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Differences between beetle communities colonizing cattle and horse dung

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Key words. Coleoptera, Aphodiidae, Hydrophilidae, Ptiliidae, Staphylinidae, cow dung, horse dung

Abstract. Piles of fresh cow and horse dung were placed in a pasture in Dziarny in north-east Poland. The differences between the beetle communities colonizing both types of dung at various stages of succession were analyzed. Beetles were sampled 2, 5, 10, 15, 20 and 25 days after placing the piles of dung in the pasture. A total of 5 343 individuals belonging to 125 species and 10 families were collected in 24 samples. None of the species of beetles collected colonized exclusively one type of dung. Several taxa showed a clear preference for cow or horse dung. Beetle succession proceeded faster in horse dung and there were significant differences in the dominant species recorded in the two types of dung. The reasons for the reported patterns are discussed.

INTRODUCTION

The faeces of large herbivores constitute a highly specific microhabitat, which is characterized by discontinuity and a very high rate of microsuccession. Significant physical and chemical changes occur within short periods of time (Dickinson & Craig, 1990). These changes result from the activity of the various organisms that colonize animal dung, including bacteria, protozoa, fungi, nematodes, arachnids, insects and earthworms, as well as local weather conditions. The species composition of the invertebrates colonizing animal dung are determined by several factors: physicochemical properties of the dung (moisture content and size of particles), weather conditions, soil type, exposure to direct sun light, season, the size of dung piles, interactions between species, the "age" and type of dung (Landin, 1961; Desiere, 1973; Olechowicz, 1974; Breymeyer & Zachareva-Stoilova, 1975; Holter, 2004).

The faeces of ruminants in the palearctic region have been studied extensively as part of ecological studies on beetles (Koskela, 1972; Koskela & Hanski, 1977; Wassmer, 1994; Šlachta et al., 2008), true flies (Hammer, 1941; Olechowicz, 1976), cattle dung (Wassmer, 1994; Šlachta et al., 2008), sheep dung (Olechowicz, 1974, 1976; Sowig & Wassmer, 1994), horse dung (Psarev, 2002) and others. These studies encompass the effect of abiotic factors on the community structure of organisms inhabiting dung at various stages in this microsuccession, their microhabitat preferences and phenology. Differences between the species composition of insects colonizing faeces of various animals, including cow and horse dung (Psarev, 2001, 2002; Dormont et al., 2004, 2007, 2010; Martinez & Suarez, 2006), are reported by some authors, but their findings are not comprehensive as they studied only a few coprophagous species or some differences were recorded only on the first and second day of succession. The main aim of this work was to describe differences between beetle communities inhabiting cow and horse dung during succession.

MATERIAL AND METHODS

This field study was carried out in May and June 2010 in a small pasture at Dziarny, approximately 4 km from the town of Iława (north-east Poland, 53°34´E, 19°37´N). The experiment was set up in a meadow where domestic cattle had been grazed for many years. In the north, the meadow is adjacent to farm buildings. Towards the south, the pasture becomes increasingly water logged and ends along the shoreline of the Iławka River. In the east and west, the meadow borders on farmland (grassland and crop fields). The experimental site never became waterlogged but large parts of the meadow were flooded seasonally. The soil in part of the field was peaty and in the rest sandy. Fresh dung was spread on the ground in the region of the field between the peat and sandy soil areas. The pasture is old and has not been ploughed or cultivated for many years. Farmers did not give their animals any treatment to rid them of parasites and their main food were grass and hay.

Six piles of cow dung from a cowshed and six piles of horse dung from a stable were spread in the meadow at the beginning of each month. Dung was spread at a distance of 100 m away from the farm building on moderately moist soil. Piles of approximately 1 kg of dung were placed at 30 cm intervals. The faeces (comprising one pile of cattle dung and one pile of horse dung) were examined 2, 5, 10, 15, 20 and 25 days later. Dung along with a 2 cm depth of the soil from immediately below the dung was transferred into a large vessel using a spatula. Small portions of about 20 g were taken from the vessel and placed in a container filled with water. After sedimentation, floating beetles were collected and placed in a container with ethyl acetate.

Samples were collected from 24 dung pats. The dominance structure was that used by Kasprzak & Niedbała (1981): eudominant (>10%), dominant (5.1–10%), subdominant (2.1–5%), receding (1.1–2%) and sub-receding (<1%). Each species was classified into one of the following trophic groups (Tr): saprophages (S) – species that feed on various organic remains, coprophages (K) – species that feed mainly on dung, mixophages (Mix) – species with different food sources (other organisms, remains, my-

Table 1. Number of specimens collected in May and June from cow and horse dung.

	Cow dung	Horse dung	Total
May	1731	1786	3517
June	1125	701	1826
Total	2856	2487	5343

celia, dung), predators (D) – species that feed on animals (mostly live). The trophic status of the beetles collected was that cited in the literature (Hinton, 1944; Koskela & Hanski, 1977; Bunalski, 2006; Szujecki, 2008). Taxa with an uncertain trophic status were labelled with a question mark. Every species was assigned to one of the following habitat specialization groups (HS): S3 – species colonizing only the faeces of large herbivores, S2 – species colonizing dung as well as carrion, decaying fungi, plant remains and compost, S1 – species colonizing various habitats (but found most abundantly in habitats other than dung) and eurytopic taxa, S0 – species that colonize dung incidentally. Two moisture preference (MP) groups were also identified: H – hygrophilous species, and M – mesohygrophilous species. Habitat specialization and moisture preferences were determined based on the literature (Burakowski et al., 1973–2000; Bunalski, 2006; Boukal et al., 2007).

In order to analyze the differences in dung beetle communities a chi-square test was used. The Shannon-Wiener Species Diversity Index (H') was used to compare beetle populations inhabiting cow and horse dung in each month. The formula is as follows:

$$H' = -\sum_{i=1}^{s} p_i \log_2 p_i$$

where s is the number of species, and p_i is the proportion of individuals of each species belonging to the i-th species of the total number of individuals. Species accumulation curves over time (based on the consecutive samples) were drawn for each type of dung.

RESULTS

In total 5,343 individuals belonging to 125 species were collected. 2,856 individuals belonging to 96 species were collected from cattle dung and 2,487 individuals belonging to 99 species from horse dung. There were significant differences in the species of beetles colonizing cow and horse dung (Jaccard Index = 0,58). A total of 3,517 specimens (100 species) were collected in May and 1,826 (83 species) in June (Table 1). The numbers of different species of beetles colonizing both types of dung are given in Table 2. The species with more than 100 individuals collected in each month of this study are listed in Tables 3 and 4.

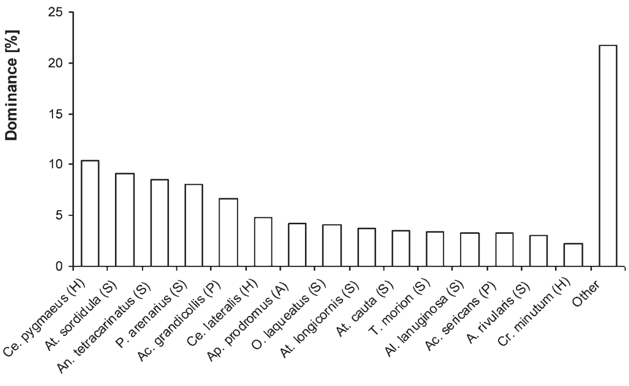

Fig. 1. Percentage dominance structure of the species of beetles collected from cow dung (N = 2856). S – Staphylinidae; P – Ptiliidae; H – Hydrophilidae; A – Aphodiidae.

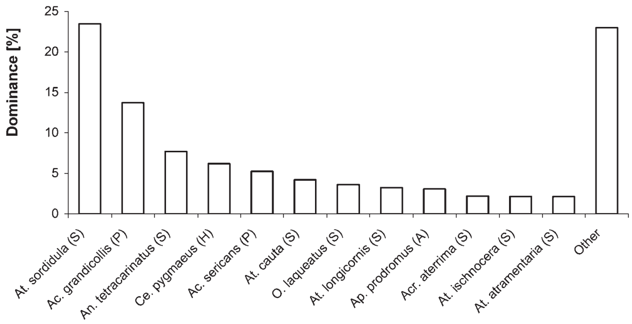

Fig. 2. Percentage dominance structure of the species of beetles collected from horse dung (N = 2487). S – Staphylinidae; P – Ptiliidae; H – Hydrophilidae; A – Aphodiidae.

In cattle dung the eudominant species was: *Cercyon pygmaeus* (Hydrophilidae, 10.4%), the dominants: *Atheta sordidula* (Staphylinidae, 9.1%), *Anotylus tetracarinatus* (Staphylinidae, 8.5%), *Platystethus arenarius* (Staphylinidae, 8.1%) and *Acrotrichis grandicollis* (Ptiliidae, 6.6%). In horse dung the eudominants were: *Atheta sordidula* (23.5%) and *Acrotrichis grandicollis* (13.7%), the dominants: *Anotylus tetracarinatus* (7.7%), *Cercyon pygmaeus* (6.2%) and *Acrotrichis sericans* (Ptiliidae, 5.3%). The dominance structures of the species of beetles in cow and horse dung are presented in Figs 1 and 2.

In May, the highest number of individuals collected from cow dung was recorded on the 10th day (694 individuals), whereas the number collected from horse dung on the 10th day was only slightly and insignificantly higher than on the 5th day (603 and 574 individuals). In June, the number collected from cow dung was greatest on the 5th day and from horse dung on the 2nd day (Fig. 3). The changes in the numbers of the four most frequent taxa collected over time indicates that the peak number collected was recorded earlier for horse than cow dung (Figs 4–7).

Coprophagous species of beetles were more abundant in cow dung (Figs 8, 9) ($\chi^2 = 324.97$, $p < 0.05$), which was also colonized for longer periods of time than horse dung. Maximum numbers of coprophagous species were recorded on the 10th day in May and 5th day of June in cow dung, and on 5th and 2nd days in horse dung. Saprophagous beetles were encountered more frequently in horse than in cow dung ($\chi^2 = 55.91$, $p < 0.05$). There were no differences in the numbers of mixophagous ($\chi^2 = 1.97$, $p < 0.05$) and predatory insects ($\chi^2 = 1.69$, $p < 0.05$) recorded. It is inter-

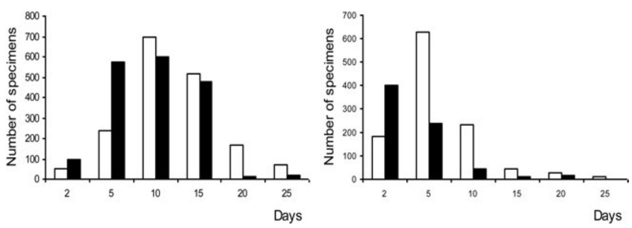

Fig. 3. Number of specimens collected in May (left) and June (right). White bars – cow dung; black bars – horse dung.

Table 2. Numbers of specimens and of the different species collected – combined data. Ncd – number of specimens collected from cow dung; Nhd – number of specimens collected from horse dung; Tr – feeding preferences; HS – habitat specialization; MP – moisture preferences; K – coprophages; S – saprophages; M – mixophages; D – predators; S3 – species colonizing only the faeces of large herbivores; S2 – species colonizing dung as well as carrion, decaying fungi, plant remains and compost; S1 – species colonizing various habitats (but found most abundantly in habitats other than dung) and eurytopic taxa; S0 – species that colonize dung incidentally; H – hygrophilous species; M – mesohygrophilous species; ? – uncertain trophic status.

Family/Species	Ncd	Nhd	Tr	HS	MP
Aphodiidae					
Aphodius ater (De Geer, 1774)	6	0	K	S3	M
Aphodius distinctus (Müller, 1776)	1	1	K	S2	M
Aphodius fimetarius (Linnaeus, 1758)	35	7	K	S2	M
Aphodius fossor (Linnaeus, 1758)	3	0	K	S3	H
Aphodius granarius (Linnaeus, 1767)	1	2	S	S2	M
Aphodius prodromus (Brahm, 1790)	122	77	K	S2	M
Aphodius subterraneus (Linnaeus, 1758)	3	1	K	S2	M
Oxyomus sylvestris (Scopoli, 1763)	22	30	S	S1	M
Carabidae Latreille, 1802					
Amara aenea (De Geer, 1774)	0	1	Mix	S0	M
Bembidion properans (Stephens, 1828)	2	3	D	S0	M
Clivina collaris (Herbst, 1784)	0	1	D	S1	H
Clivina fossor (Linnaeus, 1758)	1	0	D	S1	H
Dyschirius globosus (Herbst, 1784)	3	11	D	S1	H
Harpalus rufipes (De Geer, 1774)	0	1	Mix	S0	M
Pterostichus anthracinus (Illiger, 1798)	0	1	D	S0	H
Pterostichus vernalis (Panzer, 1796)	2	1	D	S0	H
Cryptophagidae Kirby, 1837					
Atomaria fuscata (Schoenherr, 1808)	0	1	S	S1	M
Atomaria lewisi Reitter, 1877	0	1	S	S1	M
Ephistemus globulus (Paykull, 1798) ?	2	2	S	S1	M
Ootypus globosus (Waltl, 1838)	26	16	S	S1	M
Geotrupidae Latreille, 1802					
Trypocopris vernalis (Linnaeus, 1758)	0	1	S	S1	M
Histeridae Paykull, 1811					
Margarinotus carbonarius (Hoffmann, 1803)	2	0	D	S2	M
Margarinotus ventralis (Marseul, 1854)	7	0	D	S2	M
Atholus bimaculatus (Linnaeus, 1758)	1	0	D	S2	M
Hydrophilidae Latreille, 1802					
Cercyon castaneipennis Vorst, 2009	24	10	K	S2	H
Cercyon granarius Erichson, 1837	2	2	S	S1	H
Cercyon haemorrhoidalis (Fabricius, 1775)	25	7	K	S2	H
Cercyon impressus (Sturm, 1807)	32	1	K	S2	H
Cercyon lateralis (Marsham, 1802)	136	12	K	S2	H
Cercyon marinus Thomson, 1853	0	1	S	S0	H
Cercyon melanocephalus (Linnaeus, 1758)	13	14	K	S2	H
Cercyon pygmaeus (Illiger, 1801)	297	155	K	S2	H
Cercyon quisquilius (Linnaeus, 1760)	5	5	K	S2	H
Cercyon unipunctatus (Linnaeus, 1758)	1	5	K	S1	H
Cryptopleurum crenatum (Panzer, 1794)	7	2	K	S2	H
Cryptopleurum minutum (Fabricius, 1775)	62	30	K	S2	H
Cryptopleurum subtile Sharp, 1884	1	0	K	S1	H
Megasternum concinnum (Marsham, 1802)	6	15	S	S1	H
Sphaeridium bipustulatum Fabricius, 1781	6	4	K	S3	H
Sphaeridium lunatum Fabricius, 1792	5	0	K	S3	H
Sphaeridium marginatum Fabricius, 1787	2	1	K	S3	H
Sphaeridium scarabaeoides (Linnaeus, 1758)	0	1	K	S3	H
Monotomidae Laporte, 1840					
Monotoma brevicollis Aubé, 1837	0	1	S	S1	M
Nitidulidae Latreille, 1802					
Omosita discoidea (Fabricius, 1775)	0	1	S	S0	M
Ptiliidae Erichson, 1845					
Acrotrichis atomaria (DeGeer, 1774)	1	0	S	S1	M
Acrotrichis dispar (Matthews, 1865)	2	17	S	S1	M
Acrotrichis fascicularis (Herbst, 1793)	2	8	S	S1	M
Acrotrichis grandicollis (Mannerheim, 1844)	189	342	S	S1	M
Acrotrichis sericans (Heer, 1841)	94	131	S	S1	M
Acrotrichis sp.	6	21			
Acrotrichis thoracica (Waltl, 1838)	1	2	S	S1	M
Ptenidium nitidum (Heer, 1841)	5	16	S	S1	M
Ptenidium sp.	0	3			
Staphylinidae Latreille, 1802					
Acrotona aterrima (Gravenhorst, 1802)	52	55	Mix	S1	M
Acrotona parvula (Mannerheim, 1830)	3	0	Mix	S1	M
Acrotona pusilla Brundin, 1952	7	4	Mix	S1	M
Aleochara intricata Mannerheim, 1830	3	1	D	S1	M
Aleochara lanuginosa Gravenhorst, 1802	95	44	D	S1	M
Aleochara tristis Gravenhorst, 1806	0	1	D	S1	M
Amischa analis (Gravenhorst, 1802)	2	3	Mix?	S1	M
Anotylus complanatus (Erichson, 1839)	0	1	Mix	S1	M
Anotylus rugosus (Fabricius, 1775)	10	2	Mix	S1	H
Anotylus tetracarinatus (Block, 1799)	243	192	Mix	S1	M
Aploderus caelatus (Gravenhorst, 1802)	1	0	Mix?	S1	M
Atheta atramentaria (Gyllenhal, 1810)	33	53	Mix	S1	M
Atheta cauta (Erichson, 1837)	101	105	Mix	S1	M
Atheta celata (Erichson, 1837)	1	0	Mix	S1	M
Atheta inquinula (Gravenhorst, 1802)	29	9	Mix	S2	M
Atheta ischnocera Thomson, 1870	3	54	Mix	S2	M
Atheta longicornis (Gravenhorst, 1802)	108	81	Mix	S1	M
Atheta macrocera (Thomson, 1856)	56	13	Mix	S2	M
Atheta melanaria (Mannerheim, 1831)	0	1	Mix	S1	M
Atheta nigra (Kraatz, 1856)	0	1	Mix	S2	M
Atheta nigripes (Thomson, 1856)	51	4	Mix	S1	M
Atheta palustris (Kiesenwetter, 1844)	1	1	Mix	S1	H
Atheta sordidula (Erichson, 1837)	261	585	Mix	S2	M
Atheta sp.	0	1			
Autalia rivularis (Gravenhorst, 1802)	86	12	Mix?	S2	M
Bledius gallicus (Gravenhorst, 1806)	1	0	Mix?	S0	H
Carpelimus corticinus (Gravenhorst, 1806)	2	1	Mix	S1	H
Carpelimus gracilis (Mannerheim, 1830)	6	1	Mix	S1	H
Cordalia obscura (Gravenhorst, 1802)	0	3	Mix?	S1	H
Falagria sulcatula (Gravenhorst, 1806)	0	20	Mix?	S1	M
Gabrius sp.	1	0			
Gyrohypnus angustatus Stephens, 1833	5	11	D	S1	M
Gyrohypnus fracticornis (Müller, 1776)	1	0	D	S1	M
Gyrohypnus punctulatus (Paykull, 1789)	18	27	D	S1	M
Ilyobates bennetti Donisthorpe, 1914	1	0	Mix?	S1	H
Lathrobium geminum Kraatz, 1857	1	0	D	S1	H
Leptacinus pusillus (Stephens, 1833)	0	1	D	S1	M
Leptacinus sulcifrons (Stephens, 1833)	1	0	D	S1	H
Leucoparyphus silphoides (Linnaeus, 1767)	2	0	S?	S1	M
Megarthrus denticollis (Beck, 1817)	5	4	S	S1	M
Megarthrus prosseni Schatzmayr, 1904	7	7	S	S1	M
Meotica filiformis (Motschulsky, 1860)	1	0	?	?	?
Oxypoda opaca (Gravenhorst, 1802)	0	4	Mix	S1	M
Oxytelus laqueatus (Marsham, 1802)	118	90	Mix	S1	M
Oxytelus migrator Fauvel, 1904	1	0	Mix	S1	M
Oxytelus sculptus Gravenhorst, 1806	0	3	Mix	S1	M
Pachnida nigella (Erichson, 1837)	1	0	Mix?	S0	H
Philonthus albipes (Gravenhorst, 1802)	2	28	D	S1	M

Family/Species	Ncd	Nhd	Tr	HS	MP
Philonthus alpinus Eppelsheim, 1875	4	2	D	S1	M
Philonthus coprophilus Jarrige, 1949	1	1	D	S2	M
Philonthus cruentatus (Gmelin, 1790)	3	3	D	S1	M
Philonthus longicornis Stephens, 1832	1	0	D	S1	M
Philonthus marginatus (Müller, 1764)	1	0	D	S1	M
Philonthus parvicornis (Gravenhorst, 1802)	0	1	D	S1	M
Philonthus rubripennis Stephens, 1832	0	1	D	S1	M
Philonthus sanguinolentus (Grav., 1802)	7	2	D	S1	M
Philonthus splendens (Fabricius, 1793)	6	3	D	S1	M
Philonthus tenuicornis Mulsant et Rey, 1853	2	3	D	S1	M
Philonthus varians (Paykull, 1789)	8	6	D	S1	M
Philonthus ventralis (Gravenhorst, 1802)	1	1	D	S1	M
Platystethus arenarius (Geoffroy, 1785)	231	18	K?	S2	M
Rugilus orbiculatus (Paykull, 1789)	0	4	D	S1	H
Scaphisoma agaricinum (Linnaeus, 1758)	0	1	S	S0	M
Scopaeus minutus Erichson, 1840	1	0	D	S0	M
Scydmaeus tarsatus Müller et Kunze, 1822	0	1	S?	S1	M
Stenus clavicornis (Scopoli, 1763)	2	0	D	S0	H
Tachinus laticollis Gravenhorst, 1802	0	1	Mix	S1	M
Tachinus lignorum (Linnaeus, 1758)	2	0	Mix	S2	M
Tachinus marginatus (Fabricius, 1793)	0	3	Mix	S1	M
Tachinus marginellus (Fabricius, 1781)	1	4	Mix	S1	M
Tachinus rufipes (Linnaeus, 1758)	1	1	Mix	S1	M
Tachyporus hypnorum (Fabricius, 1775)	0	1	D	S1	M
Tinotus morion (Gravenhorst, 1802)	97	36	Mix?	S1	M
Trichiusa immigrata Lohse, 1984	3	3	Mix?	S1	M
Xantholinus laevigatus Jacobsen, 1849	0	1	D	S1	M
Xantholinus longiventris Heer, 1839	1	1	D	S1	H
Xantholinus sp.	0	1	D		
TOTAL	2856	2487			

esting that most of the beetles collected from dung are not coprophagous and not dung specialists.

There were minor differences in the numbers of beetles collected that belonged to the different habitat specialization groups. Species colonizing only the faeces of large herbivores were more abundant in cow than horse dung ($\chi^2 = 9.14$, $p < 0.05$). An analysis of the moisture preferences of the beetles revealed a higher number of hygrophilous specimens in cow than in horse dung ($\chi^2 = 169.93$, $p < 0.05$). There were no differences between the remaining groups (Fig. 10): S2 species ($\chi^2 = 0.19$, $p < 0.05$), S1 species ($\chi^2 = 0.38$, $p < 0.05$), mezohygrophilous species ($\chi^2 = 0.1$, $p < 0.05$).

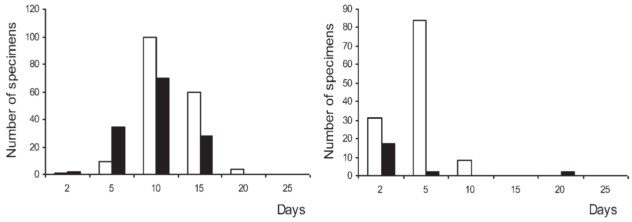

Fig. 4. Numbers of *Cercyon pygmaeus* (Hydrophilidae) collected in May (left) and June (right). White bars – cow dung; black bars – horse dung.

The Shannon-Wiener Species Diversity Index for cow dung in May was higher then that for horse dung (H' = 4.53 and H' = 4.17). A similar situation was recorded in June (H' = 4.58 and H' = 4.39). Species accumulation curves (Fig. 11) show that the numbers of species recorded initially increased rapidly over the first month and then remained relatively constant.

DISCUSSION

The beetle community that colonized cow dung was somewhat similar to that reported by Hanski (1972) in Finland. This author recorded 58 species of beetles of the family Staphylinidae in cow dung of various ages in a meadow in May and June, i.e. two more taxa than recorded in this study. Many of the species identified by Hanski were also recorded in our study (46%). Of the remaining 40 species (Koskela & Hanski, 1977) belonging to the families of Carabidae, Hydrophilidae, Histeridae and Scarabaeidae, which were recorded between June and October 1966 and in May 1967, 19 were recorded in our study. The study site in Finland is more than 1,000 km north of Dziarny and is in a different climate zone. The Polish site is characterized by a warm temperate transitional climate and the Finnish site by a cold temperate transitional climate. Many of the species collected at the two sites were identical and the number might have been even greater if the experiments

Table 3. Most abundant species collected in May – numbers of individuals collected each day.

Family/Species	Cow dung						Horse dung					
Day	2	5	10	15	20	25	2	5	10	15	20	25
Aphodiidae												
Aphodius prodromus (Brahm, 1790)	34	87	1	0	0	0	24	53	0	0	0	0
Hydrophilidae Latreille, 1802												
Cercyon lateralis (Marsham, 1802)	1	6	55	51	12	0	1	4	3	3	0	0
Cercyon pygmaeus (Illiger, 1801)	1	9	100	60	4	0	2	34	70	28	0	0
Ptiliidae Erichson, 1845												
Acrotrichis grandicollis (Mannerheim, 1844)	2	1	56	53	6	0	4	122	63	53	0	2
Staphylinidae Latreille, 1802												
Aleochara lanuginosa Gravenhorst, 1802	2	17	35	37	2	0	1	24	4	14	0	0
Anotylus tetracarinatus (Block, 1799)	1	5	119	51	4	0	26	77	54	20	0	0
Atheta sordidula (Erichson, 1837)	0	0	25	40	77	48	0	21	234	222	0	7
Oxytelus laqueatus (Marsham, 1802)	1	40	45	3	1	0	9	62	0	0	0	0
Platystethus arenarius (Geoffroy, 1785)	1	10	47	49	9	1	2	9	1	1	0	0

TABLE 4. Most abundant species collected in June – number of individuals collected each day.

Family/Species	Cow dung						Horse dung					
Day	2	5	10	15	20	25	2	5	10	15	20	25
Hydrophilidae Latreille, 1802												
Cercyon pygmaeus (Illiger, 1801)	31	84	8	0	0	0	17	2	0	0	2	0
Ptiliidae Erichson, 1845												
Acrotrichis grandicollis (Mannerheim, 1844)	9	41	19	1	1	0	54	40	3	0	1	0
Acrotrichis sericans (Heer, 1841)	2	36	51	0	0	0	59	29	3	0	0	0
Staphylinidae Latreille, 1802												
Atheta cauta (Erichson, 1837)	1	92	2	0	0	0	22	31	1	0	0	0
Atheta longicornis (Gravenhorst, 1802)	9	59	11	3	2	0	31	25	0	0	0	0
Atheta sordidula (Erichson, 1837)	0	10	36	16	9	0	51	45	5	0	0	0
Platystethus arenarius (Geoffroy, 1785)	37	67	10	0	0	0	4	0	1	0	0	0

had been carried out over corresponding periods of time. In a study conducted by Psarev (2001) in the Upper Altai region (warm temperate continental climate zone), situated 5,000 km east of Dziarny, 14 of the 29 species of beetles (48%) collected were also collected in our study.

There were significant differences in the number of specimens collected in the different months ($\chi^2 = 526.96$, $p < 0.05$). This may be due to differences in the weather. May was cloudy with relatively high rainfall and an average temperature of 12°C, whereas June was a sunny month with little rainfall and a mean temperature of 16°C (source: http://www.tutiempo.net/en/Climate/OLSZTYN/2010/122720.htm). In June, dung dried out faster (judged visually) due to higher temperatures and lower precipitation, which increased the rate of the micro-succession of coprophagous, saprophagous and mixophagous species. Our results confirm that weather conditions and dung moisture content are very important factors determining the survival of beetle communities in dung (Landin, 1961; Breymeyer, 1974; Merritt & Anderson, 1977). In June, beetles were significantly less abundant in horse than cow dung. This can be attributed to the weather conditions, which more rapidly changed the moisture and consistency of the horse dung and thereby reduced the availability of food. When the moisture content of dung is low the beetles are unable to assimilate enough nutrients because it becomes more difficult to filter out the coarse particles in the dung (Holter & Scholtz, 2007).

Cow and horse dung differ in structure, moisture content, chemical composition and type of chemical compounds they release into the environment (Frank & Shutt, 1898; Holter & Scholtz, 2007; Dortmond et al., 2010). Coprophagous beetles select habitats using olfactory cues and many species have a clear preference for a given type of faeces, but there is no evidence of the existence of European species that are attracted only to cow or horse dung (Dormont et al., 2004, 2007). The results of our study suggest that: (1) none of the species of beetles colonized only cow or horse dung, (2) several beetle taxa showed a clear preference for either the cow or horse dung, (3) beetle succession proceeded faster in horse than in cow dung and (4) there are differences in the dominance structure of beetle communities inhabiting cow and horse dung.

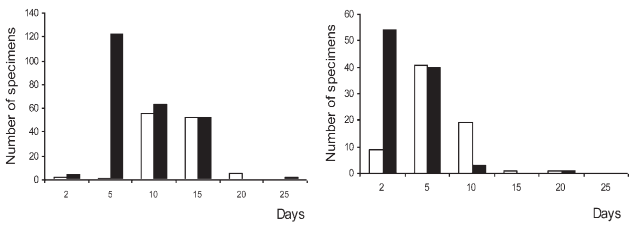

Fig. 5. Numbers of *Acrotrichis grandicollis* (Ptiliidae) collected in May (left) and June (right). White bars – cow dung; black bars – horse dung.

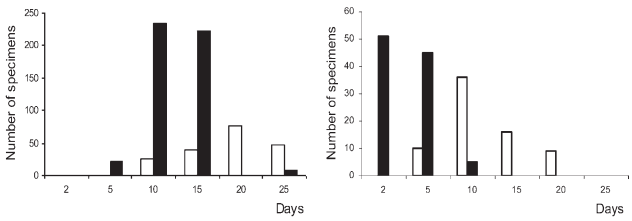

Fig. 6. Numbers of *Atheta sordidula* (Staphylinidae) collected in May (left) and June (right). White bars – cow dung; black bars – horse dung.

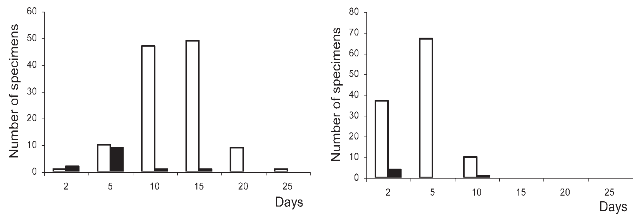

Fig. 7. Numbers of *Platystethus arenarius* (Staphylinidae) collected in May (left) and June (right). White bars – cow dung; black bars – horse dung.

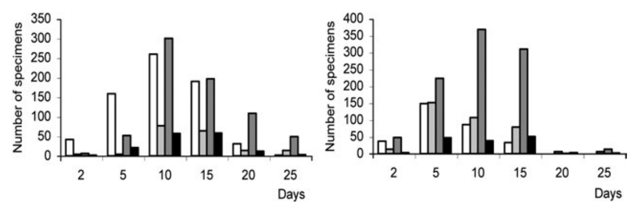

Fig. 8. Numbers of individuals collected in May belonging to the different trophic groups in the beetle communities that colonized cow dung (left) and horse dung (right). White bars – coprophagous species; light grey – saprophagous; dark grey – mixophagous; black – predators.

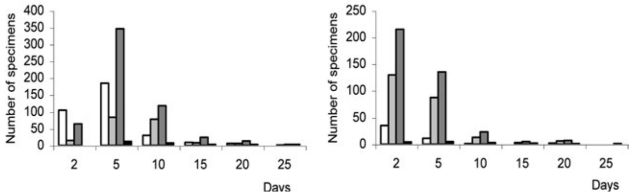

Fig. 9. Numbers of individuals collected in June belonging to the different trophic groups in the beetle communities that colonized cow dung (left) and horse dung (right). White bars – coprophagous species; light grey – saprophagous; dark grey – mixophagous; black – predators.

The species with a preference for cow dung were *Cercyon pygmaeus* (around 66% of the total population, $\chi^2 = 44.61$, $p < 0.05$) and *Platystethus arenarius* (around 93%, $\chi^2 = 182.20$, $p < 0.05$), whereas *Atheta sordidula* (around 69%, $\chi^2 = 124.09$, $p < 0.05$) and *Acrotrichis grandicollis* (around 64%, $\chi^2 = 44.08$, $p < 0.05$) were more attracted to horse dung. The higher numbers of species recorded in one of the two types of dung is probably because it was for them a higher quality food.

Our results indicate that succession was faster in horse than in cow dung. Beetle succession in dung is determined mainly by the availability of food. Fresh faeces that have a high water content are most readily colonized by coprophagous species, which are rapidly succeeded by other species as the dung dries out and the nutrients are depleted. Fresh faeces have the highest moisture content. They progressively dry out due to evaporation, which is increased by insect activity, water uptake by insects and seepage, the rate of which depends on the nature of the substrate (Hughes et al., 1975). The buccal apparatus of dung beetles is delicate and adapted for extracting fluid and small particles (Miller, 1961; Holter, 2004), therefore, beetles are unable to feed on faeces with a low moisture content and hard structure. Similar nutritional dependencies probably exist in species feeding on dead organic matter (saprophages), fungi and other organisms. The consistency and moisture content of cattle and horse dung differ significantly. Fresh cattle faeces contain more water and dehydrated at a slower rate. In the drying process, cow dung forms a hard and water-proof coat, which reduces evaporation, whereas horse dung is more susceptible to water loss due to its larger surface area. These factors affect the rate of succession. Because of this, horse dung is not degraded faster because the organisms colonizing animal excrement are only one of the factors that affect this process and adult beetles make up only a small percentage of the organisms that occupy such microhabitats. The shorter the colonization period the slower is the degradation process. In a study of cow and horse dung in the Upper Altai region, twice as many beetles were attracted to fresh horse dung (1-day-old) than to fresh cow dung (Psarev, 2001). In our experiment, beetles were collected on the second day of the study, but even then more individuals were collected from horse than cow dung.

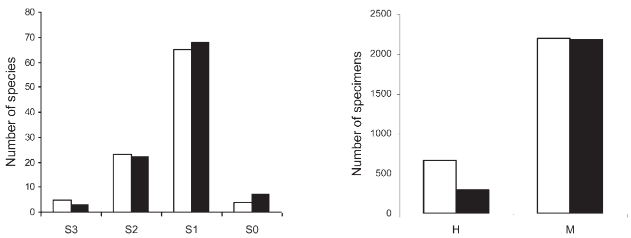

Fig. 10. Numbers of species belonging to particular habitat specialization groups (left) and numbers of individuals that prefer moist habitats (right), among the beetles that were collected from cow and horse dung. White bars – cow dung; black bars – horse dung. S3 – species that only colonize the faeces of large herbivores; S2 – species colonizing dung as well as carrion, decaying fungi, plant remains and compost; S1 – species colonizing various habitats (but found more abundantly in habitats other than dung) and eurytopic taxa; S0 – species that colonize dung incidentally. H – hygrophilous species; M – mesohygrophilous species.

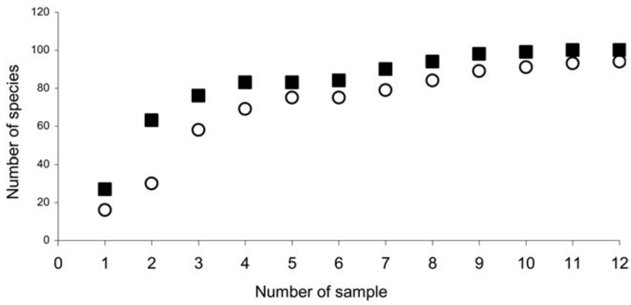

Fig. 11. Species accumulation curves over time. Black squares – species collected from cow dung; white circles – species collected from horse dung.

Differences in the physicochemical (moisture and structure) properties of cow and horse dung are associated with variations in the percentage presence of different trophic groups in the communities analyzed. Due to a greater availability of nutrients coprophagous species were nearly twice as abundant in cow as in horse dung. The above also accounts for why there were nearly twice as many species in cow dung that were dung specialists (S3). Cow dung is a more specific habitat, particularly during the early stages of succession when it is wetter and contains more nutrients than horse dung. In addition, it is likely that horse dung contains fewer nutrients suitable for coprophagous beetles (it is easier to ingest particles in a moist environment). Due to its higher moisture content, cow dung also attracts more individuals belonging to water-loving species.

The fact that most of the species we collected in dung are not coprophagous and not dung specialists is probably because the nutrients are quickly depleted and other organisms such as larvae of flies, springtails (Collembola), mites (Acarina) and fungi appears. Initially dung pats are a good source of food for coprophagous beetles, but later on this environment becomes a better source of food for mixophages such as species of the large *Atheta* genus that presumably feed on the eggs and small larvae of flies (Hanski & Koskela, 1979). Similar relations are reported by Koskela & Hanski (1977), however, these authors did not distinguish any of the beetles they collected as mixophagous.

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