

Influence of carrion smell and rebaiting time on the efficiency of pitfall traps to dung beetle sampling

Carlos Alberto Hector Flechtmann*, Vinicius Gomes Tabet & Ingrid Quintero

Department of Plant Protection, FEIS/UNESP, Av. Brasil 56, 15385-000, Ilha Solteira, SP, Brazil

Accepted: 27 November 2008

Key words: coprophagous beetles, sampling protocol, dung attractiveness, trap effectiveness, Coleoptera, Scarabaeidae, Scarabaeinae, *Sus scrofa*, *Tayassu tajacu*

Abstract

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are very useful insects, as they improve the chemo-physical properties of soil, clean pastures from dung pads, and help control simuliid flies associated with bovine cattle. Their importance makes it fundamental to sample and survey them adequately. The objectives of the present study were to determine the influence of decaying insects trapped in pitfalls on the attractiveness of Moura pig *Sus scrofa* L. (Suidae) and collared peccary *Tayassu tajacu* (L.) (Tayassuidae) dung used as baits to lure dung beetles, and to establish how long these baits remain attractive to dung beetles when used in these traps. Some dung beetle species seemed to be able to discriminate against foul smell from decaying insects within the first 24 h, hence decreasing trap efficiency. This was more evident in peccary dung-baited traps, which proved to be the least attractive bait. Attractiveness lasted only 24 h for peccary dung, after which it became unattractive, whereas the pig dung bait was highly attractive for 48 h, after which its attractiveness diminished but was not completely lost.

Introduction

Beetles of the subfamily Scarabaeinae are commonly known as dung beetles, due to the habit of adults and juveniles of most species to feed mainly on dung. This dung is buried in the ground. In the process of burying dung, the beetles improve the physical and chemical properties of the soil (Gillard, 1967; Mittal, 1993). Indirectly they also contribute to the control of species of veterinary importance, such as gastrointestinal nematodes and the larvae of flies that develop in soil (Bornemissza, 1976; Fincher, 1981). More recently, dung beetles have been used as biological indicators to evaluate diversity in natural and disturbed ecosystems (Halffter & Favila, 1993; Halffter, 1998; Davis et al., 2001; McGeoch et al., 2002; Spector, 2006).

Considering the importance of dung beetles, it is very important to adequately survey and sample them. Dung beetles are best sampled with pitfall traps, and the efficiency of the traps is enhanced when associated with baits (Lobo et al., 1988; Halffter & Favila, 1993). Several factors influence dung beetle trapping with baited pitfall traps. Some of these factors are understood and controlled for,

such as the type of trap and the most attractive baits. Modifying factors, such as trap dimensions and rebaiting time, are known to be important but there is no clear understanding of how much they influence beetle trapping. Yet other factors have been largely overlooked, for instance the influence of the decay of trapped insects (and any other captured animals for that matter) on the attractiveness of the bait.

There is disagreement in the literature on how long a bait should remain in the field before rebaiting. It seems that the attractiveness of the bait is related to the content of water in the dung, and when the moisture content of the dung drops below a certain level, it is not attractive anymore (Errouissi et al., 2004). Howden & Nealis (1975) suggested that bait loses attractiveness after 48 h, but in the literature this time varies from as little as 24 h (Larsen & Forsyth, 2005) to as long as 7 days (Errouissi et al., 2004).

Once a captured insect dies in the collecting cup, a process of putrefaction begins, usually under anaerobic conditions and aided by bacteria (Rettger & Newell, 1912; Statheropoulos et al., 2005). Decay of trapped organisms will happen in spite of the preservative used; what varies is the degree to which this process is delayed (Schmidt et al., 2006). The volatiles produced during the putrefaction

*Correspondence: E-mail: flechtma@bio.feis.unesp.br

process might interfere with the attractiveness of the bait, and the longer trapped (dead) insects remain in the collecting cup, the more volatiles are released. This aspect has received very little attention; apparently the only reference in the literature comes from an experiment that showed that carrion smell originating from trapped decaying *Ips typographus* (L.) significantly reduced attractiveness of the bait to these beetles in Theysohn slit traps (Kretschmer, 1990). There is no known information on the influence of foul smell produced by decaying insects on bait attractiveness to Scarabaeinae.

The main objectives of this study were to establish (1) the possible influence of decaying insects trapped in pitfall traps on the attractiveness of various dung baits to dung beetles, and (2) the time dung sources remain attractive to dung beetles when used as baits in pitfall traps.

Material and methods

During the end of the rainy season, from 21 March through 1 May 2007, the experiment was done in a 30-ha fragment of semideciduous latifoliate tropical forest (Atlantic Forest) in advanced stage of regeneration, located in Selvíria (20°22'S, 51°24'W), Mato Grosso do Sul, Brazil, and owned by the São Paulo State University (UNESP), at Ilha Solteira. During these 6 weeks, average maximum, minimum, and mean temperatures were 33.6, 21.2, and 26.4 °C, respectively, average air humidity was 69.7%, and total rainfall 24.6 mm.

Pitfall traps (modified from Howden & Nealis, 1975) were baited with 500 ml of fresh dung of either Moura pig, *Sus scrofa* L. (Suidae), or captive collared peccary, *Tayassu tajacu* (L.) (Tayassuidae). A previous experiment had shown that pig dung was the most attractive to dung beetles and collared peccary dung the least, among a range of dung types tested (CAH Flechtmann, F Oikawa & VG Tabet, unpubl.). Dung was suspended in a bag of plastic mosquito netting ca. 10 cm above the collecting cup, 7.0 cm in diameter and buried flush to the ground. The liquid preservative consisted of a mixture of water, a bit of unscented dish detergent, and some rock salt (NaCl).

Traps were deployed in three transects, 40 m away from the border of the fragment. Each transect consisted of four traps, two baited with pig dung and two with collared peccary dung. Traps were spaced 1.5 m apart within each transect, to provide an equal chance of a beetle to detect and choose among baits and hence being collected in any of the four traps (Scudder, 1996; Dormont et al., 2004). Trapped insects were collected at 1, 2, and 7 days. After the last collection (on day 7), dung was replaced with fresh material and traps were rerandomized within each transect to reduce positional

effects. On each collection day, in one of each set of two traps baited with the same dung type trapped insects were removed and the liquid preservative was replaced, while in the other trap all collected insects were bagged in a 2-mm mesh cloth and returned to the collecting cup, where the preservative was conserved.

Moisture content of both peccary pellets and pig dung was determined by weighing 10 samples each of recently excreted droppings and oven-drying them at ca. 56 °C for 5 days. The samples were then removed from the oven, cooled at room temperature, and reweighed. Specimens were identified using the reference collection of the Museum of Entomology of UNESP (MEFEIS), Ilha Solteira, SP, Brazil, where all voucher specimens were deposited.

The experimental design was a randomized complete block. To remove heteroscedasticity, samples were $\sqrt{(x + 0.5)}$ transformed (Phillips, 1990). Beetle catches and dung moisture content were compared using generalized linear models (Proc GLM) and treatment means were separated by the Tukey test (SAS Institute, 1990). Jaccard's similarity coefficients (Jaccard, 1901) were calculated among dung beetle assemblages captured in different days of trapping, for each dung type, and these coefficients were used to construct a dendrogram by the unweighted pair-group method of arithmetic average (UPGMA) using the Multi-Variate Statistical Package (MVSP) version 3.1 (Kovach, 1999).

Results

In 6 weeks, a total of 1 976 dung beetles were trapped, representing 26 species (Table 1). Six *Ataenius* species were also trapped but excluded from the analysis, because their relationship with dung is uncertain (Stebnicka, 1985). Only the most abundant species were included in the statistical analysis, namely *Canthon septemmaculatus histrio*, *Canthidium* spec., *Deltochilum* spec., *Dichotomius bos*, *Dichotomius nisus*, *Eurysternus* near *hirtellus*, *Ontherus appendiculatus*, *Onthophagus* near *hirculus*, *Onthophagus* near *ranunculus*, *Pedariidum bidens*, *Trichillum externepunctatum*, and *Uroxys epipleuralis*. The main factors day of trapping, bait, and insect removal yielded significant effects, as well as the interactions bait*removal, bait*day, and bait*day*removal ($P < 0.05$).

For six species, viz., *D. bos* ($F_{1,27} = 5.17$, $P = 0.0312$), *D. nisus* ($F_{1,27} = 15.88$, $P = 0.0005$), *O. appendiculatus* ($F_{1,27} = 15.71$, $P = 0.0005$), *O. nr. ranunculus* ($F_{1,27} = 10.93$, $P = 0.0022$), *P. bidens* ($F_{1,27} = 6.01$, $P = 0.0210$), and *T. externepunctatum* ($F_{1,27} = 10.38$, $P = 0.0033$), and for the whole assemblage of Scarabaeinae dung beetles (all species as a group) ($F_{1,27} = 17.85$, $P = 0.0002$), pitfall

Table 1 Number of Scarabaeinae dung beetles trapped in pitfalls baited with Moura pig (*Sus scrofa*) or collared peccary (*Tayassu tajacu*) dung, with (Y) or without (N) removal of trapped beetles, in an Atlantic forest fragment in Selvíria, state of Mato Grosso do Sul, Brazil, March through May 2007

Species	Collared peccary		Moura pig	
	Y	N	Y	N
<i>Ateuchus puncticollis</i> (Harold)	2	1	1	4
<i>Ateuchus</i> near <i>viridimicans</i> (Boucomont)	0	0	1	0
<i>Canthidium barbaticum</i> Preudhomme de Borre	0	1	1	0
<i>Canthon chalybaeus</i> Blanchard	4	0	2	3
<i>Canthidium</i> near <i>breve</i> (Germar)	1	0	0	0
<i>Canthon septemmaculatus histrio</i> Le Peletier & Serville	13	32	31	22
<i>Canthidium</i> spec.	1	2	10	9
<i>Canthon</i> spec.	0	1	4	4
<i>Deltochilum</i> spec.	8	19	12	16
<i>Diabroctis mimas</i> (L.)	1	0	0	1
<i>Dichotomius bos</i> (Blanchard)	1	1	12	7
<i>Dichotomius depressicollis</i> (Harold)	0	0	1	1
<i>Dichotomius nisus</i> (Olivier)	16	8	57	26
<i>Eurysternus caribaeus</i> (Herbst)	1	0	3	0
<i>Eurysternus</i> near <i>hirtellus</i> Dalman	43	39	99	44
<i>Malagoniella puncticollis aeneicollis</i> (Waterhouse)	0	0	1	0
<i>Ontherus appendiculatus</i> Mannerheim	90	89	310	203
<i>Ontherus digitatus</i> Harold	1	0	0	0
<i>Onthophagus</i> near <i>hirculus</i> Mannerheim	18	15	43	28
<i>Onthophagus</i> near <i>ranunculus</i> Arrow	1	0	30	13
<i>Ontherus sulcator</i> (Fabricius)	0	0	3	2
<i>Pedaridium bidens</i> Balthasar	0	1	11	10
<i>Trichillum externepunctatum</i> Preudhomme de Borre	35	28	232	230
<i>Trichillum hirsutum</i> Boucomont	0	0	1	0
<i>Uroxys epipleuralis</i> Boucomont	0	3	9	2
<i>Uroxys</i> spec.	0	1	0	1
Total	235	239	874	626

traps baited with pig dung collected significantly more dung beetles than traps baited with peccary dung. For the remaining analyzed species there were no significant differences ($P > 0.05$). Overall, these results on bait attractiveness are similar to those obtained in a previous experiment (CAH Flechtmann, F Oikawa & VG Tabet, unpubl.).

Pig dung-baited cups from which insects were removed trapped more dung beetles than cups from which they were not removed. This was observed for *D. nisus* ($F_{1,27} = 12.65$, $P = 0.0014$), *O. appendiculatus* ($F_{1,27} = 5.30$, $P = 0.0293$), *O. nr. ranunculus* ($F_{1,27} = 5.94$, $P = 0.0217$), and total Scarabaeinae ($F_{1,27} = 7.23$, $P = 0.0122$). On the

other hand, in peccary dung-baited traps, no effect from insect removal was obtained for any species ($P > 0.05$).

The same comparisons were made per day, in order to evaluate the influence of aging of dung bait and build-up of carrion smell from the decomposition of trapped insects. In traps baited with pig dung results were similar, but differences were somewhat larger on the latest trapping day. An effect of insect removal from the bait was significant on day 1 only in *O. nr. ranunculus*, whereas on day 7 it was significant in *D. nisus*, *O. appendiculatus*, and total Scarabaeinae dung beetles (Figure 1). For traps baited with peccary dung, results were similar only on day 1, where both *E. nr. hirtellus* and *T. externepunctatum* were more common in traps with insects removed. On day 2, *E. nr. hirtellus* was trapped in higher numbers in traps with no insect removal, whereas on day 7 there were no significant effect of insect removal from the peccary dung-baited traps for any of the species ($P > 0.05$, Figure 2).

Focusing on bait attractancy over time, in peccary dung-baited traps with decaying insects removed, *C. septemmaculatus histrio*, *D. nisus*, *E. nr. hirtellus*, *O. appendiculatus*, *O. nr. hirculus*, *T. externepunctatum*, and total Scarabaeinae were found in significantly higher numbers on day 1 than on day 2 or day 7. In traps without insect removal, significant differences were found only for *C. septemmaculatus histrio*, *D. nisus*, and *O. appendiculatus*, but with a similar trend: more beetles were collected on day 1 than on day 2 or day 7 (Figure 2). In pig dung-baited traps no significant differences were found between days for any dung beetle species ($P > 0.05$, Figure 1).

In peccary dung-baited traps with insects removed, similarity coefficients indicated that trapped dung beetle assemblages were more similar between day 2 and day 7 (55%) than with day 1 (33%), whereas in pig dung-baited traps assemblages were (slightly) more similar between day 1 and day 2 (70%) than with day 7 (66%) (Figure 3). Fresh pig dung contained more water than fresh peccary dung: $70.8 \pm 0.59\%$ (mean \pm SD) vs. $64.6 \pm 0.58\%$ ($F_{1,18} = 53.01$, $P < 0.0001$).

Discussion

Although traps were operated in the field for only 6 weeks, the number of individuals that were captured and the diversity of species were high for that particular area and season. Overall, pig dung proved to be a better attractant than peccary dung; of all species that were trapped in higher numbers, most were found in traps baited with pig dung (Table 1). The suitability of pig dung as a bait is known from the literature (Davis, 1994; Boonrotpong et al., 2004; Harvey et al., 2006). Peccaries are herbivores and their pads are composed of several ca. 3-cm-long pel-

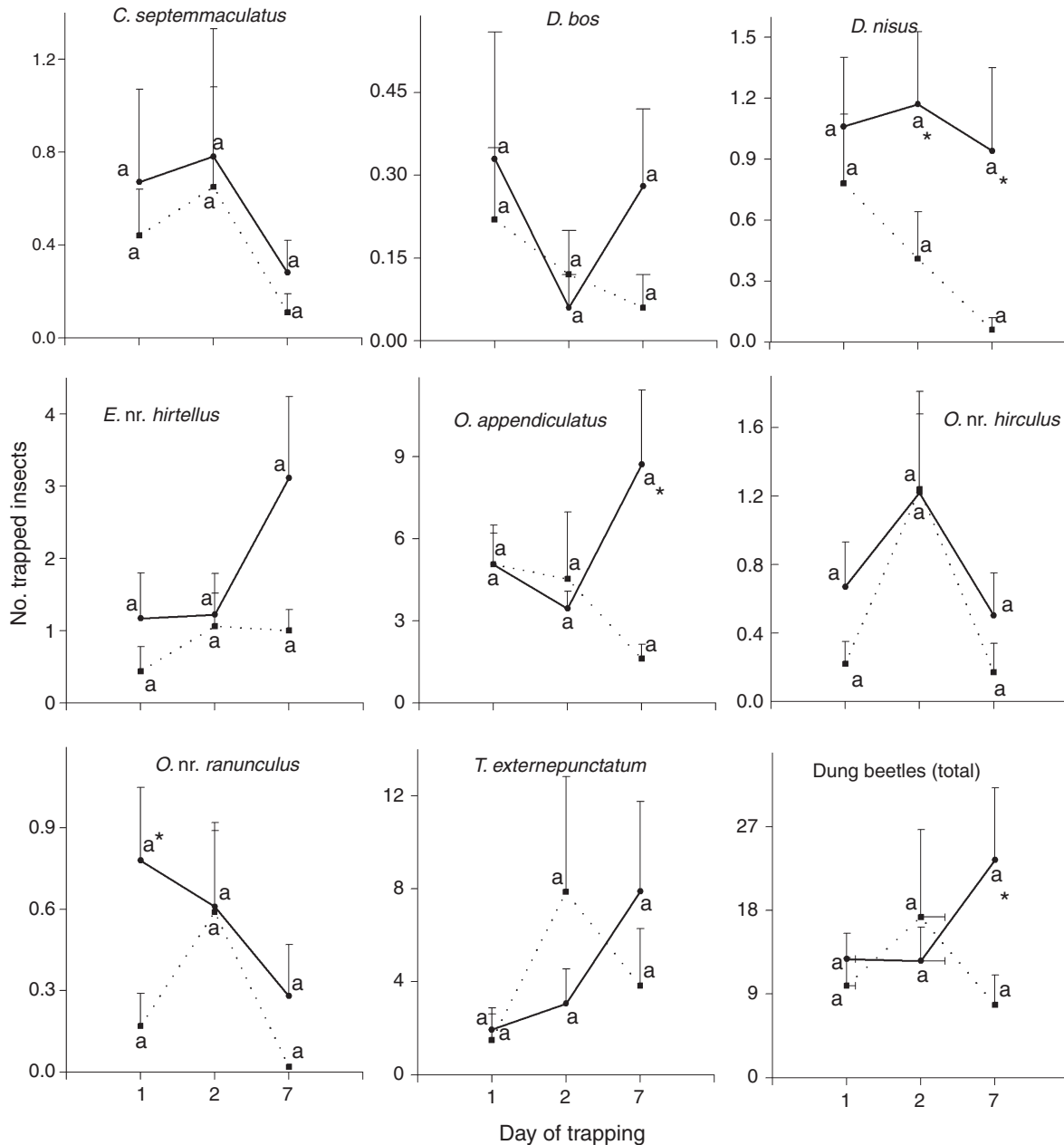


Figure 1 Mean (+ SE) weekly numbers of dung beetle species caught in pitfall traps baited with Moura pig (*Sus scrofa*) dung, with (solid line) or without (dotted line) beetle removal, in an Atlantic forest fragment in Selvíria, state of Mato Grosso do Sul, Brazil, March through May 2007. Means followed by the same letter within each treatment are not significantly different ($P > 0.05$; means followed by an * between treatments are significantly different (Tukey test: $P < 0.05$).

lets, whereas pigs are omnivores, with larger and wetter pads. Consequently, pig pads probably emit volatiles longer (Lumaret & Kirk, 1987; Gittings & Giller, 1998; Errouissi et al., 2004). Fincher et al. (1970) argue that there is a positive correlation between the odor of a bait and its attractiveness to dung beetles. Pig dung exhibits a considerably stronger smell than peccary dung, indicating that it

emits semiochemicals more and/or faster than peccary dung (Dormont et al., 2004, 2007). Even after 7 days some species were still captured in higher numbers in pig dung-baited traps with insect removal, despite dung desiccation.

Pig dung-baited traps became less attractive when insects were not removed, whereas this effect was not seen with peccary dung-baited traps. The carrion smell

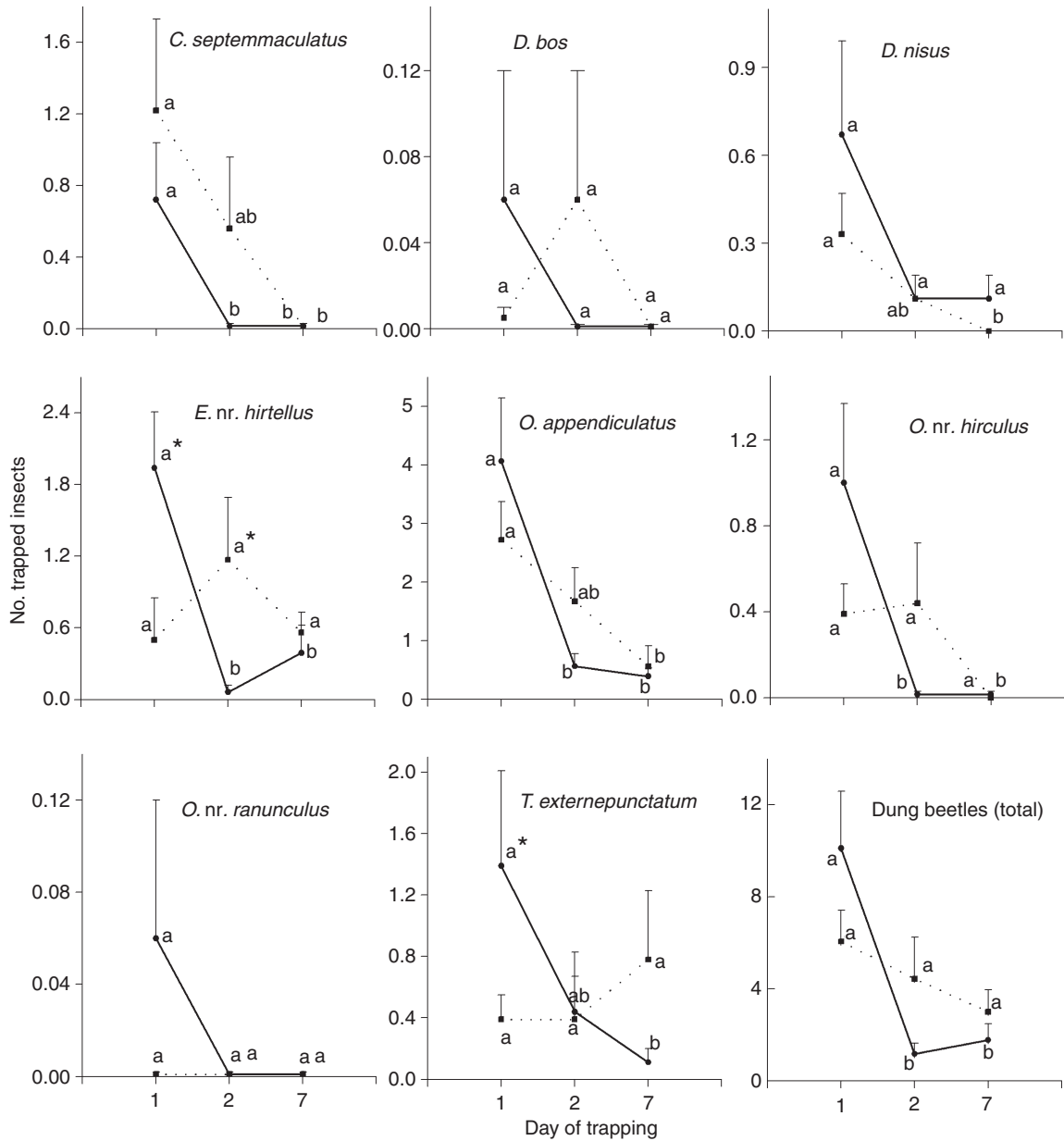


Figure 2 Mean (+ SE) weekly numbers of dung beetle species caught in pitfall traps baited with collared peccary (*Tayassu tajacu*) dung, with (solid line) or without (dotted line) beetle removal, in an Atlantic forest fragment in Selvíria, state of Mato Grosso do Sul, Brazil, March through May 2007. Means followed by the same letter within each treatment are not significantly different ($P > 0.05$); means followed by an * between treatments are significantly different (Tukey test: $P < 0.05$).

probably acted as a repellent to some of the species and to Scarabaeinae as a whole when the otherwise attractive pig dung was used. In pig dung-baited traps, the negative effect of not removing decaying insects was apparent already within 24 h (day 1), and persisted until day 7. Because peccary dung altogether lost its attractiveness quickly, the carrion smell could not make that much difference: on day 1, more dung beetles were found in the

traps without carrion smell, but not on day 2 and day 7 there were no significant differences between treatments.

It is widely accepted that dung beetles are attracted to food by the odor it releases (Ridsdill-Smith, 1991), and that they are able to discriminate among various attractive volatiles (Fincher et al., 1970; Davis, 1994; Dormont et al., 2004). In one of the few studies on the mechanism of discrimination, it was shown that the dung beetles *Copris*

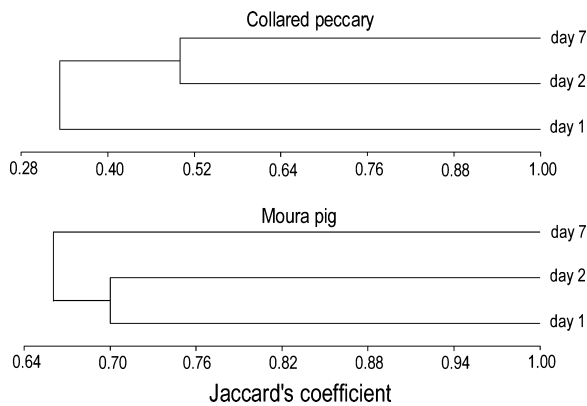


Figure 3 Jaccard's similarity coefficients among dung beetle communities collected in pitfall traps baited with collared peccary (*Tayassu tajacu*) and Moura pig (*Sus scrofa*) dung, with removal of trapped beetles, after 1 (day 1), 2 (day 2), and 7 (day 7) days, in an Atlantic forest fragment in Selvíria, state of Mato Grosso do Sul, Brazil, March through May 2007.

pecuarius Lewis and *Geotrupes auratus* Motschulsky carry olfactory cells of the basiconicum type in the lamellae of their antennae (Inouchi et al., 1987), and that in *G. auratus* these cells have different specificities and detection thresholds to attractive volatiles (Inouchi et al., 1988). The bouquets of volatiles released by carrion (Statheropoulos et al., 2005) and different dung sources, such as chicken (Kelling, 2001), cow (Kite, 1995), and pig (Schaefer, 1977; Yasuhara et al., 1984), differ in composition, even though some compounds overlap, such as skatole and indole. Apparently, dung beetles do not respond to single volatiles but to an assemblage, as shown in *G. auratus* (Inouchi et al., 1988). Hence, it is likely that dung beetles are able to discriminate between volatile blends released from pig or peccary dung and those produced by decomposing trapped insects in the cups, as shown in our experiment.

Saprophages are known to be attracted to traps with decaying insects (Lemieux & Lindgren, 1999; Porter, 2005; Schmidt et al., 2006). However, the influence of carrion smell as repellents on target insects is not widely studied. Kretschmer (1990) showed that *I. typographus* catches decreased in pheromone-baited traps when beetles were left in the traps and started to decompose and release a distinct putrid smell. Zhang et al. (2003) attempted to determine the volatiles involved and verified that verbenone and 1-hexanol were the only compounds that elicited antennal responses in this beetle, while typical carrion volatiles evoked no response. Apparently, in Kretschmer's (1990) experiment, beetles were responding either to an anti-aggregation pheromone, verbenone (Amman et al., 1989), to a non-host volatile, 1-hexanol (Visser, 1986), or to a combination of the two, and not to the putrid smell

from dead *I. typographus*. However, 1-hexanol is also known to be formed in the putrefaction process, as a carbohydrate break-down product (Statheropoulos et al., 2005). Thus, there is still a possibility that the putrefaction process is at least partially responsible for a repellent influence on bait attractiveness.

Acknowledgments

We thank Fernando Zagury Vaz-de-Mello for examination and identification of specimens of our "Museu de Entomologia da FEIS/UNESP" (MEFEIS), Rodrigo Ribeiro de Mendonça (Zoo of Ilha Solteira - Centro de Conservação de Fauna Silvestre) for providing the collared peccary dung, Gonzalo Halffter (Instituto de Ecología, A.C., Mexico), John T. Nowak (Forest Health Protection, USDA Forest Service, USA), Jorge M. Lobo (Museo Nacional de Ciencias Naturales, Spain), and Kenneth W. McCravy (Western Illinois University, USA) for comments and criticism.

References

- Amman GD, Their RW, McGregor MD & Schmitz RF (1989) Efficacy of verbenone in reducing lodgepole pine infestation by mountain pine beetles in Idaho. *Canadian Journal of Forest Research* 19: 60–64.
- Boonrotpong S, Sotthibandhu S & Pholpunthin C (2004) Species composition of dung beetles in the primary and secondary forest at Ton Nga Chang Wildlife Sanctuary. *ScienceAsia* 30: 59–65.
- Bornemissza GF (1976) The Australian dung beetle project 1965–1975. *Australian Meat Research Committee* 30: 1–30.
- Davis ALV (1994) Associations of Afrotropical Coleoptera (Scarabaeidae: Aphodiidae: Staphylinidae: Hydrophilidae: Histeridae) with dung and decaying matter: implications for selection of fly-control agents for Australia. *Journal of Natural History* 28: 383–399.
- Davis AJ, Holloway JD, Huijbregts H, Krikken J, Kirk-Springgs AH & Sutton SL (2001) Dung beetles as indicators of change in the forest of northern Borneo. *Journal of Applied Ecology* 38: 593–616.
- Dormont L, Epinat G & Lumaret JP (2004) Trophic preferences mediated by olfactory cues in dung beetles colonizing cattle and horse dung. *Environmental Entomology* 33: 370–377.
- Dormont L, Rapior S, McKey DB & Lumaret JP (2007) Influence of dung volatiles on the process of resource selection by coprophagous beetles. *Chemoecology* 17: 23–30.
- Errouissi F, Haloti S, Jay-Robert P, Janati-Idrissi A & Lumaret JP (2004) Effect of the attractiveness for dung beetles of dung pat origin and size along a climatic gradient. *Environmental Entomology* 33: 45–53.
- Fincher GT (1981) The potential value of dung beetles in pasture ecosystems. *Journal of Georgia Entomological Society* 16: 316–333.

- Fincher GT, Stewart TB & Davis R (1970) Attraction of coprophagous beetles to feces of various animals. *Journal of Parasitology* 56: 378–383.
- Gillard P (1967) Coprophagous beetles in pasture ecosystems. *Journal of the Australian Institute of Agricultural Science* 33: 30–34.
- Gittings T & Giller PS (1998) Resource quality and colonisation and succession of coprophagous dung beetles. *Ecography* 21: 581–592.
- Halfpiter G (1998) A strategy for measuring landscape biodiversity. *Biology International (Special Issue)* 36: 3–17.
- Halfpiter G & Favila ME (1993) The Scarabaeinae (Insecta: Coleoptera) an animal group for analyzing, inventorying and monitoring biodiversity and tropical rain forest and modified landscapes. *Biology International* 27: 15–21.
- Harvey CA, Medina A, Sánchez DM, Vélchez S, Hernández B et al. (2006) Patterns of animal diversity in different forms of tree cover in agricultural landscapes. *Ecological Applications* 16: 1986–1999.
- Howden HF & Nealis VG (1975) Effects of deforestation clearing in a tropical rain forest on the composition of the coprophagous scarab beetle fauna (Coleoptera). *Biotropica* 7: 77–83.
- Inouchi J, Shibuya T, Matsuzaki O & Hatanaka T (1987) Distribution and fine structure of antennal olfactory sensilla in Japanese dung beetles, *Geotrupes auratus* Mtos. (Coleoptera: Geotrupidae) and *Copris pecuarius* Lew. (Coleoptera: Scarabaeidae). *International Journal of Insect Morphology and Embryology* 16: 177–187.
- Inouchi J, Shibuya T & Hatanaka T (1988) Food odor responses of single antennal olfactory cells in the Japanese dung beetle, *Geotrupes auratus* (Coleoptera: Geotrupidae). *Applied Entomology and Zoology* 23: 167–174.
- Jaccard P (1901) Distribution de la flore alpine dans le Bassin des Dranses et dans quelques régions voisines. *Bulletin de la Société Vaudoise des Sciences Naturelles* 37: 239–272.
- Kelling FJ (2001) Olfaction in Houseflies – Morphology and Electrophysiology. PhD Dissertation, University of Groningen, Groningen, The Netherlands.
- Kite GC (1995) The floral odour of *Arum maculatum*. *Biochemical Systematics and Ecology* 23: 343–354.
- Kovach WL (1999) MVSP – A Multivariate Statistical Package for Windows, version 3.1. Kovach Computing Services, Pentraeth, Wales, UK.
- Kretschmer K (1990) Zur Wirkung von Aasgeruch auf die Fangleistung von Buchdruckerfallen. *Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz* 63: 46–48.
- Larsen TH & Forsyth A (2005) Trap spacing and transect design for dung beetle biodiversity studies. *Biotropica* 36: 322–325.
- Lemieux JP & Lindgren BS (1999) A pitfall trap for large-scale trapping of Carabidae: comparison against conventional design, using two different preservatives. *Pedobiologia* 43: 245–253.
- Lobo JM, Martín-Piera F & Veiga CM (1988) Las trampas pitfall con cebo, sus posibilidades en el estudio de las comunidades coprófagas de Scarabaeoidea (Col.). I. Características determinantes de su capacidad de captura. *Revue d'Ecologie et de Biologie du Sol* 25: 77–100.
- Lumaret JP & Kirk A (1987) Ecology of dung beetles in the French Mediterranean region. *Acta Zoológica Mexicana* 24: 1–55.
- McGeoch MA, van Rensburg BJ & Botes A (2002) The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. *Journal of Applied Ecology* 39: 661–672.
- Mittal I (1993) Natural manuring and soil conditioning by dung beetles. *Tropical Ecology* 34: 150–159.
- Phillips TW (1990) Responses of *Hylastes salebrosus* to turpentine, ethanol, and pheromones of *Dendroctonus* (Coleoptera: Scolytidae). *Florida Entomologist* 73: 286–292.
- Porter SD (2005) A simple design for a rain-resistant pitfall trap. *Insectes Sociaux* 52: 201–203.
- Rettger LF & Newell C (1912) Putrefaction with special reference to the proteus group. *Journal of Biological Chemistry* 13: 341–346.
- Ridsdill-Smith J (1991) Competition in dung-breeding insects. *Reproductive Behaviour of Insects: Individuals and Populations* (ed. by W Bailey & J Ridsdill-Smith), pp. 264–292. Chapman and Hall, London, UK.
- SAS Institute (1990) SAS/STAT User's Guide. SAS Institute, Cary, NC, USA.
- Schaefer J (1977) Sampling, characterisation and analysis of malodours. *Agriculture and Environment* 3: 121–127.
- Schmidt MH, Clough Y, Schulz W, Westphalen A & Tscharrntke T (2006) Capture efficiency and preservation attributes of different fluids in pitfall traps. *Journal of Arachnology* 34: 159–162.
- Scudder GGE (1996) Pitfall trapping: The SAGE Project; a Workshop Report on Terrestrial Arthropod Sampling Protocols for Graminoid Ecosystems. Prairie Ecozone, Terrestrial Arthropod Sampling Protocols (ed. by AT Finnamore) <http://www.eman-rese.ca/eman/reports/publications/sage/sage12.htm>, accessed 21 jun 2007.
- Spector S (2006) Scarabaeinae dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *The Coleopterists Society Monograph* 60 (Suppl. 5): 71–83.
- Statheropoulos M, Spiliopoulou C & Agapiou A (2005) A study of volatile organic compounds evolved from decaying human body. *Forensic Science International* 153: 47–155.
- Stebnicka T (1985) A new genus and species of Aulonocneminae from India with notes on comparative morphology (Coleoptera: Scarabaeidae). *Revue Suisse de Zoologie* 92: 649–658.
- Visser JH (1986) Host odor perception in phytophagous insects. *Annual Review of Entomology* 31: 121–144.
- Yasuhara A, Fuwa F & Jimbu M (1984) Identification of odorous compounds in fresh and rotten swine manure. *Agricultural and Biological Chemistry* 48: 3001–3010.
- Zhang QH, Jakuš R, Schlyter F & Birgesson G (2003) Can *Ips tyroglyphus* (L.) (Col., Scolytidae) smell the carrion odours of the dead beetles in pheromone traps? *Electrophysiological analysis. Journal of Applied Entomology* 127: 185–188.