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ORIGINAL ARTICLE

Function of coprophagous beetles (*Coleoptera: Scarabaeidae*, *Geotrupidae*, *Hydrophilidae*) in cattle pastures inferred from pitfall trapping data

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Abstract

An analysis of data on the dry weight biomass of coprophagous beetles in standardized dung (4.5 l) was conducted in order to characterize the spatial and the seasonal distribution of the beetles' biomass in cattle pastures and to elucidate their function in dung decomposition. Nested Anova with factors of farm, site (nested in farm), seasonal period and year was used to evaluate the effect of these factors on the biomass of four functional species groups: the dung dwellers of *Scarabaeidae* (subfamily *Aphodiinae*), the dung dwellers of *Hydrophilidae*, the small tunnellers of *Scarabaeidae* (subfamily *Coprinae*) and the large tunnellers of *Geotrupidae*. The spatial variation of biomass (between the sites and the farms) was insignificant (P>0.05) in the two dung-dweller groups and in the large-tunnellers group. On the other hand, a significant (P<0.05) seasonal variation of biomass was formed mainly by two species, *Aphodius prodromus* and *A. sphacelatus*. In summer, most of the biomass was accounted for by *Sphaeridium lunatum*, *S. scarabaeoides* and *A. rufipes*. In the two tunneller groups, *Onthophagus fracticornis*, *Geotrupes stercorarius* and *G. spiniger* formed a majority of the biomass in dung.

Key words: coprophagous beetles; dung decomposition; *Scarabaeidae*; *Geotrupidae*; *Hydrophilidae*; pasture

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INTRODUCTION

Coprophagous beetles contribute to dung removal from pasture sward, to its decomposition and to nutrient cycling in pastures (Hanski and Cambefort 1991, Gittings et al. 1994, Bang et al. 2005). Taxonomically, they belong to the families of *Scarabaeidae*, *Geotrupidae*, *Hydrophilidae* and

Staphylinidae. Functionally, the dung dwellers and the tunnellers used to be distinguished (Hanski and Cambefort 1991). While the dung dwellers limit their reproduction and larval development to the entire dung pat or its very near proximity (Vitner 1998), the tunnellers construct underground nests where they transport the dung on which the larval development takes place. Functionally, the tunnellers contribute most to dung removal from the pasture surface, to nutrient cycling and to improvement of the physical and chemical properties of soil (Holter and Hendriksen 1988, Bang et al. 2005, Yamada et al. 2007). The tunnellers are species from the families Geotrupidae and Scarabaeidae (subfamily Coprinae). The dung dwellers are Scarabaeidae – subfamily Aphodiinae and *Hydrophilidae* species (the majority in Europe).

In the Czech Republic, the seasonal pasturing of dairy cattle took place in the border areas, only locally since the 1950s. Since the 1990s, cattle grazing has became more common and beef husbandry based on the extensive grazing of imported breeds has spread. Despite its potential economic value, there is only limited knowledge of the community ecology and function of the coprophagous fauna. The standardized sampling design based on the application of pitfall traps baited by fresh cow dung was used by Křivan (2000) and by Slachta et al. (2008a, 2009a, b) in cattle pastures in South and West Bohemia. In the two latter studies, a total of 35,429 specimens of forty-three species were collected in 59 experimental trials from 2006 to 2008.

The aim of this study was to examine the spatial and the temporal distribution of the biomass of coprophagous beetles, on the basis of this dataset, in order to characterize their function and potential in cattle pastures.

MATERIAL AND METHODS

The experiment was carried out on three dairy farms in Novohradské hory and the Šumava Mountains in the south-west boundary region of the Czech Republic. The farms were located at an altitude of 575, 790 and 730 meters above sea level (farm 1, 2 and 3, respectively), 40–100 km apart from each other (for more details on experimental sites see Šlachta et al. 2009a). Seasonal grazing by approximately 100 cows of the Czech Fleckvieh or Holstein breeds has been practised there continuously for more than forty years. The grazing starts in May and finishes in October. The pasture sward belonged to the *Lolio-Cynosuretum* association (Frelich et al. 2006).

The beetles were collected in pitfall traps baited with 1.5 litres of fresh cow dung, which was obtained from stalls on the day the traps were set. The trap consisted of a plastic box (20 cm in diameter and 16 cm high) buried to its rim in the soil (Slachta et al. 2008b). The upper part of the trap was filled with the fresh dung placed on a wire mesh. Formaldehvde (10% solution) was used as a preserving fluid. A set of three traps at half-meter distances from each other was used in a single sampling trial and the material collected into the three traps was pooled; the total volume of bait in three traps was 4.5 l. In our experiment in 2008, a triplet of traps was placed on two pasture sites on each farm 0.6–1.5 km apart (site 1 and 2) and the sampling was carried out simultaneously on both sites (for more details see Slachta et al. 2009a). The exposure time of the traps was 7 days. The dates of the traps exposition are given in Table 1. The material collected was identified to species according to Balthasar (1964), Hansen (1987) and Vorst (2009) and the specimens were counted. The higher classification and nomenclature follows Boukal et al. (2007) and Juřena and Týr (2008).

The dry weight (DW) biomass of the beetles was calculated on the basis of weighing with 1 mg precision in each of 59 samples for each species following the methodology of Slachta et al. (2008a). The samples were sorted in six sampling periods according to calendar month (Tables 1, 2). The mean biomass in each sampling period, site and farm was calculated separately for the particular species and for the sum of species forming one of four functional groups: dung dwellers of Scarabaeidae, Aphodiinae (S-A), dung dwellers of *Hydrophilidae* (H), small tunnellers of Scarabaeidae, Coprinae (S-C) and large tunnellers of Geotrupidae (G), according to the methodology of Šlachta et al. (2008c). The nested Anova (StatSoft CR s r. o. 2008) was used for the evaluation of the spatial variation (local site effect, regional - farm effect; site nested in farm) and temporal variation (effect of year and sampling period) in the beetle biomass in samples separately for each of the four functional groups. The Post-hoc Tukey test was used for the statistical evaluation of the differences between particular levels of the factors.

		Far	m 1			Farm 2		Farm 3			
		Site 1		Site 2	Sit	e 1	Site 2	Sit	e 1	Site 2	
Period	2006	2007	2008	2008	2007	2008	2008	2007	2008	2008	
1		10 Apr	11 Apr	11 Apr	11 Apr	24 Apr	24 Apr	11 Apr	24 Apr	24 Apr	
			28 Apr								
2	19 May	18 May	12 May	12 May	23 May	22 May	22 May	23 May	23 May	23 May	
			22 May								
3	19 Jun	15 Jun	25 Jun	25 Jun	19 Jun	25 Jun	25 Jun	19 Jun	26 Jun	26 Jun	
4	24 Jul	31 Jul	30 Jul	30 Jul	25 Jul	30 Jul	30 Jul	25 Jul	31 Jul	31 Jul	
5	31 Aug	17 Sep	3 Sep	3 Sep	17 Sep	3 Sep	3 Sep	2 Aug	4 Sep	4 Sep	
								14 Sep			
6	2 Oct		9 Oct	9 Oct		9 Oct	9 Oct		10 Oct	10 Oct	

Table 1. The dates of trap exposure in 2006, 2007 and 2008 and their sorting in 6 sampling periods according to the calendar months

Table 2. Number of sample trials in particular site, farm and sampling period

			Sampling period (see Table 1)										
		1	2	3	4	5	6						
Farm 1	Site 1	3	4	3	3	3	2						
гаппт	Site 2	1	1	1	1	1	1						
F 0	Site 1	2	2	2	2	2	1						
Fami 2	Site 2	1	1	1	1	1	1						
	Site 1	2	2	2	2	3	1						
Farm 3	Site 2	1	1	1	1	1	1						

RESULTS AND DISCUSSION

The results of the nested Anova are given in Table 3. The effect of farm was insignificant in S-A, H and G functional groups (P>0.05). In S-C group, there was less biomass on farm 2 than on the other farms (P < 0.01). The site and year effects were insignificant in all functional groups (P>0.05). The significant differences (P<0.05)were found between the sampling periods in all but the G group (P<0.05; Fig. 1). The spatial (local and regional) variation in biomass thus revealed was lower than the seasonal variation in Scarabaeidae and Hydrophilidae beetles. The exception is the Scarabaeidae-Coprinae group. This is because on farm 2 the most common species of this group, Onthophagus fracticornis (Preyssler 1790), was less frequent than on the other farms (Ślachta et al. 2009a).

The significant seasonal variation in biomass of *Scarabaeidae* and *Hydrophilidae* relates to

their species-specific difference of adult flight actitivity and their reproduction (Waßmer 1994, Gittings and Giller 1997, Šlachta et al. 2009a). In the first sampling period (April), two species of dung dwellers of Aphodius prodromus (Brahm 1790) and A. sphacelatus (Panzer 1798) formed on average 51% and 26% of biomass in the samples, respectively (Table 4). These two species thus contributed substantially to the biomass peak in April. They are known to have an early-spring and autumn peak of occurrence (Gittings and Giller 1997, Šlachta et al. 2009a). Their contribution to dung removal from pasture surface may consist in the penetration of the upper crust of the dung pat thus accelerating its destruction by weathering. Their larval development can run without the dung, in decaying vegetables for example, and the occurrence of adults in dung may thus indicate mainly maturation feeding in spring. The next peak in the activity of Scarabaeidae dung dwellers was found in sampling period 4

(late July). This is attributed mainly to the occurrence of *Aphodius rufipes* (Linnaeus 1758). This large species contributes significantly to dung decomposition both by adult and larvae feeding (Holter 1979a, b). The aggregation of about one hundred specimens in a single dung pat may take place in this species (Holter 1979b). The highest number of specimens recorded in this study was 471 specimens in a single sampling trial at the end of August 2006 (sampling period 5; Šlachta et al. 2009a). The summer peak of biomass in *Hydrophilidae* (sampling period 3,

4) was formed by the two largest species of this group, *Sphaeridium lunatum* Fabricius 1792 and *S. scarabaeoides* (Linnaeus 1758), which dominated the biomass of H group for all the sampling season (Table 5). The adults feed on dung and their larvae are predatory. Their contribution to dung decomposition may be in the penetration of the upper crust of dung thus accelerating its destruction by weathering and enabling better access for other decompositors to the lumen of the dung pat.

Table 3. Results of nested Anova – achieved levels of significance (*P*). n.s. – P>0.05. S-A – dung dwellers of *Scarabaeidae*, *Aphodiinae*, H – dung dwellers of *Hydrophilidae*, S-C – small tunnellers of *Scarabaeidae*, *Coprinae*, G – large tunnellers of *Geotrupidae*.

	S-A	Н	S-C	G
Farm	n.s.	n.s.	<i>P</i> <0.01	n.s.
Site (Farm)	n.s.	n.s.	n.s.	n.s.
Year	n.s.	n.s.	n.s.	n.s.
Period	<i>P</i> <0.05	<i>P</i> <0.001	<i>P</i> <0.01	n.s.



Fig. 1. Mean DW biomass of four functional groups of beetles in six sampling periods according to nested Anova results (data from different years, farms and sites put together). S-A – dung dwellers of *Scarabaeidae*, *Aphodiinae*, H – dung dwellers of *Hydrophilidae*, S-C – small tunnellers of *Scarabaeidae*, *Coprinae*, G – large tunnellers of *Geotrupidae*.

Table 4. Mean biomass dry weight (DW) of the species and functional group of dung dwellers of S	Scarabaeidae,
Aphodiinae (S-A) in six sampling periods and the contribution of the DW species biomass to a tot	al biomass in
the sampling periods. A – Aphodius, O – Oxyomus.	

	Mean DW (mg/4.5 l dung)							Weight percentage					
	Sampling period (see Table 1)							Sampling period					
Species	1	2	3	4	5	6	1	2	3	4	5	6	
A. prodromus (Brahm 1790)	3 554	363	6	0	35	2 103	51	19	<1	0	1	71	
A. sphacelatus (Panzer 1798)	1 850	170	1	0	3	146	26	9	<1	0	<1	5	
A. rufipes (Linnaeus 1758)	0	22	310	4 531	2 336	92	0	1	19	91	73	3	
A. fimetarius (Linnaeus 1758)	1 195	265	108	120	416	376	17	14	7	2	13	13	
A. pusillus (Herbst 1789)	5	57	30	1	1	0	<1	3	2	<1	<1	0	
A. contaminatus (Herbst 1783)	0	0	0	0	252	156	0	0	0	0	8	5	
A. erraticus (Linnaeus 1758)	30	149	351	56	24	9	<1	8	22	1	1	<1	
A. depressus (Kugelann 1792)	97	168	367	99	4	0	1	9	23	2	<1	0	
A. rufus (Moll 1782)	0	0	80	19	122	6	0	0	5	<1	4	<1	
A. ater (De Geer 1774)	98	17	8	1	0	0	1	1	1	<1	0	0	
A. fossor (Linnaeus 1758)	93	716	303	122	5	0	1	37	19	2	<1	0	
A. distinctus (O. F. Müller 1776)	2	0	0	0	<1	60	<1	0	0	0	<1	2	
A. luridus (Fabricius 1775)	75	3	0	0	0	0	1	<1	0	0	0	0	
<i>A. haemorrhoidalis</i> (Linnaeus 1758)	0	4	27	10	1	0	0	<1	2	<1	<1	0	
O. sylvestris (Scopoli 1763)	3	1	1	0	0	0	<1	<1	<1	0	0	0	
A. sticticus (Panzer 1798)	2	7	1	0	<1	0	<1	<1	<1	0	<1	0	
A. uliginosus (Hardy 1847)	1	0	0	0	<1	2	<1	0	0	0	<1	<1	
A. granarius (Linnaeus 1767)	2	<1	0	0	0	0	<1	<1	0	0	0	0	
A. biguttatus (Germar 1824)	<1	0	0	0	0	0	<1	0	0	0	0	0	
Total S-A	7 008	1 941	1 593	4 959	3 199	2 950	100	100	100	100	100	100	

In the small tunnellers of the S-C group, the most common species Onthophagus fracticornis formed also the bulk of the biomass in this group (on average 60-100% in particular sampling periods; see Table 6). As mentioned above, this species was rare on farm 2 in comparison to the other farms, which accounts for the lower biomass and significant farm effect found in this study (P<0.01; Table 3). Its tunneller activity (reproduction) takes place in spring and the depth of their nests can be 25 cm. The most buried dung in pastures may probably be accounted for by Geotrupidae. These large tunnellers (up to 26 mm) construct their nests up to 50 cm deep and the total amount of buried dung can be up to 2.8 kg fresh weight per a parental pair in case of Geotrupes spp. (Kühne 1995). The main

shaft of the nest has a diameter of about 1.5 cm and it is filled with soil after the construction is accomplished. The two most common species. Geotrupes stercorarius (Linnaeus 1758) and G. spiniger (Marsham 1802) (Šlachta et al. 2009a) formed also the bulk of the collected biomass in this functional group (on average 54-100% of biomass in particular species and sampling period; Table 6). Interestingly, the biomass distribution was not significantly different between the sampling periods. This is accounted for by the fact that G. stercorarius has a reproductive activity (and a peak of occurrence) in spring, which G. spiniger has in late summer and in autumn (Kühne 1995), which may be an adaptation of these two largest dung feeders in Central Europe to limited food source in pastures.

Table 5. Mean biomass dry weight (DW) of the species and functional groups of dung dwellers of *Hydrophilidae* (H) in six sampling periods and the contribution of the DW species biomass to a total biomass in the sampling periods. C - Cercyon, S - Sphaeridium, Cr - Cryptopleurum, M - Megasternum.

	Mean DW (mg/4.5 I dung)							Weight percentage						
_	Sampling period (see Table 1)							Sampling period						
Species	1	2	3	4	5	6	1	2	3	4	5	6		
S. lunatum (Fabricius 1792)	66	926	1 685	1 515	104	23	23	84	69	65	65	68		
S. scarabaeoides (Linnaeus 1758)	117	103	593	576	37	7	41	9	24	25	23	21		
C. impressus (Sturm 1807)	15	24	17	69	8	1	5	2	1	3	5	3		
C. castaneipennis (Vorst 2009)	8	15	60	37	2	<1	3	1	2	2	1	1		
C. lateralis (Marsham 1802)	2	11	13	31	3	<1	1	1	1	1	2	1		
Cr. minutum (Fabricius 1775)	6	1	2	3	1	<1	2	<1	<1	<1	<1	0		
S. bipustulatum (Fabricius 1781)	27	11	38	68	4	0	10	1	2	3	2	0		
<i>C. melanocephalus</i> (Linnaeus 1758)	12	2	2	8	1	<1	4	<1	<1	<1	1	1		
S. marginatum (Fabricius 1787)	22	3	19	9	<1	1	8	<1	1	<1	<1	2		
Cr. crenatum (Panzer 1794)	2	<1	<1	1	0	0	1	<1	<1	<1	0	0		
<i>C. haemorrhoidalis</i> (Fabricius 1775)	3	1	2	<1	<1	<1	1	<1	<1	<1	<1	1		
C. pygmaeus (Illiger 1801)	1	<1	<1	1	<1	<1	<1	<1	<1	<1	<1	1		
C. unipunctatus (Linnaeus 1758)	2	0	0	<1	<1	<1	1	0	0	<1	<1	1		
C. quisquilius (Linnaeus 1761)	1	<1	<1	<1	0	<1	<1	<1	<1	<1	0	<1		
<i>M. concinnum</i> (Marsham 1802)	0	0	0	<1	<1	0	0	0	0	<1	<1	0		
C. alpinus (Vogt 1969)	0	<1	0	0	0	0	0	<1	0	0	0	0		
Total H	283	1 097	2 433	2 317	160	34	100	100	100	100	100	100		

Table 6. Mean biomass dry weight (DW) of the species and functional groups of tunnellers in six sampling periods and the contribution of the DW species biomass to a total biomass in the sampling periods. S-C – small tunnellers of *Scarabaeidae*, *Coprinae*, G – large tunnellers of *Geotrupidae*, G – *Geotrupes*, A – *Anoplotrupes*, T – *Trypocopris*, O – *Onthophagus*.

	Mean DW (mg/4.5 I dung)						Weight percentage								
		Sampling period (see Table 1)							Sampling period						
Species	1	2	3	4	5	6	1	2	3	4	5	6			
O. fracticornis (Preyssler 1790)	1 133	988	99	73	438	204	99	93	60	99	100	100			
<i>O. joannae</i> (Goljan 1953)	10	75	65	1	1	0	1	7	39	1	<1	0			
O. similis (L. G. Scriba 1790)	5	0	0	0	0	0	<1	0	0	0	0	0			
O. coenobita (Herbst 1783)	0	0	2	0	0	0	0	0	1	0	0	0			
Total S-C	1 148	1 062	167	74	439	204	100	100	100	100	100	100			
G. spiniger (Marsham 1802)	0	0	0	663	733	93	0	0	0	80	100	83			
G. stercorarius (Linnaeus 1758)	689	225	26	130	0	19	96	54	57	16	0	17			
<i>A. stercorosus</i> (Hartmann in L. G. Scriba 1791)	30	100	10	30	0	0	4	24	22	4	0	0			
T. vernalis (Linnaeus 1758)	0	91	10	10	0	0	0	22	22	1	0	0			
Total G	719	415	46	833	733	111	100	100	100	100	100	100			

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REFERENCES

- BalthasarV(1964): Monographie der Scarabaeidae und Aphodiidae der palaearktischen und orientalischen Region. Coleoptera: Lamellicornia. Band 3. Aphodiidae. Verl Tschechoslowak Akad Wiss, Prague.
- Bang HS, Lee J-H, Kwon OS, Na YE, Jang YS, Kim WH (2005): Effects of paracoprid dung beetles (*Coleoptera: Scarabaeidae*) on the growth of pasture herbage and on the underlying soil. Appl Soil Ecol 29: 165–171.
- Boukal DS, Boukal M, Fikáček M, Hájek J, Klečka J, Skalický S, Šťastný J, Trávníček D (2007): Catalogue of water beetles of the Czech Republic. Klapalekiana 43(Suppl.): 1–289.
- Frelich J, Pecharová E, Klimeš F, Ślachta M, Hakrová P, Zdražil V (2006): Landscape management by means of cattle pasturage in the submountain areas of the Czech Republic. Ekológia (Bratislava) 25(Suppl. 3): 116–124.
- Gittings T, Giller PS (1997): Life history traits and resource utilisation in an assemblage of north temperate *Aphodius* dung beetles (*Coleoptera: Scarabaeidae*). Ecography 20: 55–66.
- Gittings T, Giller PS, Stakelum G (1994): Dung decomposition in contrasting temperate pastures in relation to dung beetle and earthworm activity. Pedobiologia 38: 455–474.
- Hansen M (1987): The Hydrophiloidea (Coleoptera) of Fennoscandia and Denmark.
 E. J. Brill/Scandinavian Science Press Ltd., Leiden, Copenhagen.
- Hanski I, Cambefort Y (1991): Dung beetle ecology. Princeton University Press, Princeton, New Jersey.
- Holter P (1979a): Effect of dung-beetles (*Aphodius* spp.) and earthworms on the disappearance of cattle dung. Oikos 32: 393–402.
- Holter P (1979b): Abundance and reproductive strategy of dung beetle *Aphodius rufipes* (L.) (*Scarabaeidae*). Ecol Entomol 4: 317–326.
- Holter P, Hendriksen NB (1988): Respiratory loss and bulk export of organic matter from cattle dung pats: a field study. Holarctic Ecol 11: 81–86.
- Juřena D, Týr V (2008): Checklist of *Scarabaeoidea* (*Coleoptera*) of the Czech Republic and Slovakia. Klapalekiana 44(Suppl.): 3–15.

- Křivan V (2000): Coprophagous beetles of *Scarabaeidae* after the restoration of grazing management in Novobystřicko region. Master thesis, University of South Bohemia, Faculty of Agriculture (in Czech).
- Kühne R (1995): Data to the biology of selected Geotrupes species: G. spiniger Marsham, G. vernalis Linné, and G. stercorosus Scriba. Dtsch Ent Z 42: 343–367 (in German).
- StatSoft CR s. r. o. (2008): STATISTICA, version 8.0. www.statsoft.cz.
- Šlachta M, Frelich J, Svoboda L (2008a): Seasonal biomass distribution of dung beetles (Scarabaeidae, Geotrupidae, Hydrophilidae) in mountain pastures of South-West Bohemia. J Agrobiol 25: 163–176.
- Šlachta M, Frelich J, Váchal J (2008b): Measurement of diversity of coprophagous beetles. Uplatněná certifikovaná metodika. Jihočeská univerzita v Českých Budějovicích, Zemědělská fakulta (in Czech).
- Šlachta M, Frelich J, Váchal J (2008c): Assessment of the functional structure of dung beetles community. Uplatněná certifikovaná metodika. Jihočeská univerzita v Českých Budějovicích, Zemědělská fakulta (in Czech).
- Slachta M, Frelich J, Tonka T (2009a): Application of dung-baited pitfall trapping in monitoring study on diversity of coprophagous beetles (*Scarabaeidae*, *Geotrupidae*, *Hydrophilidae*) in cattle pastures. J Agrobiol 26: 83–99.
- Slachta M, Frelich J, Tonka T (2009b): Composition of community of coprophagous beetles (Coleoptera: Scarabaeidae, Geotrupidae, Hydrophilidae) in beef cattle pasture in Western Bohemia – an application of dung-baited pitfall trapping in monitoring study on coprophagous fauna. Erica 16: 97– 112 (in Czech).
- Vitner J (1998): Reproductive biology of the Central European Aphodius species with large scutellum (*Coleoptera: Scarabaeidae: Aphodiinae*). Acta Soc Zool Bohem 62: 227– 253.
- Vorst O (2009): Cercyon castaneipennis sp.n., an overlooked species from Europe (Coleoptera: Hydrophilidae). Zootaxa 2054: 59–68.
- Waßmer T (1994): Seasonality of coprophagous beetles in the Kaiserstuhl area near Freiburg (SW-Germany) including the winter months. Acta Oecol 15: 607–631.
- Yamada D, Imura O, Shi K, Shibuya T (2007): Effect of dung beetles on dung decomposition, soil nutrients and herbage growth. Grassl Sci 53: 121–129.