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Diel activity patterns of carrion-visiting Coleoptera studied by time-sorting pitfall traps

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Ninety-three species from 13 beetle families were obtained during a one-year field study of diel activity in carrion-visiting Coleoptera. The daily activity patterns were observed using carrion-baited automatic traps placed in a grassy meadow and a deciduous forest in the surroundings of Opava (Silesia, Czech Republic). The traps were operated for three months each: in spring (May), summer (July) and autumn (October). Significantly more individuals were collected during the daylight period than in the night time. Total diel activity of carrion-visiting Coleoptera culminated around the sunset. The diel activities of all collected species are presented. In total, more individuals and species were collected at the forest site.

Key words: Coleoptera, carrion, carcass, necrobionts, diel activity, habitat preference, Czech Republic.

Introduction

Carrion is a spatially and temporally well-defined habitat and food resource, which under aerobic conditions will allow characteristic sequences of organisms to feed, grow and reproduce (HANSKI, 1990). The structure of carrion arthropod communities is primarily characterised by a large number of co-occurring species. At least 100 typical carrion insect species at a single carcass of small mammal are usually found in the course of decomposition and several hundred other arthropod species, which are found by chance in addition (KENTNER & STREIT, 1990).

Carrion is a limited and ephemeral food source and therefore subject to interspecific competition (PUTMAN, 1983). Generally, when animal species coexist and use a similar resource, they tend to segregate in niches to avoid conflicts (SHOENER, 1974). The intense competition for food resource leads to segregation by niches of the dominant carrion occupying species (PESCHKE et al., 1987). The niche segregation can be observed from four basic perspectives – phenology (seasonal differences in life cycles), habitat preferences, preferences of type or degree of decomposition (in succession), and daily periodicities (KOČÁREK, 1998, 2001b). The diel activity patterns of the decomposers, predators and parasites are modified by their interspecific interactions. The groups that play the role of main competitors are the burying beetle (Coleoptera: Silphidae) and the carrion blowflies (Diptera: Calliphoridae, Muscidae, Sarcophagidae) (PUTMAN, 1983).

There is very little information about the diel activity of carrion-visiting Coleoptera. The

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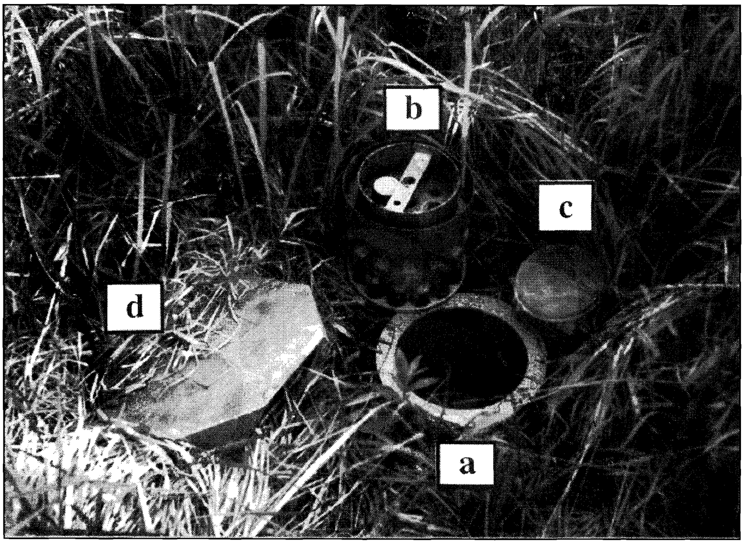

Fig. 1. Automatic time-sorting pitfall trap used in this research. a external metal case (20 cm in diameter) buried in the soil; b - internal part with 12 collecting vessels laid on a clock mechanism; c - basin with the bait protected by nylon-netting; d - a metal roof (30 × 30 cm).

diel activity and the temporal niche segregation in Silphidae were studied by KOČÁREK (2001b) and OHKAWARA et al. (1998). Data about the diel activity of some individual carrion-visiting Coleoptera species were published by ŠPICAROVÁ (1972, 1974), SHUBECK (1975), NOVÁK (1976), PETRUŠKA (1978, 1979) and KOROBEINIKOV & ESYUNIN (1984); the diel activity patterns in assemblages of carrion visitors were studied by SHUBECK (1971) and SCHOENLY (1983). Results on habitat associations of carrion-visiting Coleoptera in Central European conditions were presented by NOVÁK (1962, 1964, 1965, 1966), PETRUŠKA (1964, 1968a, b), LIKOVSKÝ (1967), ERBELING & ERBELING (1986), PESCHKE et al. (1987), KENTNER & STREIT (1990), RŮŽIČKA (1994), KOČÁREK & BENKO (1997) and KOČÁREK (2001b, in press).

Ninety-three species from 13 beetle families were obtained during a one-year field study on diel activity in carrion-visiting Coleoptera. The aim of our study was to obtain data about diel activity patterns and habitat preference of individual carrion-visiting beetles in each season and two different habitats.

Material and methods

The daily periodicities of carrion-visiting beetles were studied in the surroundings of the town of Opava (Suché Lazce village; 49°54″ N; 18°00″ E) in the Czech Republic.

Diel activity patterns were observed using carrion-baited automatic traps with two-hour periods of catches. The traps consisted of four basic parts (Fig. 1): a – an external metal case (20 cm in diameter) buried in the ground with the lip flush with the soil surface; b – an internal part with 12 collecting vessels (filled with water solution of ethylene glycol) laid on a clock mechanism; c – a basin with the bait (approximately 100 g of raw beef heart) protected by nylon-netting and lodged in the centre of the internal part and d – a metal roof (30 × 30 cm). Traps were placed in two different habitats: grassy meadow and deciduous forest. The traps in the meadow habitat were placed at a distance of 100 m from the meadow-forest edge; while the traps in the forest habitat were placed 100 m from the forest-meadow edge. The distance between the sampling sites was 1.5 km.

The traps were serviced every day, the insects in the solution were partly preserved in 70% ethyl alcohol and partly prepared by drying and sticking on entomological cards. The daily maximum and minimum ground surface temperatures were recorded by a min.-max. thermometer of ethanol type; the values are presented as mean ± standard deviation. Sampling was conducted during three one-month periods, which were chosen in spring (May 1998), summer (July 1997) and autumn (October 1998). These months are characterised by the following average climatic characteristics: May – ca 70 mm precipitation, 13 °C temperature; July – ca 100 mm precipitation, 17 °C temperature; October – ca 60 mm precipitation, 8 °C temperature (Collective, 1958). The average annual temperature is 8 °C and the annual rainfall is ca 650 mm (Collective, 1958).

The following groups were identified by specialists: Histeridae part., Dermestidae, Leiodidae part., Anobiidae – J. Vávra (Ostrava, Czech Rep.); Leiodidae part. – Z. Švec (Prague, Czech Rep.); Carabidae part. – J. Stanovský (Ostrava, Czech Rep.); Nitidulidae – J. Jelínek (Prague, Czech Rep.); Cryptophagidae, Lathrididae part. – P. Průdek (Brno, Czech

Table 1. Number of species and individuals of Coleoptera caught in each season and in each habitat.

Season	Meadow		Forest		Total	
	Individuals	Species	Individuals	Species	Individuals	Species
Spring (May)	341	30	858	51	1 199	62
Summer (July)	394	26	533	43	927	55
Autumn (October)	322	36	216	21	538	43
Total	1 057	58	1 607	74	2 664	93

Table 2. Numbers of individuals of carrion-visiting Coleoptera caught during daylight and darkness periods and the results of their comparisons by Chi-square test.

Period	Spring	Summer	Autumn	Total
Daylight	818	687	326	1831
Darkness	401	235	213	849
χ^2	142.65***	221.59***	23.69***	359.82***

Key: ***$P < 0.001$.

Rep.); Lathrididae part. – P. Míka (Prague, Czech Rep.); Staphylinidae: Staphylininae: Philonthini – P. Krásenský (Pardubice, Czech Rep.); Stapylinidae: Proteininae, Omaliinae, Oxytelinae, Tachyporinae part. – J. Jászay (Bardejov, Slovakia); Staphylinidae: Steniinae – L. Hromádka (Prague, Czech Rep.); Staphylinidae: Aleocharinae – S. Snäll (Tumba, Sweden); Scydmaenidae – P. Hlaváč (Košice, Slovakia); Hydrophyilidae – M. Boukal (Olomouc, Czech Rep.). The other groups of Coleoptera were identified by the author. The classification followed the paper of JELÍNEK (1993).

Results

A total of 2,664 individuals belonging to 93 Coleoptera species (Tab. 1, Appendix 1) were obtained by pitfall traps placed in two habitats during three seasons. 1,119 individuals belonging to 62 species were collected in spring, 927 individuals belonging to 55 species were collected in summer and 538 individuals belonging to 43 species were collected in autumn (Tab. 1).

Diel activity

Significantly more individuals were collected during daylight, overall as well as in individual seasons (Tab. 2). Total diel activity of carrion-visiting Coleoptera peaked around the interval between daylight and night periods, i.e. around sunset (Fig. 2). The autumn course of activity was rather different: the activity of beetles rose slowly and the peak of activity was not as pronounced as in the previous seasons. The period of 24.00–08.00 was characterised by a minimum activity of carrion-visiting Coleoptera.

A complete list of species collected during this study is presented in Appendix 1, with numbers of individuals captured at each sampling 2-h interval in May, July and October. Total activity of individual beetle families is presented in Table 3.

Carabidae – 12 species belonging to 8 genera were collected (Tab. 4); the majority of individuals were collected in summer (Tab. 3).

Hydrophilidae – three species belonging to three genera were collected (Tab. 4); the majority of individuals were collected in spring (Tab. 3). All species showed a nocturnal activity pattern (Appendix 1).

Histeridae – four species belonging to three genera were collected (Tab. 4); the majority of specimens were collected in summer (Tab. 3). The activity culminated in late afternoon and about sunset (Tab. 3, Appendix 1).

Silphidae – 8 species belonging to three genera were collected (Tab. 4); the majority of individuals were collected in spring (Tab. 3). In general, activity peaked in the afternoon (Tab. 3), but there were considerable differences among individual species. Species of the genera *Thanatophilus* and *Oiceoptoma* showed diurnal activity patterns; *Nicrophorus humator* showed a nocturnal activity pattern; *N. fossor* and *N. investigator* were ac-

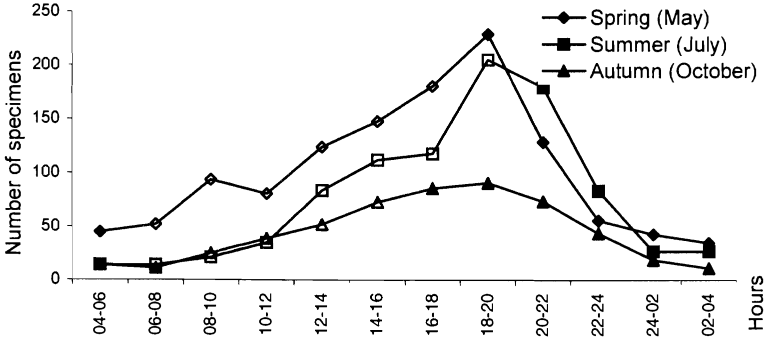

Fig. 2. Diel activity of Coleoptera expressed as total numbers of all individuals caught during each 2-hour period at each season. Full black symbols mean darkness period of day, open symbols mean daylight period of day.

Table 3. Total diel activity of individual families of carrion-visiting Coleoptera collected in Opava (Czech Republic).

Family	Time of collection (hour)												
Period	06	08	10	12	14	16	18	20	22	24	02	04	Total
Carabidae													
spring	1		2	2	1	2			3	1		1	13
summer	2		5	6	2	6	4	1	4	3	2	2	37
autumn	1		1			1	1	2	1		1	1	9
Hydrophilidae													
spring							1	3	8	1			13
summer		1				1			1	1			4
autumn									1				1
Histeridae													
spring		1	3	1	4	6	9	10	6	3			43
summer	2		1		1	9	20	47	22	17	10	4	133
autumn													1
Silphidae													
spring	7	10	8	28	62	53	64	55	21	13	9	2	332
summer	2		1	14	56	41	45	58	21	8	1	2	220
autumn			1	8	14	25	25	19	12	3			107
Leiodidae													
spring	3	5	13	4	6	29	34	80	26	12	7	4	223
summer	5	7	5	11	11	24	21	49	82	31	4	10	260
autumn	1		7	8	7	14	16	22	15	6	4	3	103
Staphylinidae													
spring	33	35	67	46	50	57	72	82	64	25	27	27	585
summer	3	6	11	6	14	28	25	49	50	23	10	7	232
autumn	12	11	15	16	27	23	38	46	45	35	14	6	288
Geotrupidae													
spring						1							1
summer						5	1						0
autumn			1	7	4	9	5	2					28
Nitidulidae													
spring	1	1	1							1			4
summer	1						1	2	3	2			9
autumn												1	1

Key: time of collection (hour) – the end of the two-hour catch period (e.g. 22 = the range of 20.00–22.00 h); white part – daylight, ordered white part – sunrise or sunset, grey part – night. The families Scydmaenidae, Dermestidae, Anobiidae, Cryptophagidae and Lathrididae with low abundance are omitted in this table.

Table 4. Trophic groups of carrion-visiting Coleoptera collected in Opava (Czech Republic), including the type of diel activity.

Family	Genus or no. of genera	No. of species	Trophic group	Diurnal (D) / Nocturnal (N)
Carabidae	8	12	predators	D / N
Hydrophilidae	3	3	saprophagous	N
Histeridae	3	4	predators	D / N
Silphidae	*Thanatophilus*	2	necrophagous / predators	D
	Oiceoptoma	1	necrophagous / predators	D
	Nicrophorus	5	predators / necrophagous	D / N
Leiodidae	*Catops*	11	necrophagous / saprophagous	D / N
	Ptomaphagus	2	necrophagous / saprophagous	D / N
	Sciodrepoides	3	necrophagous / saprophagous	D / N
	3 others	3	other	D / N
Scydmaeindae	2	2	other	–
Staphylinidae	*Aleochara*	1	parasitoids / predators / necrophagous	D
	Atheta	9	saprophagous	D / N
	Omalium	2	saprophagous	D / N
	Ontholestes	2	predators	D
	Philonthus	5	predators	D
	Quedius	1	predators	–
	Tachinus	2	saprophagous	D / N
	7 others	9	saprophagous / predators	D / N
Geotrupidae	1	1	coprophages	D
Dermestidae	2	2	dermato- / keratophages	–
Anobiidae	1	1	other	–
Nitidulidae	*Omosita*	3	dermato- / keratophages	D / N
	2 others	2	other	D / N
Cryptophagidae	1	1	saprophagous	–
Lathrididae	2	2	saprophagous	–

tive around sunset. The other species did not show any restricted pattern of diel activity (Appendix 1). Leiodidae – 19 species belonging to 6 genera were collected (Tab. 4); the majority of individuals were collected in the summer (Tab. 3). Their activity peaked around sunset, but the majority of species were active at lower densities throughout the day (Tab. 3, Appendix 1).

Scydmaenidae – in total only two specimens of two species belonging to two genera were collected in spring (Tabs 3, 4, Appendix 1).

Staphylinidae – 31 species belonging to 14 genera were collected (Tab. 4); the majority of individuals were collected in spring (Tab. 3). In general, their activity peaked around sunset (Tab. 3). The majority of species showed indefinite pattern of activity with undistinct peaks around sunset (f.e. *Atheta* spp.), but there are groups with clear diurnal activity (*Philonthus, Ontholestes*). Some species were active nearly all the day, e.g. *Omalium rivulare*, *Aleochara curtula* and *Tachinus signatus* (Appendix 1).

Geotrupidae – Only one species was collected (Tab. 4); the majority of individuals were collected in autumn (Tab. 3). Activity peaked in the afternoon (Tab. 3, Appendix 1).

Dermestidae – Only two species (and individuals) belonging to one genus were collected in summer and autumn (Tabs 3, 4, Appendix 1).

Anobiidae – Only one species was collected in summer (Tabs 3, 4, Appendix 1).

Nitidulidae – five species belonging to three genera were collected (Tab. 4); the majority of individuals were collected in summer (Tab. 3). Their activity peaked around sunset, but the species were also active to a lesser extent at night, around sunrise and during late afternoon (Tab. 3, Appendix 1).

Cryptophagidae – only one species was collected in spring (Tab. 3, Tab. 4, Appendix 1).

Lathrididae – two species belonging to two genera (Tab. 4) were collected in summer and spring (Tab. 3, Appendix 1).

Habitat associations

In total, significantly more individuals (χ^2 = 113.55, d.f. = 1, $P < 0.001$) of carrion-visiting Coleoptera were collected at the forest site, however, the number of species did not differ significantly between the two sites ($\chi^2 = 1.94$, d.f. = 1, $P = 0.16$) (Tab. 1). Significantly more individuals and species were collected at the forest site in spring (individuals: $\chi^2 = 222.93$, d.f. = 1, $P < 0.001$; species: $\chi^2 = 5.44$, d.f. = 1, $P < 0.05$) and summer (individuals: $\chi^2 = 20.84$, d.f. = 1, $P < 0.001$; species: $\chi^2 = 4.19$, d.f. = 1, $P < 0.05$). Conversely, significantly more individuals and species were collected at the meadow site in autumn (individuals: $\chi^2 = 20.88$, d.f. = 1, $P < 0.001$; species: $\chi^2 = 3.95$, d.f. = 1, $P < 0.05$). The numbers of individuals of each species collected at the two sites are presented in Appendix 1.

Discussion

In general, carcass colonisation by beetles is a stochastic process to some extent, not only because vertebrate remains are rare but also because there is a wide spectrum of natural conditions and behavioural traits of the beetles (PINERO, 1997). Carcass is commonly assumed to be a rare resource of patchy distribution and transient nature (PESCHKE et al., 1987). The scarcity of carcasses suggests that beetles must search over large distances. This factor alone makes carcass colonisation a random event, a function of the availability of other carrion in the area and the distance from other possible carrion sources via emigration (GILPIN & HANSKI, 1991).

Most of the frequent carrion visitors, such as *Nicrophorus*, *Dermestes*, *Omosita*, are necrophagous specialists. However, some species are not only restricted to carcasses. For example, *Anoplotrupes* and *Ontholestes* can be regularly found in dung. In addition to the problem of quantifying the degree of habitat specialisation of Coleoptera, the trophic level cannot be clearly defined for some of these insects. The classification in Table 4 gives only a rough estimation of the trophic levels in Coleoptera groups collected during this study. The relative composition of the individual function groups was influenced by the bait used in this study (meal). The pure meal can represent only a part of food niches used by necrobiont insects (KOČÁREK, in press a), because other tissues of naturally decomposing carcass are absent there. In particular, groups associated with the final stages of carcass decomposition (dry stage), and the species associated with hair and skin remains were not collected at all or were collected in very low numbers (i.e. Dermestidae, Cleridae, Nitidulidae, Trogidae). These groups have been collected in traps baited by carrion of small mammals during experiments at the same locations (KOČÁREK, in press a). If we compare species composition obtain by these two baits, we found a higher total number of species collected on carrion (145 species) than on meal (93 species).

The rate and course of carcass decomposition is strongly influenced by blowfly maggot activity (PUTMAN, 1983). Their activities completely dominates the pattern of decomposition during the active decay (aerobic protein decomposition) (PUTMAN, 1978; KOČÁREK, in press a). Many Coleoptera species are associated with the maggots as predators (e. g. Histeridae, some Staphylinidae or Silphidae). The movement of maggots on the surface of a carcass is mainly nocturnal (SCHOENLY, 1983; KOČÁREK, 2001a; a number of authors' own observations on carrion). Maggots are present on the carcass all day and beetles can predate them not only on the surface of the corpse but also inside it or under it in the soil. The association of Coleoptera predator activity with the diel cycles of blowfly maggots is not yet understood.

Generally, the communities which include both nocturnal and diurnal animals use the resources more efficiently than a community with a single phase of activity (WILLIAMS, 1959). Carrion, as well as the larvae of carrion blowflies (Diptera: Calliphoridae, Muscidae, Sarcophagidae) which compose the basic food resource for predators, are limited and ephemeral resources (food sources) and therefore subject to interspecific competition (PUTMAN, 1983). The activity of beetles at different times of the day allows resource partitioning among the beetles co-occurring within the guilds.

WILLIAMS (1959) studied the diel activity of undistinguished epigaeic invertebrates (i.e. invertebrates associated with the soil surface). The fauna was predominantly diurnal in his study. He found the peak of activity during the afternoon. Significantly more individuals were collected during daylight in this study (Tab. 2); but the diel activity of carrion-visiting Coleoptera peaked around sunset (Fig. 2).

The activity of carrion-visiting Coleoptera was found to be minimal between 24.00 and 08.00. It coincides with the peak of the postfeeding dispersal activity of the carrion blowfly larvae before their pupation in the soil in the surroundings of the carcass. The mass emigration of larvae from the corpse during the night appears to be an adaptation to minimise predation by the carrion-visiting Coleoptera (KOČÁREK, 2001a).

The majority of species observed in this study were active during both day and night (Appendix 1). Only a few species showed activity restricted to one day-phase. It was distinct particularly in Silphidae, where the intense competition lead to segregation by niches (Kočárek, 2001b).

Diel activity of Carabidae has been the most frequently studied among Coleoptera (Novák, 1973; Dennison & Hodkinson, 1983; Alderweireldt & Desender, 1992). Carabid beetles are non-specialised predators or scavengers, and their occurrence on carrion is mainly accidental. Some species (particularly large *Carabus* species) occasionally feed on carrion of mammals (Thiele, 1977). However, there are only limited data obtained during this study, which do not allow comparisons between species.

The diel activity of two carrion-visiting species from the family Histeridae was studied by Petruška (1978, 1979). Both species, *Margarinotus carbonarius* (Hoffmann, 1803) and *Saprinus semistriatus* (L. G. Scriba, 1790), showed diurnal activity with peaks in the afternoon. In the present study, the dominant species *Margarinotus striola succicola* (Thomson, 1862) was active in the afternoon, about sunset and to a lesser extent at night, with a peak in the late afternoon. Shubeck (1971) observed the activity of Histeridae in New Jersey exclusively during the daylight period. Schoenly (1983) recorded the activity of *Saprinus discoidalis* LeConte, 1851 both during daylight and at night, with a distinct peak 2 h before sunset.

The diel activity of Silphidae obtained during this study was published separately (Kočárek, 2001b).

From the family Leiodidae, only the diel activity of *Ptomaphagus subvillosus* (Goeze, 1777) was studied by Novák (1976). The species was active during daylight with a peak in the afternoon.

The diel activity of the carrion-visiting Staphylinid *Philonthus politus* (L., 1758) was studied by Novák (1976). The species showed diurnal activity with a peak in the afternoon, but with less activity at sunset and night. His results are similar to the results obtained in this study. The diel activity of other Coleoptera families has not been studied yet.

Some Coleoptera species are restricted either to forests i.e. *Oiceoptoma thoracica* (L., 1758), *Nicrophorus humator*, *Catops nigrita* Erichson, 1837, *Anoplotrupes stercorosus* (Hartmann, 1791) or non-forest sites, i.e. *Thanatophilus* spp.; the majority of these species are necrophagous or saprophagous. The strong habitat preferences are caused by strong competition between these species (Peschke et al., 1987). Among the groups of predators, habitat preferences are conspicuous: Histeridae and Staphylinidae are more or less evenly distributed at both sites (Appendix 1).

Williams (1959) found that the locomotory activity of epigaeic invertebrates is generally greater in woods than in non-forest areas., which is probably associated with the presence of a definite litter layer. Meadow habitats with low heterogeneity of vegetation are generally accompanied by a lower diversity of epigaeic invertebrates, e.g. Carabidae (Refseth, 1980; Waliczky, 1991; Magura & Tóthmérész, 1997). In carrion-visiting Coleoptera, Likovský (1967) obtained significantly more individuals and species in forests than in meadows. The same results were obtained in this study.

An interesting phenomenon is the shift in total numbers of individuals and species found in the forest and the meadow during autumn. There were more individuals and species found in autumn than in the previous seasons. The reason for this change may be that the species found exclusively in a forest habitat during spring and summer were also (or only) found in the field habitat in late autumn. For example, no carrion beetles (Silphidae) were found in the forest during this season (October) (Kočárek, 2001b). The ground temperatures (and the possibility of passive warming of the beetles' bodies from their environment) in the open non-forest habitat was increased during sunshine. The maximum day temperatures in the meadow habitat ($r = 16.3 \pm 4.9\,^{\circ}\mathrm{C}$) were higher than the same in the forest ($r = 13.6 \pm 5.0\,^{\circ}\mathrm{C}$) (paired t-test: $t_{(1,20)} = 4.97$, $P < 0.01$) and the minimum day temperatures were significantly lower in meadow habitat ($r = 5.7 \pm 3.9\,^{\circ}\mathrm{C}$) than in the forest one ($r = 6.6 \pm 3.4\,^{\circ}\mathrm{C}$) (paired t-test: $t_{(1,20)} = -2.66$, $P < 0.01$). The temperature in the forest is very low in late autumn without the possibility of direct sunshine during daylight. The implication is the immigration of typical forest species into the open non-forest habitats neighbouring the forest

Conclusion

The majority of species observed in this study were active during both day and night periods. Only a few species showed activity restricted to only one phase of the day. The activity of beetles at different times of day allows resource partitioning among the beetles co-occurring within guilds. This was particularly distinct in Silphidae where strong competition lead to segregation by niches.

Total diel activity of carrion-visiting Coleoptera peaked around sunset; minimal activity was observed between 24.00 – 08.00.

Some species were restricted to forest or non-forests sites; the majority of these species are necrophagous or saprophagous. The strong habitat preference is caused by competition amongst these species. In predators, habitat preferences were not conspicuous: Histeridae and Staphylinidae were more or less evenly distributed at both sites. In total, more individuals and species of carrion-visiting Coleoptera were collected in forest than in meadow.

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Appendix 1. Complete list of species obtained during each season in Opava (Czech Republic) with the data of diel activity and habitat associations.

Spring (May)															
Family	Time of collection (hour)												Numbers		
Species	06	08	10	12	14	16	18	20	**22**	**24**	**02**	**04**	Meadow	Forest	Total
Carabidae															
Abax ovalis (Duftschmid, 1812)			1	1										2	2
Abax parallelepipedus (Piller et Mitterpacher, 1783)									**1**					1	1
Carabus intricatus L., 1761			1											1	1
Carabus linnaei Panzer, 1810	1													1	1
Nebria brevicollis (F., 1792)										**1**				1	1
Poecilus cupreus (L., 1758)				1		1							2		2
Poecilus versicolor (Sturm, 1826)						1							1		1

Pterostichus niger (Schaller, 1783)									**1**					1	1
Pterostichus oblongopunctatus (F., 1787)					1				**1**			**1**	3		3
Hydrophilidae															
Cercyon lateralis (Marsham, 1802)								1	**5**	**1**			5	2	7
Cryptopleurum minutum (F., 1775)							1	2	**3**				4	2	6
Histeridae															
Gnathoncus nannetensis (Marseul, 1862)					1									1	1
Margarinotus striola succicola (C.G. Thomson, 1862)		1	3	1	3	6	9	8	**5**	**3**			26	13	39
Saprinus semistriatus (L.G. Scriba, 1790)								2	**1**				2	1	3
Silphidae															
Nicrophorus humator Olivier, 1790			3					1	**8**	**12**	**7**	**2**		33	33
Nicrophorus vespillo (L., 1758)				1	3	4	5	3	**1**				11	6	17
Nicrophorus vespilloides Herbst, 1784	6	8	4	5	16	16	45	39	**4**	**1**	**1**			145	145
Oiceoptoma thoracica (L., 1758)		2		14	33	13	4	4						70	70
Thanatophilus rugosus (L., 1758)				1	3	3	1	1					9		9
Thanatophilus sinuatus (F., 1775)	1		1	7	7	17	9	7	**8**		**1**		58		58
Leiodidae															
Catops coracinus Kellner, 1846								1						1	1
Catops fuliginosus Erichson, 1837	1		1				1	1						4	4
Catops nigrita Erichson, 1837		1	4	2	3	7	6	9	**1**		**2**		5	30	35
Catops subfuscus Kellner, 1846	1		1			2	3	3	**1**	**1**				12	12
Catops tristis (Panzer, 1794)							1				**1**			2	2
Catops sp. (females)			2	1	1	8	10	9	**3**	**1**	**1**		7	29	36
Choleva cisteloides (Frolich, 1799)							2						1	1	2
Ptomaphagus sericatus (Chaudoir, 1845)			1											1	1
Ptomaphagus subvillosus (Goeze, 1777)							1							1	1
Sciodrepoides alpestris Jeannel, 1934							1	5	**4**	**1**				11	11
Sciodrepoides fumatus (Spence, 1815)		3		1		2	3	4	**9**	**4**	**1**	**2**	6	23	29
S. fumatus + *S. alpestris* (females)	1	1			2	6	4	23	**8**	**5**	**2**	**1**	13	40	53
Sciodrepoides watsoni (Spence, 1815)			4			4	2	25				**1**	25	11	36
Scydmaenidae															
Euconnus pubicollis (Muller et Kunze, 1822)							1							1	1
Neuraphes elongatulus (Muller et Kunze, 1822)												**1**		1	1
Staphylinidae															
Aleochara curtula (Goeze, 1777)	1	1		7	6	8	3	2	**3**	**2**	**1**		29	5	34
Anotylus tetracarinatus (Block, 1799)	1						1	2	**1**				3	2	5
Atheta corvina (C.G Thomson, 1856)			1	1			5	3						10	10
Atheta crassicornis (F., 1792)						4	12	16	**2**		**1**		8	27	35
Atheta divisa (Markel, 1845)							3	4	**1**				2	6	8
Atheta indubia (Sharp, 1869)						1	1						2		2
Atheta laticollis (Kirby, 1832)			2				2	1					1	4	5
Atheta subtilis (W. Scriba, 1866)							1	3		**1**				5	5
Atheta sp.							2	2			**1**		2	3	5
Omalium caesum Gravenhorst, 1806				1	1				**2**	**1**			1	4	5
Omalium rivulare (Paykull, 1789)	27	31	58	19	16	23	33	39	**45**	**18**	**23**	**25**	39	318	357
Ontholestes murinus (L., 1758)	3		3	1	4		2	3	**3**				19		19
Ontholestes tesselatus (Fourcroy, 1785)					1				**1**				2		2
Oxypoda alternans (Gravenhorst, 1802)		1								**1**				2	2
Oxypoda lividipennis Mannerheim, 1830							1							1	1
Oxytelus rugosus (F., 1775)			1										1		1
Philonthus addendus Sharp, 1867				4	6	4	1		**2**				12	5	17
Philonthus fimetarius (Gravenhorst, 1802)						2		5						7	7
Philonthus politus (L., 1758)		1		6	7	4	1		**1**	**1**	**1**	**1**	18	5	23
Philonthus succicola C.G. Thomson, 1860			1	7	8	11	4	1	**2**			**1**	28	7	35

Philonthus varians (Paykull, 1789)					1									1	1
Proteinus crenulatus Pandellé, 1867	1		1											2	2
Quedius mesomelinus (Marsham, 1802)		1												1	1
Tachinus laticollis Gravenhorst, 1802								1						1	1
Tachinus signatus (Gravenhorst, 1802)									**1**	**1**			2		2
Geotrupidae															
Anoplotrupes stercorosus (Hartmann, 1791)						1								1	1
Nitidulidae															
Omosita colon (L., 1758)										**1**			1		1
Omosita discoidea (F., 1775)	1	1	1											3	3
Cryptophagidae															
Cryptophagus subdepressus Gyllenhal, 1828					1									1	1
Lathrididae															
Corticaria longicornis (Herbst, 1793)									**1**					1	1

Summer (July)

Family	Time of collection (hour)												Numbers		
Species	**06**	08	10	12	14	16	18	20	22	**24**	**02**	**04**	Meadow	Forest	Total
Carabidae															
Abax parallelpipedus (Piller et Mitterpacher, 1783)			1					1		**1**	**1**			4	4
Carabus hortensis L., 1758	**1**		2			1					**1**	**1**	4	2	6
Loricera pilicornis (F., 1775)				1			1						1	1	2
Molops piceus (Panzer, 1793)										**1**				1	1
Poecilus cupreus (L., 1758)									1					1	1
Pterostichus niger (Schaller, 1783)				1									1		1
Pterostichus oblongopunctatus (F., 1787)				2	1	3	3						9		9
Hydrophilidae															
Cercyon lateralis (Marsham, 1802)		1				1				**1**			3		3
Megasternum obscurum (Marsham, 1802)									1				1		1
Histeridae															
Saprinus lautus Erichson, 1839						1							1		1
Saprinus semistriatus (L.G. Scriba, 1790)						1		1	2	**1**			4	1	5
Margarinotus striola succicola (C.G. Thomson, 1862)	**2**		1		1	7	20	46	20	**16**	**10**	**4**	98	29	127
Silphidae															
Nicrophorus fossor Erichson, 1837					2	2	13	22	3				6	36	42
Nicrophorus humator Olivier, 1790							1	3	6	**4**	**1**			11	11
Nicrophorus investigator Zetterstedt, 1824	**1**					1	1	5	6	**1**				11	11
Nicrophorus vespillo (L., 1758)							4	9	2	**1**		**1**	12	5	17
Nicrophorus vespilloides Herbst, 1784				4	5	5	12	16	3	**2**				26	26
Oiceoptoma thoracica (L., 1758)	**1**			2	28	19	8		1			**1**		60	60
Thanatophilus rugosus (L., 1758)				2	3	1	1						7		7
Thanatophilus sinuatus (F., 1775)			1	6	18	13	5	3					46		46
Leiodidae															
Anisotoma orbicularis (Herbst, 1792)									1					1	1
Catops coracinus Kellner, 1846	**1**			1	1			3	2	**1**			9		9
Catops morio (F., 1792)						1							1		1
Catops nigrita Erichson, 1837	**3**	4		2	4	11	12	16	18	**6**	**1**	**1**	2	76	78
Catops westi Krogerus, 1931						2								2	2
Catops sp.(females)		2	2	3	5	9	7	13	21	**7**	**1**		11	59	70
Colenis immunda (Sturm, 1807)								1						1	1
Sciodrepoides alpestris Jeannel, 1934								3	2	**2**				7	7
Sciodrepoides fumatus (Spence, 1815)	**1**			1	1		1	3	6	**3**		**5**		21	21

S. fumatus + *S. alpestris* (females)				1		1	1	5	5	**1**				14	14
Sciodrepoides watsoni (Spence, 1815)		1	3	3				5	27	**11**	**2**	**4**	50	6	56
Staphylinidae															
Aleochara curtula (Goeze, 1777)				1	1		3	4	5	**1**		**1**	6	10	16
Anotylus tetracarinatus (Block, 1799)										**1**			1		1
Atheta corvina (C.G. Thomson, 1856)			2											2	2
Atheta crassicornis (F., 1792)			4	1		2	1	18	23	**12**	**2**	**1**	33	31	64
Atheta divisa (Markel, 1845)		1	1						5		**2**	**1**	8	2	10
Atheta subtilis (W. Scriba, 1866)					1									1	1
Atheta sp.								4					4		4
Omalium rivulare (Paykull, 1789)					1		1	3	2	**1**	**2**			10	10
Ontholestes murinus (L., 1758)		2		2		2	3					**1**	10		10
Ontholestes tesselatus (Fourcroy, 1785)			1			3	1	2					1	6	7
Oxypoda alternans (Gravenhorst, 1802)								2						2	2
Philonthus addendus Sharp, 1867									1				1		1
Philonthus fimetarius (Gravenhorst, 1802)									1					1	1
Philonthus politus (L., 1758)					3	11	8	6	2	**3**			23	10	33
Philonthus succicola C.G. Thomson, 1860				1	4	9	6	3	2	**1**			21	5	26
Philonthus varians (Paykull, 1789)					1								1		1
Philonthus sp.					1								1		1
Quedius mesomelinus (Marsham, 1802)								1						1	1
Tachinus laticollis Gravenhorst, 1802								2	1					3	3
Tachinus signatus (Gravenhorst, 1802)	**3**	2	3	1	2	1	2	4	7	**4**	**4**	**3**	25	11	36
Tachinus sp.		1							1				2		2
Geotrupidae															
Anoplotrupes stercorosus (Hartmann, 1791)						5	1							6	6
Dermestidae															
Dermestes lardarius L., 1758												**1**	1		1
Anobiidae															
Stegobium paniceum (L., 1758)					1							**2**		3	3
Nitidulidae															
Epurea unicolor (Olivier, 1790)								1						1	1
Glischrochilus quadripunctatus (L., 1758)							1	1	1	**1**				4	4
Omosita discoidea (F., 1775)	**1**								2	**1**				4	4
Lathrididae															
Aridius nodifer (Westwood, 1839)							1							1	1

Autumn (October)

Family	Time of collection (hour)												Numbers		
Species	**06**	08	10	12	14	16	18	**20**	**22**	**24**	**02**	**04**	Meadow	Forest	Total
Carabidae															
Pterostichus oblongopunctatus (F., 1787)	**1**		1				1	**2**	**1**		**1**	**1**		8	8
Poecilus cupreus (L., 1758)						1							1		1
Hydrophilidae															
Cercyon lateralis (Marsham, 1802)									**1**				1		1
Histeridae															
Margarinotus striola succicola (C.G. Thomson, 1862)							1						1		1
Silphidae															
Nicrophorus humator Olivier, 1790					1	1	3	**6**	**2**	**1**			14		14
Nicrophorus investigator Zetterstedt, 1824						2	6	**3**					11		11
Nicrophorus vespillo (L., 1758)					1	1	2	**4**	**3**	**1**			12		12
Nicrophorus vespilloides Herbst, 1784			1	4	5	9	11	**4**	**5**	**1**			40		40

Thanatophilus rugosus (L., 1758)				3	3	4	1						11		11
Thanatophilus sinuatus (F., 1775)				1	4	8	2	**2**	**2**				19		19
Leiodidae															
Catops coracinus Kellner, 1846									**1**				1		1
Catops fuliginosus Erichson, 1837			1				1	**1**	**2**		**1**		5	1	6
Catops grandicollis Erichson, 1837					1		1	**1**	**1**	**1**	**1**		6		6
Catops chrysomeloides (Panzer, 1798)								**1**					1		1
Catops kirbyi (Spence, 1815)							3	**1**				**2**	2	4	6
Catops nigricans (Spence, 1815)			1										1		1
Catops nigrita Erichson, 1837				2	3	1		**2**	**1**				1	8	9
Catops tristis (Panzer, 1794)	**1**		3		3	9	4	**10**	**3**	**2**	**1**		17	19	36
Catops sp.(females)			2	4		4	6	**6**	**6**	**2**	**1**	**1**	21	11	32
Sciodrepoides fumatus (Spence, 1815)				1										1	1
Sciodrepoides watsoni (Spence, 1815)				1			1		**1**	**1**			2	2	4
Staphylinidae															
Acidota cruentata (Mannerheim, 1831)										**1**			1		1
Aleochara curtula (Goeze, 1777)		1		2	3	4	1	**1**	**2**	**4**			18		18
Atheta corvina (C.G. Thomson, 1856)							1	**1**					1	1	2
Atheta divisa (Markel, 1845)								**1**						1	1
Atheta fungi (Gravenhorst, 1806)		1					1	**1**					2	1	3
Atheta laticollis (Kirby, 1832)					1		1	.						2	2
Atheta subtilis (W. Scriba, 1866)							2	**3**	**1**				2	4	6
Atheta trinotata (Kraatz, 1856)			1			1		**1**					1	2	3
Atheta vaga (Heer, 1839)						1	3	**1**					1	4	5
Atheta sp.					2		1			**1**			3	1	4
Megarthrus sinuatocollis (Boisduval et Lacordaire, 1835)								**1**						1	1
Omalium rivulare (Paykull, 1789)	**11**	6	10	8	12	6	15	**28**	**35**	**13**	**9**	**5**	68	90	158
Ontholestes murinus (L., 1758)			1		1					**1**			3		3
Ontholestes tesselatus (Fourcroy, 1785)		2	2	1	1	1	3			**1**	**1**		12		12
Oxypoda alternans (Gravenhorst, 1802)										**1**				1	1
Oxypoda lividipennis Mannerheim, 1830				1		1					**1**		3		3
Philonthus politus (L., 1758)			1	3	3	4	4	**2**	**2**	**3**	**1**	**1**	24		24
Philonthus sp.					2	3	1						3	3	6
Proteinus crenulatus Pandellé, 1867	**1**	1		1	2	1	4	**6**	**5**	**7**	**1**		6	23	29
Quedius mesomelinus (Marsham, 1802)										**3**	**1**		4		4
Stenus clavicornis Scopoli, 1863						1								1	1
Stenus similis (Herbst, 1784)							1						1		1
Geotrupidae															
Anoplotrupes stercorosus (Hartmann, 1791)			1	7	4	9	5	**2**					2	26	28
Dermestidae															
Dermestes murinus L., 1758						1							1		1
Nitidulidae															
Omosita depressa (L., 1758)												**1**		1	1

Key: Time of collection (hour) – the end of the two-hours catch period (e.g. 22 = the range of 20.00-22.00 h); regular font style – daylight, underlined – sunrise or sunset, bold – night.