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Decomposition and Coleoptera succession on exposed carrion of small mammal in Opava, the Czech Republic

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Abstract

In 1997 and 1998, field studies on exposed rat carcasses were conducted in Opava, the Czech Republic, to describe the decomposition process and Coleoptera succession patterns. Coleoptera assemblages were monitored during three 40-d succession series conducted in spring, summer and autumn in two different habitats: meadow and deciduous forest. The rate of decomposition was studied in carcasses open to insects and isolated from them. The stages of decomposition recognised in this study follow Reed's classification: fresh, bloated, decay and dry stage. Carcass in summer decayed much faster than in spring and autumn and the decomposition of insect-free carcasses was less rapid than that of carcasses exposed to insects. A total of 145 Coleoptera species belonging to 22 families was recorded on the carcasses. The number of species in the succession series increased from the fresh stage, reached a maximum in the decay stage and gradually declined in the dry stage. The greatest diversity of Coleoptera was found in spring, followed by summer and autumn. More species were collected in forest site than in meadow. Four ecological groups, each characterised by a specific type of carrion association and varying in food specialisation and species biology, have been distinguished.

1. Introduction

Decomposition is a natural and necessary process responsible for the return of organic material, such as dead plant or animal matter, to the ecosystem. Carrion, or dead animal matter, represents a temporary and changing food source for a varied and distinct community of organisms [30]. Insects, especially Coleoptera and Diptera, are the major components of this community and constitute a primary element involved in the decomposition process. Specialisation is a consequence of the ephemeral nature and patchy distribution of animal remains [12,13] and the dietary chemistry of necrophagous animals. Necrophages have enzymatic complements similar to carnivorous species (e.g. Silphidae) or chemical agents to digest peptide chains of keratin, col-

lagen or elastin (e.g. Dermestidae, Trogidae) [30]. Many other species of predators and parasites are associated with necrophages. Altogether, at least 100 typical carrion insect species are found at a single carcass, and in addition, many other species, which are trapped by chance (e.g. [22,23,27]). Previous studies have shown that in the absence of vertebrate scavengers, arthropods arrive at remains in definite and predictable patterns (e.g. [3,22,27,28]) and play a major role in carrion decomposition. Many studies have focussed on the influence of niche dimensions on species assemblages, such as the influence of different decomposition stages, different environments and seasons ([4,6,9,10,16,28,35] and others).

The study of seasonal insect succession on carrion is of special concern. It provides a dynamic profile of seasonal abundance of individual carrion species and a perspective on the shifting species composition of the carrion community with changing seasons. There are few studies that span more

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than one season and attempt to describe the succession of the entire carrion insect community in each season [16,26,31,35]. We lack data particularly from Central Europe. Carrion decomposition and succession as well as the biology, phenology, biogeography or habitat preference of necrophagous insect communities are fundamental to forensic entomology, but relatively few studies have dealt with these aspects [5].

2. Materials and methods

2.1. Site descriptions

The study was conducted in the surroundings of the town of Opava (Suché Lazce village; 49°54 N; 18°00 E), in the Opavská pahorkatina hills, the Czech Republic. This area is characterised by an average annual temperature of 7.9 °C and average annual precipitation of 629 mm (data from the observatory in Opava). Two different sites were selected 1.5 km apart: grassy meadow and deciduous forest. Both sites were situated in gradual north-west slopes, at an altitude of around 320 m.

2.2. Sampling procedure

Grey laboratory rats (*Rattus norvegicus* Berk), representing typical small mammals, were used as bait. Fresh rat carcasses (weight 70–80 g) were placed into baited traps as described below.

The trap was based around two modified plastic garden vessels: the external width of the bottom outlet was 20 cm in diameter and the upper outlet was 25 cm in diameter (20 cm deep); the internal width of the bottom outlet was 15 cm in diameter and the upper outlet was 20 cm in diameter (25 cm deep). The external vessel was cut down so that the external one was 10 cm taller after installation. The lip of the internal vessel was protected by a net, in basic version with meshes of 1 cm in diameter. The trap has been described in detail previously [17].

The traps were installed by burying the external vessel in the ground with the lip flush with the soil surface. The internal vessels were filled with soil, with the surface flush with the soil surface around the trap. The baits (carcasses) were placed on the soil surface in the internal vessels and fixed on pieces of metal net (for easy service during weighing). The external vessels were filled with a preservative solution (formaldehyde), and detergent.

Sampling was conducted during three 40-d periods which were chosen in spring (5th May–13th June 1998), summer (16th July–24th August 1997) and autumn (1st October–9th November 1997). The traps were serviced every day in 24-h intervals during the first 20 d of carcass decomposition, the last inspection was carried out on the 40th day. The time of manipulation and sampling did not exceed 10 min to keep the disturbance of carcasses at a minimum and maintain the

integrity of the microcommunity. One of the traps in each stand was always isolated from insects by a net with the diameter of meshes 0.8 mm to enable comparisons of decomposition processes with and without insect participation. The insects in the solution were sieved with a tea strainer, preserved in 70% ethyl alcohol and identified in the laboratory. Only the insects that fell into the trap were collected; individuals observed on the carcass body were not collected in order to retain all the factors that affected the natural decomposition processes. The daily maximum and minimum ground surface temperatures and humidity were recorded in the surroundings of the individual carcasses during the first 20 d of decomposition (Fig. 1). Actual humidity was measured between 10 and 11 AM.

Some of the live blowfly maggots were separated from corpses and put into breeding vessels with soil to obtain adults. These adults were used for species determination.

2.3. Determinations

Listed specialists identified the following Coleoptera groups: Histeridae part., Dermestidae, Leiodidae part., Anobiidae, Rhizophagidae—J. Vávra (Ostrava); Leiodidae part.—Z. Švec (Praha); Carabidae part.—J. Stanovský (Ostrava); Nitidulidae—J. Jelínek (Praha); Cryptophagidae, Lathrididae part.—P. Průdek (Brno); Lathrididae part.—P. Míka (Praha); Staphylinidae: Staphylininae: Philonthini—P. Krásenský (Pardubice); Staphylinidae: Proteininae, Omaliinae, Oxytelinae, Tachyporinae part.—J. Jaszay (Bardejov, Slovakia); Staphylinidae: Steniinae—L. Hromádka (Praha); Staphylinidae: Aleocharinae—S. Snäll (Tumba, Sweden); Scydmaenidae, Pselaphidae—P. Hlaváč (Košice, Slovakia); Hydrophilidae, Byrrhidae—M. Boukal (Olomouc); Scarabaeidae—A. Bezděk (České Budějovice). The remaining groups of Coleoptera were identified by the author. Classification follows the paper of Jelínek [15].

F. Gregor (Brno) identified the adults of Calliphoridae and Muscidae (Diptera).

3. Results

3.1. Decomposition of carcasses

The stages of decomposition recognised in this study follow the classification of Reed [31] who divided decomposition into four stages: fresh, bloated, decay and dry. The stages were recognised visually by characteristic morphological changes on the carcass body described below.

3.1.1. Carcasses open to insects

Carcasses in summer decayed much faster than those in spring and autumn. In summer, the carcass in the meadow reached the dry stage in only 6 d, when the average daily temperature was 17.4 °C (Table 1). In contrast, during autumn, 18 d were required for the carcasses to reach the dry
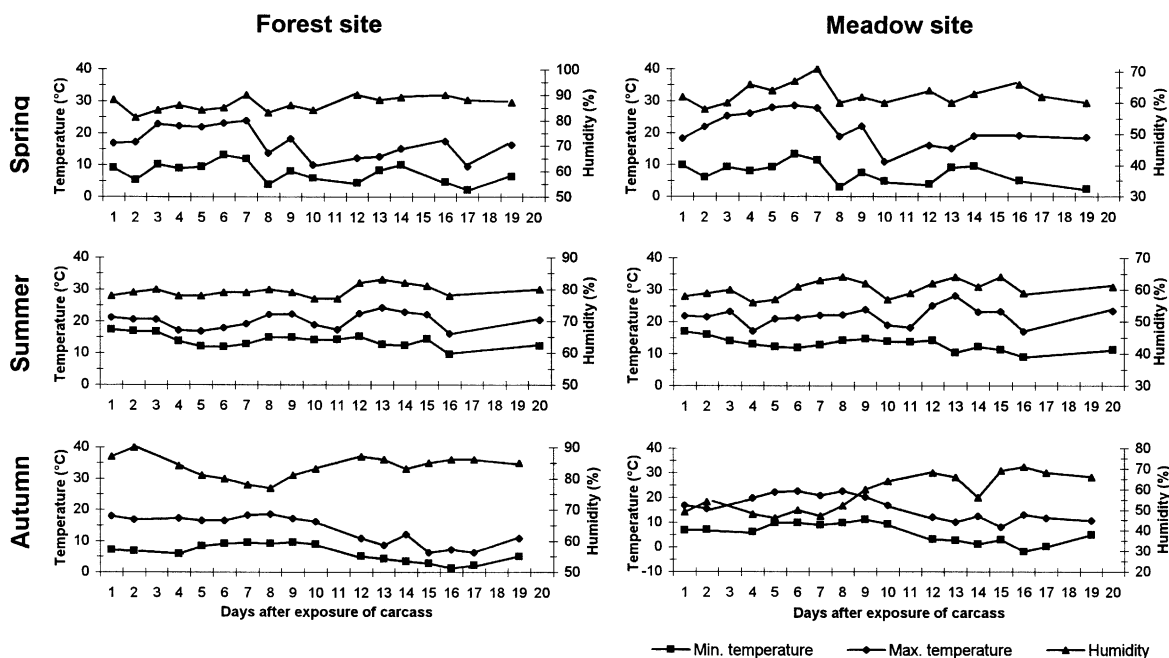
Fig. 1. Ground surface temperature and humidity values measured during the decomposition of individual carcasses.

stage in meadow habitat when the average daily temperature was 10.9 °C. Carcasses placed at the meadow site with higher average temperature (Table 1) decayed much faster than those at the forest site (Fig. 2). The above data indicate a direct correlation between the rate of carrion decomposition and temperature. The decomposition curves of the carcasses exposed in forest and meadow habitats have the same S-curve shape with only small differences in the same season (Fig. 2).

Fresh stage lasted only 1–2 d after the exposure of carcass. There were no morphological changes visible on the carcass.

Bloated stage begins when bloating of the carcass is first observed. This is caused by a build up of gases inside the carcass which result from anaerobic protein decomposition. This stage lasted from two (summer) to six (autumn) days, and 8.1% (summer, meadow) to 15.6% (autumn, meadow) of

the total biomass were removed during the bloated stage (Table 1).

Decay stage begins with the onset of aerobic protein decomposition. The greatest percentage of biomass was removed during this stage mainly as a result of the blowfly maggot feeding masses. Maggots of *Lucilia caesar* (Linnaeus, 1758), *Calliphora vomitoria* (Linnaeus, 1758), *Calliphora vicina* Robineau-Désvoidy, 1830 (Calliphoridae) and *Hydrotaea similis* Maede, 1887 (Muscidae) dominated. Their activities totally determine the pattern of decomposition during this stage. In summer, over 60% of the total biomass were removed during the decay stage at each site; in spring and autumn, about 50% of the biomass were removed (Table 1). The duration of this stage varied from 3 (summer, meadow) to 10 (autumn, both sites) days. Towards the end of this stage, the blowfly maggots leave the carcass as preapupae (see [18]).

Table 1

Comparisons of decomposition processes in each season, habitat and with or without insect participation. Climatological data (daily average) were recorded during each experimental series

Season	Habitat	Stage of decomposition								Total remains (%)		Average	
		Fresh		Bloated		Decay		Dry		With insects	Without insects	Temperature (°C)	Humidity (%)
		d	r	d	r	d	r	d	r				
Spring	Forest	1	1.2	4	8.7	31.2	71.0	12.3	86.4	5	47.9	29	11.0
	Meadow	1	1.0	4	10.9	24.7	60.3	14.3	62.8	4	51.9	30	11.5
Summer	Forest	1	1.1	2	9.6	17.2	50.9	16.9	79.4	5	70.3	31	1.8
	Meadow	1	0.9	2	8.1	19.9	38.1	17.4	60.4	3	67.3	33	3.8
Autumn	Forest	2	1.3	6	11.1	30.3	77.7	9.9	83.7	10	50.6	21	6.7
	Meadow	2	0.8	6	15.6	29.5	61.8	10.9	58.4	10	49.5	21	4.2

d, duration of the decomposition stage (in days); r, percentage of carcass removal during the decomposition stage (%).
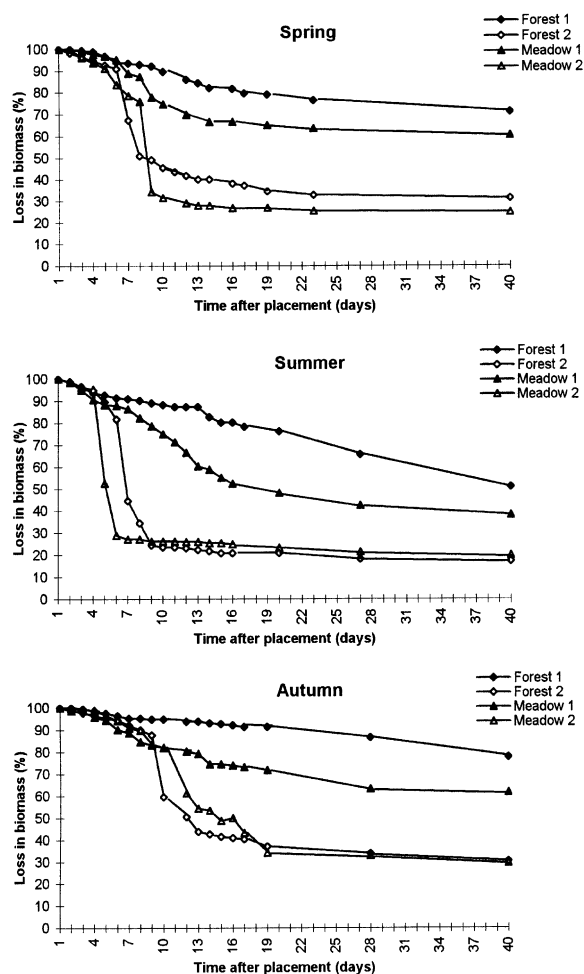
Fig. 2. Rate of carcass decomposition expressed as a percentage of initial carcass weight against time (days) for which the carcass had been exposed. Access of insects to carcasses marked 1 (full black symbols) was reduced by the net with the diameter of meshes 0.8 mm; carcasses marked 2 (open symbols) were fully exposed to insects. For details, see the text.

Dry stage begins when no maggots remain on the carcass and lasts until carrion fauna are no longer found associated with the remains. The carcasses were in the process of drying up and most of the flesh had been removed. By the end of the experiment, only dried skin, fur, cartilage and bones were left of the carcasses. There were less final remains of carcass biomass in summer (17.2%, 19.2%) than in spring (24.7%, 31.2%) and autumn (29.5%, 30.3%) (Table 1).

3.1.2. Carcasses free from insects

The decomposition of carcasses free from insects was less rapid than in exposed carrion. The stages of decomposition were not distinguished in these carcasses, because when the insects, especially carrion blowflies, were excluded from the carcass, it was very difficult to divide the decomposition into well-defined stages. During the first four (summer) to seven

(autumn) days, the decomposition curves of insect-free carcasses and carcasses open to insects were very much alike (Fig. 2). Then, the two types of carrion underwent their characteristic courses of decomposition. Insect-free carrion decomposed and dried very slowly—the loss of weight was gradual and thus gave a gently sloping curve (Fig. 2). After 40 d, from 50.9% (summer, forest) to 77.7% (autumn, forest) of the original carrion remained in the form of a mummified body (Table 1). The decomposition was always faster and with smaller final remains in meadow habitat in the same season. The remains of carrion exposed in the meadow in summer (38.1%) were influenced by the incident penetration of several blowfly maggots about 6–8 d after exposure.

A few colonies of fungi grew on the carcasses at the second half of carcass decomposition.

3.2. Coleoptera associated with carrion

A total of 145 Coleoptera species belonging to 22 families was recorded on the rat carcasses (Appendix A).Figs. 3–5 illustrate the patterns of Coleoptera succession in different seasons with the rate of carcass removal and the duration of each decomposition stage placed at the top of each figure. Major temporal features of carrion beetles development included a period of invasion by predominantly burying beetles of genus *Nicrophorus*, species of Leiodidae and some Staphylinidae (fresh/bloated stage), a period of maximum Coleoptera diversity achieved when carcass tissues were presumably most attractive to consumers (decay stage), and a period of monotonic decline in Coleoptera arthropod richness (dry stage) (see Fig. 6). The late dry stage was characterised by low diversity of specialised species (Dermestidae, Trogidae, Cleridae, some Staphylinidae) (Figs. 3–5).

The greatest diversity of Coleoptera was collected in spring (118 species), followed by summer (106 species) and autumn (74 species). In total, more species were collected at a forest site (121 species) than at a meadow site (93 species).

Four ecological groups have been distinguished, each characterised by a specific type of carrion association and varying in food specialisation and biology of species. These are specialised or obligate necrophages (Section 3.2.1), that are regularly found on carrion and associated with it as with a major food source; saprophagous species (Section 3.2.2) associated with decaying organic (animal and plant) matter, that are regularly found on carrion but are not associated with only this food source; predatory or parasitic species (Section 3.2.3) feeding on invertebrates visiting carrion, and accidental species (Section 3.2.4) whose representatives are found on carrion by chance and normally occupy other habitats.

3.2.1. Necrophages

Silphidae. Eight species of necrophagous carrion beetles were found (Appendix A). *Nicrophorus fossor* Erichson, 1837, *N. humator* Olivier, 1790, *N. investigator* Zetterstedt, 1824, *N. vespilloides* Herbst, 1784 and *Oiceoptoma thoracica* (L., 1758) showed distinct preferences for the forest
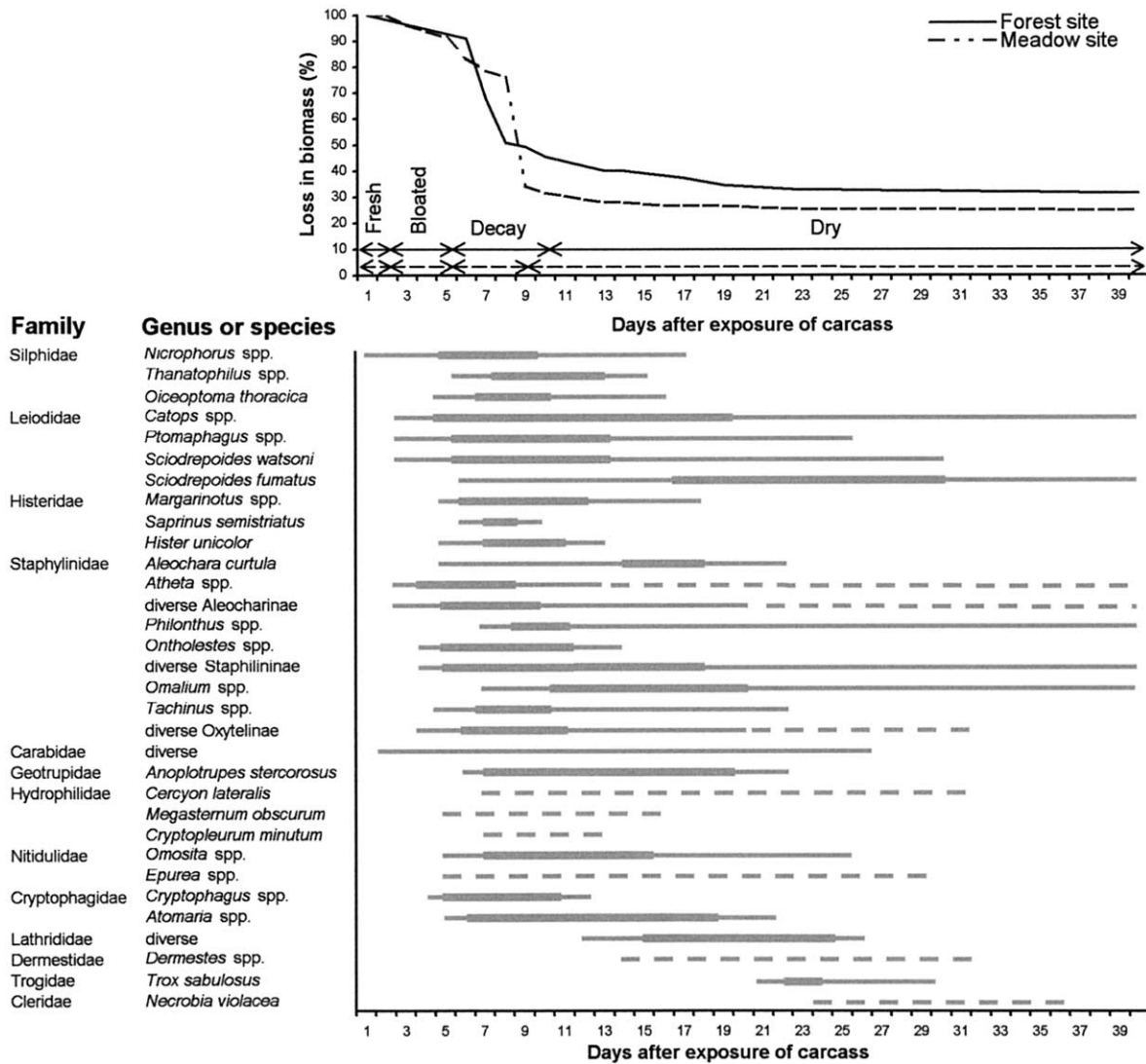
Fig. 3. Rate of carcass removal and the Coleoptera succession on exposed rat carcasses during spring in Opava, the Czech Republic. The thickness of bands indicates relative abundance of each species at different times, the interrupted band indicates irregular occurrence of few individuals.

habitat, whereas *N. vespillo* (L., 1758), *Thanatophilus rugosus* (L., 1758) and *T. sinuatus* (F., 1775) showed a preference for the open meadow. *N. fossor* occurred only in summer, *N. investigator* occurred in summer and autumn and *O. thoracica* occurred only in spring and summer (Appendix A). The other species occurred in all seasons. All five species of *Nicrophorus* were among the first to colonise the carcasses and were found till the early part of the dry stage (Figs. 3–5). *Thanatophilus* and *Oiceoptoma* colonised the carcass later than *Nicrophorus* and were collected firstly from the end of the bloated stage (spring, autumn) or from the decay stage (summer). The occurrence ended in the early dry stage (Figs. 3–5).

Trogidae. Only one species, *Trox sabulosus* (L., 1758), was found. This species was collected only in spring, pre-

ferred meadow habitat (Appendix A) and colonised carrion in the dry stage (Fig. 3).

Dermestidae. Two species of genus *Dermestes* were found (Appendix A). Both species showed preference for the meadow habitat. *D. murinus* L., 1758 occurred during all three seasons and *D. lardarius* L., 1758 occurred in spring and summer (Appendix A), but both with the highest abundance in spring. The species of *Dermestes* were typical for the dry stage of decomposition (Figs. 3–5).

Nitidulidae. Three species of genus *Omosita* and one species of *Nitidula* can be classified as necrophagous (Appendix A). *Omosita colon* (L., 1758) and *Nitidula bipuncata* (L., 1758) were collected at both habitats in spring and summer; *O. depressa* (L., 1758) and *O. discoidea* (F., 1775) preferred forest site and were collected during all three sea-
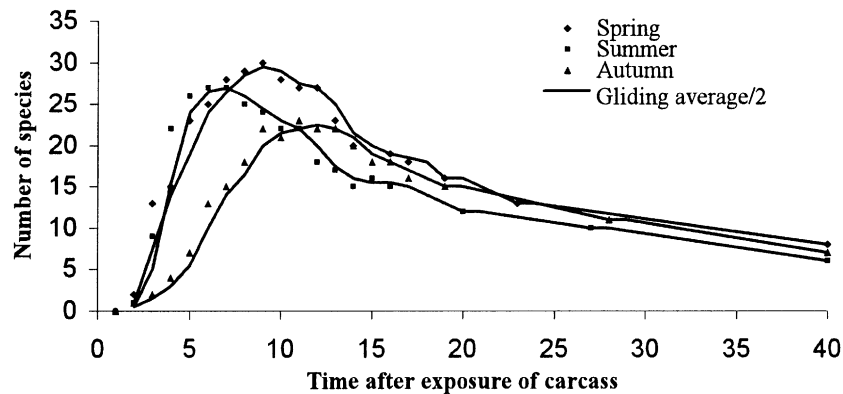
Fig. 6. Diversity of Coleoptera species during the decomposition of rat carcasses exposed at the meadow site in spring, summer and autumn (Opava, the Czech Republic).

sons (Appendix A) with the highest abundance in spring period. All these species appeared from decay to dry stages of decomposition (Figs. 3–5).

3.2.2. Saprophages

Hydrophilidae. Three species of three genera were found (Appendix A). *Cercyon lateralis* (Marsham, 1802) was collected at both habitats during all three seasons; *Cryptopleurum minutum* (F., 1758) preferred meadow habitat and occurred only in spring; *Megasternum obscurum* (Marsham, 1802) occurred only in meadow habitat during spring and summer (Appendix A). Hydrophilidae appeared from decay to dry stages of decomposition (Figs. 3–5).

Leiodidae. 16 saprophagous species belonging to genera *Catops*, *Ptomaphagus* and *Sciodrepoides* were found (Appendix A). Species *C. fuliginosus* Erichson, 1837, *C. grandicollis* Erichson, 1837, *C. chrysomeloides* (Panzer, 1798), *C. morio* (F., 1792), *C. nigricans* (Spence, 1815), *P. sericarus* (Chaudoir, 1845) and *S. watsoni* (Spence, 1815) showed a preference for the meadow habitat; *C. coracinus* Kellner, 1846, *C. nigrita* Erichson, 1837, *C. subfuscus* Kellner, 1846, *C. westi* Krogerus, 1931, *P. subvillosus* Goeze, 1777, *S. alpestris* Jeanel, 1934, *S. fumatus* (Spence, 1815) showed a preference for the forest habitat; species *C. kirbyi* (Spence, 1815) and *C. tristis* (Panzer, 1794) did not show restricted habitat preference (Appendix A). The activity culminated in autumn in the majority of these species (e.g. *C. fuliginosus*, *C. grandicollis*, *C. chrysomeloides*), only in one species the activity culminated in spring (*C. subfuscus*) and in two species in summer (*C. coracinus*, *S. alpestris*) (Appendix A). Species of *Catops* appeared from the early bloated stage all through the rest of the decomposition. Species of *Ptomaphagus* appeared from the bloated stage to the middle of the dry stage of decomposition. Species of *Sciodrepoides* differed in their occurrence during the succession. *S. watsoni* appeared from fresh or early bloated stage to dry stage with the highest abundance in decay and early dry stages; *S. fumatus* appeared from decay to dry stage of decomposition with the highest abundance in the middle dry stage (Figs. 3–5).

Staphylinidae. 15 predominantly saprophagous species belonging to six genera were found (Appendix A). *Anotylus tetracarinatus* (Block, 1799) did not show restricted habitat preference and occurred in spring and summer. Among *Atheta*, *A. divisa* (Markel, 1845) preferred meadow habitat, *A. corvina* (C.G. Thomson, 1856) and *A. subtilis* (W. Scriba, 1866) preferred forest habitat. The other species did not show restricted habitat preference. *A. fungi* (Gravenhorst, 1806) occurred only in autumn; the other species occurred during all the three seasons. *Omalium caesum* (Gravenhorst, 1806) preferred the meadow habitat and occurred in spring and summer, whereas *O. rivulare* (Paykull, 1789) preferred the forest habitat and occurred during all the three seasons. *Oxypoda alternans* (Gravenhorst, 1802) preferred the forest habitat and occurred during all the three seasons, *O. lividipennis* Mannerheim, 1830 preferred meadow habitat and occurred in spring and autumn. *Proteinus crenulatus* Pandellé, 1867 preferred forest habitat and occurred only in autumn. *Tachinus signatus* (Gravenhorst, 1802) preferred forest habitat and occurred in spring and summer. The following three saprophagous species occurred at low abundance which did not allow further evaluations (Appendix A). *Atheta* spp. occurred from early bloated to dry stages with the highest abundance in the decay stage (Figs. 3–5). *Omalium* spp. occurred from decay to dry stage with the highest abundance in the early dry stage (Figs. 3–5). *Tachinus* spp. occurred from the bloated to dry stage with the highest abundance in the decay stage (Figs. 3 and 4).

3.2.3. Predators/parasites

Histeridae. Four species of three genera were found (Appendix A). *Hister unicolor unicolor* L., 1758 was collected at both habitats without distinct habitat preference; *Margarinotus carbonarius* (Hoffmann, 1803), *M. striola succicola* (Thomson, 1862) and *Saprinus semistriatus* (L.G. Scriba, 1790) preferred meadow habitat. *H. unicolor unicolor* and *M. striola succicola* occurred during all three seasons, *M. carbonarius* and *S. semistriatus* occurred during spring and summer (Appendix A). The highest total abundance was found in spring. Both *Margarinotus* species occurred from
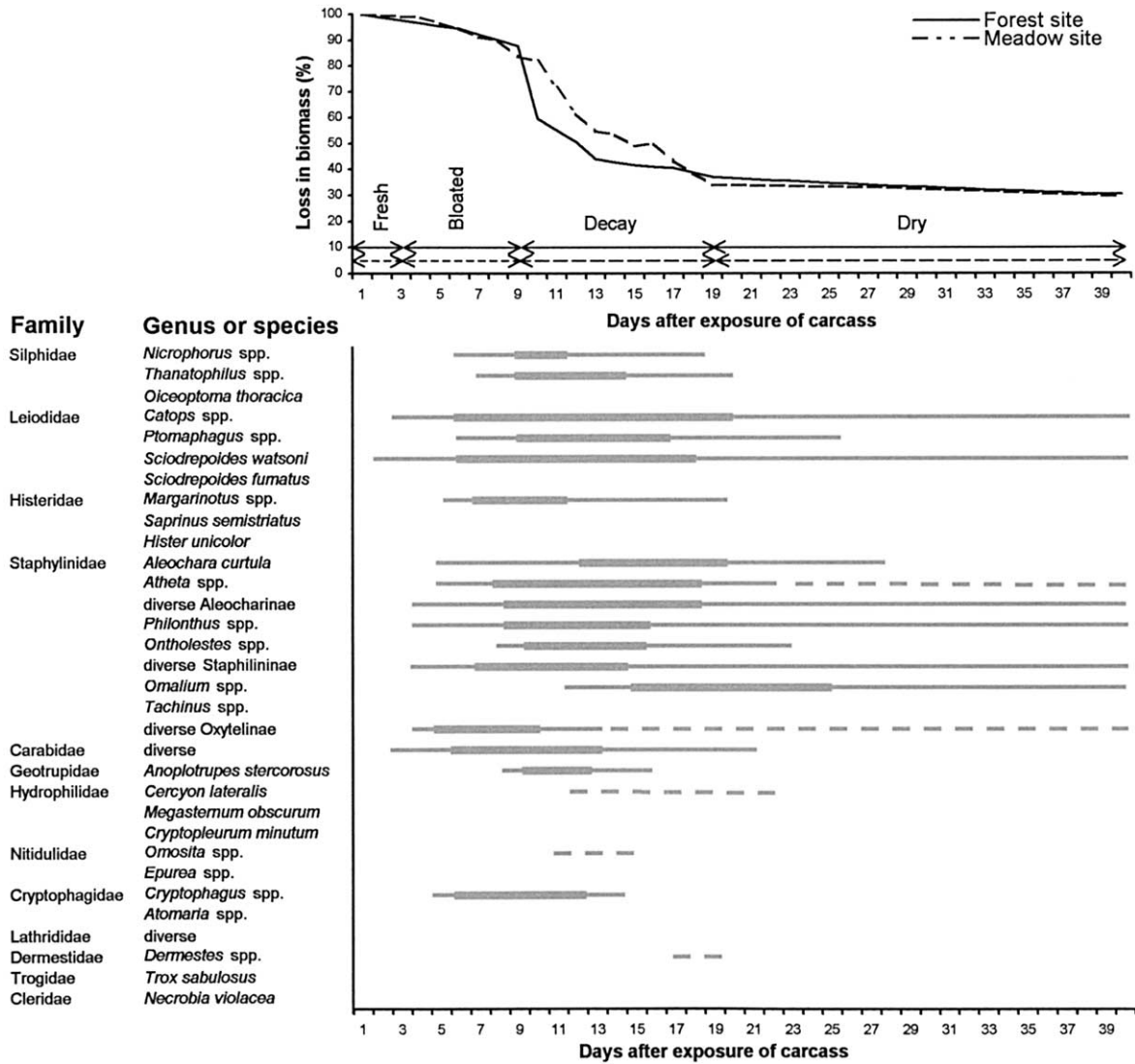
Fig. 5. Rate of carcass removal and the Coleoptera succession on exposed rat carcasses during autumn in Opava, the Czech Republic. The thickness of bands indicates relative abundance of each species at different times, the interrupted band indicates irregular occurrence of few individuals.

bloated to early dry stage with the highest abundance in decay stage; *S. semistriatus* occurred from bloated to decay stage and *H. unicolor unicolor* from bloated to early dry stage of decomposition (Figs. 3–5).

Silphidae. Carrion beetles belong to both necrophages and predators categories. Adult *Nicrophorus* are predators and feed on decaying meat only rarely, their larvae are exclusively necrophagous. Other Silphidae species are predators and necrophages together and their larvae are necrophagous. Their occurrence is summarised in Section 3.2.1.

Staphylinidae. 10 predominantly predator species belonging to five genera were found (Appendix A). Larvae of one of them, *Aleochara curtula* (Goeze, 1777), feed as parasitoids on blowfly maggots [28]. This species preferred meadow habitat and occurred during all three seasons. Both *Ontho-*

lestes murinus (L., 1758) and *O. tesselatus* (Fourcroy, 1785) preferred the meadow habitat and occurred during all the three seasons. In genus *Philonthus*, *P. addendus* Sharp, 1867, *P. politus* (L., 1758) and *P. succicola* C.G. Thomson, 1860 preferred meadow habitat, and *P. fimetarius* (Gravenhorst, 1802) preferred forest habitat. *P. politus* occurred during all the three seasons, the next three *Philonthus* species occurred in spring and summer with higher abundance in spring. The following three predator species occurred at low abundance, which did not allow further evaluations (Appendix A). *A. curtula* occurred from the late bloated stage to dry stage with the highest abundance in bloated or early dry stage (Figs. 3–5). *Ontholestes* spp. occurred from bloated to early dry stage with the highest abundance in the decay stage (Figs. 3–5). *Philonthus* spp. occurred from bloated to dry

stage with the highest abundance in the decay stage (Figs. 3–5).

Cleridae. Only one species, *Necrobia violacea* (L., 1758), was found. This species showed preference for meadow habitat and occurred in spring and summer (Appendix A) irregularly in the dry stage of decomposition (Figs. 3 and 4).

3.2.4. Accidental species

Carabidae. Carabidae are predatory species that only occasionally visited carrion. Some species (especially *Carabus* spp.) can occasionally feed on decaying meat [21,37]. 17 species belonging to eight genera that occurred irregularly from bloated to dry stages (Appendix A) were found. *Abax* spp., *Carabus auronitens* F., 1792, *C. linnaei* Panzer, 1810, *C. violaceus*, *Loricera pilicornis* (F., 1775) preferred meadow habitat, *Poecilus* spp. and *Pterostichus oblongopunctatus* (F., 1775) preferred forest site. *C. scheidleri* Panzer, 1799 and *P. niger* (Schaller, 1783) did not show distinct habitat preference (Appendix A).

Silphidae. *Phosphuga atrata* (L., 1758) is an accidental species on carrion where it feeds on molluscs [34]. It preferred forest site and occurred during all the three seasons (Appendix A).

Leiodidae. *Agathidium*, *Anisotoma* and *Colenis* are mycetophagous species. *Choleva sturmi* Brisout de Barneville, 1863 and *Leptinus testaceus* J. Müller, 1817 are saprophagous species associated with tunnels and nests of small mammals. Only *Anisotoma humeralis* (F., 1792) and *C. immunda* (Sturm, 1807) were found in sufficient number for further evaluation. Both species preferred forest site and occurred in spring and summer (Appendix A).

Scydmaenidae. Saprophagous and mycetophagous species. Three species belonging to three genera were found in low abundance, which did not allow further evaluation (Appendix A).

Staphylinidae. 13 species belonging to 10 genera were categorised as accidental on carrion (Appendix A). There are predatory (e.g. *Staphilinus* spp., *Stenus* spp.), mycophagous (*Bolitochara* spp., some *Atheta* spp.) or myrmecophilous species (*Zyras* spp.). All these species were found in low abundance, which did not allow further evaluation.

Pselaphidae. Saprophagous and mycetophagous species. Two species belonging to two genera were found (Appendix A). *Brychyglutta fossulata* (Reichenbach, 1816) preferred meadow habitat and occurred only in spring (Appendix A).

Geotrupidae, Scarabaeidae. Species of these two families are coprophagous and they are associated with the dung of mammals. *Anoplotrupes stercorosus* (Hartmann, 1791) also regularly visited carcasses. This species preferred forest site and occurred during all the three seasons (Appendix A).

Byrrhidae. Only one bryophagous species, *Simplocaria semistriata* (F., 1794), was recorded (Appendix A).

Elateridae, Lycidae. Phytophilous species. *Athous subfuscus* (O.F. Müller, 1767) and *Dictyoptera aurora* Latreille, 1829 were recorded (Appendix A).

Anobiidae, Rhizophagidae. Species associated with decaying wood; one species of Anobiidae and two species of Rhizophagidae were recorded (Appendix A). *Rhizophagus dispar* (Paykull, 1800) preferred the forest site and was collected only in spring (Appendix A).

Nitidulidae. Four species of genus *Epurea* were categorised as accidental on carrion (Appendix A). They are phytophilous or xylophilous species. *E. unicolor* (Olivier, 1790) and *E. variegata* (Herbst, 1793) preferred forest site and occurred in spring and summer (Appendix A).

Cryptophagidae. Saprophagous, xylophagous and mycetophagous species associated with decaying organic matter, either plant or animal. 12 species belonging to three genera were found (Appendix A). *Atomaria atricapilla* Stephens, 1830, *A. fuscata* (Schönherr, 1808), *Cryptophagus nitidulus* Miller, 1858, *C. pallidus* Sturm, 1845 (Appendix A). *A. atricapilla* Stephens, 1830 and *A. nodifer* occurred during all the three seasons; *A. fuscata*, *C. nitidulus*, *E. transversus* and *S. angusticollis* occurred in spring and summer and *C. pallidus* in spring and autumn (Appendix A). *Atomaria* spp. occurred from decay to dry stage with the highest abundance in the dry stage (Figs. 3 and 4); *Cryptopahus* spp. occurred from bloated or decay to dry stage with the highest abundance in decay or early dry stage (Figs. 3–5).

Endomychidae. Mycophagous species. One species, *Lycoperdina bovistae* (F., 1792), was recorded.

Lathridiidae. Saprophagous, xylophagous and mycetophagous species associated with decaying organic matter, either plant or animal. 11 species belonging to six genera were found (Appendix A). *Stephostethus lardarius* (De Geer, 1775) preferred the forest site; *Enicmus transversus* (Olivier, 1790) preferred the meadow site and *Aridius nodifer* (Westwood, 1839) occurred at both sites with the same abundance (Appendix A). *A. nodifer* occurred during all the three seasons, the other two species occurred in spring and summer (Appendix A). Species of this family occurred from decay to dry stages (Fig. 4) or only in the dry stage (Fig. 3).

4. Discussion

4.1. Decomposition of carcass

Decomposition of the bodies of dead animals is a microsuccessive process in which it is possible to distinguish several stages with their corresponding forms of carrion and the necrophage fauna proper to them. The categorisation varies depending mainly on the length of the decomposing period and the type of carrion. Bornemissza [3] included five stages of decomposition in the carrion of guinea pigs over a span of 450 d. Payne [27] recorded five stages in piglets; however, Reed [31] reported four stages of decomposition. Fuller [10] used division into only three stages. Cornabay [7] studied the carrion of toads and lizards where no stages of decomposition can be visually observed. The stages of decomposition recognised in my study follow Reed's classifi-
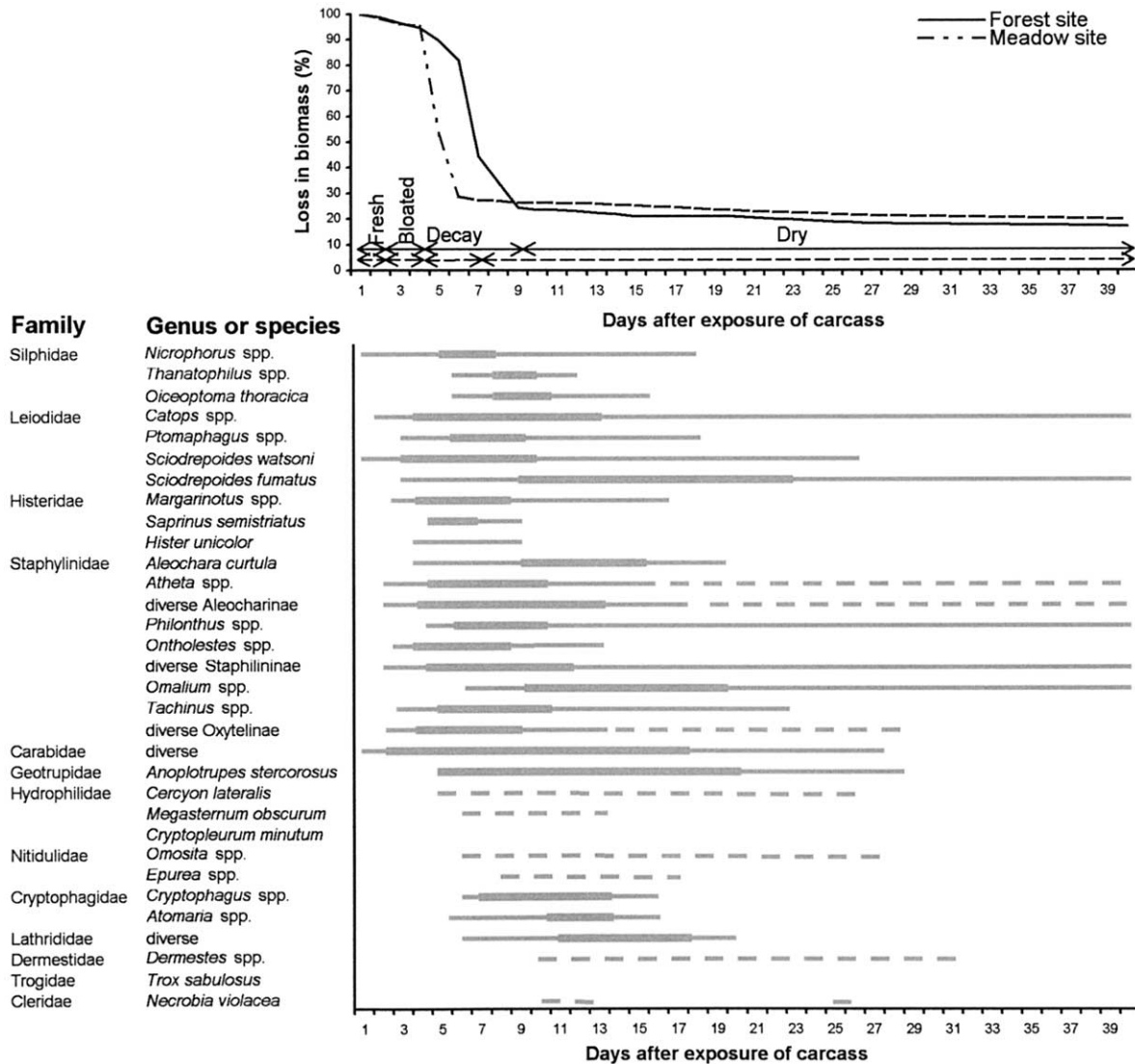
Fig. 4. Rate of carcass removal and the Coleoptera succession on exposed rat carcasses during summer in Opava, the Czech Republic. The thickness of bands indicates relative abundance of each species at different times, the interrupted band indicates irregular occurrence of few individuals.

cation, widely followed by other authors (e.g. [16,36,38]). Morris [25] states that Reed's classification is the most satisfactory description of decomposition stages and recommends its adoption by all researches concerning medicolegal application of entomology. We must keep in mind the fact that decomposition is a continuous process and discrete stages do not actually exist in nature [33]. The above mentioned decay stages only have a descriptive value.

Reed [31] and Johnson [16] have shown that the duration of a particular stage of decomposition is shorter than that of its successor in the same season. In the current study, similar results were obtained with an exception regarding the bloated stage in the meadow during spring (Table 1). The bloated stage in spring and autumn lasted longer than in summer.

These data are consistent with the average daily temperatures recorded in each season (Table 1). These observations can be attributed to differences in breeding biology of blowflies. The development of blowfly larvae, which are responsible for the process of skin puncturing that ended the bloated stage earlier by passing to aerobic decomposition (decay stage), is faster in the warmer season [2,5,35]. Tantawi et al. [36] noted, that the period of the bloated stage depends more on the number of larvae infesting the carcass rather than on temperature. During the decay stage, temperature plays a primary role in the length of the stage—the carcass is open and its flesh dries rapidly especially in hot weather.

The results of arthropod exclusion experiments demonstrate accelerated breakdown and decay of rat carrion in the

presence of necrophagous and saprophagous insects. Payne [27] and Abell et al. [1] obtained the same results.

Differences in the microclimate, depending on the position of carcasses relative to trees and shrubs, obviously influenced the rate of decay [3] as well. In this study, carcasses placed at the meadow site with higher average temperature (Table 1), increased by the insulation during sunshine, decayed much faster than those at the forest site (Fig. 2). Rates of decomposition vary with the temperature [8], which especially affects bacterial activity [30] and developmental rates of carrion frequenting insects [2]. On the other hand, humidity was higher at the forest site with the undergrowth and a layer of forest litter. With the exclusion of extreme habitats, humidity influenced the rate of decomposition less than temperature [27,31,38]. In arid zones, high temperature in combination with low humidity dehydrates small carcasses and induces the mummification [14].

4.2. Coleoptera succession

The sequence of Coleoptera succession observed in this study follows the same general patterns found in both temperate and tropical areas [3,4,7,9,10,16,22,26–28,31,32, 36,38]. The succession of species on a carcass develops primarily as a continuum of change [33], when various stages are characterised by a different number of associated species (Fig. 6). The number of species reaches maximum during the stage of active decomposition (decay stage). The initial period and the late dry stage were characterised by the low diversity of specialised species (*Nicrophorus*, *Dermestes*, *Trox*, *Necrobia*, some Staphylinidae). Nabaglo [26] obtained the same results.

Burying beetles (genus *Nicrophorus*) have a special position within the guild of carrion insects. The beetles bury carcasses in order to raise their brood upon, by which carrion use by other insects is excluded [24,30]. Other insects would act as food competitors for the slowly developing larvae [11], and therefore, only those carcasses, which have not been colonised by other insects yet, can be used for offspring production. In my experiments, the carcasses were partially isolated from these beetles due to the type of trap used. Burying beetles that entered carcass, could not bury it because the carcass was fixed on a metal net. For this reason, the burying beetles were relieved of their participation in the decomposition process in this study. Adult burying beetles are predators and feed only rarely on decaying meat. Therefore, they are also attracted by older carrion, where they feed upon fly larvae [30].

Species of *Nicrophorus* showed no niche differentiation with respect to different arriving times, as all are dependent mainly on fresh breeding material. Similar to the other studies (e.g. [19,22,29]), I also found the spatial separation in this genus to be stronger than in other carrion insects.

The different appearance of the two *Sciodrepoides* species during the succession (Figs. 3 and 4) represents niche differentiation at carrion. Kentner and Streit [22] obtained the same results. Besides the niche differentiation in the

course of decomposition, there is also a certain spatial separation, as *S. fumatus* occurs rather in the forest, whereas *S. watsoni* occurs rather in the open field [20]. In individual species of *Catops* and *Ptomaphagus*, differences in habitat preference and seasonality were found, but no important differences were observed with respect to different arriving times during the carcass succession. Some authors (e.g. [26]) found some variances during the underground decomposition of rodent carcass, when *C. neglectus*, *C. kirbyi*, *C. coracinus* and *C. chrysomeloides* occurred only in the dry stage.

So far, little and somewhat problematic knowledge has been obtained on the role of the various species participating in the decomposition of dead animals. The classification (Section 3.2 and Appendix A) gives only a rough estimation of the trophic levels, as it cannot be clearly defined for some carrion-visiting Coleoptera. Some species, like the adults of *Thanatophilus* or *Nicrophorus*, feed on maggots as well as on decaying meat. Further detailed observations in laboratory are necessary to ascertain the feeding preferences in many species (especially small species of Staphylinidae), because their trophic levels are rather supposed than confirmed. In saprophagous species (especially Cryptophagidae, Lathridiidae), it is very problematic to ascertain whether they prefer carcasses or occur on carcasses only by chance and are associated mainly with some other decaying matter (plant litter, fungi). Also, some predatory Coleoptera are not restricted to carcass only. Especially some Staphylinidae (e.g. *Philonthus*) are generalists with respect to habitat (they occupy carrion as well as dung) but specialists concerning prey (maggots of distinct size) [28]. In contrast, specialists with respect to habitats (e.g. *Thanatophilus*) may be generalists concerning their nutrition (maggots as well as decaying meat). In addition, the feeding habits and distribution in time and space were different for adults and larvae. Some of the species, which as adults feed on a variety of foods, have exclusively necrophagous larvae (e.g. *Oiceoptoma*). Another example is predatory *Aleochara curtula* with parasitic larvae.

The occurrence of predaceous beetles on carrion correlates with the abundance of their basic prey. Since blowfly maggots as the predominant prey are typical for the decay stage, the activity of predaceous beetles (especially Histeridae and Silphidae) culminated during this stage. Blowfly maggots grow very quickly and synchronously and before pupation the majority of them disperses from the corpse into the surroundings [18]. By dispersing, the larvae minimise interactions with predators highly concentrated at carcass.

This study resulted in an extensive inventory of carrion-associated Coleoptera found in habitats typical for the landscape of the northern part of the Czech Republic. Most necrophilous species are not specific to a particular type of carrion, therefore, beetles observed during this study may be also attracted to human corpses and used to estimate postmortem interval in forensic cases. The temporal pattern of Coleoptera activity on rat carcass cannot be easily applied to

human cases, because the rates of decomposition and, consequently, beetles succession accelerate on small carcasses.

Acknowledgements

Appendix A

Complete list of Coleoptera species collected during the study of carcass decomposition in Opava, the Czech Republic and their ecological characteristics.

| Family | Habitat preference | | Seasonality | | | Ecological |
Species	Meadow	Forest	Spring	Summer	Autumn	group
Carabidae						
Abax ovalis (Duftschmid, 1812)		••••	•••	••		acc./pre.
Abax parallelepipedus (Piller et Mitterp., 1783)		••••	••	••		acc./pre.
Carabus auronitens (Fabricius, 1792)		••••	••	••	••	acc./pre.
Carabus coriaceus (Linnaeus, 1758)	–	–	–	–	–	acc./pre.
Carabus hortensis (Linnaeus, 1758)	–	–	–	–	–	acc./pre.
Carabus linnaei (Panzer, 1810)		••••	••	••••	••	acc./pre.
Carabus scheidleri (Panzer, 1799)	••	••	••	••	••	acc./pre.
Carabus ullrichii (Germar, 1924)	–	–	–	–	–	acc./pre.
Carabus violaceus (Linnaeus, 1758)	•	•••	••	••	••	acc./pre.
Cychrus attenuatus (Fabricius, 1794)	–	–	–	–	–	acc./pre.
Loricera pilicornis (Fabricius, 1775)	•	•••	••	••	•	acc./pre.
Molops piceus (Panzer, 1793)	–	–	–	–	–	acc./pre.
Poecilus cupreus (Linnaeus, 1758)	••••		••	••	•	acc./pre.
Poecilus versicolor (Sturm, 1826)	••••		•••	••		acc./pre.
Pterostichus niger (Schaller, 1783)	••	••	••	•	••	acc./pre.
Pterostichus oblongopunctatus (Fabricius, 1787)	•••	•	••	••	•	acc./pre.
Stomis pumicatus (Panzer, 1796)	–	–	–	–	–	acc./pre.
Hydrophilidae						
Cercyon lateralis (Marsham, 1802)	••	••	••	••	•	sap.
Cryptopleurum minutum (Fabricius, 1775)	•••	•	•••••			sap.
Megasternum obscurum (Marsham, 1802)	••••		•••	••		sap.
Histeridae						
Hister unicolor unicolor (Linnaeus, 1758)	••	••	••	••	•	pre.
Margarinotus carbonarius (Hoffmann, 1803)	•••	•	•••	••		pre.
Margarinotus striola succicola (Thomson, 1862)	•••	•	••	••	•	pre.
Saprinus semistriatus (L.G. Scriba, 1790)	•••	•	•••	••		pre.
Silphidae						
Nicrophorus fossor (Erichson, 1837)	•	•••		•••••		pre./nec.
Nicrophorus humator (Olivier, 1790)	•	•••	••	••	•	pre./nec.
Nicrophorus investigator (Zetterstedt, 1824)	•	•••		•••	••	pre./nec.
Nicrophorus vespillo (Linnaeus, 1758)	•••	•	••	•	••	pre./nec.
Nicrophorus vespilloides (Herbst, 1784)	•	•••	•••	•	•	pre./nec.
Phosphuga atrata (Linnaeus, 1758)	•	•••	•••	•	••	pre./acc.
Oiceoptoma thoracica (Linnaeus, 1758)		••••	•••	••		nec./pre.
Thanatophilus rugosus (Linnaeus, 1758)	••••		••	••	•	nec./pre.
Thanatophilus sinuatus (Fabricius, 1775)	••••		••	••	•	nec./pre.

| Family | Habitat preference | | Seasonality | | | Ecological |
Species	Meadow	Forest	Spring	Summer	Autumn	group
Leiodidae						
Agathidium confusum (Brisout de Barneville, 1863)	–	–	–	–	–	acc.
Agathidium mandibulare (Sturm, 1807)	–	–	–	–	–	acc.
Agathidium seminulum (Linnaeus, 1758)	–	–	–	–	–	acc.
Anisotoma humeralis (Fabricius, 1792)		••••	••	•••		acc.
Anisotoma orbicularis (Herbst, 1792)	–	–	–	–	–	acc.
Catops coracinus (Kellner, 1846)	•	•••	•	•••	•	sap.
Catops fuliginosus (Erichson, 1837)	•••	•	••		•••	sap.
Catops grandicollis (Erichson, 1837)	••••				•••••	sap.
Catops chrysomeloides (Panzer, 1798)	••••				•••••	sap.
Catops kirbyi (Spence, 1815)	••	••		••	•••	sap.
Catops morio (Fabricius, 1792)	••••			•	••••	sap.
Catops nigricans (Spence, 1815)	••••		•		••••	sap.
Catops nigrita (Erichson, 1837)	•	•••	••	••	•	sap.
Catops subfuscus (Kellner, 1846)		••••	••••			sap.
Catops tristis (Panzer, 1794)	••	••	•		••••	sap.
Catops westi (Krogerus, 1931)	•	•••	•	••••		sap.
Colenis immunda (Sturm, 1807)		••••		•••••		acc.
Choleva sturmi (Brisout de Barneville, 1863)	–	–	–	–	–	acc.
Leptinus testaceus (J. Müller, 1817)	–	–	–	–	–	acc.
Ptomaphagus sericatus (Chaudoir, 1845)	•••	•	••	•	••	sap.
Ptomaphagus subvillosus (Goeze, 1777)		••••	••	•	•	sap.
Sciodrepoides alpestris (Jeannel, 1934)		••••	••	•••		sap.
Sciodrepoides fumatus (Spence, 1815)	•	•••	••	••	•	sap.
Sciodrepoides watsoni (Spence, 1815)	•••	•	••	•	•	sap.
Scydmaenidae						
Cephenium majus (Reitter, 1881)	–	–	–	–	–	acc.
Euconnus pubicollis (Muller et Kunze, 1822)	–	–	–	–	–	acc.
Neuraphes elongatulus (Mulller et Kunze, 1822)	–	–	–	–	–	acc.
Staphylinidae						
Acidota cruentata (Mannerheim, 1831)	–	–	–	–	–	acc.
Aleochara curtula (Goeze, 1777)	•••	•	••	••	••	pre./sap./par.
Anotylus tetracarinatus (Block, 1799)	••	••	•••	••		sap.
Atheta corvina (C.G. Thom., 1856)	•	•••	••	••	••	sap.
Atheta crassicornis (Fabricius, 1792)	••	••	••	••	•	sap.
Atheta divisa (Markel, 1845)	•••	•	••	••	•	sap.
Atheta fungi (Gravenhorst, 1806)	••	••			••••	sap.
Atheta subtilis (W.Scriba, 1866)	•	•••	••	••	•	sap.
Atheta trinotata (Kraatz, 1856)	–	–	–	–	–	sap.
Atheta vaga (Heer, 1839)	–	–	–	–	–	sap.
Bolitochara bella (Märkel, 1845)	–	–	–	–	–	acc.
Bolitochara oblique (Erichson, 1837)	–	–	–	–	–	acc.
Creophilus maxillosus (Linnaeus, 1758)	–	–	–	–	–	pre.
Drusilla canaliculata (Fabricius, 1787)	–	–	–	–	–	acc.
Eusphalerum semicoleoptratum (Panzer, 1794)	–	–	–	–	–	acc.
Megarthrus sinuatocollis (Bois. et Lac., 1835)	–	–	–	–	–	acc.
Omalium caesum (Gravenhorst, 1806)	•••	•	•••	••		sap.
Omalium rivulare (Paykull, 1789)	•	•••	••	••	••	sap.
Ontholestes murinus (Linnaeus, 1758)	••••		••	••	••	pre.
Ontholestes tesselatus (Fourcroy, 1785)	•••	•	••	••	••	pre.
Oxypoda alternans (Gravenhorst, 1802)		••••	••	•	••	sap.
Oxypoda lividipennis (Mannerheim, 1830)	•••	•	••		•••	sap.
Oxytelus rugosus (Fabricius, 1775)	–	–	–	–	–	acc./pre.
Philonthus addendus (Sharp, 1867)	•••	•	••••	•		pre.

| Family | Habitat preference | | Seasonality | | | Ecological |
Species	Meadow	Forest	Spring	Summer	Autumn	group
Philonthus fimetarius (Gravenhorst, 1802)		●●●●	●●●●	●		pre.
Philonthus politus (Linnaeus, 1758)	●●●	●	●●	●●	●●	pre.
Philonthus succicola (C.G.Thom., 1860)	●●●	●	●●●	●●		pre.
Philonthus varians (Paykull, 1789)	–	–	–	–	–	pre.
Proteinus crenulatus (Pandellé, 1867)	●	●●●	●●		●●●	sap.
Quedius mesomelinus (Marsham, 1802)	–	–	–	–	–	pre.
Rugilus orbiculatus (Paykull, 1789)	–	–	–	–	–	acc./pre.
Staphylinus melanarius (Heer, 1839)	–	–	–	–	–	acc./pre.
Staphylinus pubescens (De Geer, 1774)	–	–	–	–	–	acc./pre.
Stenus clavicornis (Scopoli, 1863)	–	–	–	–	–	acc./pre.
Stenus similis (Herbst, 1784)	–	–	–	–	–	acc./pre.
Tachinus laticollis (Gravenhorst, 1802)	–	–	–	–	–	sap.
Tachinus signatus (Gravenhorst, 1802)	●	●●●	●●	●●●		sap.
Zyras humeralis (Gravenhorst, 1802)	–	–	–	–	–	acc.
Zyras lugens (Gravenhorst, 1802)	–	–	–	–	–	acc.
Pselaphidae						
Brachygluta fossulata (Reichenbach, 1816)	●●●●		●●●●●			acc.
Euplectus piceus (Motschulsky, 1835)	–	–	–	–	–	acc.
Trogidae						
Trox sabulosus (Linnaeus, 1758)	●●●	●	●●●●●			nec.
Geotrupidae						
Anoplotrupes stercorosus (Hartmann, 1791)		●●●●	●	●●	●●	acc.
Scarabaeidae						
Aphodius depressus (Kugelann, 1792)	–	–	–	–	–	acc.
Byrrhidae						
Simplocaria semistriata (Fabricius, 1794)	–	–	–	–	–	acc.
Elateridae						
Athous subfuscus (O.F. Müller, 1767)	–	–	–	–	–	acc.
Lycidae						
Dictyoptera aurora (Latreille, 1829)	–	–	–	–	–	acc.
Dermestidae						
Dermestes murinus (Linnaeus, 1758)	●●●	●	●●	●●	●	nec.
Dermestes lardarius (Linnaeus, 1758)	●●●	●	●●●	●●		nec.
Anobiidae						
Stegobium paniceum (Linnaeus, 1758)	–	–	–	–		acc.
Cleridae						
Necrobia violacea (Linnaeus, 1758)	●●●●		●●●	●●		pre.
Nitidulidae						
Epurea marseuli (Reitter, 1872)	–	–	–	–	–	acc./sap
Epurea pygmaea (Gyllenhal, 1808)	–	–	–	–	–	acc./sap.
Epurea unicolor (Olivier, 1790)		●●●●	●●●	●●		acc./sap.
Epurea variegata (Herbst, 1793)		●●●●	●●●●	●		acc./sap
Nitidula bipuncata (Linnaeus, 1758)	●●	●●	●●●	●●		nec./sap.
Omosita colon (Linnaeus, 1758)	●●	●●	●●●	●●		nec./sap.
Omosita depressa (Linnaeus, 1758)	●	●●●	●	●●	●●	nec./sap.
Omosita discoidea (Fabricius, 1775)	●	●●●	●●	●●	●	nec./sap.
Rhizophagidae						
Rhizophagus dispar (Paykull, 1800)		●●●●	●●●●			acc.
Rhizophagus bipustulatus (Fabricius, 1792)	–	–	–	–	–	acc.
Cryptophagidae						
Antherophagus nigricornis (Fabricius, 1787)	–	–	–	–	–	acc./sap.
Atomaria analis (Erichson, 1846)	–	–	–	–	–	acc./sap.
Atomaria atricapilla (Stephens, 1830)	●	●●●	●●	●●	●	acc./sap.
Atomaria fuscata (Schönherr, 1808)		●●●●	●●●	●●		acc./sap.

| Family | Habitat preference | | Seasonality | | | Ecological |
Species	Meadow	Forest	Spring	Summer	Autumn	group
Atomaria procerula (Erichson, 1846)	–	–	–	–	–	acc./sap.
Atomaria scutellaris (Motschulsky, 1849)	–	–	–	–	–	acc./sap.
Cryptophagus dentatus (Herbst, 1793)	–	–	–	–	–	acc./sap.
Cryptophagus nitidulus (Miller, 1858)		••••	••	•••		acc./sap.
Cryptophagus pallidus (Sturm, 1845)	•	•••		••	•••	acc./sap.
Cryptophagus pilosus (Gyllenhal, 1828)	–	–	–	–	–	acc./sap.
Cryptophagus setulosus (Sturm, 1845)	–	–	–	–	–	acc./sap.
Cryptophagus sporadum (Bruce, 1934)	–	–	–	–	–	acc./sap.
Endomychidae						
Lycoperdina bovistae (Fabricius, 1792)	–	–	–	–	–	acc.
Lathrididae						
Aridius nodifer (Westwood, 1839)	••	••	••	••	•	acc./sap.
Corticaria impressa (Olivier, 1790)	–	–	–	–	–	acc./sap.
Corticaria longicornis (Herbst, 1793)	–	–	–	–	–	acc./sap.
Corticaria longicornis (Herbst, 1793)	–	–	–	–	–	acc./sap.
Cortinicara gibbosa (Herbst, 1793)	–	–	–	–	–	acc./sap.
Dienerella elongata (Curtis, 1830)	–	–	–	–	–	acc./sap.
Enicmus transverses (Olivier, 1790)	•••	•	•••	••		acc./sap.
Melanophthalma curticollis (Mannerheim, 1844)	–	–	–	–	–	acc./sap.
Stephostethus angusticollis (Gyllendal, 1827)	•	•••	•••	••		acc./sap.
Stephostethus lardarius (De Geer, 1775)	–	–	–	–	–	acc./sap.
Stephostethus rugicollis (Olivier, 1790)	–	–	–	–	–	acc./sap.

Spr., spring sampling period (5th May–13th June 1998); Sum., summer sampling period (16th July–24th August 1997); Aut., autumn sampling period (1[sh] October–9th November 1997); nec., necrophagous species; sap., saprophagous species; pre., predator species; par., parasitic species; acc., species accidental on carrion. The black dots mean the relative abundance at each habitat and in each season; it is not shown in species collected in a total number lower than 10 individuals.

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