The blue arrows represent arthropod groups, and the pink arrows represent vertebrate scavengers. The dashed lines indicate the active period of different groups. Figure 4.5.1 and Figure 4.5.3 exclude wolves.

Figure 4.5.1 shows that in spring the decomposition process of a carcass includes five phases, the 1st phase is from early March to end of April (the fresh stage and the decay

stage), the 2nd phase is from May to early June (the wet decay stage), the 3rd phase is from early June to early July (the dry decay stage), the 4th phase is from early July to end of August (the skeletal stage), and the 5th phase is from end of August to middle of September (the remain stage).

The 1st phase lasts quite long in the early spring because of the low temperature. In this phase the carcass is decomposing slowly, and the physical appearance has no significant change. The main carcass consumers are vertebrate scavengers. In the middle of 1st phase, Diptera, Silphidae, and Staphylinidae occur, the number of arthropods increases slowly, at the end of the 1st phase, Geotrupidae, Dermestidae, and Cleridae occur.

In the 2nd phase, the main carcass consumers are arthropods and vertebrate scavengers. In this phase, the number of arthropods increases very fast and reaches the highest peak, and most of the flesh is consumed. In the 3rd phase (the dry decay stage), some dry flesh, bones, skin and hair are left, main carcass consumers are arthropods. Coleoptera-larvae are present between the 2nd and the 3rd phase. In the 4th phase, only hair and bones are left. The number of arthropods decreases, no Silphidae, Diptera, and Staphylinidae are found anymore after the 4th phase. In the 5th phase, several pieces of bones are left, sometimes nothing left at all. Dermestidae and Cleridae are found on the small pieces of bones and around.

Figure 4.5.2 describes the variation pattern of six taxa of arthropods in spring. No arthropods occur in March except small amount of Diptera. From April on, the number starts to increase and most taxa reach the peak in May. The numbers of Silphidae and Coleoptera-larvae start to decrease after the 2nd phase. Staphylinidae, Geotrupidae, Diptera, and Dermestidae are present during the whole decomposition process, and the numbers of these four taxa fluctuate during the whole decomposition process with no conspicuous peaks.

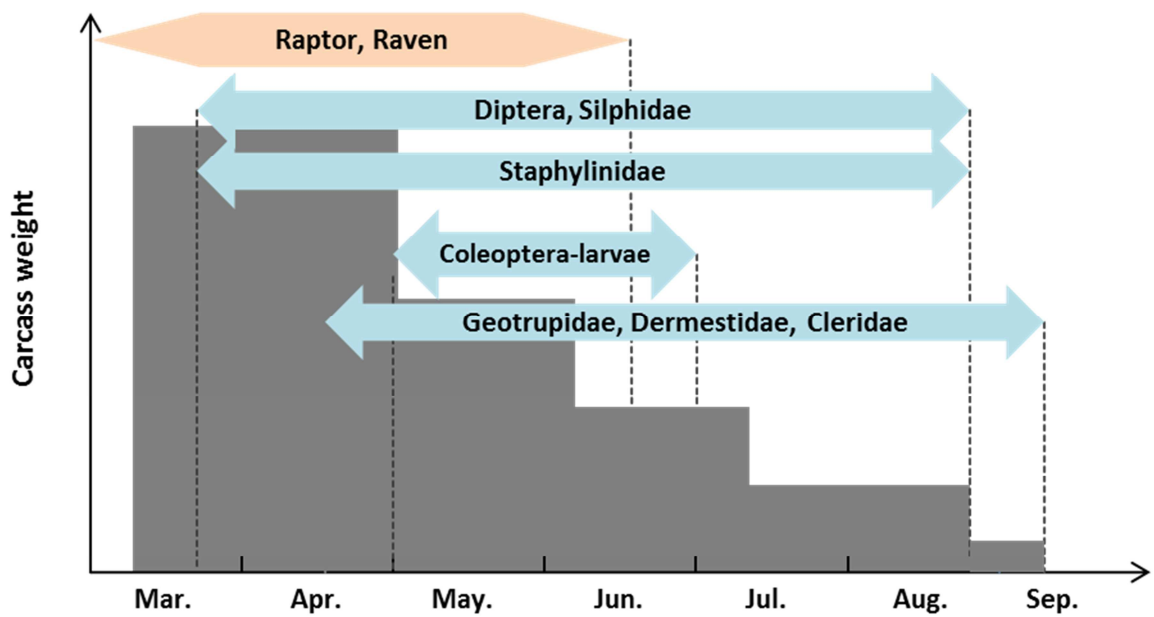


Figure 4.5.1 Food web model based on carcasses in spring.

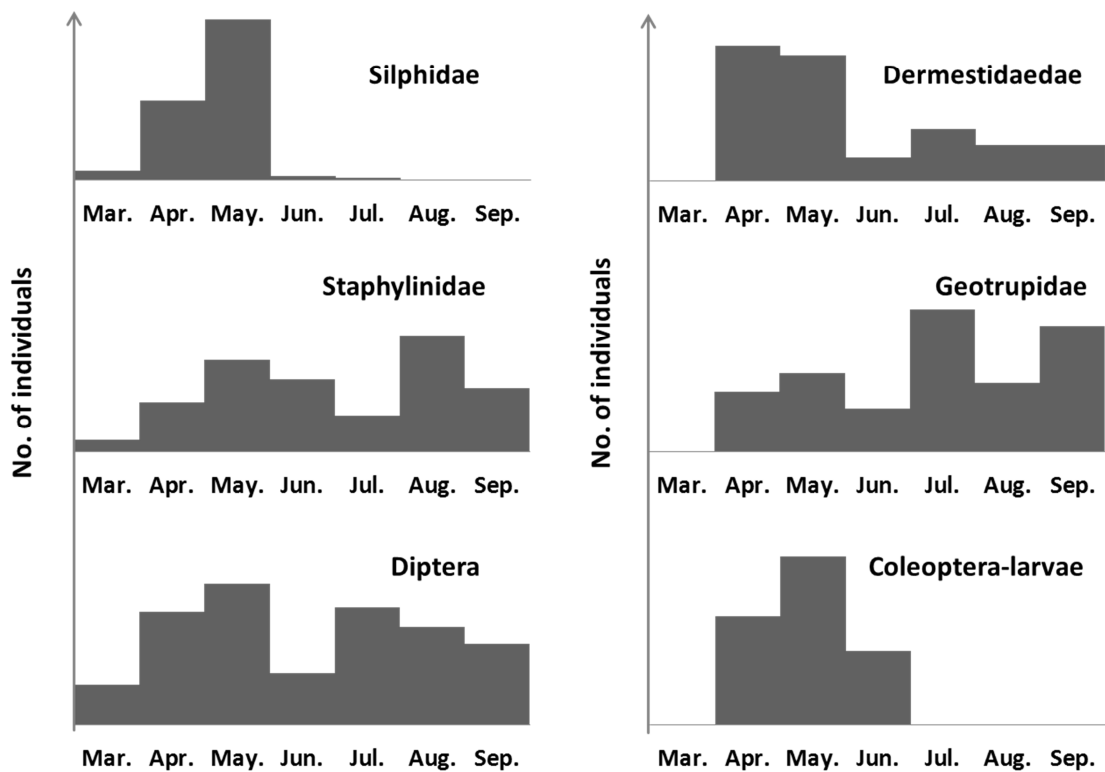


Figure 4.5.2 Variation of six arthropod taxa in spring.

Figure 4.5.3 describes the decomposition process of the carcass and the main carcass consumers in summer. The decomposition process includes four phases. When a carcass is exposed at the beginning of June, the 1st phase is from early June to late June (the fresh stage and the wet decay stage), the 2nd phase is from late June to late July (the dry decay stage), the 3rd phase is from late July to the middle of August (the skeletal stage), the 4th phase is from the middle of August to early September (the remain stage). Compared to the food web model in spring (Figure 4.5.1), all decomposition stages are much shorter, and the carcass is depleted faster.

At the beginning of the 1st phase, vertebrate scavengers, Silphidae, Histeridae, Staphylinidae, Geotrupidae, and Diptera occur as soon as the carcass is exposed. Brachycera - larvae occur in the middle of the 1st phase and disappear about five days later. Histeridae occur since the middle of the 1st phase and last till the end of the 3rd phase. Coleoptera-larvae occur in the end of the 1st phase, and last till the end of the 3rd phase. Most flesh of the carcass is consumed in the 1st phase. In the 2nd phase, skin, hair, bones and a few dry fleshies are left. In the 3rd phase, dry skin, hair and bones are left. In the 4th phase, several pieces of bones are left; sometimes nothing is left at all. From the 2nd phase to the end, arthropods are the main consumers. Geotrupidae, Staphylinidae, Dermestidae, and Cleridae are present during the whole decomposition process.

Figure 4.5.4 shows that the numbers of Silphidae, Diptera, Staphylinidae, Histeridae, Coleoptera-larvae, and Brachycera-larvae reach the highest peak in the 1st phase, after that the numbers decrease sharply. The numbers of Geotrupidae and Dermestidae increase in the 1st phase, and reach the peak in the 2nd phase, after that the numbers decrease.

Schoenly & Reid (1987) mentioned that the carrion arthropod community develops primarily as a continuum of gradual change: rapid at first, slow during peak activity, and erratic in the final days as carcass resources become depleted. The succession of arthropods in summer in this study followed this pattern, however, in spring no pattern was found.

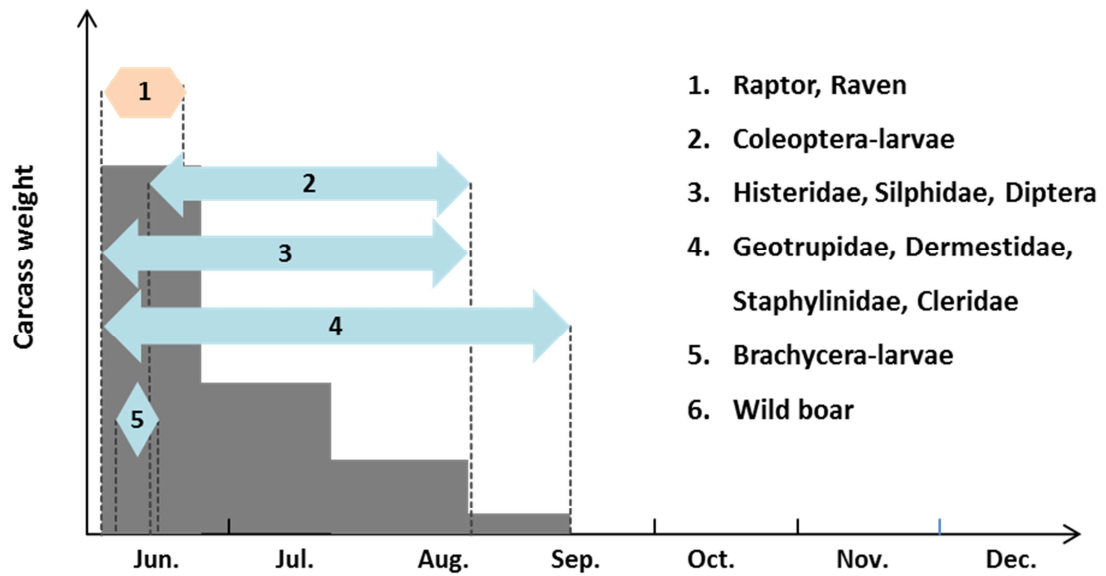


Figure 4.5.3 Food web model based on carcasses in summer.

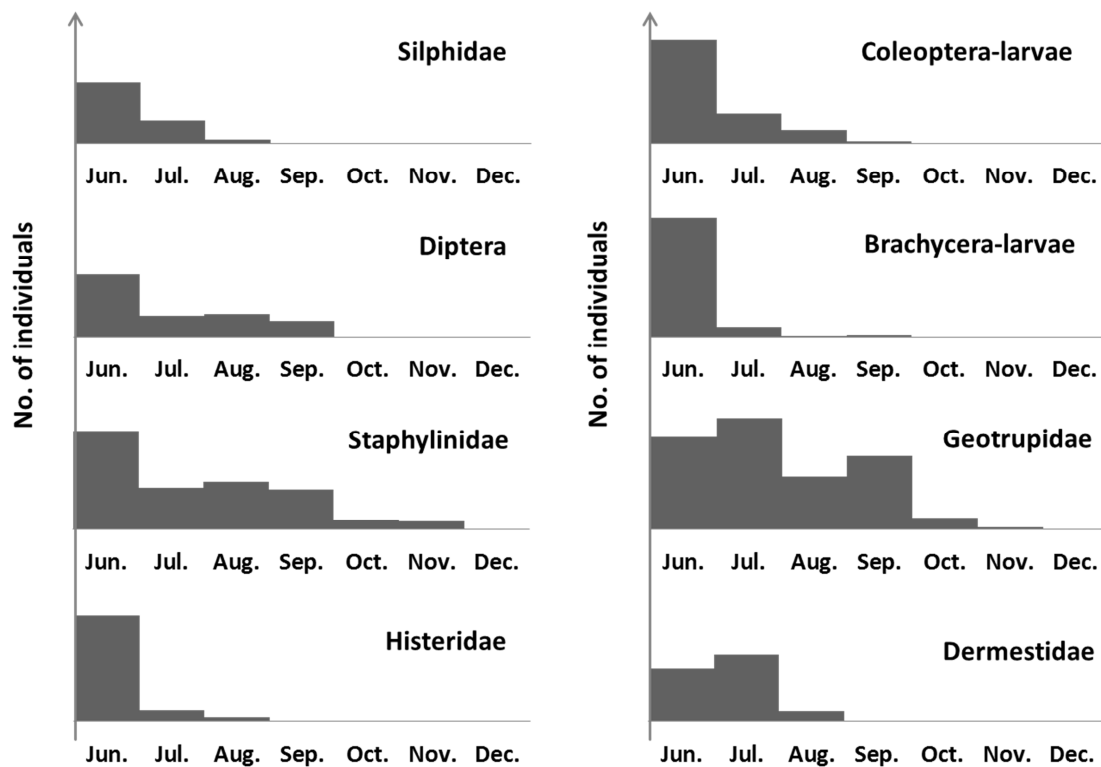


Figure 4.5.4 Variation of eight arthropod taxa in summer.

Figure 4.5.5 describes the decomposition process of a carcass in winter. In winter no significant decomposition stages exist, since carcasses are fast depleted. The main carcass consumers in winter are vertebrate scavengers. When wolves exist, the carcass would be completely consumed in several hours. Raptors and ravens always find the carcass first. In most cases, they share the carcass peacefully, but competitions also happen sometimes.

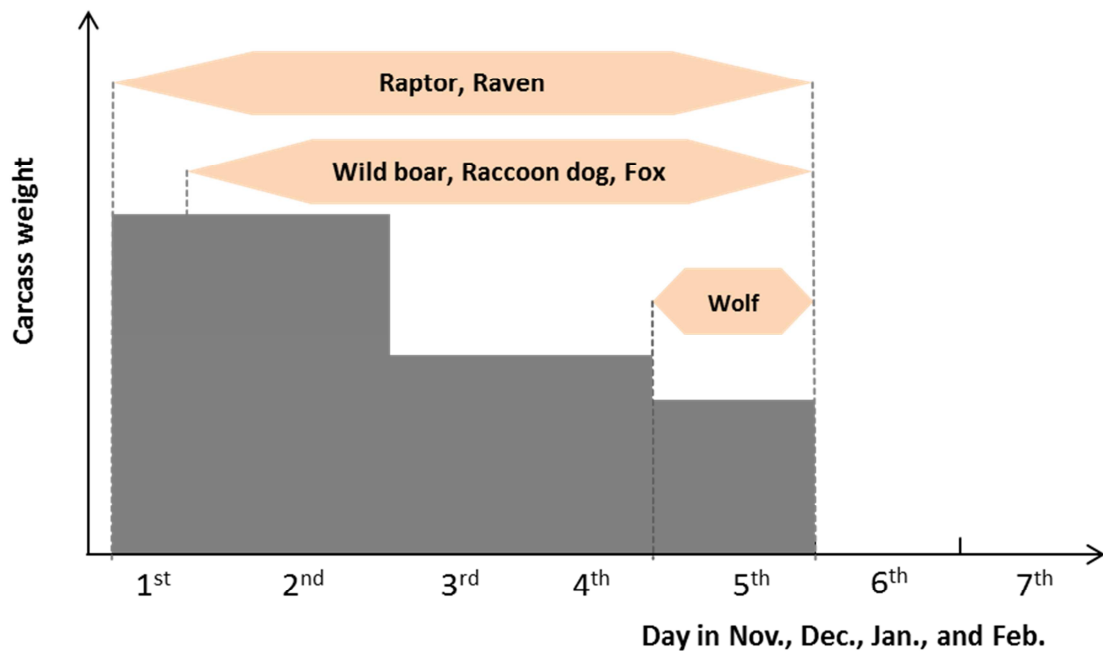


Figure 4.5.5 Food web based on carcasses in winter.

Figure 4.5.6 is a part of the trophic position between the omnivore-detritus and the omnivore-animals (Schoenly 1991). Schoenly (1991) mentioned that Hemiptera are not direct carrion consumers, but as omnivores they are involved in the carrion food web. In the research area, three species of Hemiptera were found on carcasses. *Pyrrhocoris apterus* (Linnaeus) and *Coriomeris denticulatus* (Scopoli) were found frequently on carcasses without observing any specific behavior. *Alydus calcaratus* (Linnaeus) was found not only sucking on fresh carcasses but also feeding on carcasses during the dry stage after rain (Gu et al. 2014).

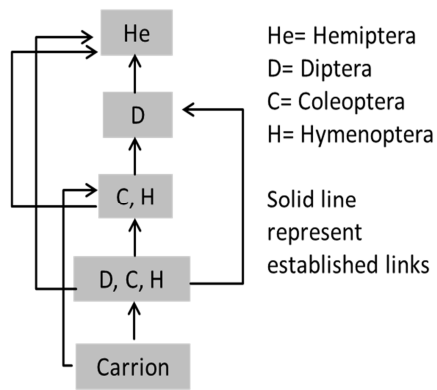


Figure 4.5.6 Omnivore interactions for each omnivore-detritus and omnivore-animal trophic position (according to, Schoenly 1991, modified).

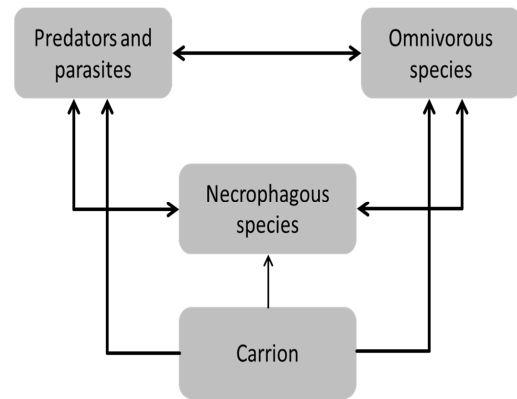


Figure 4.5.7 Interactions among three important carrion communities according to guilds.



Figure 4.5.8 Maggots on carcass no. 6.



Figure 4.5.9 *Necrodes littoralis* preys on maggots.



Figure 4.5.10 Formicidae scavenges on Diptera.



Figure 4.5.11 Mites phoresy on *Thanatophilus rugosus*.

Schoenly (1991) mentioned that Hymenoptera do not only use carcasses directly but they are also involved in different trophic levels (Figure 4.5.6). According to the results of our research, bees of the genera *Megachile* and *Andrena* frequently have visited the carcasses in spring. Formicidae have also been observed at larger carcasses. They preyed on maggots, scavenged dead insects of the families Calliphoridae (Figure 4.5.10) and Geotrupidae and in some cases carried bits of decaying material.

Figure 4.5.7 shows the interaction among different carrion communities: predators and parasites, omnivorous species, and necrophagous species in the research area. Figure 4.5.8 shows Brachycera-larvae are consuming the carcass. Figure 4.5.9 shows a predator (*Necrodes littoralis*) is preying on necrophagous species (Brachycera-larvae). Figure 4-5-11 shows phoresy of adventive species (Acari). A *Thanatophilus rugosus* individual is transferring the mites to the carcass.

The food web based on large vertebrate carcasses is very complex. Besides the direct carcass consuming activities, there are many known and unknown interactions among the carcass consumers and visitors. Figure 4.5.1, Figure 4.5.3, and Figure 4.5.5 present a rough view of how the weights of carcasses decrease during the decomposition, the focus is on the interaction between the carcass and the consumers, interactions between the consumers can be added on these basic models when more related data are available.

5 Conclusions and recommendations

There was no certain model of decomposition stages for all carcasses. In the research area, when the carcass was not open, a conspicuous bloated stage was observed. After the bloated stage there was a long black putrefaction stage, normally no vertebrates used such carcasses any longer. When the carcass was open (large enough for small scavenger to access, e.g. ravens), no bloated stage occurred. During the decay, the black putrefaction stage also existed, but for a shorter time. When no large scavengers existed in the exposition habitat, the main factor influencing the decomposition process was the openness index and the weight of the carcass. However, when large scavengers existed,

especially wolves, the carcass was finished in several hours, and no decomposition stage was observed.

In the research area, the main carcass consumers in summer were arthropods (Coleoptera-larvae, Dermestidae, Diptera, Geotrupide, Histeridae, Brachycera-larvae, Silphidae, and Staphylinidae), ravens and raptors. Besides the well-known carrion arthropods, grasshoppers, butterflies, bees were also observed using carcasses directly. However, because of the collection method (pitfall traps are only able to collect the crawling insects) no exact number was available. In winter, the main consumers of carcasses were wild boars, foxes, wolves, ravens and raptors.

In summer, there was a certain assemblage of carrion arthropods at carcasses with open wounds. It is the same as the results from Schoenly & Reid (1987) that the carrion arthropod community develops primarily as a continuum of gradual change: rapid at first, slow during peak activity, and erratic in the final days as carcass resources become depleted. But in spring and late autumn, no assemblage model was advanced. Under cold weather condition the fresh stage was relatively long and arthropods were inactive. The main factors influencing the occurrences of arthropods were the habitat where the carcass was exposed, the weight and the openness of the carcass. Temperature and precipitation also had influences, but not as strong as the properties of carcass itself.

The distribution and occurrence of arthropods around the carcasses has provided a new view for indicating the decomposition stages. In forensic science, Diptera are always considered as the most important indicators for identifying the decomposing stages. But in nature, because of complex interactions (prey of maggots), the amount of Diptera and maggots are difficult to evaluate. From the results of this research, Silphidae were the most conspicuous indicators for the end of the decay stage.

The existence of carcasses in the research area has significantly increased the animal diversity and abundance. In the pitfall traps near to the carcass, significantly more arthropods are collected. Carcasses have positive influences on the vertebrates, the vegetation and the surrounding soil. Cadaver decomposition islands around carcasses have been frequently observed.

The ideal carcass using for food web restoration should merit following three requirements: firstly, it should be a large carcass (roe deer, red deer, and wild boar). Compared to small carcasses (rabbit and mouse) larger carcasses remain in the habitat much longer and have more potential to develop to a carrion decomposition island. Secondly, the carcass should have big open wounds on the abdomen, as an access for small sized scavengers which cannot open the carcass by themselves (for example, ravens, fox, raccoon dog, and pine marten). Thirdly, the carcass should not be treated with any drugs. Medicine pollution of carrion consumers must be avoided. Therefore, wild games which did not die of disease are the optimal carcass resource. The carcass should be distributed in the research area randomly and discrete, which is exactly the same as killed by a prey.

At natural reserve areas, dead local wild animals should be kept in the original area where they lived. It saves the transport fees, and guarantees the nutrient recirculation within the environment. For using carcasses in destroyed areas for restoration, for example, post-mining areas or some polluted area are not yet investigated, this would be a new research direction.

Some improvements can be suggested for further research. When the decreasing weight of carcass and the weight of carrion consumers are measured every sampling day, then a more specific carrion food web including energy transform pulse can be calculated and modelled. Collecting the pitfall traps and doing long time direct observation at the carcass area every day can provide a more exact successional pattern of arthropods on carcasses.

The models of food web based on carcasses and the arthropod distribution models in this study were built under strict limitations. They are only suitable to habitats in the research area. The carcass must be opened before exposition. The models should not be used as a standard model for all studies. However, people can follow the research method and statistical procedures to set up similar carrion food web models in other habitats. Before using carcasses as a method of restoration, it is necessary to do the

basic research on the carrion food web in certain areas which is necessary for a feasibility evaluation.

Public acceptance of carcasses is also an important issue. Can people accept that in the forest they always visit occurs a carcass? Can people accept that the number of wolves, and wild boars increase in their living area? How people think about putting carcasses back to the nature will influence the new regulation and legislation concerning carcasses.

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