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Dung scent profiles or single scent compounds:

What do dung beetles use to detect their food?

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DUNG SCENT PROFILES OR SINGLE SCENT COMPOUNDS: WHAT DO DUNG BEETLES USE TO DETECT THEIR FOOD?

Viktoria Zagler

ABSTRACT

In coprophagous beetles the successful detection of suitable food sources as well as the selection of preferred dung types most likely are facilitated by volatile odorants emitted by the dung. However, it is largely unknown whether entire dung scent profiles or individual dung scent compounds are used by dung beetles to detect their food source. This study quantified species richness and composition of dung beetle assemblages as well as food preferences of individual species attracted to different dung types. Field work was conducted in a farmland area in Lower Austria between 3 August and 3 September 2007. The odors of used dung types were analyzed to evaluate the importance of emitted volatile odorants for species composition and the occurrence of individual species. A total of 1,057 dung beetle individuals belonging to 15 species were caught by pitfall traps, each baited with dung from one of seven different dung producers represented by herbivores (sheep, horse, cattle, and goose), omnivores (human, and pig) and one carnivore (dog). One additional control trap remained unbaited. The dung scent composition emitted by different dung types was analyzed using gas chromatography-mass spectrometry. A total of 17 dung scent odorants out of 6 compound classes (fatty acid derivates, benzenoids, sulphur-containing compounds, nitrogen-containing compounds, ketones, sesquiterpenoids) were detected in the scent samples. Composition of dung beetle communities as well as dung scent profiles differed significantly between dung types. Seven dung odorants (4-Propylphenol, 3-Methylindole, unknown fatty acid derivate, β-Caryophyllene, Indole, unknown nitrogen-containing compound and Dimethyl disulfide) were found to affect the occurrence of the 4 most abundant dung beetle species, all belonging to the genus *Onthophagus*, in the pitfall trap samples. Some compounds are closely associated with the nutrition of the dung producers and therefore may be used by dung-feeding beetles as indicator for food quality. Not all dung scents related to the occurrence of individual dung beetle species acted as attractant, but appeared to have a strong negative effect on the attractiveness of exposed dung baits. Our study indicates that both single dung scent compounds and a combination of different scents are used by dung beetles to detect suitable dung sources. The importance of determined dung scents possible acting as cues for the selection of adequate food by coprophagous beetles has to be further evaluated by choice experiments.

Key words: infochemicals, dung types, herbivore dung, carnivore dung, omnivore dung, dung beetle assemblages, species composition, food preferences, olfactory cues, dung scents, dung scent profiles

ZUSAMMENFASSUNG

Das erfolgreiche Auffinden geeigneter Nahrungsressourcen sowie die Auswahl bevorzugter Dungtypen durch koprophage Käfer hängen wahrscheinlich massgeblich von Duftstoffen ab, welche vom Dung abgegeben werden. Es ist allerdings weitgehend unbekannt, ob einzelne Duftstoffe oder das gesamte Duftstoffgemisch von Dungkäfern genutzt wird, um geeignete Nahrung aufzufinden. Diese Studie untersuchte Artenreichtum und Artenzusammensetzung von Dungkäfergemeinschaften sowie die Häufigkeit des Auftretens einzelner Arten an verschiedenen Dungsorten. Die Freilandarbeit wurde in einem landwirtschaftlich genutzten Gebiet in Niederösterreich zwischen 3. August und 3. September 2007 durchgeführt. Um die Bedeutung der vom Dung abgegebenen Duftstoffe für die Artenzusammensetzung und das Auftreten einzelner Dungkäferarten zu testen, wurde das Duftstoffgemisch der verschiedenen Dungsorten untersucht,. Insgesamt wurden 1.057 Dungkäfer, zugehörig zu 15 Arten mit Hilfe von Barberfallen gefangen, die jeweils mit einem von sieben unterschiedlichen Dungtypen beködert waren. Die sieben verschiedenen Dungproduzenten repräsentierten vier Herbivore (Schaf, Pferd, Kuh, Gans), zwei Omnivore (Mensch, Schwein) und ein Karnivore (Hund). Die Zusammensetzung der von einzelnen Dungsorten abgegebenen volatilen Stoffgemische wurde mittels Gaschromatographie-Massenspektroskopie analysiert. Insgesamt konnten 17 flüchtige Verbindungen im Dungduft nachgewiesen werden, die zu 6 verschiedenen Verbindungsklassen (Fettsäurederivate, Benzene, Schwefelverbindungen, Stickstoffverbindungen, Ketone, Sesquiterpene) zählen. Sowohl

die angelockten Dungkäfergemeinschaften als auch die Duftstoffzusammensetzungen unterschieden sich signifikant zwischen den einzelnen Dungtypen. Für sieben Duftstoffe (4-Propylphenol, 3-Methylindol, unbekanntes Fettsäurederivat, β-Caryophyllen, Indol, unbekannte Stickstoffverbindung und Dimethyldisulfid) zeigte sich ein deutlicher Effekt auf das Auftreten der vier am häufigsten in den beköderten Barberfallen gefangenen Dungkäferarten, vier Vertreter der Gattung *Onthophagus*. Einige dieser Duftstoffe stehen in engem Zusammenhang mit der Ernährung der Dungproduzenten und könnten daher von Dungkäfern als Indikator für die Qualität der Nahrungsresource verwendet werden. Jedoch wirkten nicht alle Duftstoffe als Lockmittel, sondern für einzelne konnte eine negative Wirkung auf die Anzahl auftretender Individuen gezeigt werden. Unsere Ergebnisse liefern deutliche Hinweise darauf, dass sowohl einzelne Duftstoffe als auch Duftstoffgemische von Dungkäfern genutzt werden, um geeignete Nahrung aufzufinden. Für eine detaillierte Untersuchung der Bedeutung einzelner Duftstoffe als olfaktorische Reize für koprophage Käfer sind weiterführende Wahlversuche unabdingbar.

INTRODUCTION

Many insects such as herbivores (Ahmad 1983, Harborne 1993), parasitoids (Vet & Dicke 1992, Wäckers 1994) and coprophagous species (Landin 1961, Dormont *et al.* 2007) detect their food sources or hosts through emitted volatile substances, so called infochemicals (see Dicke & Sabelis 1988), carrying food-specific information. This information not only facilitates the detection of a preferred food source but also helps reducing the time required searching for adequate food or hosts (e.g. Vet & Dicke 1992).

Coprophagous beetles can be generalists or specialists concerning their dung preferences (Hanski & Cambeforte 1991, Dormont *et al.* 2007). In African dung beetles the functional group of rollers appears to prefer omnivore dung, whereas large tunnelers tend to use exclusively large herbivore dung (like elephant dung) (Hanski & Cambeforte 1991). Recent studies from European regions showed prominent differences between dung beetle assemblages attracted to dung of various vertebrates even when belonging to the same feeding guild (Martín-Piera & Lobo 1996, Gittings & Giller 1998, Galante & Cartagena 1999, Finn & Giller 2002, Dormont *et al.* 2004). For example, a study in France documented clear preferences for the majority of dung beetles species for either cattle or horse dung (Dormont *et al*. 2004).

Although dung beetles can exploit a variety of resources, the majority of species feed on dung of larger herbivores and omnivores (Hanski & Cambefort 1991). Carnivore dung does only attract few dung beetle species that often also feed on carrion (Hanski, 1987). Herbivore dung is the quantitatively most abundant dung in all major terrestrial ecosystems. It is carbohydrate-rich and consists of two components: low-quality undigested plant remains and high-quality products of the mammalian gut fauna and flora. Omnivore dung is less abundant but a qualitatively attractive resource, because of its high nitrogen content (Hanski & Cambeforte 1991).

The option to use different dung types could be one possibility for dung beetle species to deplete interspecific competition. In this study, we did not only quantify differences between dung beetle assemblages attracted to different dung types, but also tried to evaluate the importance of chemical volatiles released by the dung for acting as cues for coprophagous beetles to detect adequate dung sources (e.g. Dormont *et al*. 2004). Particularly, we addressed the following questions:

(1) Does dung type affect abundance and composition of attracted dung beetle species?

Because of its high availability in most geographical regions and ecosystems herbivore dung does attract the largest number of dung beetle species (Barbero *et al.* 1999). Carnivore and omnivore dung is only used by a smaller number of European dung beetle species (Martín-Piera & Lobo 1996). However, human dung represents an exception and is very attractive for most dung beetle species (Howden & Nealis 1975). In species restricted to herbivore dung polyphagy is common (Martín-Piera & Lobo 1996), but also species-specific preferences to one dung type can be commonly found (Dormont *et al.* 2004, Gittings & Giller 1998). Therefore, we expect that dung beetles attracted to the seven dung types exposed in our study show pronounced dung preferences but are not strictly monophagous (e.g. Hanski & Cambeforte 1991).

(2) How do dung scent profiles differ between dung producers?

As result of their different diets and digestion, herbivorous and carnivorous mammals have distinct dung scent profiles (Aii *et al.* 1980, Moore *et al.* 1987). The dung of carnivores and carrion seem to have several similarities in scent composition because both sources attract partly the same dung beetle species (Hanski 1987). Various scents consist of chemical volatiles responsible for fecal odor common in every type of dung (such as methyl sulfide compounds, but also Indole and Skatole; Moore *et al*. 1987). In contradiction, other scent compounds are characteristic for individual dung types and are influenced by dietary and endogenous products (Aii *et al.* 1980, Moore *et al.* 1987). Therefore, we expected to detect volatile compounds typical for fecal odor and scent compounds specific for the dung types exposed in this study.

(3) Can dissimilarities between dung beetle communities colonizing different dung types be related to differences in the dung scent profiles?

Based on olfactometer bioassays, Dormont *et al*. (2007) provided clear evidence that emitted dung scent volatiles are responsible for the detection of a dung location and the selection of suitable dung pats by coprophagous beetles. Dung preferences of individual species may depend on such "Infochemicals" characteristic for individual dung types. Consequently, the scent composition may shape the entire dung beetle assemblage attracted to different dung types.

(4) Which scent characteristics do individual dung beetle species use to detect their food?

Dung beetles can differentiate between different dung producers due to specific emitted dung volatiles (Dormont *et al*. 2007). However, it is largely unknown if they use individual scents or the composition of volatiles for the selection of food and breeding resources. A previous study on houseflies showed that a mixture of only three scent compounds (Butanoic acid, Skatole, Dimethyl trisulphide) was sufficient to attract similar numbers than pig dung (9 odor compounds identified) (Cossé & Baker 1996). We assume that dung beetles do not only use one volatile compound, but a composition of several infochemicals to detect and select adequate dung sources.

MATERIAL AND METHODS

Study area and study sites

Field work was conducted at Niederkreuzstetten (in vicinity of Kreuzstetten; 224 m asl, 48°28' N 16°28' E) located in the district Mistelbach, Lower Austria. The region is dominated by agricultural areas interspersed with small patches of woodland, and cattle and sheep pastures. Other large mammals occurring in the region are roe deer and wild boar. The study area is characterized by a Pannonian climate with hot and dry summers and cold winters with little snow. The mean annual temperature is about 9°C, the annual precipitation about 500 mm (ZAMG 2002), measured at the nearest weather station at Poysdorf (209 m asl, 48°40´ N 16°38´ E).

Experimental design

To quantify food preferences, dung beetles were attracted to pitfall traps baited with different dung types at eight different dates: 3 August, 7 August, 13 August, 16 August, 20 August, 24 August, 27 August, and 3 September 2007. Each pitfall trap consisted of a plastic cup with a volume of 0.5 l, a height of 14 cm, and a diameter of 9 cm at the top and 6.5 cm at the bottom. Filter paper bags (8.4 cm x 18.4 cm) were filled with 40 g of fresh dung and were fixed in the cup with a cord, which was threaded in two opposing little holes at the top of the cups. The dung used was collected in the morning of every sampling day, prepared for the pitfall traps and deployed in the afternoon. After exposure in the field, about 0.2 l of water mixed with a special soap without any "own" smell (Tween®80) was added to the cups. As controls, reference traps were prepared in the same manner with filter paper bags filled with wadding instead of dung. All traps were protected by a wooden roof against rainfall and sunshine.

Dung of two omnivores (human and pig), four herbivores (cattle, horse, sheep and goose), and one carnivore (dog) was used for bait trapping. Traps were exposed in two circles with a diameter of 20 m in a distance of 200 m from each other. One circle was located in grassland (sampling site 1), the second one in a fallow with surrounding cropland and wood (sampling site 2). In each circle, eight holes stabilized with plastic tubes were prepared in the ground. Subsequently, at each circle 8 pitfall traps, each baited with a different dung type (7 traps) or without dung (1 trap), were randomly inserted into the prepared holes (Fig. 1). Consequently, attracted beetles had the opportunity to choose between all exposed baits and the control. Exposure time of traps was 28 ± 1 hours. All insects trapped were preserved in 80% alcohol, however, only scarabid dung beetles were identified (after Bunalski 1999 and Lohse & Lucht 1992) and used for further analysis.

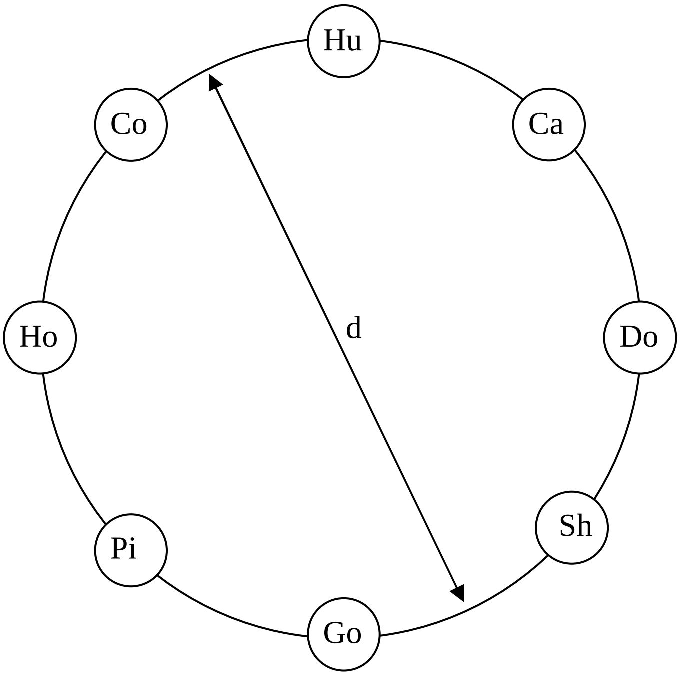

Figure 1. Spatial design of the 8 traps exposed in a circle with a diameter (d) of 20 m. Seven pitfall traps were baited with human (Hu), cattle (Ca), dog (Do), sheep (Se), goose (Go), pig (Pi), and horse (Ho) dung, respectively. One control trap (Co) remained unbaited. For every individual sampling date traps were randomly replaced with each other.

Dung scent analysis

During four trapping experiments the dung scents of the exposed baits were analyzed: 3 August, 16 August, 20 August, and 27 August. Details of trapping dates and experimental treatments are given in Table 1. The first step of dung scent analyses was to weigh the fresh dung. For each sampling day, the dog was limiting the initial weight, which was used as standard. The amount of dung was transferred in a glass with a volume of 0.75 l, which was subsequently closed with an aluminum foil. After the air had accumulated with the compounds emitted from the dung for a certain time (Tab. 1), it was collected by sucking it through a micro-tube filled with a mixture of 1.5 mg Tenax-TA (mesh 60–80) and 1.5 mg Carbotrap (mesh 20–40). Therefore, the adsorbent tube was introduced in the headspace through a little hole in the aluminum foil. The extraction was activated by a membrane pump (G12/01 EB, ASF Thomas, Inc.) with a flow rate of about 200 ml per minute and lasted for 5 minutes. To detect possible contaminants, volatiles were collected from an empty glass bottle. After collecting the scents, the micro-tubes were hermetically sealed and sent to the University of Bayreuth for further analyses. A mixture of the same dung used for the scent extraction was afterwards used for preparing the pitfall traps.

Table 1. Dates of the dung scent extraction with initial weight of the dung, steeping time and suction time for every date.

No.	Date	Weighted sample of fresh dung (g)	Accumulation time (min)	Suction time (min)
1	3 August 2007	170	30-60	5
2	16 August 2007	95	30-60	5
3	20 August 2007	100	30-90	5
4	27 August 2007	125	60-90	5

Dung scent samples were analyzed on a Varian Saturn 3800 gas chromatograph (GC) fitted with a 1079 injector, and a Varian Saturn 2000 mass spectrometer (MS). To insert the absorbent tubes into the GC injector, Varians Chromatoprobe was used (Amirav & Dagan 1997). The injector vent was opened (1/20) and the injector was heated at 40 °C to flush any air from the system. After 2 minutes the split vent was closed and the injector heated at 200 °C per minute, then held at 200 °C for 4.2 minutes. Afterwards the split vent was opened (1/20) and the injector was cooled down. The analyses were conducted by a ZB-5 column (5 % phenyl polysiloxane, length 60 m, inner diameter 0.25 mm, film thickness 0.25 µm, Phenomenex). A constant helium carrier gas flow rate (1.8 ml per minute) was perpetuated by the use of electronic flow control. For 7 minutes the GC oven temperature was held at 40 °C, then increased by 6 °C per minute to 260 °C and held for 1 minute at this temperature. The mass spectra were taken at 70 eV with a scanning speed of 1 scan per second from m/z 30 to 350.

For data analysis the Saturn Software package 5.2.1 was used. The dung scent compounds were identified by using the data bases NIST 02 and MassFinder 3, and identifications were confirmed by comparison of retention times with published data (Adams 1995). Identification of some compounds was also confirmed by comparison of mass spectra and retention times with those of authentic standards. To quantify the amount of each volatile in the blend, known amounts of monoterpenoids, benzenoids, and fatty acid derivatives were injected, and the mean peak area of these compounds was used for quantification (see Dötterl *et al.* 2009).

Statistical analysis

Because arthropod assemblages are usually incompletely sampled, we estimated species richness with the four different nonparametric estimators ACE, Chao1, Chao2 and Jackknife1 (Colwell 2006). The median of all four estimates was used as species richness measurement and to estimate the completeness of recorded species inventories. The software EstimateS version 8.0.0 was used to calculate the estimates by randomizing samples 100 times (Colwell 2006). Additionally, species accumulation curves with 95% confidence intervals were calculated (Colwell 2006) to detect differences in species richness between dung beetle assemblages attracted to different dung baits.

The mean number of dung beetles trapped with pitfall traps baited with different dung types was compared using the non-parametric Kruskal-Wallis test, because even after transformations data did not achieve normal distribution. The post-hoc test used for pairwise comparison was a standard range test. Parametric ANOVA (type VI) and subsequent Tukey's HSD test were used to detect differences in the mean amount of individual dung scents between dung types. For all tests the software STATISTICA version 7.1 was used (StatSoft 2005).

Bray-Curtis similarities were calculated to quantify differences in the structure of dung beetle assemblages (using square root transformed abundance data) attracted by different dung types and differences between dung scent profiles (based on relative amounts of dung scents) emitted by different dung types. All Bray-Curtis similarities and subsequent non-metric multidimensional scaling (NMDS) to visualize similarity relationships between dung types were calculated with Primer version 5 (Clarke & Gorley 2002). Stress values for NMDS ordination plots lower than 0.2 were used as indication for an acceptable two-dimensional representation of the original distance matrix values by the ordination (Clarke 1993). One-way analyses of similarities

(ANOSIMs) were used to test for differences of species composition and dung scent profiles between dung types. Additionally, two-way crossed ANOSIMs were computed to test for effects of dung type and study site on species composition of dung beetles. Pairwise tests (ANOSIMs) were calculated to detect significant differences within the set of used dung types. All ANOSIMs were computed with Primer version 5 (Clarke & Gorley 2002) with a maximum number of 999 allowed permutations. The structures of scent compounds (see Fig. 7) were created using IsisDraw 2.5 (MDL Information systems Inc. 1990-2002). To test for relationships between dung beetle species compositions and dung scent profile, Spearman matrix rank correlations (max. permutations = 999) were calculated with Primer version 5 (Clarke & Gorley 2002).

Pearson correlations were calculated (using STATISTICA version 7.1, Statsoft 2005) to test for effects of the total amount of scent emitted by different dung types on the number of attracted dung beetles.

A Canonical Correspondence Analysis (direct CCA) was used to analyze the occurrence of the most abundant dung beetle species in the multidimensional niche space described by the dung scent compounds (focus scaling on inter-species distance; biplot scaling to reduce the large set of environmental variables; best variables are selected sequentially on the basis of maximum extra fit by automatic forward selection; see ter Braak & Smilauer 2002). The analyses were evaluated by using Monte-Carlo permutation tests to test for the significance of the first ordination axis and of the canonical axes together (number of unrestricted permutations = 499 under reduced model). For the analyses the software CANOCO for Windows version 4.55 was used (ter Braak & Smilauer 2002).

RESULTS

Dung beetles

General results

A total of 1,057 dung beetle individuals belonging to 15 species were captured in the pitfall traps baited with the seven different dung types at two different sites. The control traps did not attract a single dung beetle. Four of the trapped dung beetle species and a total of 19 individuals belonged to the genus *Aphodius* (family Aphodiidae). Aphodiidae represented only 25 % of all collected dung beetle species and 1.8 % of the total number of trapped individuals. The family Scarabaeidae was represented by *Euoniticellus vulvus* with 6 trapped individuals and 9 species of the genus *Onthophagus* with a total of 1,003 individuals. The family Scarabaeidae was most abundant with a total number of 1,019 individuals (97.9% of all trapped dung beetle individuals) and represented 62.5 % of the collected dung beetle species. Only one large dung beetle species was found in the traps, *Geotrupes stercorarius* (family Geotrupidae). Two specimens of *G. stercorarius* were attracted by pig dung and one by human dung.

Effect of dung type on species richness and abundance

The species richness estimates (Tab. 2) and the species accumulation curves indicate highest species richness for dung beetle assemblages attracted by pig, human and cattle dung (Fig. 2). However, according to the confidence intervals of the species accumulation curves (not shown in the graph) differences in species richness did not prove to be significant. A species accumulation curve was not calculated for beetles attracted by horse dung due to the small sample size (compare Tab. 2).

Table 2. Abundance as well as observed and estimated species richness of dung beetles attracted by different dung types.

Dung types	Individuals	**Observed species (O)**	Estimated species					Completeness [(O/M)*100]
			ACE	Chao1	Jack1	Chao2	**Median (M)**	
Pig	266	**11**	13.56	12.00	13.63	11.66	**12.78**	86.07
Human	479	**11**	12.70	11.33	13.63	11.88	**12.29**	89.50
Cattle	42	**7**	19.89	13.00	10.20	8.60	**11.60**	60.34
Dog	160	**7**	7.93	7.00	8.75	7.44	**7.69**	91.09
Sheep	78	**7**	7.00	7.00	7.00	7.00	**7.00**	100.00
Goose	26	**4**	7.90	5.00	5.71	4.43	**5.36**	74.70
(Horse)	6	**3**	4.00	3.00	4.50	4.50	**4.25**	70.59
All	**1057**	**15**	**16.80**	**19.5**	**19.38**	**21.25**	**19.44**	**77.16**

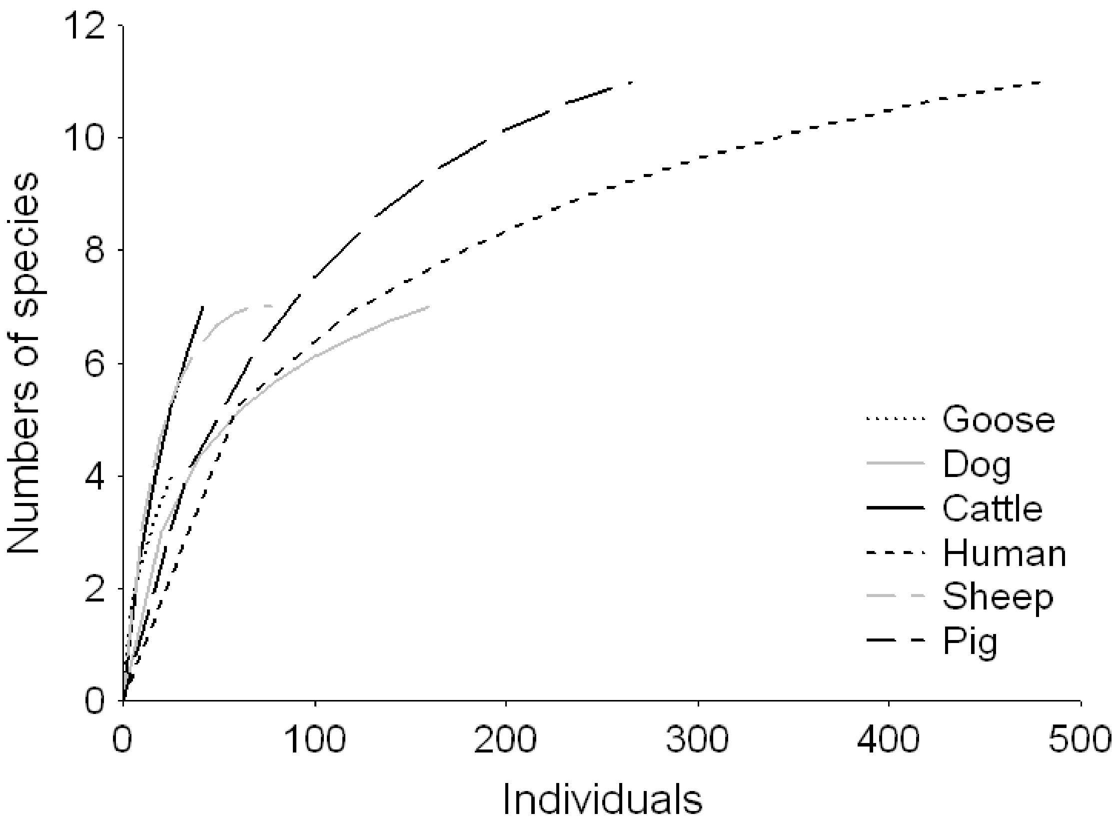

Figure 2. Species accumulation curve for dung beetle assemblages attracted by dung of human, pig, dog, cattle, sheep and goose.

The mean total number of dung beetle specimens attracted per sampling date by the different dung types did not significantly differ between the two sampling sites (paired t test: $t = 1.91$, N = 8, $p = 0.097$). The mean numbers of trapped individuals (± SD) were 3.94 (± 0.98) and 3.28 (± 1.54) at sampling site 1 and 2, respectively. Therefore, for further analyses, samples from both sites were pooled for individual sampling dates and pitfall traps baited with the same dung type. The mean number of sampled dung beetles (N = 8 sampling dates) differed significantly between dung types (Kruskal-Wallis ANOVA: $H_{6,\ 36} = 30.99$, $p < 0.001$). Highest numbers of dung beetles were attracted by omnivore dung of humans and pigs. Smallest beetle numbers were found for pitfall traps baited with dung of the herbivores goose, cattle, horse and sheep. Intermediate numbers were attracted by dog dung (Fig. 3).

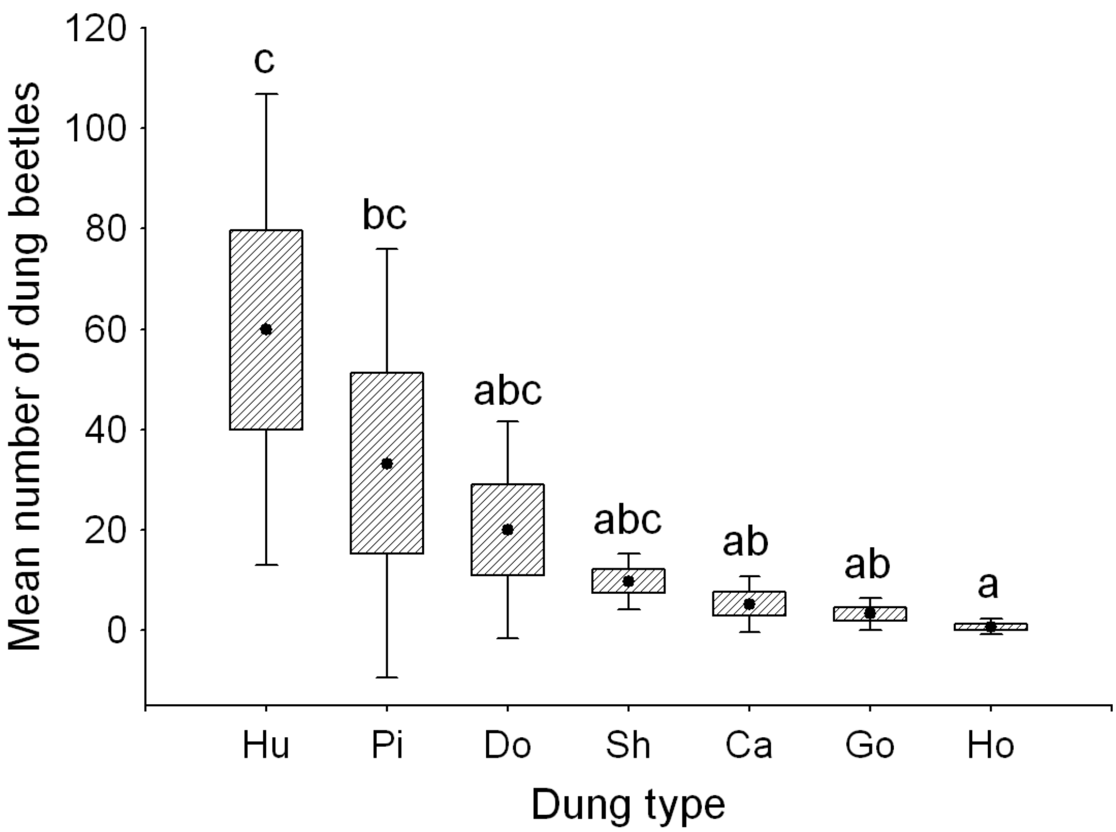

Figure 3. Mean number of dung beetle individuals ± standard error (box) and 95% confidence intervals (whiskers) per sampling date (N = 8) attracted by seven different dung types. Dung producers: human (Hu), pig (Pi), dog (Do), sheep (Sh), cattle (Ca), goose (Go) and horse (Ho). N = 8 samples per dung type. Different letters indicate significant differences between means (Kruskal–Wallis all pairwise comparisons).

When only the six most abundant dung beetle species (total of >10 individuals) were considered, there is no species which was exclusively attracted by one dung type (Tab. 3). All abundant species, except of *Aphodius erraticus*, occurred most frequently in traps baited with human dung, and then in traps with pig and dog dung. However, only the number of trapped specimens of the *Onthophagus* species differed significantly between dung types (Fig. 4).

Table 3. Total number of specimens of all recorded dung beetle species collected by pitfall traps baited with different dung types. For abbreviations of dung producers see Fig. 3.

Species	**Dung type**							
	Hu	Pi	Do	Sh	Ca	Go	Ho	**Total**
Subfamily Aphodiinae								
Aphodius (Colobopterus) erraticus (Linnaeus 1758)	2	3	0	6	1	0	0	**12**
Aphodius (Limarus) maculatus (Sturm 1900)	0	0	0	0	1	0	0	**1**
Aphodius (Teuchestes) haemorrhoidalis (Linnaeus 1758)	0	1	0	2	0	0	0	**3**
Aphodius (Volinus) sticticus (Panzer 1798)	2	1	0	0	0	0	0	**3**
Subfamily Geotrupinae								
Tribe Geortrupini								
Geotrupes stercorarius (Linnaeus 1758)	1	2	0	0	0	0	0	**3**
Subfamily Scarabaeinae								
Tribe Oniticellini								
Euoniticellus vulvus (Goeze 1777)	8	4	0	2	1	1	0	**16**
Tribe Onthophagini								
Onthophagus coenobita (Herbst 1783)	25	8	18	4	1	0	0	**56**
Onthophagus fracticornis (Preyssler 1790)	238	139	15	11	14	0	2	**419**
Onthophagus gibbulus (Pallas 1781)	0	0	2	0	0	0	0	**2**
Onthophagus joannae (Goljan 1953)	12	6	7	4	3	4	0	**36**
Onthophagus nuchicornis (Linnaeus 1758)	3	2	2	0	0	1	1	**9**
Onthophagus ovatus (Linnaeus 1767)	183	99	115	49	21	20	3	**490**
Onthophagus similis (Scriba 1790)	0	0	1	0	0	0	0	**1**
Onthophagus taurus (Schreber 1759)	4	1	0	0	0	0	0	**5**
Onthophagus vitulus (Fabricius 1776)	1	0	0	0	0	0	0	**1**
Total	**479**	**266**	**160**	**78**	**42**	**26**	**6**	**1057**

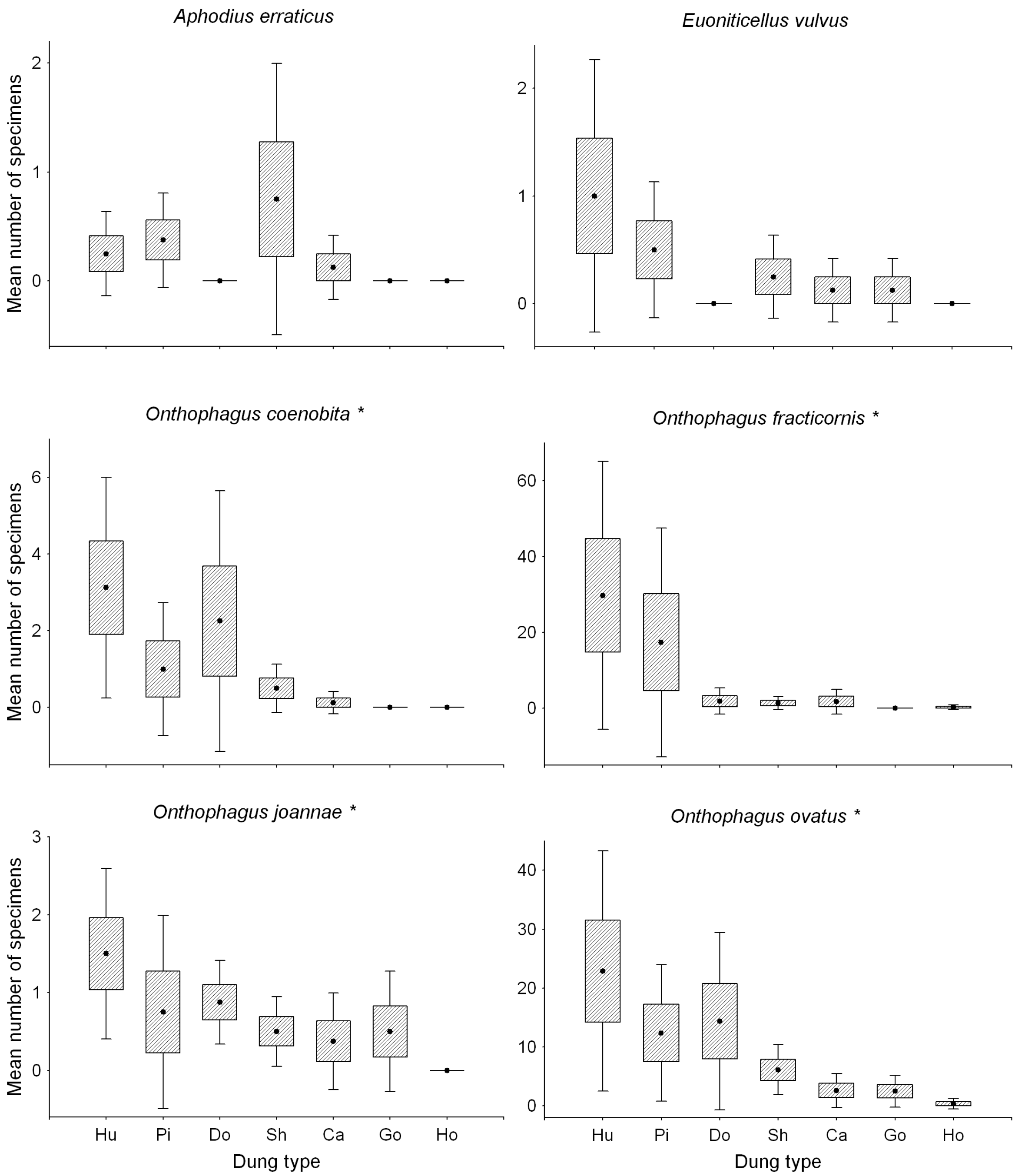

Figure 4. Mean number of individuals collected per sampling date (N = 8) with pitfall traps baited with different dung types ± standard error (box) and 95% confidence intervals (whiskers) shown for the six most abundant dung beetle species. For abbreviations of dung types see Figure 3. * indicates a significant effect of dung type on the number of collected beetles (Kruskal-Wallis test; $p < 0.05$).

Effect of dung type on species composition

Due to the small total number of only six beetle specimens attracted by horse dung samples of this dung type were rejected from all subsequent similarity analyses. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis similarities was used to visualize similarities of dung beetle assemblages attracted by different dung baits (Fig. 5). The resulting ordination plot clearly indicates that species composition of dung beetles differs between dung types, changing from species assemblages attracted by dung of the two omnivores human and pig (on left site of ordination plot) to assemblages attracted by the dung of the herbivores sheep, cattle and goose (towards right side of ordination plot). Beetle assemblages attracted by dog dung have an intermediate position between omnivores and herbivores (Fig. 5).

That the composition of dung beetle assemblages is related to the used dung bait is also supported by a one-way ANOSIM (Global $R = 0.44$, $p = 0.001$). The difference remained significant even when including the factor sampling site, which itself did not prove to affect species composition (two-way ANOSIM; dung type: Global $R = 0.38$, $p = 0.013$; sampling site: Global $R = 0.04$, $p = 0.420$).

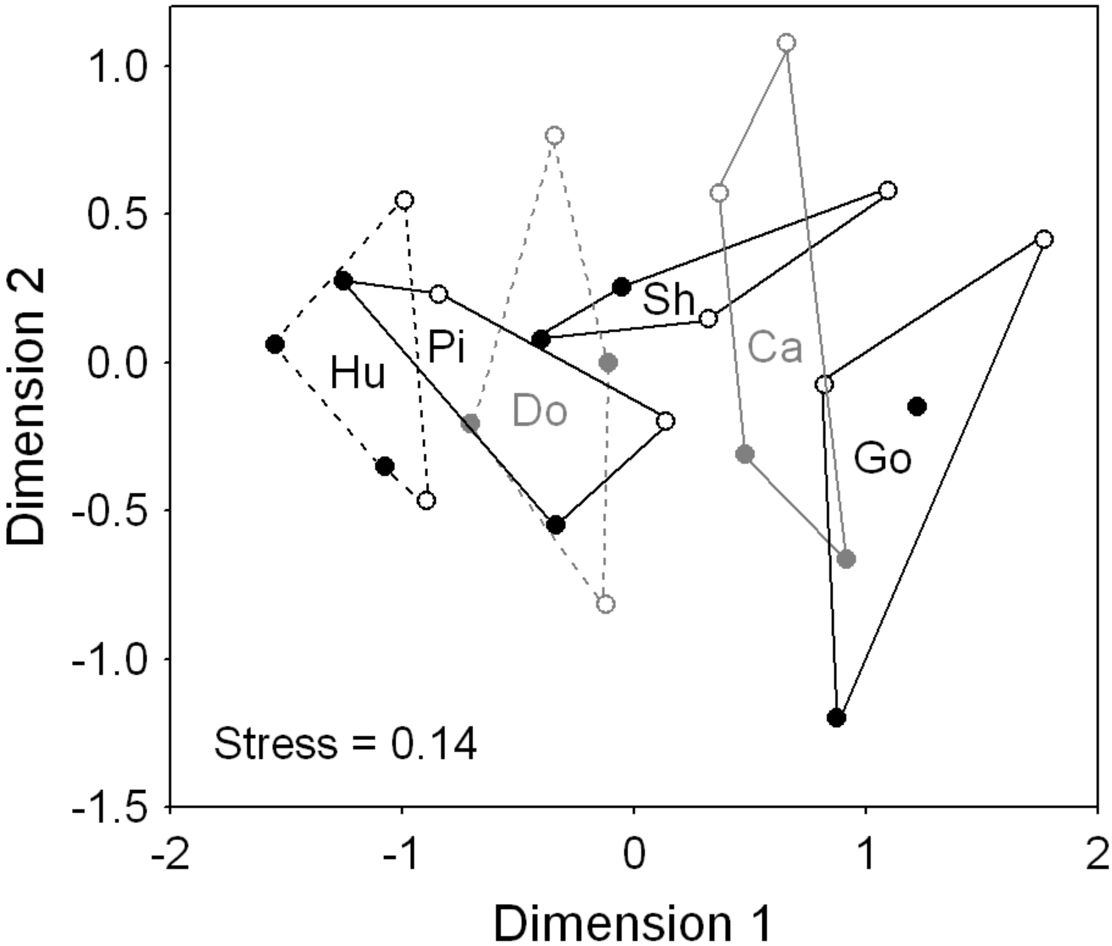

Figure 5. Similarity of dung beetle assemblages attracted by six different dung types, visualized in a non-metric multidimensional scaling plot based on Bray-Curtis similarities (square-root transformed abundance data). Dung types: Human (Hu), Pig (Pi), Dog (Do), Sheep (Sh), Cattle (Ca) and Goose (Go). Sampling sites are indicated by filled (Sampling site 1) and empty symbols (Sampling site 2). For both sites the first and second four sampling dates were pooled to achieve samples large enough to calculate reliable similarity values. Samples from identical dung types are connected by lines.

Pairwise tests (one-way ANOSIMs) support differences between similarities (Bray-Curtis) of dung beetle assemblages attracted to different dung baits (Tab. 4). Species composition of beetles attracted by human dung differed significantly from the one at cattle, goose, sheep and dog dung, whereas differences between beetle assemblages caught by traps baited with dung of omnivores (human and pig) did not achieve significance. Species composition of dung beetles attracted by goose dung differed significantly from those of dog, pig and human dung but not from those of the two herbivores cattle and sheep. Among the group of herbivores (sheep, cattle and goose) the composition of dung beetle species showed no significant differences. Species composition recorded at dog dung could be significantly distinguished from those found at all other dung types except pig dung (Tab. 4).

Table 4. Results of pairwise tests (one-way ANOSIMs) to detect significant differences of species composition between dung types. Significant differences are printed bold.

Pairwise tests	***R***	***p***
Cattle vs. Sheep	-0.07	0.629
Dog vs. Cattle	**0.53**	**0.029**
Dog vs. Goose	**0.73**	**0.029**
Dog vs. Sheep	**0.26**	**0.029**
Goose vs. Cattle	0.46	0.057
Goose vs. Sheep	0.43	0.086
Human vs. Cattle	**0.94**	**0.029**
Human vs. Dog	**0.40**	**0.029**
Human vs. Goose	**1.00**	**0.029**
Human vs. Pig	-0.02	0.571
Human vs. Sheep	**0.71**	**0.029**
Pig vs. Cattle	0.46	0.057
Pig vs. Dog	0.04	0.343
Pig vs. Goose	**0.72**	**0.029**
Pig vs. Sheep	0.12	0.286

Dung scents

A total of 17 dung scent compounds were detected in the scent samples, 9 of which could be identified. Table 5 shows the compounds divided into the compound classes with their odor description and their relative amounts (%) in the particular dung type (mean of the 4 samples for every dung type). Goose dung was excluded from the dung scent analyses because of the low total amount of emitted dung scents, which did not allow a reliable identification of individual scent compounds in the gas chromatography-mass spectrometry (GC-MS) analysis. The detected dung scent compounds belong to six different compound classes: Fatty acid derivates (5 scent compounds), Sesquiterpenoids (4), Nitrogen-containing compounds (3), Ketones (2), Benzenoids (2) and Sulphur-containing compounds (1).

Table 5. Average relative amounts (%) of dung scent volatiles of 6 different dung types. For every dung type 4 samples were collected and analyzed. Unknown substances were labeled with the abbreviation of the compound class and the retention time (seconds). The odor descriptions refer to Acree & Arn (2004) or GSC (1980-2009), when marked with *. For Dihydroneoclovene no odor description was found.

Compounds	**Odor description**	**Dung type**					
		Cattle	Dog	Horse	Human	Pig	Sheep
Total number of compounds		11	4	9	5	6	3
Fatty acid derivates							
Unknown FAD 1172	–	0.2	–	–	–	0.2	–
Unknown FAD 1720	–	0.2	–	–	–	–	–
Unknown FAD 2324	–	0.2	–	–	0.3	–	–
Unknown FAD 2385	–	0.5	–	1.1	–	–	–
Unknown FAD 2571	–	0.3	–	0.5	–	–	–
Ketones							
2-Decanone	orange, floral*	–	–	–	–	0.4	–
2-Undecanone	orange, fresh, green	0.2	–	–	–	0.2	–
Nitrogen-containing compounds							
Indole	mothball, burnt	0.6	26.8	0.9	18.9	5.3	6.0
Unknown NCC 1770	–	–	0.1	–	–	–	–
3-Methylindole	mothball, fecal	0.2	–	0.2	0.5	1.4	–
Sulphur-containing compounds							
Dimethyl disulfide	onion, cabbage, putrid	–	47.1	–	–	–	–
Benzenoids							
p-Cresol	medicine, phenol, smoke	97.3	26.0	89.1	79.6	92.5	87.9
4-Propylphenol	medicinal, phenolic*	0.2	–	–	–	–	–
Sesquiterpenoids							
Unknown ST 1862	–	–	–	5.9	–	–	–
Dihydroneoclovene	–	0.2	–	0.4	–	–	6.1
Unknown ST 1907	–	–	–	0.3	–	–	–
β-Caryophyllene	wood, spice	–	–	1.7	0.7	–	–

The total amount of volatiles emitted by the dung differed significantly between dung types (ANOVA: $F_{5,18} = 12.28$, $p < 0.0001$). Pig dung emitted significantly more scent than all other dung types. Also human and dog dung emitted relatively high amounts, but only human dung differed significantly from the dung of herbivores (cattle, horse and sheep). The lowest total scent amounts per extraction were found for sheep (Fig. 6).

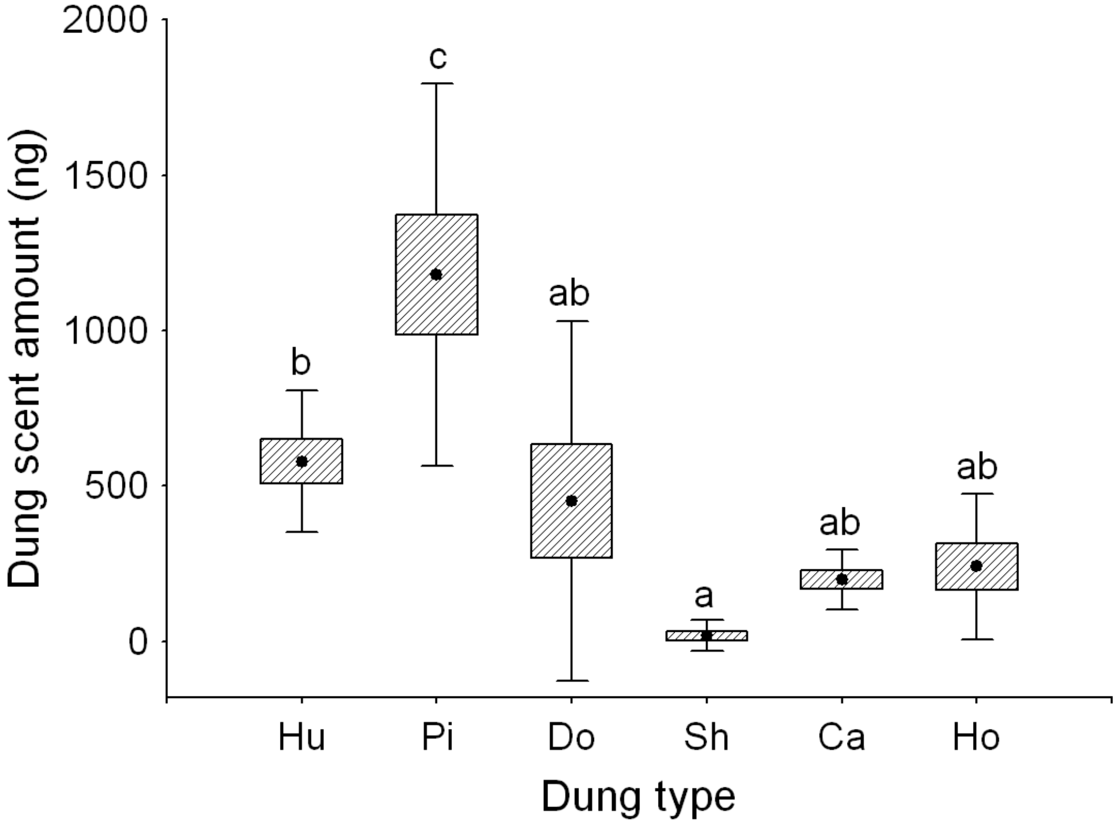

Figure 6. Mean total amount of dung scents emitted from dung of different dung producers ± standard error (box) and 95% confidence intervals (whiskers). N = 4 samples per dung type. Dung producers: human (Hu), pig (Pi), dog (Do), sheep (Sh), cattle (Ca), and horse (Ho). Different letters indicate significant differences between means (Tukey HSD test).

Non-metric multidimensional scaling (NMDS) based on Bray-Curtis similarities was used to visualize similarities between scent profiles of different dung types (Fig. 7). The resulting graph indicates a distinct scent composition of the different dung types which is corroborated by a one-way ANOSIM (Global R = 0.71, p = 0.001). Pairwise tests (one-way ANOSIMs) achieved a significant level for all pairwise comparisons of scent compositions between dung types except for the comparison human vs. sheep dung (results not shown).

The structural formular of the three chemical compounds with the highest total amounts are shown in Figure 7. The compounds p-Cresol and Indole were emitted by every dung type although their relative amount differed prominently (Tab. 5). p-Cresol reached the highest relative amount of all emitted scents in all dung types, except in dog dung. In the latter dung type the highest relative concentration was reached by Dimethyl disulfide (DMDS), which was not found in any other dung type (Tab. 5).

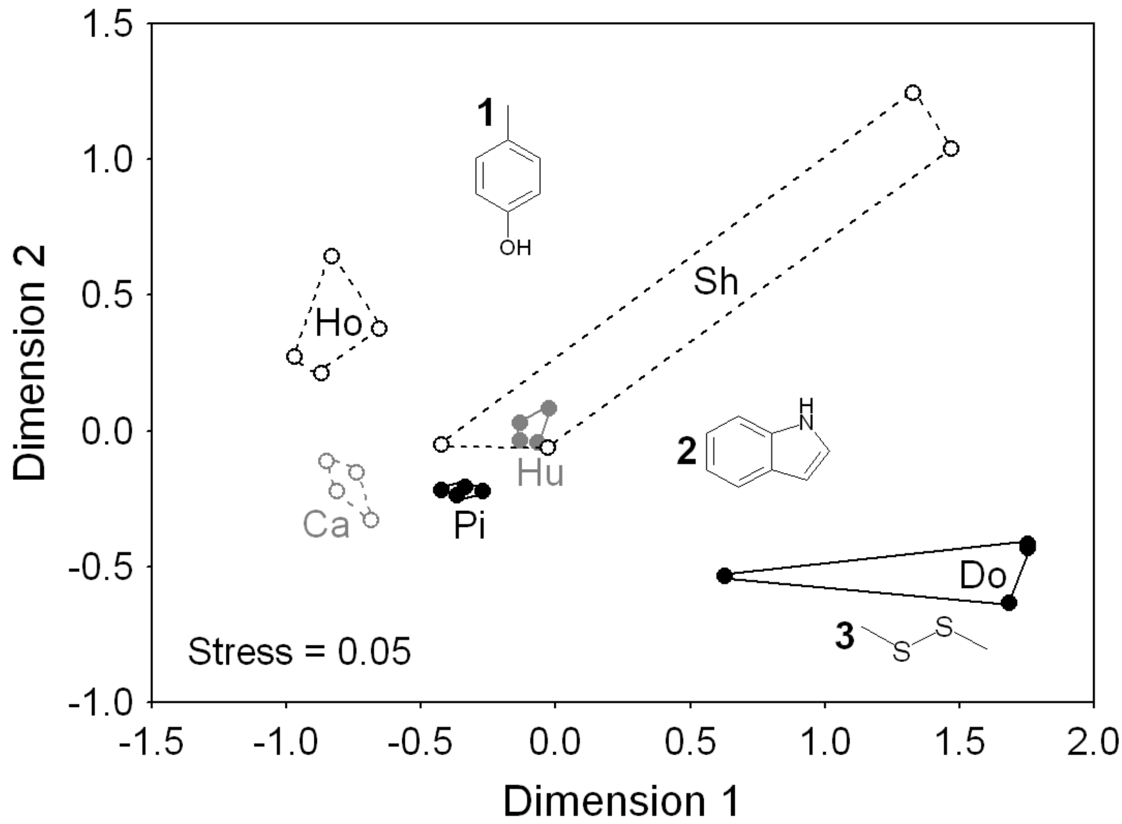

Figure 7. Non-metric multidimensional scaling visualizing (Bray-Curtis) similarities of dung scent profiles of 6 different dung types (N = 4 per dung type). Dung types: cattle (Ca), dog (Do), horse (Ho), human (Hu), pig (Pi), and sheep (Sh). Additionally, structural formulas of scents emitted in high concentrations by dung of all (1: p-Cresol, 2: Indole) or individual dung producers (dog; 3: Dimethyl disulfide) are shown.

Relationship between dung scent profiles and dung beetle assemblages

In all subsequent analyses goose dung had to be excluded because GC-MS analyses did not produce reliable data on its scent profile due to the extremely low total amounts of detectable scent. The number of dung beetle specimens (log (x + 1) transformed) caught in individual pitfall traps during the four sampling rounds, for which data of emitted dung scent amounts were available, was not significantly related to the total amount of extracted dung scents (log (x + 1) transformed) (r = 0.24, N = 24, p = 0.24; Fig. 8). However, a strong positive effect of total dung scent amount on the number of trapped dung beetle specimens was found, when dung beetles sampled by sheep dung were excluded from the analysis (r = 0.57, N = 20, p = 0.008). Sheep dung strongly deviated by emitting relatively small total amounts of dung scents but attracted relatively high numbers of dung beetles (compare Fig. 8).

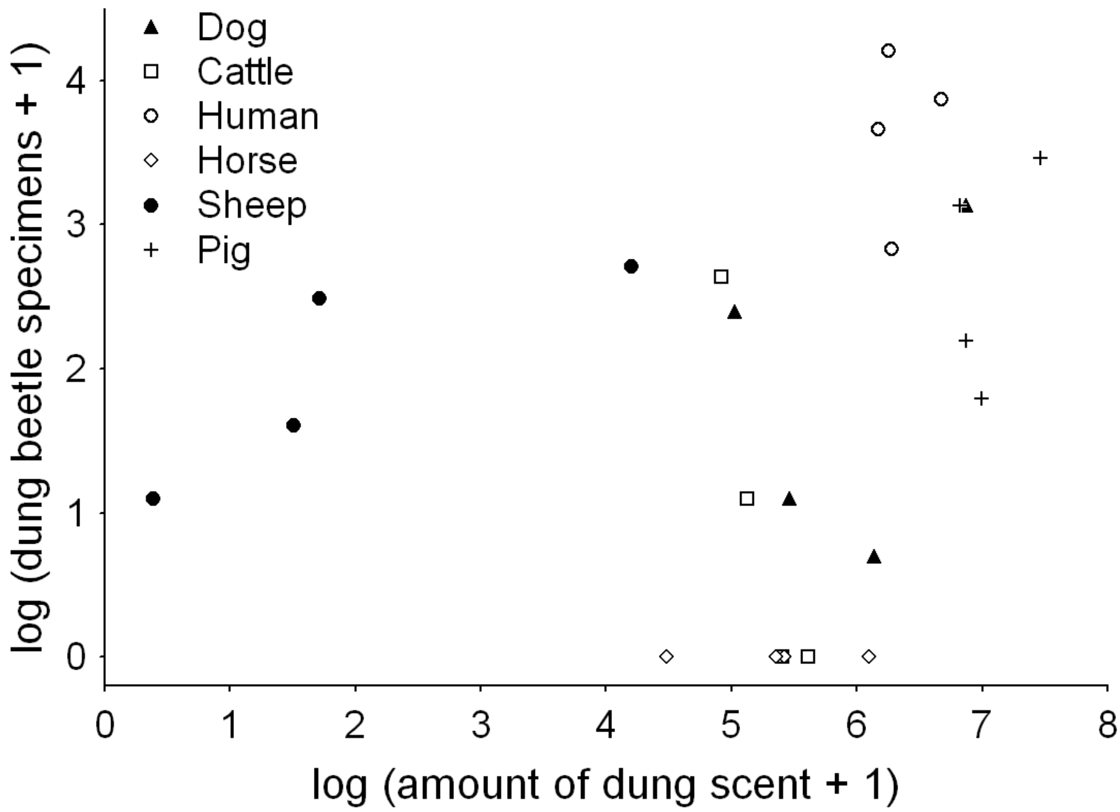

Figure 8. Relationship between the total amount of scents emitted by different dung types and the number of attracted dung beetle specimens (N = 4 scent and beetle sample replicates per dung type).

A Spearman matrix rank correlation relating (Bray-Curtis) similarities of dung scent profiles and dung beetle species composition (only samples with ≥10 individuals included) did not find a significant relationship (*Rho* = 0.022, *p* = 0.409).

Furthermore, we analyzed for the four most abundant dung beetle species *Onthophagus ovatus*, *O. fracticornis*, *O. coenobita* and *O. joannae* (for dates of the dung scent extractions >10 individuals), which differed significantly in their dung preferences (Fig. 3) if the number of trapped specimens is related to the amounts of individual dung scent compounds. Due to the extremely low number of trapped dung beetle specimens, horse samples were excluded from all subsequent analyses. Effects of amounts of individual dung scent compounds on the number of trapped specimens of the four most abundant beetle species were analyzed using a Canonical Correspondence Analysis (CCA). As abundance measurement for each species, we calculated the relative number of individuals attracted by different dung types for all individual dates. Two of the 17 detected compounds (two unknown sesquiterpenoids: ST 1862 and ST 1907) were excluded from the analysis because they only were emitted by horse dung. To quantify the relative amount of the 15 compounds for the each sampling date, their peak areas were divided by the total amount of dung scent. Subsequently, all values were log-transformed and standardized. A CCA including all 15 compounds did not show a significant result (Monte-Carlo Test, all canonical axes: $F = 1.48$, $p = 0.204$), although the 15 environmental variables explained about 64% of variance. Supplementary collinearity was detected when fitting the two unknown compounds FAD 2385 and FAD 2571. These two compounds were for that reason deleted from the set of predictive scent compounds. To determine which variables of the 13 remaining best explain the species data, a stepwise forward selection was performed. Every step the model was reduced by one compound, which explained least of the variance. The eigenvalues (EV) and the test of significance for the first and for all canonical axes of the different models were noted. The ordination plot shown in Figure 9 represents the achieved model with the highest significance (Monte-Carlo Test; first canonical axis: EV = 0.35, $F = 8.08$, $p = 0.036$; all canonical axes: EV = 0.54, $F = 3.36$, $p = 0.002$) and includes seven scent compounds (4-Propylphenol, 3-Methylindole, unknown FAD 1720, β-Caryophyllene, Indole, unknown NCC 1770 and DMDS). The CCA ordination indicated that the four dung beetle species responded to different scent compounds or combinations of them. Only *O. coenobita* and *O. ovatus*, which showed similar preferences for human, dog, pig, and sheep dung (compare Fig. 3), appeared to respond to similar dung scents.

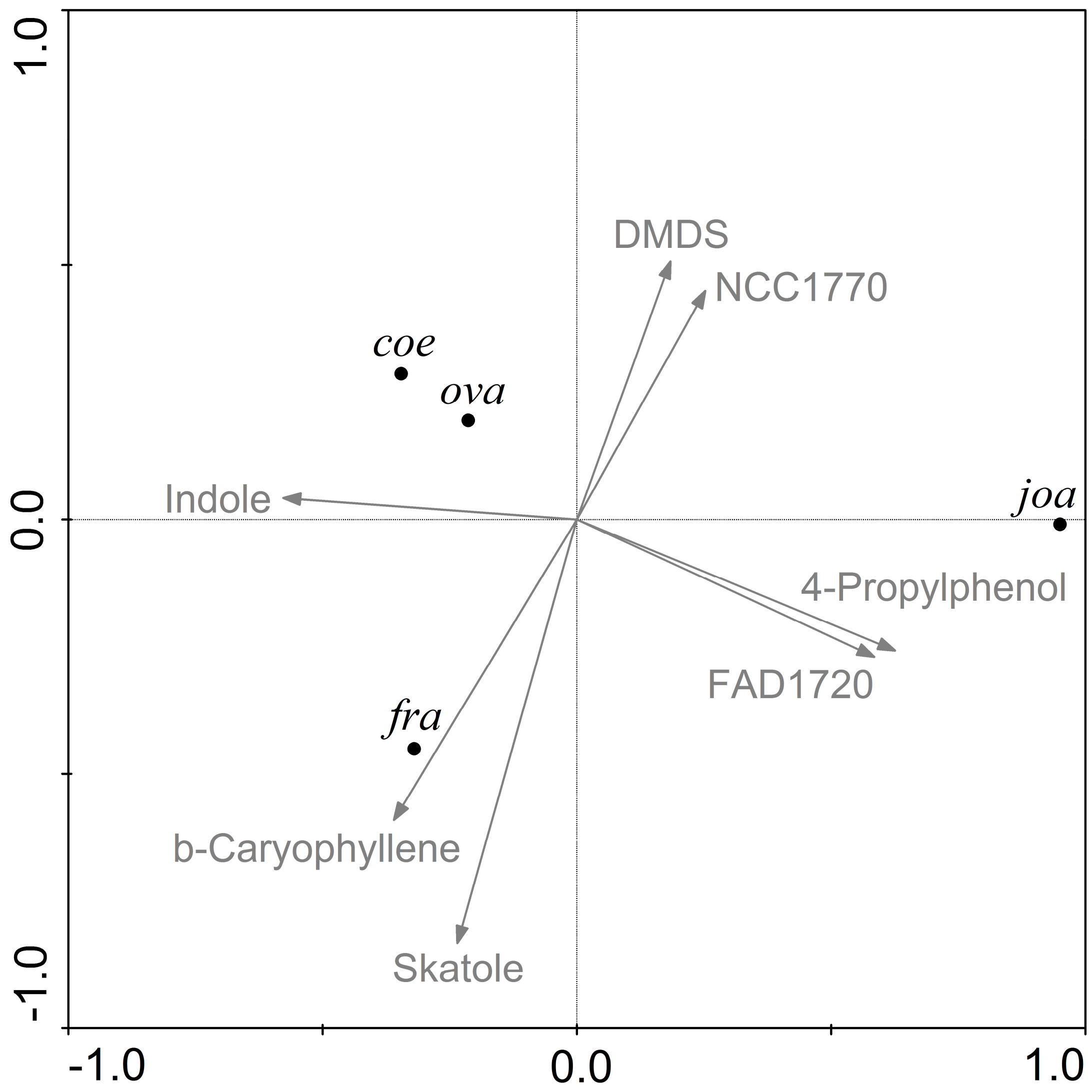

Figure 9. Canonical Correspondence Analysis indicating effects of amounts of 7 different dung scents (standardized) on the abundance variation of the four abundant dung beetle species, *Onthophagus fracticornis* (fra), *O. coenobita* (ova), *O. joannae* (joa), and *O. ovatus* (ova).

DISCUSSION

Food specificity of dung beetles

The European dung beetle species live almost entirely from dung of pasture livestock, like cattle, sheep, and horse (Rainio 1966, Hanski 1991b) and consume dung of carnivores, wild omnivores and carrion only infrequently (Martín-Piera & Lobo 1996, Barbero *et al.* 1999). Although the majority of species generally use all types of herbivore feces, feeding preferences are reported from different European areas (Lumaret & Kirk 1987, Wassmer 1995, Martín-Piera & Lobo 1996, Dormont *et al.* 2004, Dormont *et al.* 2007).

In our study dung beetles could choose between dung of different herbivores, omnivores and one carnivore. In general, human feces proved to be most attractive, a phenomenon also documented in tropical dung beetle species (Howden & Nealis 1975, Larsen & Forsyth 2005) and reported for certain dung beetle species by a study conducted in Spain (Martín-Piera & Lobo 1996).

The four most abundant species in our study, all belonging to the genus *Onthophagus*, significantly preferred certain dung types. The species *O. coenobita* appears to be predominantly restricted to human dung, but also occurs on cattle, horse, goat, sheep, and pig excrements (Horion 1958, Petrovitz 1956). Additionally, it is also regularly observed on carrion. However, this food source may only be used for nutrition by adult beetles and not as breeding site (Burmeister 1930). In our study this species was also found in traps baited with dog and pig dung, but only marginally occurred in traps baited with herbivore feces. Like *O. coenobita*, also *O. fracticornis*, *O. ovatus* and *O. joannae* reached their highest numbers in pitfall traps baited with human dung. *O. joannae* and *O. ovatus* were additionally collected frequently by traps baited with pig and dog dung. In contradiction, it was mentioned by other authors that *O. ovatus* occurs primarily on sheep, but also on goat, cattle, dog, and game feces, and carrion and rooting vegetables (Horion 1958, Lohse & Lucht 1992, Baum 1989). For *O. joannae* sheep, cattle and other dung types were already recorded as food sources (Lohse & Lucht 1992, Bunalski 1999). The only beetle which appeared to be mainly restricted to the two omnivore dung types (not using dog dung) in this study was *O. fracticornis*. However, also this species is known to exploit (in varying frequency) all kinds of dung (Horion 1958). Further studies have to show if intraspecific differences in dung preferences are perhaps the result of a seasonal or geographical variation.

All four species of the genus *Onthophagus* are paracoprid beetles (tunnelers), which prepare nests in the soil below droppings (Hanski & Cambeforte 1991, Finn & Gittings 2003). By contrast the endocrips (dwellers) breed directly in the dung patch and are represented predominantly by Aphodiidae species. In this study the only at least moderately abundant (> 10 trapped individuals) *Aphodius* species was *A. erraticus*, which belongs as an exceptional case also to the group of tunnelers (Rojewski 1983, Vitner 1998). We found most specimens on the excrements of sheep dung, although this species was described as predominantly occurring under cattle and horse droppings (Horion 1958). The tunneler *E. vulvus* is known as consumer of horse and cattle excrements (Lohse & Lucht 1992, Bunalski 1999), but in our study most specimens were found in traps baited with human dung. However, the abundance of the latter two species did not prove to differ significantly between dung baits, which might be related to the generally small numbers of only 12 and 16 collected specimens in *A. erraticus* and *E. vulvus*, respectively.

As mentioned before, the feeding habits of most coprophagous beetles are not restricted to certain dung types. The majority of dung beetle species utilize various kinds of dung, although for many species specific food preferences are reported (Al-Houty & Al-Musalam 1996, Finn & Giller 2002, Martín-Piera & Lobo 1996). In this study, no significant differences in richness of dung beetle assemblages attracted by different dung types were found, although the abundance of trapped individuals and species composition differed significantly between dung types. Martín-Piera and Lobo (1996) also found similar species richness, but a species composition significantly differing between dung types, clearly indicating that feeding preferences of species shaping species assemblage composition.

The key question is why individual dung beetle species prefer certain dung types for their own nutrition as adults and as reproduction site. Gittings and Giller (1998) pointed out three factors which potentially may influence food preferences of coprophagous beetles. First, detectability may be directly related to the odor dispersion of a dung patch. Secondly, the suitability of a dung patch as dung beetle habitat for adults, larvae and eggs may change with increasing dung age. Finally, the nutritional qualities may affect the selection of the food resource for dung beetles, whereas adults choose other dung types for their own nutrition than for their offspring.

Specificity of scents emitted from different dung types

Feces of carnivorous, omnivorous and herbivorous mammals vary in their volatile odor composition and their nutritive composition and, consequently, attractiveness for dung beetles (Hanski & Cambeforte 1991). The source material for the dung odor is composed by exogenous products (undigested feeding components) and endogenous products (e.g. microbial conversion of proteins and fermentable carbohydrates) (Aarnink *et al.* 2007, Moore *et al.* 1987). For that reason the odor differs between animals with different nutrition and digestion. Similarities between the chemical composition of carnivore dung and carrion, for example, are demonstrated by the attraction of relatively few, but similar dung beetle species (Hanski 1987). Also the 8 specimens of carrion beetles (e.g. *Necrophorus* sp., *Oeceoptoma* sp.) found in dog feces during our study indicate that at least some beetles feeding on carrion are also attracted to carnivore dung. Dung volatile composition of herbivorous animals, such as grassing cattle, depends on their different plant incorporation (Aii *et al.* 1980).

In this study two volatile compounds are detected in the odor of most dung types, p-Cresol and Indole. They were found to represent two of the most important volatile components in cattle dung (Aii *et al.* 1980) and in livestock house air (O'Neill & Phillips 1992). We found p-Cresol as the major compound in the odor of all dung types, except of dog dung. For pig manure p-Cresol was also found as the main scent compound in a study on houseflies attracted to pig dung (Cossé & Baker 1996). p-Cresol was already identified as an infochemical for several other insects (Kite 1992). For example, it acts as olfactory attractant for the Japanese dung beetle *Geotrupes auratus* (Inouchi *et al.* 1988) and is applied as odor to traps for baiting tsetse flies

Glossina longipennis (Kyorku *et al.* 1990). Furthermore, it is emitted by sapromyiophilous flowers, such as *Arum maculatum*, imitating fecal or urinous odor character to attract coprophagous insects acting as pollinators (Kite 1995).

Indole as well as Skatole are also characteristic for the odor of feces (Kelling & den Otter 2001, Aii *et al.* 1980, O'Neill & Phillips 1992) and are additionally found as constituents in the scent of tainted meat (Mottram 1991). Therefore these two compounds appear to be highly attractive for houseflies (Cossé & Baker 1996, Brown *et al.* 1961). However, unlike Indole, Skatole could not be detected in every type of feces in our study.

DMDS represented the major fraction found in the scent of dog feces, the only investigated carnivorous mammal in this study. DMDS was also found as very important volatile for the typical fecal odor of human dung (Moore *et al.* 1987), although this could not be confirmed by our study. Belonging to the group of sulphides, it is found in dung and meat as a product of degradation (Kelling & den Otter 2001).

Furthermore five fatty acids were detected in our studied dung samples. They were most abundant in cattle dung, which could be due to the plant material (e.g. grasses) consumed by cattle. For example, Italian ryegrass silage contains many fatty acid volatiles and cattle feeding on it produce dung including these volatiles (Aii *et al.* 1980). Also other studies found that high concentrated short-chained fatty acids contribute to the odor of dung (Moore *et al.* 1987).

Dung types used in this study showed both differences in emitted scent amount and composition of dung scent volatiles. While the first may have important consequences for the detectability of a dung patch, the later may be particularly important for indicating type and nutritional quality of the dung. If scent composition plays a major role, specific single volatiles or entire volatile mixtures could potentially affect the attractiveness of dung for coprophagous beetles.

Potential olfactory cues for dung beetles

For locating dung patches, dung beetles use their olfactory sense (Landin 1961). In contrast to other studies (e.g. Lumaret *et al.* 1993) our results indicate that not only the amount of dung scent influences the arrival of dung beetles, but also the composition or single compounds of the dung scent seemed to be pivotal. Gittings and Giller (1998) showed that the colonization of dung by coprophagous beetles is mainly influenced by differences in the suitability of various dung types as dung beetle microhabitats (for example qualities as breeding medium, nutritional quality) and not by the odor strength. Therefore, the odor of dung must carry information important for dung beetles to find a preferred pat. For example, the size and age of dung patches (Finn & Giller 2000) – due to their crust formation (Thome & Desière 1979) – influence odor dispersion properties (Gittings & Giller 1998). Furthermore, the nitrogen content, important for the nutrition of adult dung beetles (Hanski & Cambeforte 1991), could be indicated by volatile nitrogen-containing compounds emitted by the dung.

Our results suggest that there are 7 different scent compounds which most likely affect the occurrence of the four most abundant dung beetle species, all belonging to the genus *Onthophagus*. Three of these scent compounds represent nitrogen-containing volatiles (Indole, Skatole and one unknown NCC 1770). The other four compounds belong to different compound classes (sulphur-containing compounds; DMDS; benzenoids: 4-Propylphenol; fatty acid derivates: FAD 1720; sesquiterpenoids: β-Caryophyllene). Surprisingly, p-Cresol, the scent with the highest concentration in all dung types, except dog dung, had no significant effect on the occurrence of dung beetles, although it usually attracts many insects utilizing dung or similar resources. As indicated by our and other studies (Aii *et al.* 1980, Cossé & Baker 1996, Kelling & den Otter 2001) p-Cresol seems to be emitted by all dung types. Therefore, it could be potentially of overall importance for attracting dung beetles. However, so far its importance as attractant is only proven for some species, such as *Geotrupes auratus* (Inouchi *et al.* 1988). p-Cresol could be important for the detectability of dung over larger distances. However, the study on *Geotrupes auratus* indicated 2-Butanone, a very volatile substance, to be responsible for guiding food searching and locating behavior, while p-

Cresol appeared to be effective not until beetles reached the close vicinity of the exposed dung (Inouchi *et al.* 1988).

It is plausible that several volatile compounds contribute to the information of the nutritional qualities of a dung source. The occurrence of two dung beetle species *O. coenobita* and *O. ovatus* appeared to be related predominantly to Indole, known as an important attractant for several insects like houseflies (Kelling & den Otter 2001) and the dung beetle *Geotrupes auratus* (Inouchi *et al.* 1988). But also DMDS in combination with an unknown nitrogen-containing compound (NCC 1770), both restricted to the scent of dog feces in this study, had an influence on the arrival. As mentioned before both species, *O. coenobita* and *O. ovatus*, are found abundantly on human dung and carrion and the compounds described above are characteristic for these food sources. Omnivore/carnivore dung is nitrogen-rich (Hanski & Cambeforte 1991) and contains sulfides, which are also found as degradation products in meat (Kelling & den Otter 2001). In our study DMDS was only recorded in the scent of dog feces. However, it is also known to occur as a major fecal odorant in human feces (Moore *et al.* 1987).

Despite of their morphological similarities and the observation that *O. joannae* occurs along with *O. ovatus* in several dung types (Lohse & Lucht 1992), our results showed that *O. joannae* responded to quite different scents. The occurrence of *O. joannae* was best explained by the benzenoid 4-Propylphenol and an unknown fatty acid derivate (FAD 1720), both restricted to cattle excrements. 4-Propylphenol was already found to attract – in combination with other phenolic compounds – the biting midge *Culicoides impunctatus*, which is also decoyed by cattle urine (Bhasin *et al.* 2001). Indole seemed to have a negative effect on *O. joannae* in our study, a finding quite contrary to the conclusions drawn by other studies (Kelling & den Otter 2001, Cossé & Baker 1996).

For the dung beetle species *O. fracticornis*, we found a high preference for Skatole (nitrogen-containing compound), a typical fecal odorant, and β-Caryophyllene (sesquiterpenoid). Furthermore, *O. fracticornis* showed a negative response to some volatiles, particularly two compounds emitted from dog feces (DMDS, NCC 1770). β-Caryophyllene is a major plant volatile found in essential oils of several spice plants, like oregano (Mockute *et al.* 2001), cinnamon (Jayaprakasha *et al.* 2003) and black pepper (Orav *et al.* 2004). It is also found in the scent of the sapromyiophilous flower *Arum maculatum* (Jürgens *et al*. 2006) and in cattle dung (Kite 1995). *O. fracticornis* is known as generalist. The positive effects of Skatole and also Indole confirm this acceptance, because these two compounds are strongly related with fecal odor (Moore *et al*. 1987, Kelling & den Otter 2001) and occurred in most dung types analyzed in this study.

To summarize, our data indicate that the preferences of dung beetle species to certain dung types are not necessarily linked to only one emitted volatile compound, but often to a combination of several different scents. Moreover, same compounds, which appear to be a major attractant for certain dung beetle species, can be negatively related to the occurrence of other species.

Conclusions

Gittings (1994) pointed out that the reproductive success of *Aphodius* species was usually higher in preferred dung types, highlighting the important link between fitness and food preferences and the necessity for dung beetles to detect and select the best food source. Dung beetles locate and select their food source on the basis of olfactory cues (Dormont *et al.* 2007). They can distinguish between different dung types because of the emitted volatile compounds. As documented by this study, dung beetle assemblages and scent composition clearly differ between dung types. However, differences in species composition were not directly related to differences in scent composition, indicating that certain subsets of scents may be of higher importance for resource selection than the entire scent composition. Furthermore, our study clearly demonstrated that several volatiles better predicted the occurrence of individual dung beetle species than just individual scents, which was already recognized by another study. Traps baited with five different odor compounds (2-Butanone, Phenol, p-Cresol, Indole, Skatole) attracted much more individuals of the dung beetle *Geotrupes auratus* than traps baited with only one of these volatiles (Inouchi *et al.* 1988).

For parasitoid insects a learning process is recorded, which increase the effectiveness of host-foraging behavior (Lewis *et al.* 1990, Vet & Groenewold 1990, Turlings *et al.* 1993, Lewis *et al.* 1998). Host and food availability for parasitoids varies spatially and temporarily and it is an advantage for them to adapt their foraging behavior (Lewis *et al.* 1998). Also food and breeding habitats of dung beetles are only patchily distributed and temporarily available (Hanski 1991a). Therefore, a learning process based on feeding experience associated with olfactory cues could be also advantageous in dung beetles to increase the chance of finding high quality food sources and to gain better access to potential mating partner and breeding sites. Experiments quantifying the importance of individual dung scents potentially acting as infochemicals, combined with studies on potential effects of feeding experiences on dung preferences, will offer an interesting field of further research on coprophagous beetles.

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APPENDIX

Table A. Dung beetle species and individuals collected at 8 sampling dates (1 = 3 August 2007, 2 = 7 August 2007, 3 = 13 August 2007, 4 = 16 August 2007, 5 = 20 August 2007, 6 = 24 August 2007, 7 = 27 August 2007, 8 = 3 September 2007) with pitfall traps baited with seven different dung types.

Species	Dung type – sampling days															
	Cattle								Dog							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Subfamily Aphodiinae																
Aphodius (Colobopterus) erraticus			1													
Aphodius (Limarus) maculatus	1															
Aphodius (Teuchestes) haemorrhoidalis																
Aphodius (Volinus) sticticus																
Subfamily Geotrupinae																
Tribe Geotrupini																
Geotrupes stercorarius																
Subfamily Scarabaeinae																
Tribe Oniticellini																
Euoniticellus vulvus		1														
Tribe Onthophagini																
Onthophagus (Palaeonthophagus) coenobita						1					2		2	12		2
Onthophagus (Palaeonthophagus) fracticornis	3					11					1		2	12		
Onthophagus (Palaeonthophagus) gibbulus														2		
Onthophagus (Palaeonthophagus) joannae	1						2		2	1	1	1		1		1
Onthophagus (Palaeonthophagus) nuchicornis											1			1		
Onthophagus (Palaeonthophagus) ovatus	8	7	1			5			20	34	5	1	6	48	1	
Onthophagus (Palaeonthophagus) similis														1		
Onthophagus taurus																
Onthophagus (Palaeonthophagus) vitulus																

Table A. cont.

Species	Dung type – sampling days															
	Goose								Horse							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Subfamily Aphodiinae																
Aphodius (Colobopterus) erraticus																
Aphodius (Limarus) maculatus																
Aphodius (Teuchestes) haemorrhoidalis																
Aphodius (Volinus) sticticus																
Subfamily Geotrupinae																
Tribe Geotrupini																
Geotrupes stercorarius																
Subfamily Scarabaeinae																
Tribe Oniticellini																
Euoniticellus vulvus			1													
Tribe Onthophagini																
Onthophagus (Palaeonthophagus) coenobita																
Onthophagus (Palaeonthophagus) fracticornis														2		
Onthophagus (Palaeonthophagus) gibbulus																
Onthophagus (Palaeonthophagus) joannae				2		2										
Onthophagus (Palaeonthophagus) nuchicornis			1							1						
Onthophagus (Palaeonthophagus) ovatus	2	1	2		3	10	2							3		
Onthophagus (Palaeonthophagus) similis																
Onthophagus taurus																
Onthophagus (Palaeonthophagus) vitulus																

Table A. cont.

Species	Dung type – sampling days															
	Human								Pig							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Subfamily Aphodiinae																
Aphodius (Colobopterus) erraticus	1	1							1	1	1					
Aphodius (Limarus) maculatus																
Aphodius (Teuchestes) haemorrhoidalis										1						
Aphodius (Volinus) sticticus						2								1		
Subfamily Geotrupinae																
Tribe Geotrupini																
Geotrupes stercorarius						1								1		1
Subfamily Scarabaeinae																
Tribe Oniticellini																
Euoniticellus vulvus		4	2			2			1		2			1		
Tribe Onthophagini																
Onthophagus (Palaeonthophagus) coenobita	1		3	1	3	11	2	4						6	1	1
Onthophagus (Palaeonthophagus) fracticornis	9	9	12	14	55	126	12	1	2	1	2		21	105	5	3
Onthophagus (Palaeonthophagus) gibbulus																
Onthophagus (Palaeonthophagus) joannae	2	1	2	2	1	4				4				2		
Onthophagus (Palaeonthophagus) nuchicornis		2	1								1	1				
Onthophagus (Palaeonthophagus) ovatus	25	74	12	29	6	35	1	1	18	21	4	4	9	41	2	
Onthophagus (Palaeonthophagus) similis																
Onthophagus taurus		2			1		1						1			
Onthophagus (Palaeonthophagus) vitulus				1												

Table A. cont.

Species	**Dung type – sampling days**							
	Sheep							
	1	2	3	4	5	6	7	8
Subfamily Aphodiinae								
Aphodius (Colobopterus) erraticus			4			2		
Aphodius (Limarus) maculatus								
Aphodius (Teuchestes) haemorrhoidalis		1	1					
Aphodius (Volinus) sticticus								
Subfamily Geotrupinae								
Tribe Geotrupini								
Geotrupes stercorarius								
Subfamily Scarabaeinae								
Tribe Oniticellini								
Euoniticellus vulvus			1	1				
Tribe Onthophagini								
Onthophagus (Palaeonthophagus) coenobita				1		2	1	
Onthophagus (Palaeonthophagus) fracticornis		1	6			2	1	1
Onthophagus (Palaeonthophagus) gibbulus								
Onthophagus (Palaeonthophagus) joannae		1	1		1	1		
Onthophagus (Palaeonthophagus) nuchicornis								
Onthophagus (Palaeonthophagus) ovatus	4	13	6	12	10	4		
Onthophagus (Palaeonthophagus) similis								
Onthophagus taurus								
Onthophagus (Palaeonthophagus) vitulus								

Table B. Sent compounds and peak areas for the different dung types analyzed for four sampling days corresponding to dates of dung beetle trapping (1 = 3 August 2007, 4 = 16 August 2007, 5 = 20 August 2007, 7 = 27 August 2007). In the last row the total scent amounts (ng) of the individual dung scent extraction samples are provided.

Scent compounds	**Dung types – Sampling dates**							
	Cattle				Dog			
	1	4	5	7	1	4	5	7
Fatty acid derivates								
Unknown FAD 1172	200000	0	0	5000	0	0	0	0
Unknown FAD 1720	80000	50000	30000	5000	0	0	0	0
Unknown FAD 2324	21354	59730	0	80000	0	0	0	0
Unknown FAD 2385	124465	253731	10000	153783	0	0	0	0
Unknown FAD 2571	0	140000	1000	140000	0	0	0	0
Ketones								
2-Decanone	0	0	0	0	0	0	0	0
2-Undecanone	50000	110000	5000	5000	0	0	0	0
Nitrogen-containing compounds								
Indole	232626	300000	5000	30000	14966732	15233738	3761431	27943090
Unknown NCC 1770	0	0	0	0	195119	10000	5000	20000
3-Methylindole (Skatole)	112644	40000	1000	10000	0	0	0	0
Sulphur-containing compounds								
Dimethyl disulfide	0	0	0	0	47498432	14707052	15492182	31035150
Benzenoids								
p-Cresol	16270352	27311276	34544700	20924870	60102532	0	0	0
4-Propylphenol	100000	30000	80000	10000	0	0	0	0
Sesquiterpenoids								
Unknown ST 1862	0	0	0	0	0	0	0	0
Dihydroneoclovene	133748	80000	5000	30000	0	0	0	0
Unknown ST 1907	0	0	0	0	0	0	0	0
β-Caryophyllene	0	0	0	0	0	0	0	0
Scent amount (ng)	*135.48*	*221.88*	*271.20*	*167.29*	*959.96*	*234.20*	*150.60*	*461.34*

Table B. cont.

Scent compounds	Dung types – Sampling dates							
	Horse				Human			
	1	4	5	7	1	4	5	7
Fatty acid derivates								
Unknown FAD 1172	0	0	0	0	0	0	0	0
Unknown FAD 1720	0	0	0	0	0	0	0	0
Unknown FAD 2324	0	0	0	0	0	0	0	900000
Unknown FAD 2385	409124	50000	660348	229815	0	0	0	0
Unknown FAD 2571	0	644250	0	500	0	0	0	0
Ketones								
2-Decanone	0	0	0	0	0	0	0	0
2-Undecanone	0	0	0	0	0	0	0	0
Nitrogen-containing compounds								
Indole	10000	0	1147672	0	11712296	17005602	16648529	10576420
Unknown NCC 1770	0	0	0	0	0	0	0	0
3-Methylindole (Skatole)	20000	40000	134344	10000	0	1095870	150000	250000
Sulphur-containing compounds								
Dimethyl disulfide	0	0	0	0	0	0	0	0
Benzenoids								
p-Cresol	8810182	26425562	48986488	25783780	49339168	82496200	48461908	55810488
4-Propylphenol	0	0	0	0	0	0	0	0
Sesquiterpenoids								
Unknown ST 1862	1327133	1200229	4463770	300000	0	0	0	0
Dihydroneoclovene	40000	10000	247497	150000	0	0	0	0
Unknown ST 1907	70000	50000	134671	60000	0	0	0	0
β-Caryophyllene	538438	260804	883354	356555	54275	733934	885788	347309
Scent amount (ng)	*87.77*	*224.27*	*443.05*	*210.27*	*477.82*	*792.38*	*517.24*	*530.83*

Table B. cont.

Scent compounds	Dung types – Sampling dates							
	Pig				Sheep			
	1	4	5	7	1	4	5	7
Fatty acid derivates								
Unknown FAD 1172	1000000	0	0	90000	0	0	0	0
Unknown FAD 1720	0	0	0	0	0	0	0	0
Unknown FAD 2324	0	0	0	0	0	0	0	0
Unknown FAD 2385	0	0	0	0	0	0	0	0
Unknown FAD 2571	0	0	0	0	0	0	0	0
Ketones								
2-Decanone	50000	800000	1000000	651272	0	0	0	0
2-Undecanone	168129	293228	501422	190405	0	0	0	0
Nitrogen-containing compounds								
Indole	9337142	4698584	12391068	5552282	100000	281064	150000	40000
Unknown NCC 1770	0	0	0	0	0	0	0	0
3-Methylindole (Skatole)	1185434	1187292	3892649	2436183	0	0	0	0
Sulphur-containing compounds								
Dimethyl disulfide	0	0	0	0	0	0	0	0
Benzenoids								
p-Cresol	105230568	132772640	205979840	114113240	350000	8000000	0	0
4-Propylphenol	0	0	0	0	0	0	0	0
Sesquiterpenoids								
Unknown ST 1862	0	0	0	0	0	0	0	0
Dihydroneoclovene	0	0	0	0	0	126175	428968	20000
Unknown ST 1907	0	0	0	0	0	0	0	0
β-Caryophyllene	0	0	0	0	0	0	0	0
Scent amount (ng)	*914.67*	*1092.81*	*1749.76*	*962.08*	*3.52*	*65.74*	*4.53*	*0.47*

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