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# Attractiveness of Different Bait to the Scarabaeinae (Coleoptera: Scarabaeidae) in Forest Fragments in Extreme Southern Brazil

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**Pedro Giovâni da Silva, Fernando Z. Vaz-de-Mello, and Rocco Alfredo Di Mare (2012)** Attractiveness of different bait to the Scarabaeinae (Coleoptera: Scarabaeidae) in forest fragments in extreme southern Brazil. *Zoological Studies* **51**(4): 429-441. The aim of this study was to investigate the attractiveness of different types of bait to the Scarabaeinae. Scarabaeinae fauna was sampled using pitfall traps in 3 forest fragments of Santa Maria, Rio Grande do Sul, Brazil, between May 2009 and Apr. 2010. Each habitat received 27 traps placed on 3 transects, each containing 3 sets of 3 traps, respectively baited with human excrement, rotten meat, and rotten banana. Of the total number of species and individuals collected, 33 species and 75.02% of individuals were attracted to human excrement, 29 species and 20.26% of individuals to meat, and only 25 species and 4.72% of individuals to the banana. Kruskal-Wallis tests showed significant statistical differences among the mean species richness (H = 20.65, *d.f.* = 2, $p < 0.01$) and abundance (H = 21.56, *d.f.* = 2, $p < 0.01$) of beetles attracted to each bait type. An ordination analysis showed the formation of different groups according to feeding habits and trophic niche overlap. According to Levins' index, 14 species were coprophagous, 13 were generalists, and 2 necrophagous. Differences found occurred due to the great change in dung beetle assemblages from each type of baited trap during the study period. In this study, human feces was the most attractive bait, differing significantly from carrion and rotten banana in both species richness and abundance of the Scarabaeinae. http://zoolstud.sinica.edu.tw/Journals/51.4/429.pdf

**Key words:** Dung beetles, Trophic guild, Coprophagy, Necrophagy, Saprophagy.

The subfamily Scarabaeinae (Coleoptera: Scarabaeidae) includes dung beetles, a globally distributed group of detritus-feeding insects, which contribute to important ecological functions, such as nutrient recycling, secondary seed dispersal, bioturbation, and natural control of cattle parasites (Nichols et al. 2008). These beetles mainly eat mammal feces (coprophagy), carrion (necrophagy), and rotting plant matter (saprophagy), and they may be specialists or generalists (Halffter and Matthews 1966, Halffter and Edmonds 1982, Hanski and Cambefort 1991, Halffter and Halffter 2009).

Apparently, the Scarabaeinae evolved from saprophagous ancestors, which lived in Afrotropical forests at the Mesozoic-Cenozoic boundary (~65 million years ago [Mya]) (Cambefort 1991, Gill 1991, Halffter 1991, Davis et al. 2002, Monaghan et al. 2007, Halffter and Halffter 2009). Their great global diversification seems to have followed the increase in mammal dung types during the Cenozoic, which would have influenced the high specialization of the group to coprophagy (Cambefort 1991, Davis et al. 2002, Monaghan et al. 2007, Arillo and Ortuño 2008, Davis 2009, Sole and Scholtz 2010, Philips 2011).

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Necrophagy in the Neotropical Scarabaeinae may be linked to reduced dung resources owing to mass extinctions of mammal megafauna between the Pliocene and Pleistocene (5-2 Mya) (Halffter and Matthews 1966, Halffter 1991). Although saprophagy is currently the preferred eating habit of some species (Halffter and Halffter 2009), it was hypothesized to have resurfaced as a new behavior, different from primitive saprophagy (Cambefort 1991, Halffter and Halffter 2009). The ingestion of decaying plant material is an alternative diet which may promote a decrease in competition among species, especially within forests. However, coprophagy is the predominant current feeding habit of dung beetles, followed by necrophagy (Halffter and Matthews 1966, Halffter and Edmonds 1982, Hanski and Cambefort 1991, Simmons and Ridsdill-Smith 2011).

The current range of trophic niches occupied by scarabaeine species would reflect the wide availability of different food resources available throughout their evolution, since there are species associated with other resources. These include fungi (Halffter and Matthews 1966, Navarrete-Heredia and Galindo-Miranda 1997, Falqueto et al. 2005), rotten eggs (Louzada and Vaz-de-Mello 1997, Pfrommer and Krell 2004), and even predation on other arthropods (Pereira and Martínez 1956, Hertel and Colli 1998, Larsen et al. 2006 2009, Silveira et al. 2006). Ecosystem complexity, a high diversity of mammals (and their feces), past inter- and intraspecific competition, and the availability of other food resources during the evolutionary history of the Scarabaeinae may have been some of the factors that led species to develop food alternatives which differ from the ancestral diet (Gill 1991, Halffter 1991, Hanski and Cambefort 1991, Monaghan et al. 2007).

The current worldwide distribution of dung beetles is strongly influenced by the diversity of mammal dung and climate (Davis and Scholtz 2001, Davis et al. 2002) with the tropical region having a high diversity of the Scarabaeinae (Halffter and Matthews 1966, Hanski and Cambefort 1991, Davis et al. 2002). In the Neotropical Region, scarabaeine species richness is primarily centered on forests and differs from the Afrotropical fauna which shows greater diversity in savannas, although species richness of each is related to the diversity of excrement provided by vertebrates present in the ecosystems in their respective regions (Gill 1991, Halffter 1991, Davis et al. 2002). Although subtropical forests possess a smaller number of scarabaeine species than tropical forests (Halffter and Matthews 1966), the relationship of dung beetles with the mammalian fauna (and its feces) is also expected in the subtropics.

With reference to the evolutionary ecological origins of the subfamily, the current paper examines trophic associations of the scarabaeine fauna of 3 subtropical forest fragments in southern Brazil using 3 principal food types: plant matter (represented by rotten bananas), dung (represented by human feces), and carrion (represented by rotten chicken offal).

## MATERIALS AND METHODS

### Study area

The municipality of Santa Maria is located in the central region of Rio Grande do Sul, Brazil (Fig. 1). It lies in the transition zone between the 'Depressão Central' and the 'Planalto Meridional Brasileiro' (Southern Brazilian Plateau) at the edge of the Atlantic Forest and Pampa biomes (IBGE 2010). The city is typified by grassland areas and deciduous seasonal forest vegetation belonging to the 'Fralda da Serra Geral' (Pereira et al. 1989), variously situated on floodplains, lowlands, and mountains, with elevations ranging 40-500 m. The climate is hot, wet, and subtropical of type Cfa according to the Köppen-Geiger classification (Pell et al. 2007). The annual precipitation averages around 1700 mm, with rainfall well distributed throughout the year (Pereira et al. 1989). The average annual temperature is approximately 19°C, with minima varying between 8 and 10°C, maxima between 32 and 40°C, and frequent frost in winter (Nimer 1990).

In order to conduct the present and other studies, species of the Scarabaeinae were sampled in 3 non-contiguous forest fragments of different sizes and levels of anthropic disturbance. They are identified as follows.

1) Morro do Elefante (29°40'33"S, 53°43' 14"W) is an around 730-ha, non-isolated area of deciduous seasonal forest of the scarp of 'Planalto Médio Riograndense' (Rio Grande do Sul Medium Plateau) or of 'Fralda da Serra Geral' (Machado and Longhi 1990). On its southern edge, there are some small plantations of *Pinus* spp., *Eucalyptus* spp., and *Citrus* spp., and a few trails and glades. Its surroundings are characterized by fields, agricultural plantations, and a sequence of other mountains with similar forest vegetation. Based on

the classification by Silva (2011b), it is regarded as a fragment with a high level of preservation.

2) Morro do Cerrito (29°42'07"S, 53°47'08"W) is a 140-ha isolated area of deciduous seasonal forest of 'Serra Geral' belonging to the 'Depressão Central' of Rio Grande do Sul (Pereira et al. 1989). It has areas of glades, exotic trees, and buildings and is largely surrounded by housing and a number of similar but smaller forest fragments. Based on the classification by Silva (2011b), it is considered a forest fragment with an intermediate level of preservation.

3) Campus of Univ. Federal de Santa Maria (29°43'27"S, 53°43'29"W) is a 53-ha forest fragment with secondary native vegetation in the understory encompassed by a mixed plantations of *Pinus* spp. and *Eucalyptus* spp., which replaced areas of grassland and riparian vegetation nearly 30 yr ago (Soares and Costa 2001, Dambros et al. 2004, Madruga et al. 2007). It is surrounded by grasslands, agricultural plantations, a few buildings, and some similar neighboring forest fragments. This habitat is considered to have a high level of disturbance due to the presence of exotic trees and the great transformation of the fragment and its surroundings (Silva 2011b).

Monthly temperature and precipitation data were obtained from the meteorological station of Univ. Federal de Santa Maria, Santa Maria, Brazil.

### Sampling method

Individuals of the Scarabaeinae were captured using baited pitfall traps. This is considered the most efficient sampling method for collecting the majority of this group (Lobo et al. 1988, Halffter and Favila 1993, Milhomem et al. 2003, Spector 2006).

A trap consisted of a 1000-ml plastic container, 13 cm in diameter and 10 cm deep, which was buried so that its rim was at ground level (Lobo et al. 1988, Ausden 1996). To accommodate the bait, a smaller plastic pot was placed into the larger container. A solution of water (350 ml), formalin (10%), and detergent was put inside the trap. The study was conducted between 1 May 2009 and 30 Apr. 2010, encompassing the 4 seasons of the year (winter, 21 June to 21 Sept.; spring, 22 Sept. to 20 Dec.; summer, 21 Dec. to 20 Mar.; and autumn, 21 Mar. to 20 June). Collections took place in 2-wk periods, in the middle and end of each month, totaling 24 samplings. Traps remained at the study sites during the entire period, and the bait was periodically renewed.

Traps were baited with human feces (20 g), chicken organs (40 g), or bananas (50 g). The 2 latter bait types were allowed to rot for 3 d at room temperature before use. Such bait represents the 3 major trophic guilds of these insects: coprophagy, necrophagy, and saprophagy (Halffter and Matthews 1966).

In total, 27 traps were installed in each fragment, arranged in 3 transects. Transects were separated from one another by 100 m and contained 3 sets of 3 traps, each set separated by 30 m. Each set of 3 traps was arranged in a triangular shape with each trap separated by 2 m and baited with one of the 3 kinds of bait in order to enable the selection of a resource by the beetles (Almeida and Louzada 2009).

Separate beetle samples are stored at the Laboratory of Evolutionary Biology at Univ. Federal de Santa Maria (UFSM). They were first identified to the generic and subgeneric levels

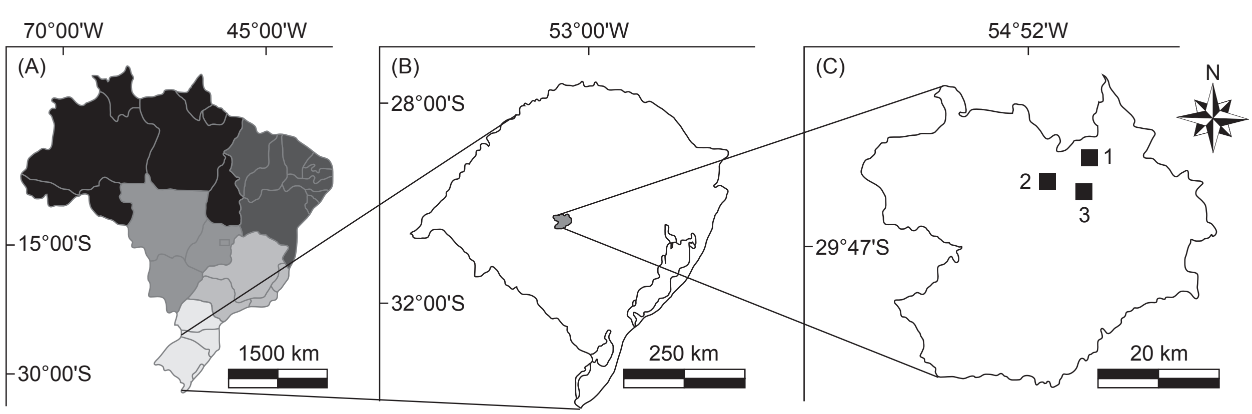


**Fig. 1.** Location of 3 habitats in Santa Maria (C), Rio Grande do Sul (B), Brazil (A), sampled for species of the Scarabaeinae between May 2009 and Apr. 2010, using pitfall traps baited with human excrement, rotten meat, and rotten banana. Forest fragments sampled: 'Morro do Elefante' (1), 'Morro do Cerrito' (2), and 'Campus of Univ. Federal de Santa Maria (3).

using a dichotomous key for the Scarabaeinae of the Americas (Vaz-de-Mello et al. 2011), and their identification was subsequently confirmed by the 2nd author. Voucher specimens are deposited in the collections of UFSM and at Univ. Federal de Mato Grosso (UFMT).

**Data analysis**

The proximity of the pitfall traps allowed dung beetles to choose between traps baited with different food types (i.e., a cafeteria experiment, see Almeida and Louzada 2009). The trophic guild of each species was inferred using Levins' standardized index of niche breadth ($B_A$) (Levins 1968, Krebs 1999) for species with an abundance of > 15 individuals. This index is scaled from 0 to 1, and the greater the value, the greater the degree of trophic generalization of the species. Species were classified into coprophagous, necrophagous, or saprophagous specialists when the Levins' index was ≤ 0.5, and as generalists when the value of the index was higher (Krebs 1999, Filgueiras et al. 2009). The simplified index of Morisita-Horn ($I_{MH}$) (Horn 1966) was used to determine the degree of niche overlap in food resource use by scarabaeine species. These indices were calculated using Ecological Methodology software (Kenney and Krebs 2000).

Ordination analyses were conducted to (1) determine temporal differences in the association of scarabaeine assemblages with different bait types, and (2) verify the degree of specialization by a species in relation to feeding habits. Bray Curtis similarity matrices were constructed from (1) seasonal data on species abundance for the 3 kinds of baits, excluding months with fewer than 10 individuals to minimize bias, and (2) from a Morisita-Horn data matrix on niche overlap between species' feeding habits. Due to the great heterogeneity in initial values, data for species abundance were square root-transformed to homogenize the variances (Filgueiras et al. 2009). Ordination analyses (nonmetric multidimensional scaling [NMDS]) were performed using the program Primer 6 (Clarke and Gorley 2005). The dimensional configuration of NMDS was evaluated by the level of stress, which ranged 0-1.

Kruskal-Wallis tests, conducted with the program PAST 2.02 (Hammer et al. 2001), were performed to determine possible differences in richness and abundance between the kinds of bait used. A two-way analysis of variance (ANOVA) test, conducted in BioEstat 5.0 (Ayres et al. 2007), was used to determine differences in abundance and richness of the Scarabaeinae throughout the seasons of the year on the different kinds of bait. Here, collections were arranged according to each seasonal period. In order to homogenize the variance, the data were square root-transformed. Normality was checked by Shapiro-Wilk tests in the program PAST 2.02.

## RESULTS

In total, 33 species were recorded with 25 species (75.75%) attracted to all 3 bait types. Of the total number of individuals collected (19,699), 75.02% were attracted to human feces, 20.26% to rotten meat, and 4.72% to fermented banana. All 33 of the species were attracted to human feces (Table 1), where *Canthidium* aff. *trinodosum* (Boheman, 1858) (27.49%), *Dichotomius assifer* (Eschscholtz, 1822) (19.07%), and *Canthon latipes* Blanchard, 1845 (17.44%) were the most abundant species. In traps baited with rotten meat, 29 species were captured, where *C.* aff. *trinodosum* (16.58%), *C. latipes* (13.88%), and *Canthon lividus* Blanchard, 1845 (10.57%) were the most abundant species. In traps baited with rotten banana, 25 species were collected, and *C.* aff. *trinodosum* (21.44%), *Canthidium* aff. *dispar* Harold, 1867 (14.26%), and *C. latipes* (10.72%) were the most abundant species. Kruskal-Wallis tests showed significant statistical differences in the average species richness (H = 20.65, *d.f.* = 2, $p < 0.01$) and abundance (H = 21.56, *d.f.* = 2, $p < 0.01$) among bait types.

Thirteen species (39.40%) were considered to have generalist habits according to Levins' standardized index of niche breadth, and they represented 15.48% of the total number of captured individuals (with an average number of individuals per species of 234.61 ± 246.50). Four species (12.12%) could not be classified into food categories because the number of individuals ($n < 15$) was insufficient. Other species ($n = 16$) were classified as having specialist food associations in this study. Of these, 14 species were coprophagous and represented 79.25% of the total number of captured individuals (with an average number of individuals per species of 1115.21 ± 1525.52); another 2 species were necrophagous and represented 15.48% of the total number of captured individuals (with an average number of individuals per species of 511.5 ± 64.34). No species showed saprophagy as the preferential feeding habit. Although classified as specialists, all of these species were attracted to more than 1 kind of bait. Trophic associations were consistent among seasons.

According to the ordination analysis conducted on food niche overlap (the simplified index of Morisita-Horn), scarabaeine species ($n > 15$) with coprophagous feeding habits formed 2 clear groups. Generalist species with high values of niche overlap (Fig. 2) formed no concise group, and neither did the 2 necrophagous species. Generalist and necrophagous species were widely scattered across the graph, and most were statistically distant from coprophagous species.

*Dichotomius* Hope, 1838, *Eurysternus* Dalman, 1824, *Onthophagus* Latreille, 1802, and *Ontherus* Erichson, 1847, included a large group of coprophagous species with low food niche overlap. The 2nd group of coprophagous species

**Table 1.** Numbers of individuals of species of the Scarabaeinae captured with pitfall traps baited with rotten banana (RB), rotten meat (RM), and human excrement (HE) in forest fragments in Santa Maria, Rio Grande do Sul, Brazil, between May 2009 and Apr. 2010. %, Percentage of the total captured; $B_A$, standardized index of Levins niche breadth for species with > 15 individuals. TH, trophic habit of the species (C, coprophagous; N, necrophagous; G, generalist; IN, insufficient number of individuals)

| Species | Bait | | | Total | % | $B_A$ | TH |
|---|---|---|---|---|---|---|---|
| | RB | RM | HE | | | | |
| *Ateuchus* aff. *carbonarius* (Harold, 1868) | 0 | 0 | 1 | 1 | 0.01 | - | IN |
| *Ateuchus* aff. *robustus* (Harold, 1868) | 0 | 7 | 61 | 68 | 0.35 | 0.227 | C |
| *Canthidium* aff. *dispar* Harold, 1867 | 133 | 183 | 152 | 468 | 2.38 | 0.974 | G |
| *Canthidium moestum* Harold, 1867 | 10 | 30 | 12 | 52 | 0.26 | 0.682 | G |
| *Canthidium* aff. *trinodosum* (Boheman, 1858) | 200 | 662 | 4061 | 4923 | 24.99 | 0.214 | C |
| *Canthidium* sp. | 62 | 121 | 863 | 1046 | 5.31 | 0.217 | C |
| *Canthon amabilis* Balthasar, 1939 | 53 | 125 | 71 | 249 | 1.26 | 0.821 | G |
| *Canthon chalybaeus* Blanchard, 1845 | 46 | 270 | 117 | 433 | 2.20 | 0.557 | G |
| *Canthon latipes* Blanchard, 1845 | 100 | 554 | 2577 | 3231 | 16.40 | 0.250 | C |
| *Canthon lividus* Blanchard, 1845 | 97 | 422 | 167 | 686 | 3.48 | 0.592 | G |
| *Canthon* aff. *luctuosus* Harold, 1868 | 60 | 232 | 210 | 502 | 2.55 | 0.741 | G |
| *Canthon oliverioi* Pereira and Martínez, 1956 | 0 | 5 | 75 | 80 | 0.41 | 0.133 | C |
| *Canthon quinquemaculatus* Castelnau, 1840 | 16 | 366 | 84 | 466 | 2.37 | 0.269 | N |
| *Coprophanaeus milon* (Blanchard, 1845) | 4 | 24 | 13 | 41 | 0.21 | 0.604 | G |
| *Coprophanaeus saphirinus* (Sturm, 1826) | 27 | 366 | 164 | 557 | 2.83 | 0.460 | N |
| *Deltochilum brasiliense* (Castelnau, 1840) | 5 | 9 | 10 | 24 | 0.12 | 0.898 | G |
| *Deltochilum morbillosum* Burmeister, 1848 | 0 | 17 | 14 | 31 | 0.16 | 0.981 | G |
| *Deltochilum rubripenne* (Gory, 1831) | 40 | 224 | 233 | 497 | 2.52 | 0.664 | G |
| *Deltochilum sculpturatum* Felsche, 1907 | 2 | 10 | 5 | 17 | 0.09 | 0.620 | G |
| *Dichotomius* aff. *acuticornis* (Luederwaldt, 1930) | 5 | 7 | 14 | 26 | 0.13 | 0.752 | G |
| *Dichotomius assifer* (Eschscholtz, 1822) | 36 | 152 | 2817 | 3005 | 15.25 | 0.067 | C |
| *Dichotomius nisus* (Olivier, 1789) | 2 | 4 | 22 | 28 | 0.14 | 0.278 | C |
| *Eurysternus aeneus* Génier, 2009 | 0 | 0 | 1 | 1 | 0.01 | - | IN |
| *Eurysternus caribaeus* (Herbst, 1789) | 11 | 70 | 1361 | 1442 | 7.32 | 0.060 | C |
| *Eurysternus parallelus* Castelnau, 1840 | 2 | 9 | 122 | 133 | 0.68 | 0.091 | C |
| *Homocopris* sp. | 0 | 0 | 2 | 2 | 0.01 | - | IN |
| *Ontherus azteca* Harold, 1869 | 1 | 10 | 32 | 43 | 0.22 | 0.322 | C |
| *Ontherus sulcator* (Fabricius, 1775) | 6 | 69 | 553 | 628 | 3.19 | 0.135 | C |
| *Onthophagus catharinensis* Paulian, 1936 | 4 | 5 | 499 | 508 | 2.58 | 0.018 | C |
| *Onthophagus* aff. *tristis* Harold, 1873 | 4 | 17 | 335 | 356 | 1.81 | 0.063 | C |
| *Phanaeus splendidulus* (Fabricius, 1781) | 0 | 7 | 18 | 25 | 0.13 | 0.676 | G |
| *Sulcophanaeus rhadamanthus* (Harold, 1875) | 0 | 0 | 4 | 4 | 0.02 | - | IN |
| *Uroxys* aff. *terminalis* Waterhouse, 1891 | 7 | 15 | 104 | 126 | 0.64 | 0.216 | C |
| Number of individuals | 933 | 3,992 | 14,774 | 19,699 | | | |
| Number of species | 25 | 29 | 33 | 33 | | | |

comprised 2 species of *Canthidium* Erichson, 1847, 1 *Ateuchus* Weber, 1801, and 1 *Canthon* Hoffmannsegg, 1817. Although classified as coprophagous, high proportions of individuals of these species were also captured in traps baited with rotten meat and rotten fruit.

The 3-dimensional NMDS ordination plot (Fig. 3) shows clear clustering of species assemblages attracted to each bait type. Thus, the pattern of species attracted to particular bait types remained consistent throughout each month of the year considered in the analysis.

Essentially, peaks in species richness and abundance coincided with the seasonal peak in rainfall (Sept. to Jan., but especially Oct. to Dec.) (Fig. 4), then declined with a reduction in rainfall under high temperatures (Feb. to May) becoming low from June to Aug. under the low rainfall and temperatures of the cool dry season.

Throughout the period, a majority of the Scarabaeinae were attracted to human excrement (Fig. 4). Species captured in rotten meat more frequently occurred in Nov. (43.14%) and Dec. (21.84%), while those captured in the fermented banana more frequently occurred in Dec. (23.79%) and Oct. (22.07%) (Fig. 4). These results are related to the greater richness and abundance of dominant and generalist species in this period. The lowest percentages of captures for meat and fruit bait in terms of individuals and species occurred between June and Aug., and in July, no individuals occurred in these traps. These results were apparently related to seasonal distributions of temperature and precipitation in this region.

In total, 63.64% of species occurred in all seasons of the year, 15.15% in 3 seasons, and 12.12% in 2 seasons. The 2 latter groups, although present in more than 1 season, were more frequent in spring. Three species occurred in specific seasons: *Ateuchus* aff. *carbonarius*

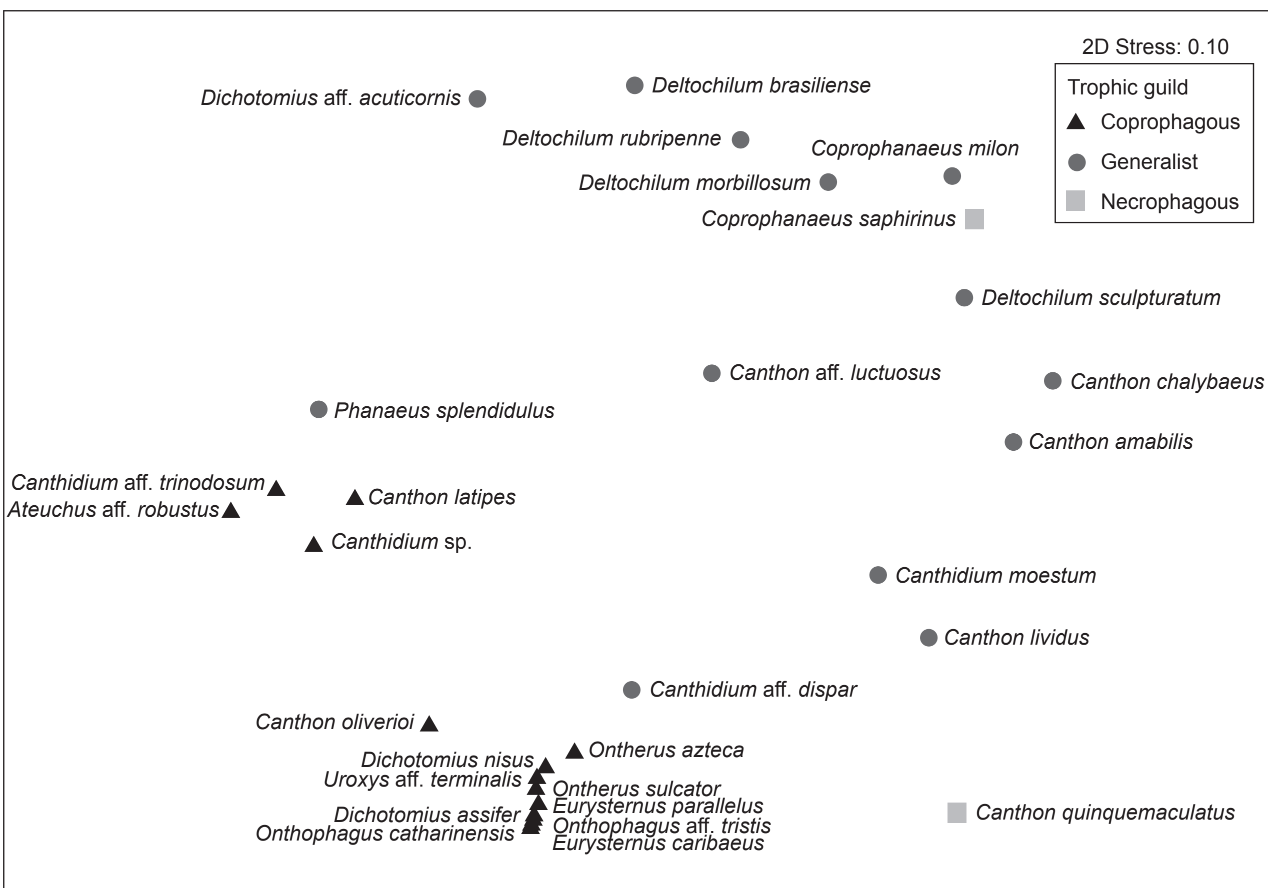


**Fig. 2.** Non-metric multidimensional scaling (NMDS) with Bray-Curtis similarity based on the Morisita-Horn index of food niche overlap showing the distribution of scarabaeine species according to each trophic guild (coprophagous, necrophagous, or generalist), captured by pitfall traps in forest fragments in Santa Maria, Rio Grande do Sul, Brazil, between May 2009 and Apr. 2010. Species with fewer than 15 individuals were excluded.

(Harold, 1868) occurred only in spring (Oct.) and *Eurysternus aeneus* Génier, 2009 only in summer (Dec.), while *Sulcophanaeus rhadamanthus* (Harold, 1875) was only collected in autumn (May).

When the richness of the Scarabaeinae was tested for the different kinds of bait among seasons, significant differences among bait types ($F$ = 16.175, *d.f.* = 2, $p$ = 0.004) and seasons ($F$ = 17.581, *d.f.* = 3, $p$ = 0.003) were found (Fig. 5A). Significant differences in bait types, according to an a posteriori Tukey's test, was found between averages of human excrement and fermented fruit (Q = 8.021, $p < 0.01$) and between human excrement and rotten meat (Q = 4.533, $p < 0.05$). Significant differences among seasons occurred between averages of spring and winter (Q = 6.644, $p < 0.05$) and between spring and autumn (Q = 7.047, $p < 0.01$).

When abundances of the Scarabaeinae within different kinds of bait were compared among the seasons, significant differences among the bait used ($F$ = 22.446, *d.f.* = 2, $p$ = 0.002) and seasons ($F$ = 10.100, *d.f.* = 3, $p$ = 0.01) were found (Fig. 5B). According to the a posteriori Tukey's test, only human excrement, the average of which was the highest, significantly differed from the bait of fruit (Q = 9.187, $p < 0.01$) and meat (Q = 6.600, $p < 0.01$), while spring (highest average) significantly differed from autumn (Q = 6.580, $p < 0.05$) and winter (Q = 6.883, $p < 0.05$).

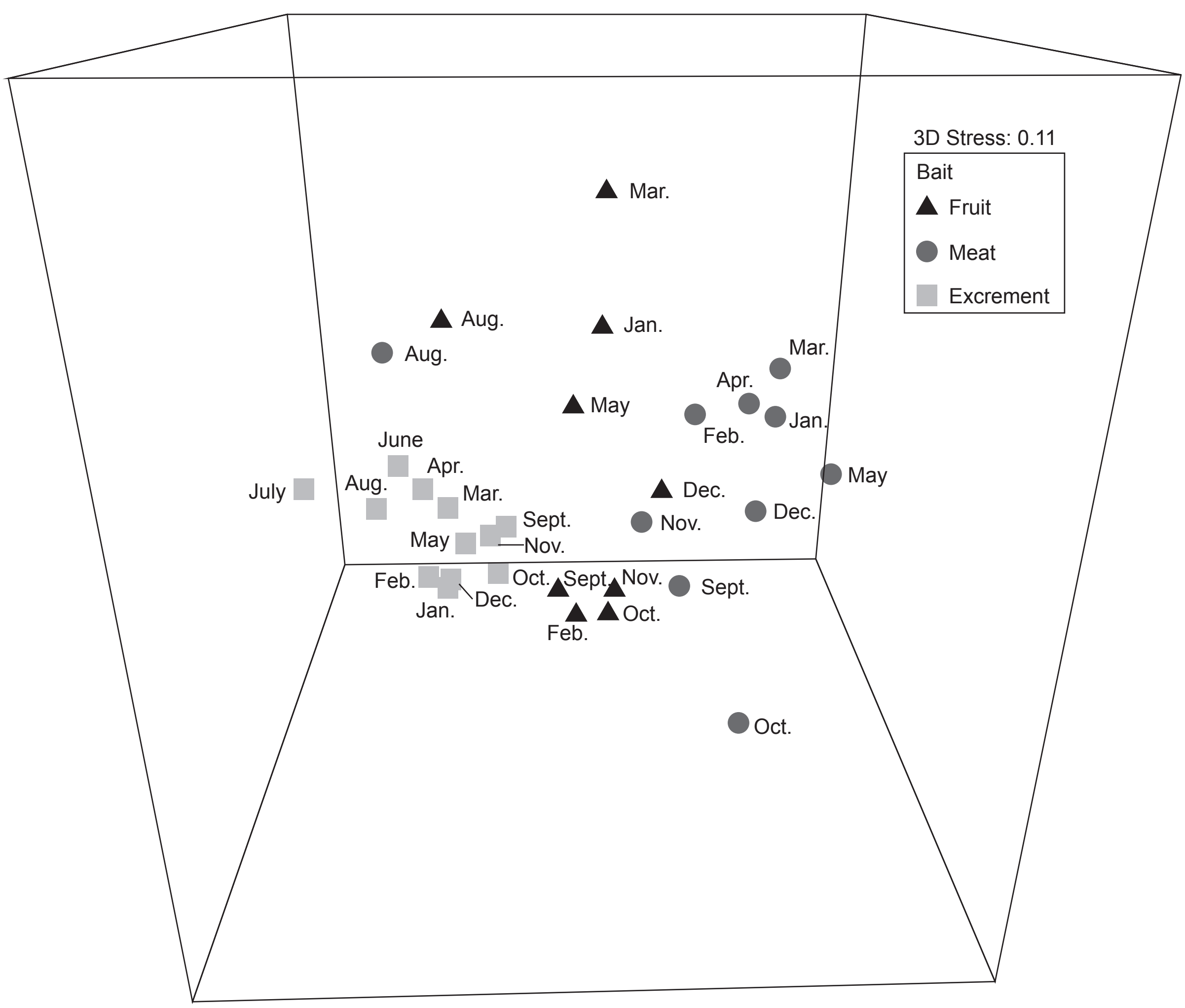


**Fig. 3.** Non-metric multidimensional scaling (NMDS 3D plot) with Bray-Curtis similarity showing the distribution of the Scarabaeinae according to each kind of bait, captured by pitfall traps in forest fragments in Santa Maria, Rio Grande do Sul, Brazil, between May 2009 and Apr. 2010. The symbols are the initials of the months. Months with fewer than 10 individuals were excluded from this analysis.

## DISCUSSION

There was a clear distinction between the levels of attraction of scarabaeine species to human excrement, rotten meat, and rotten fruit during the study period. Human feces was the most attractive bait in terms of both the number of individuals and species. Numbers consistently showed significant differences from the other bait types across months and seasons. These differences occurred due to great changes in the composition, richness, and abundance of scarabaeine assemblages in each type of baited trap throughout the study period. All species were classified into trophic groups with feeding preferences that remained the same among the months and seasons.

The results of this study on the relative attractiveness were as we expected, because the dung of omnivorous and herbivorous mammals is the main food source used by most species of the Scarabaeinae for nesting and feeding by adults and larvae (Halffter and Matthews 1966, Halffter and Edmonds 1982, Hanski and Cambefort 1991,

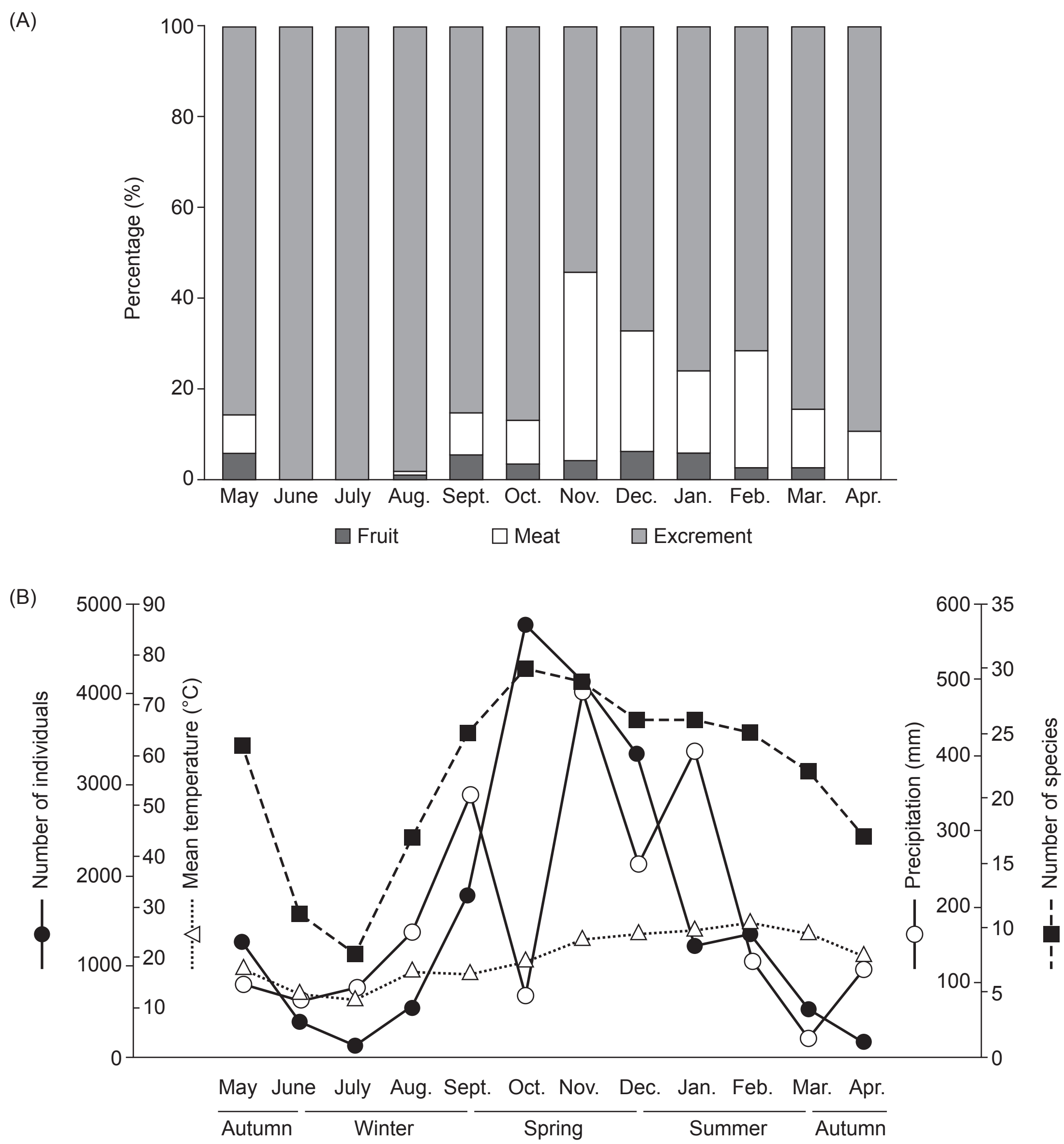


**Fig. 4.** Monthly number of individuals and species of the Scarabaeinae, and proportion of individuals for each type of bait used in forest fragments of Santa Maria, Rio Grande do Sul, Brazil, between May 2009 and Apr. 2010, and distribution of environmental variables of mean temperature and precipitation during the study period.

Simmons and Ridsdill-Smith 2011). In this study, all species and 75% of individuals were attracted to human feces, confirming it to be one of the most important bait for the effective capture of Neotropical Scarabaeinae, both in forests and pastures (Halffter and Matthews 1966, Falqueto et al. 2005, Larsen et al. 2006, Filgueiras et al. 2009, Audino et al. 2011).

Other researchers obtained similar results. Fincher et al. (1970), Estrada et al. (1993), and Filgueiras et al. (2009) found higher proportions of individuals in traps baited with excrement of omnivorous mammals (such as humans) in relation to other kinds of dung (carnivorous or herbivorous mammals). Silva et al. (2009) found higher proportions of species and individuals in traps baited with human excrement than in traps baited with rotten chicken meat. Audino et al. (2011) sampled dung beetles using the same bait types used in this study, and they collected 84.68% of the total number of individuals and 89.28% of all species in traps baited with human feces. Those results suggest that the excrement of omnivorous mammals potentially is of better quality or is more attractive than other kinds of dung (Cambefort and Hanski 1991, Hanski and Cambefort 1991). When different types of bait were used (excrement vs. carrion vs. rotten fruit), it is probable that the coprophagous eating habit of most collected species contributed to the high abundance in traps baited with human feces.

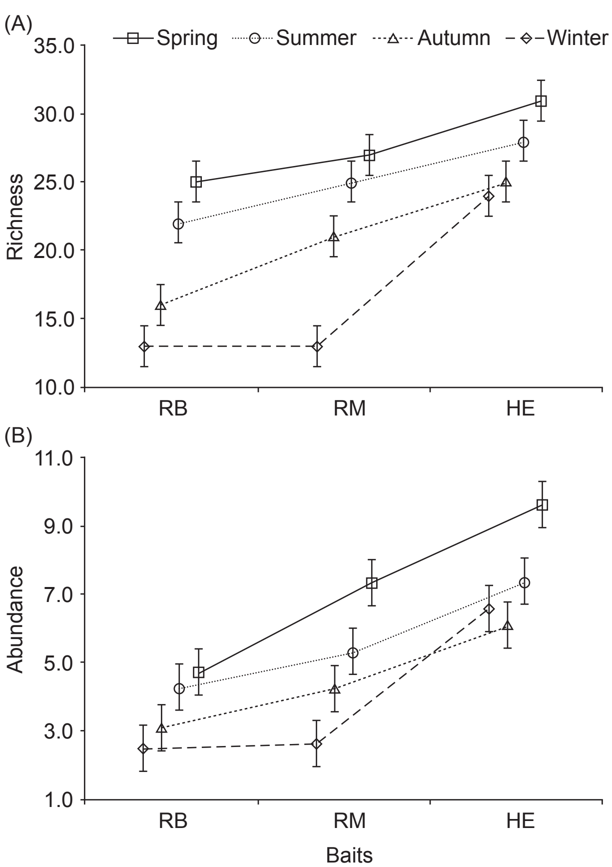


**Fig. 5.** Two-way ANOVA analysis characterizing differences between species richness (A) and abundance (B) of the Scarabaeinae by season for each bait type (RB, rotten banana; RM, rotten meat; HE, human excrement) in forest fragments of Santa Maria, Rio Grande do Sul, Brazil, between May 2009 and Apr. 2010. Values are presented as the mean ± standard deviation.

In relation to eating habits, the high number of species considered coprophagous (14) demonstrated greatest attraction to bait with human excrement compared to other kinds of bait (Larsen et al. 2006) and even to non-baited traps (Filgueiras et al. 2009, Silva 2011a). However, 13 species showed generalist eating habits, and 2 others were specialist necrophages. The results were similar to those of Almeida and Louzada (2009) for the scarabaeine fauna of different vegetation types captured with pitfall traps baited with human excrement and carrion in the Cerrado in Carrancas, Minas Gerais, Brazil. Those authors also collected a large number of coprophagous species, some generalists, and a smaller number of necrophagous species. Neither published results nor the present findings support the hypothesis that assemblages of Neotropical Scarabaeinae include a higher proportion of generalist species in relation to specialists (Halffter and Matthews 1966, Halffter 1991).

Besides historical and evolutionary processes (Halffter and Matthews 1966, Halffter and Edmonds 1982, Halffter 1991, Hanski and Cambefort 1991, Davis et al. 2002, Davis 2009), the high specialization to coprophagy in the Scarabaeinae seems to be related to the greater availability of mammal dung in the ecosystem (Halffter and Matthews 1966), since there appear to be fewer rotting fruits and carcasses of dead animals, and they may be seasonally and spatially limited (Howden and Young 1981, Louzada and Lopes 1997).

However, necrophagy in the Scarabaeinae is considered particularly important in Neotropical forests where the occurrence of large mammals is low (Halffter and Matthews 1966). For example, Silva et al. (2008) sampled dung beetles using pitfall traps baited with rotten meat and excrement of bovines across a field-forest ecotone and found a greater number of individuals in the 1st bait type. Furthermore, Silva (2011a) sampled dung beetles in 2 non-native habitats and found greater species richness in traps baited with human dung but greater abundance in traps baited with carrion. In this study, only 2 necrophagous species were found, *Canthon quinquemaculatus* Castelnau, 1840, and *Coprophanaeus saphirinus* (Sturm, 1826), but 87.87% of the captured species were found in traps baited with rotten meat.

*Canthon quinquemaculatus* has a wide Neotropical distribution and is common in animal carcasses in the early stages of decomposition (Martínez 1959, Halffter and Matthews 1966). Although Martínez (1987) cited it as being exclusively necrophagous, there are also records of its capture after attraction to the fetid smell liberated by recent cuttings of liana (Pereira and Martínez 1956). In contrast to this study, Martínez (1959) considered *C. saphirinus* a coprophagous species mainly found in the dung of herbivorous mammals from southern Brazil to Bahia and also in Argentina and Paraguay (Martínez 1959, Arnaud 2002, Edmonds and Zídek 2010), where there were color variations among populations from different localities (Edmonds and Zídek 2010). Although classified as necrophagous, these 2 species also occurred in human excrement and rotten banana. Due to the less-frequent occurrence of carcasses compared to excrement, the use of other food resources (feces or fruit) by specialist necrophagous species appears to be a process of maintaining themselves in periods when their preferred food is unavailable. These results are in line with the findings of Halffter and Matthews (1966) who asserted that necrophages are not exclusively necrophagous, since the species may use more than 1 kind of dietary resource according to its availability in the ecosystem. Coprophagous species that preferentially use human excrement also show a greater tendency to occasional necrophagy (Halffter and Mathews 1966). As assumed by Falqueto et al. (2005), species that use rarer resources than excrement (such as carrion and rotten fruit) seem to have a higher trophic generality.

Mature and decaying fruit is particularly attractive to a variety of species of the Scarabaeinae (Gill 1991). In this study, 75.75% of species represented by only 4.74% of individuals occurred in traps baited with rotten banana, although always in lower abundances than those found in human excrement and rotten meat. As bananas are not native to subtropical forests of southern Brazil, this bait type might not have been sufficiently attractive to species of the Scarabaeinae in this region. Future studies will compare the attractiveness banana to fruits of jelly palm trees (*butiá*), since a significant number of sarabaeine species are attracted to the fruits of these native palms (Pereira and Martínez 1956, Gill 1991, Halffter and Halffter 2009), which occur in forests of southern Brazil (Nunes et al. 2010).

A high number of species (13) were found to have generalist eating habits. According to Halffter and Matthews (1966), some species may vary their preference for different kinds of food resources according to its local availability. Many typically coprophagous or copro-necrophagous species may use fruit as a food resource. In other cases, specialist saprophagous species are occasionally collected in traps baited with feces or carrion. In Neotropical forests, species being attracted to decaying fruit or plant material may be the result of an evolutionary process in recent geological times that is related to the great availability of this resource compared to the low diversity of mammals and, consequently, the lower diversity of dung and carcasses (Halffter and Halffter 2009).

Although most species of the Scarabaeinae which are attracted to rotten fruit are also captured in feces and carrion, some species of *Onthophagus* and *Canthidium* may feed predominantly or exclusively on this resource (Gill 1991, Halffter and Halffter 2009), while species of other typically copro-necrophagous groups (such as *Canthon*, *Deltochilum* Eschscholtz, 1822, and *Dichotomius*) are often captured or attracted by rotten or fermented fruit (Pereira and Halffter 1961, Halffter and Halffter 2009).

Thus, trophic generalization or the use of more than 1 type of food resource decreases competition for scarce and ephemeral food such as excrement, animal carcasses, and rotten plant matter (Halffter and Halffter 2009). Apparently, trophic generalization can also give a species a wider use of the environment, while specialization tends to limit the occupation of new ecosystems where the preferred food is not available. The ability to utilize alternative foods would have contributed to the high diversity of the Neotropical Scarabaeinae (Halffter and Halffter 2009).

In this study, human feces was the most attractive bait, differing significantly from carrion and rotten banana in both species richness and abundance of the Scarabaeinae. Coprophagous species showed the greatest abundance and distinctly differed in patterns of attraction to bait compared to generalist and necrophagous species. Differences between patterns of attraction to the bait persisted throughout the entire study period. Species captured during periods of low temperatures were frequently coprophagous taxa that showed the highest abundances in this study. Generalist species always occurred at lower abundances, and most of them were found in greater numbers in traps baited with rotten meat and at greater frequencies during the spring.

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