

ORIGINAL ARTICLE

Abundance and diversity of coprophagous beetles (Coleoptera: Scarabaeidae) caught with a light trap in a pasture area of the Brazilian Cerrado

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(Received 15 July 2010; accepted 30 January 2012)

Coprophagous beetles (Coleoptera: Scarabaeidae) play an important ecological role in grazing agroecosystems, especially for the removal and bury of herbivore feces. In this study we identified coprophagous Scarabaeidae species found in an area of *Brachiaria brizantha* (Poaceae) pasture in the Brazilian Cerrado, analyzing community structure with environmental variables in the area. The insects were captured with a light trap from November 2007 to October 2008 every 15 days, totaling 24 hours of sampling/month. A total of 2541 individuals were collected and from two subfamilies (Aphodiinae and Scarabaeinae), 17 genera and 33 species. The numbers of individuals and species captured were positively correlated with monthly precipitation.

Os besouros coprófagos (Coleoptera: Scarabaeidae) desempenham importante papel ecológico em agroecossistemas de pastagens, com ênfase na remoção e enterrio das fezes de herbívoros. Nesse estudo nós identificamos as espécies de Scarabaeidae coprófagos que ocorrem em área de pastagem de *Brachiaria brizantha* (Poaceae) no Cerrado brasileiro, analisando a estrutura da comunidade com as variáveis ambientais da área. Os insetos foram capturados com uma armadilha luminosa a cada quinze dias de novembro de 2007 a outubro de 2008, totalizando 24 horas de amostragem/mês. Um total de 2.541 indivíduos foram capturados e estão distribuídos em duas subfamílias (Aphodiinae e Scarabaeinae), 17 gêneros e 33 espécies. O número de indivíduos e de espécies capturadas foram positivamente correlacionados com a precipitação mensal.

Keywords: agro-pastoral landscape; Brazil; dung beetle; ecology; insect community; Scarabaeoidea

Introduction

Tropical pastures have conditions extremely different from native forests, including higher temperatures, less shade, and an absence of predators and refuge locations (Martínez-Garza & González-Montagut 1999). The destruction of natural environments for the creation of pastures causes alterations in the structure and composition of communities, which may suffer the loss of species not adapted to the new environmental conditions (Medri & Lopes 2001).

Pasture areas commonly present a large quantity of cattle feces which contains abundant organic nutrients that are used by foragers (Anduaga 2004). Despite the benefits, bovine manure can be considered a problem. Various arthropod species develop in fecal mass and some are considered pests, such as the horn fly *Haematobia irritans* (Linnaeus, 1758) (Diptera: Muscidae). Selection of populations resistant to insecticides justifies the growing need for implementation of alternative programs for fly control of bovine feces from pastures and its incorporation into the soil is the use of coprophagous beetles (Scarabaeidae, principally Scarabaeinae). The feeding and reproduction of most of these species involves the allocation of food sources in tunnels dug into the soil, which removes the reproductive medium of the flies (Bornemissza 1970; Ridsdill-Smith & Matthiessen 1981; Flechtmann, Rodrigues, Araújo, et al. 1995). The activity of these beetles also promotes the degradation of organic materials and cycling of nutrients in the soil (Halffter & Matthews 1966; Halffter & Edmonds 1982; Yokoyama et al. 1991; Yamada et al. 2007).

(Marchiori et al. 2001). One alternative for the removal

Scarabaeinae includes about 5000 species and Aphodiinae has about 1850 species (Hanski & Cambefort 1991). Aphodiinae forms an important part of the guild of coprophagous beetles (Arellano & Halffter 2003). In southern South America 27 Aphodiinae species occur (Smith & Skelley 2007).

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In Brazil, 618 species in 59 genera of Scarabaeinae have been registered, of which 75 were recorded in the state of Mato Grosso do Sul (MS) (Vaz-de-Mello 2000).

Scarabaeid beetles can be captured with several trap types including baited and unbaited pitfall traps (e.g., Halffter & Favila 1993; Milhomem et al. 2003; Gardner et al. 2008; Silva, Diniz, et al. 2010), flight intercept traps (e.g., Chung 2004; Larsen et al. 2006; Costa et al. 2009), and light traps (e.g., Flechtmann, Rodrigues, & Couto 1995; Kato et al. 1995; Ronqui & Lopes 2006). Light traps are useful to monitor trends of insect abundance (Kato et al. 2000) and are capable of catching species that are not captured in pitfall or flight intercept traps (Hill 1996).

Livestock production is one of the most important economic activities in MS, occupying areas of native and exotic pastures. In exotic pastures, native vegetation of the Cerrado gives way to the exploration of livestock production. Pasture agroecosystems normally occupy areas that were once native forests and coprophagous beetle species encountered in these locations are likely adapting to the newly created environment or moving to other habitats, thereby changing the number of species in the area (Rodrigues & Marchini 2000). Due to the great importance of these beetles in agro-pastoral systems, the aim of this work was to identify the Scarabaeidae coprophagous beetle fauna that are attracted to light traps in a pasture area of Brachiaria brizantha (Hochst. ex A. Rich) Stapf (Poaceae) in the Brazilian Cerrado, analyzing community structure (abundance and richness) with environmental variables in the area (precipitation and temperature).

Materials and methods

The study was performed at the Manga Rosa farm (212 ha) located in the Brazilian Cerrado, 7 km from the municipality of Guia Lopes da Laguna, MS, Brazil (21° 24' 56.6" S; 56° 09' 41.5" W). Nelore cattle occupy *B. brizantha* pastures in a rotational grazing system.

Capture of coprophagous beetles was carried out by installing a light trap (Luiz de Queiroz model) in the pasture area every two weeks, from November 2007 to October 2008. The trap, which utilized a 20 W fluorescent lamp, was installed 1 m above the soil and remained in the field from 18:00 h until 6:00 h the next day, when the captured insects were placed in 70% ethanol. The insects were sorted under a stereomicroscope and one sample (1 to 20 specimens) was mounted on entomological pins. Beetles were compared with a reference collection of coprophagous Scarabaeidae at the Entomology Laboratory of the "Universidade Estadual de Mato Grosso do Sul" (UEMS; Aquidauana, MS, Brazil), and posteriorly identified by Prof. Dr. Fernando Zagury Vaz-de-Mello (Universidade Federal de Mato Grosso, UFMT, Instituto de Biociências, Cuiabá, Mato Grosso, Brazil). Voucher specimens were stored in the Entomology Laboratory at the UEMS, and in the "Seção de Entomologia da Coleção Zoológica" of the UFMT.

To assess capture efficiency, a species accumulation curve and its confidence interval (95%) was constructed. The four non parametric estimators (Chao 1, 2, Jackknife 1, 2) were used to calculate richness estimates. A ranking of abundance was constructed to observe the aspects of the community. All richness estimates were performed with the statistical program Estimates 7.5, utilizing 500 randomizations (Colwell 2005). The correlation of monthly precipitation and average monthly temperature with the abundance and richness was done using a non parametric test (Spearman test). Meteorological data were obtained from the weather station located in the municipality of Porto Murtinho, MS, roughly 170 km from the site at which this study was conducted.

Results

Richness and abundance

During the study period the trap was set 24 times, capturing 2541 individuals belonging to the subfamilies Aphodiinae and Scarabaeinae, distributed among 17 genera and 33 species. Aphodiinae was represented by 16 species in eight genera with *Ataenius* Harold, 1867 being most species rich. Beetles of the subfamily Scarabaeinae belonged to 17 species in nine genera (Table 1).

The richness estimate (Chao 1, 2, Jackknife 1, 2) indicated a maximum of 36 species (Table 2). The average of these estimates and observed richness indicates that sampling efficiency was roughly 98.5%. When we analyzed the curve produced using the number of species (Sobs) we observed that the species accumulation curves tended towards an asymptote (Figure 1).

The majority of species were represented by few individuals, with large numbers of singleton and doubleton species. Of 2541 individuals captured, *Labarrus pseudolividus* (Olivier, 1789) and *Dichotomius bos* (Blanchard, 1843) were most abundant, representing respectively 36.40 and 14.68% of the individuals captured (Table 1).

Effect of abiotic factors on seasonality

The number of individuals (R = 0.73; p < 0.05) and species (R = 0.78; p < 0.05) captured were positively

| Taxon | Abundance | |
|---|-----------|--------|
| | п | (%) |
| Aphodiinae | | |
| Aidophus flechtmanni Stebnicka & Dellacasa, 2001 | 10 | 0.39 |
| Ataenius aff. complicatus | 2 | 0.08 |
| Ataenius aff. platensis | 10 | 0.39 |
| Ataenius aff. scutellaris | 35 | 1.38 |
| Ataenius crenulatus Schmidt, 1910 | 179 | 7.04 |
| Ataenius forsteri Balthasar, 1960 | 113 | 4.45 |
| Ataenius gracilis Melsheimer, 1845 | 17 | 0.67 |
| Ataenius imbricatus Melsheimer, 1845 | 8 | 0.31 |
| Ataenius sp. | 184 | 7.24 |
| Flechtmanniella laticollis (Petrovitz, 1973) | 39 | 1.53 |
| Labarrus pseudolividus (Olivier, 1789) | 925 | 36.40 |
| Lomanoxoides sp. 1 | 30 | 1.18 |
| Lomanoxoides sp. 2 | 4 | 0.16 |
| Nialaphodius nigrita (Fabricius, 1801) | 240 | 9.45 |
| Pleuraphodius sp. | 120 | 4.72 |
| Trichiopsammobius brasiliensis Petrovitz, 1963 | 21 | 0.83 |
| Scarabaeinae | | |
| Ateuchus latus Boucomont, 1928 | 8 | 0.31 |
| Ateuchus pauperatus (Germar, 1824) | 18 | 0.71 |
| Ateuchus sp. | 3 | 0.12 |
| Besourenga sp. | 4 | 0.16 |
| Canthidium aff. pinotoides | 3 | 0.12 |
| Dichotomius bos (Blanchard, 1843) | 373 | 14.68 |
| Dichotomius nisus (Olivier, 1789) | 15 | 0.59 |
| Dichotomius sexdentatus (Luederwaldt, 1925) | 1 | 0.04 |
| Dichotomius aff. piceus | 2 | 0.08 |
| Dichotomius glaucus Harold, 1869 | 2 | 0.08 |
| Dichotomius opacipennis Luederwaldt, 1931 | 1 | 0.04 |
| Digitonthophagus gazella (Fabricius, 1787) | 22 | 0.87 |
| Eutrichillum hirsutum (Boucomont, 1928) | 27 | 1.06 |
| Genieridium bidens (Balthasar, 1942) | 36 | 1.42 |
| Ontherus appendiculatus (Mannerheim, 1829) | 64 | 2.52 |
| Ontherus carinicollis Luederwaldt, 1930 | 2 | 0.08 |
| Trichillum externepunctatum Preudhomme de Borre, 1886 | 23 | 0.91 |
| Total | 2541 | 100.00 |

Table 1. Spectrum and abundance (n, %) of coprophagous beetles (Aphodiinae and Scarabaeinae) caught with a light trap in a pasture area in the Brazilian Cerrado (Guia Lopes da Laguna, Mato Grosso do Sul, Brazil), from November 2007 to October 2008.

Table 2. Richness estimates of coprophagous beetles (Aphodiinae and Scarabaeinae) caught with a light trap in a pasture area in the Brazilian Cerrado (Guia Lopes da Laguna, Mato Grosso do Sul, Brazil), from November 2007 to October 2008.

| | Number of species | Standard deviation |
|-------------------|-------------------|--------------------|
| Observed richness | 33 | ±0.73 |
| Chao 1 | 33.20 | ± 0.62 |
| Chao 2 | 33.32 | ± 0.74 |
| Jackknife 1 | 35.88 | ±1.59 |
| Jackknife 2 | 31.61 | ± 0.00 |

correlated with monthly precipitation, with a greater abundance of individuals collected between November and May (Figure 2). Average monthly temperature did not influence the number of individuals captured (p > 0.05), but was positively related to the number of species collected (R = 0.69; p < 0.05) (Figure 2).

Labarrus pseudolividus specimens were observed during almost the entire year, but with a strong reduction in abundance during the winter, when no specimens were captured in June and September (Figure 2, 3). Dichotomius bos individuals were principally observed during the rainy period of the year, and were not captured from June to September which corresponds to the cold and dry season (Figure 2, 3).

Discussion

Richness and abundance pattern

Our study of the coprophagous beetle community in a pasture agroecosystem located in the Cerrado

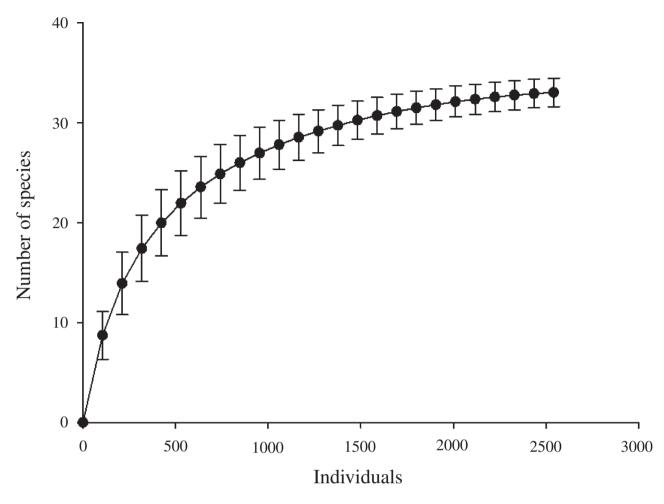


Figure 1. Species accumulation curve of coprophagous beetles (Aphodiinae and Scarabaeinae) caught with a light trap in a pasture area in the Brazilian Cerrado (Guia Lopes da Laguna, Mato Grosso do Sul, Brazil), from November 2007 to October 2008.

confirmed the occurrence of dung beetle species common to open areas such as pastures with exotic (Flechtmann, Rodrigues, & Couto 1995; Koller et al. 1999, 2007; Aidar et al. 2000) and native grasses (Rodrigues et al. 2010; Almeida et al. 2011). It also contributes to the understanding of local diversity of these insects and increases knowledge on their distribution. The long period of sampling allowed for capture of species with different activity during the year.

The number of species registered here was greater than the 24 captured by a light trap in a pasture located in Selvíria, MS (Flechtmann, Rodrigues, & Couto 1995). Ronqui & Lopes (2006), also using a light trap installed in a pasture (Tamarana, Paraná, Brazil), collected almost the same number of Aphodiinae species, but only one third of the number of Scarabaeinae recorded in our study. The richness pattern obtained in the present study is different from other exotic pastures cultivated in Brazil. Therefore, the factors that might explain this pattern must still be investigated in large studies involving native and exotic pastures.

The pattern of species dominance is the same as that encountered in other Neotropical pastures (e.g., Louzada & Silva 2009; Almeida et al. 2011). It is believed that the dominance of few species in Brazilian pastures is a direct reflection of the availability of resources (mainly cattle feces), as well as the soil conditions and micro-climate that vary according to forage management techniques. In these agroecosystems, the sustentation of a great diversity and high population densities would only be possible with the adoption of different management strategies for these landscapes, such as animal rotation in the area, which would include periods of grazing and abandonment. Management must meet the requirements of plants (e.g., fertilization, time for regrowth) and the consumption of fresh mass by cattle (e.g., grazing time, carrying capacity) without adversely affecting the dung beetle communities present at the site (Lobo

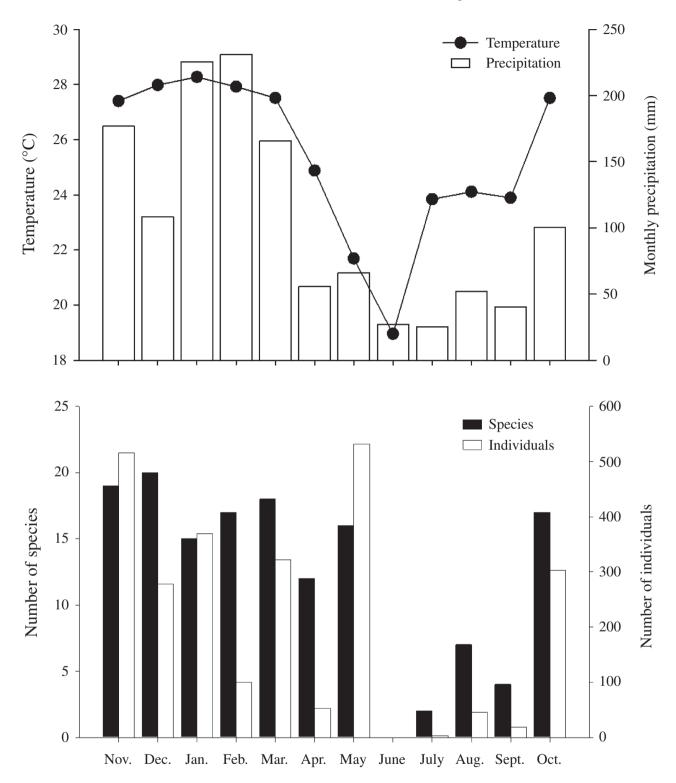


Figure 2. Average monthly temperature and precipitation, species richness and abundance of coprophagous beetles (Aphodiinae and Scarabaeinae) caught with a light trap in a pasture area in the Brazilian Cerrado (Guia Lopes da Laguna, Mato Grosso do Sul, Brazil), from November 2007 to October 2008.

et al. 1998, 2006; Verdú et al. 2007). Grazing intensity may be considered a key factor in determining the variation in diversity and composition of the dung beetle community (Lobo et al. 2006; Verdú et al. 2007). As grazing pressure increases, the rate of herbivore feces renewal would increase, favoring larger dung

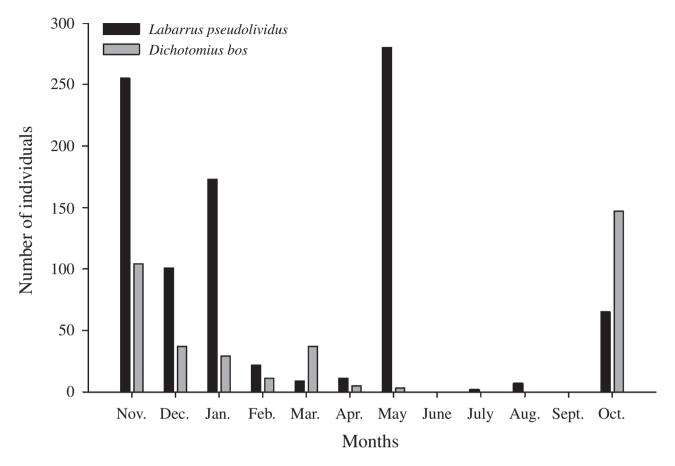


Figure 3. Monthly pattern of abundance of *Labarrus pseudolividus* (Aphodiinae) and *Dichotomius bos* (Scarabaeinae) individuals caught with a light trap in a pasture area in the Brazilian Cerrado (Guia Lopes da Laguna, Mato Grosso do Sul, Brazil), from November 2007 to October 2008.

beetle populations (Lobo et al. 2006). In locations where cattle grazing is continuous and the number of cattle is constant, the diversity and abundance of dung beetles is higher compared to pastures recently used (Lobo et al. 1998). However, in areas of livestock activity abandonment with the suspension of grazing for long periods and/or irregular spatial distribution for grazing, a decrease in beetle diversity may occur (e.g., Lobo et al. 2006).

The dominant species *L. pseudolividus* is widely distributed throughout the Brazilian territory, abundantly sampled in open environments such as pastures with light traps (Flechtmann, Rodrigues, & Couto 1995; Ronqui & Lopes 2006) and/or baited with cattle feces (Rodrigues & Marchini 2000). These small beetles (Flechtmann, Rodrigues, & Seno 1995) feed and nest inside the dung (Waterhouse 1974), significantly contributing to the control of flies by destroying their habitat (Ridsdill-Smith et al. 1987). Many species of Aphodiinae move between patches of dung present in the same pasture (Roslin 2000), indicating that the same individual can control more than a single patch of manure.

Dichotomius bos, the second most abundant species, presents great potential for use in biological control of flies, principally due to its large size $(\sim 20 \text{ mm})$ and ability to bury feces (Flechtmann, Rodrigues, & Couto 1995; Flechtmann, Rodrigues, & Gaspareto 1995). Dichotomius bos is widely distributed and abundant in Brazilian pasture systems (Marchiori et al. 2003; Koller et al. 2007; Rodrigues et al. 2010; Almeida et al. 2011), although it has also been sampled in areas of closed native vegetation (Rodrigues 2008: César Murilo de Albuquerque Correa, Anderson Puker, Vanesca Korasaki, & Kleyton Rezende Ferreira, unpublished data) and Eucalyptus plantations with understory (Rodrigues & Marchini 2000) using traps baited with cattle feces. This species is probably a specialist coprophagous beetle (Silva et al. 2007) and its ample distribution in pastures and high abundance suggest its adaptation to open environments and/or cattle feces. Therefore, D. bos potentially appears to be the best option for future use in biological control of flies by native dung beetle species (Louzada & Silva 2009).

Seasonality

Our results show that with the increase in precipitation there is an increase in the richness and number of individuals captured, which was also observed in several other studies (Novelo et al. 2007; Nyeko 2009; Silva, Costa, et al. 2010; Lopes et al. 2011). Our results are similar to those encountered by Koller et al. (2007) who registered high abundance of coprophagous beetles between October and May (rainy season) in a pasture of the Brazilian Cerrado (Campo Grande, MS). As in this study, Flechtmann, Rodrigues, & Couto (1995) captured a greater number of coprophagous beetles in a light trap during the rainy season (pasture in Selvíria, MS). Silva, Costa, et al. (2010) offered two hypotheses that may explain the lower abundance and richness of adult beetles in the dry season: (1) adults in open habitats must be sensitive to the effects of drought and remain underground during this period; or (2) the adults die in the dry season and only the immature beetles survive in the nest, reaching the adult stage at the beginning of the rainy season. Such data are important to predict the best period for studies on these beetle species, especially L. pseudolividus and D. bos species as they had the greatest abundance.

Abundance pattern of *L. pseudolividus* was similar to that in pastures of Selvíria, MS (Flechtmann, Rodrigues, & Couto 1995) and Tamarana, PR (Ronqui & Lopes 2006). The biology of *L. pseudolividus* is not known, but the biological cycle of other Aphodiinae is relatively short, varying from 50 to 100 days (Wegner & Niemczyk 1981; Verdú & Galante 1997, 2000; González-Vainer et al. 2003). In this case, the presence of *L. pseudolividus* during nearly the entire year may be related to the short duration of its cycle, favoring the appearance of various generations per year.

The absence of D. bos in the dry season coincides with the results of Flechtmann, Rodrigues, & Couto (1995) who reported that beetles with paracoprid nesting behavior (tunnelers) significantly reduced their activities in the dry season, remaining underground. The biological cycle of D. bos is annual (Alves & Nakano 1978), therefore the absence of adult beetles in winter appears to be an adaptation to the dry and cold period. Thus, in Brazilian pastures, the best period to sample high abundance and richness of these beetles is during the rainy and hot season.

Acknowledgments

We thank Prof. Dr. Fernando Z. Vaz-de-Mello (Universidade Federal de Mato Grosso, Brazil) for identification of the Scarabaeidae species collected in this research. We thank Patty Ramirez (University of Lancaster, Lancaster, UK) for reviewing the English of this article. We are also grateful for the valuable criticisms and suggestions provided by anonymous reviewers and the editor of the SNFE, Dr. Anne Zillikens, on the final version of this manuscript.

References

- Aidar T, Koller WW, Rodrigues SR, Correa AM, Silva JCC, Balta OS, Oliveira JM, Oliveira VL. 2000. Besouros coprófagos (Coleoptera: Scarabaeidae) coletados em Aquidauana, MS, Brasil. An Soc Entomol Bras. 29:817–820.
- Almeida S, Louzada J, Sperber C, Barlow J. 2011. Subtle-use change and tropical biodiversity: dung beetle communities in Cerrado grasslands and exotic pastures. Biotropica. 43:704–710.
- Alves SB, Nakano O. 1978. Estudo da biologia do *Dichotomius anaglypticus* (Mannerheim, 1829) (Coleoptera: Scarabaeidae). Ecossistema. 3:11–20.
- Anduaga S. 2004. Impact of the activity of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) inhabiting pasture land in Durango, Mexico. Environ Entomol. 33:1306–1312.
- Arellano L, Halffter G. 2003. Gamma diversity: derived from and a determinant of alpha diversity and beta diversity. An analysis of three tropical landscapes. Acta Zool Mex. 90:27–76.
- Bornemissza GF. 1970. Insectary studies on the control of the dung breeding flies by the activity of the dung beetle, *Onthophagus* gazella F. (Coleoptera, Scarabaeidae). J Aust Entomol Soc. 9:31–41.
- Chung AYC. 2004. Vertical stratification of beetles (Coleoptera) using flight intercept traps in a lowland rainforest of Sabah, Malaysia. Sepilok Bulletin. 1:29–41.
- Costa CMQ, Silva FAB, Farias AMI, Moura RC. 2009. Diversidade de Scarabaeinae (Coleoptera, Scarabaeidae) coletados com armadilha de interceptação de vôo no Refúgio Ecológico Charles Darwin, Igarassu-PE, Brasil. Rev Bras Entomol. 53:88–94.
- Colwell RK. 2005. EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5. [cited 2010 Apr]. Available from: http://viceroy.eeb.uconn.edu/estimates
- Flechtmann CAH, Rodrigues SR, Araújo SD, Wenzel RL. 1995. Levantamento de insetos fimícolas em Ilha Solteira, São Paulo, Brasil. Rev Bras Entomol. 39:115–120.
- Flechtmann CAH, Rodrigues SR, Couto HTZ. 1995. Controle biológico da mosca-dos-chifres (*Haematobia irritans irritans*) em Selvíria, Mato Grosso do Sul. 4. Comparação entre métodos de coleta de besouros coprófagos (Scarabaeidae). Rev Bras Entomol. 39:259–276.
- Flechtmann CAH, Rodrigues SR, Gaspareto CL. 1995. Controle biológico da mosca-dos-chifres (*Haematobia irritans irritans*) em Selvíria, Mato Grosso do Sul. 5. Seleção de besouros coprófagos. Rev Bras Entomol. 39:277–286.
- Flechtmann CAH, Rodrigues SR, Seno MCZ. 1995. Controle biológico da mosca-dos-chifres (*Haematobia irritans irritans*) em Selvíria, Mato Grosso do Sul. 3. Levantamento de espécies fímicolas associadas à mosca. Rev Bras Entomol. 39:249–258.
- Gardner TA, Hernández MIM, Barlow J, Peres CA. 2008. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for Neotropical dung beetles. J Appl Ecol. 45:883–893.
- González-Vainer P, Morelli E, Canziani C. 2003. Biología y estados inmaduros de *Ataenius perforatus* Harold, 1867 (Coleoptera: Scarabaeidae: Aphodiinae). Monog Tercer Milên. 3:67–74.
- Halffter G, Edmonds WD. 1982. The nesting behaviour of dung beetles (Scarabaeinae): an ecological and evolutionary approach. Instituto de Ecología/MAB, México, D.F. 242 p.
- Halffter G, Favila ME. 1993. The Scarabaeinae (Insecta: Coleoptera) an animal group for analysing, inventorying and

monitoring biodiversity in tropical rainforest and modified land-scapes. Biol Int. 27:15–21.

- Halffter G, Matthews EG. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). Folia Entomol Mex. 12/14:1–312.
- Hanski I, Cambefort Y, editors. 1991. Dung beetle ecology. Princeton University Press, Princeton, New Jersey, 481 p.
- Hill CJ. 1996. Habitat specificity and food preference of an assemblage of tropical Australian dung beetles. J Trop Ecol. 12:449–460.
- Kato M, Inoue T, Hamid AA, Nagamitsu T, Merdek MB, Nona AR, Itino T, Yamane S, Yomoto T. 1995. Seasonality and vertical structure of light-attracted insect communities in a dipterocarp forest in Sarawak. Res Popul Ecol. 37:59–79.
- Kato M, Itioka T, Sakai S, Momose K, Yamane S, Hamid AA, Inoue T. 2000. Various population fluctuation patterns of lightattracted beetles in a tropical lowland dipterocarp forest in Sarawak. Popul Ecol. 42:97–104.
- Koller WW, Gomes A, Rodrigues SR, Alves RGO. 1999. Besouros coprófagos (Coleoptera: Scarabaeidae) coletados em Campo Grande, MS, Brasil. An Soc Entomol Bras. 28:403–412.
- Koller WW, Gomes A, Rodrigues SR, Goiozo PFI. 2007. Scarabaeidae e Aphodiidae coprófagos em pastagens cultivadas em área do Cerrado Sul-Mato-Grossense. Rev Bras Zooc. 9:81–93.
- Larsen TH, Lopera A, Forsyth A. 2006. Extreme trophic and habitat specialization by Peruvian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). Coleopt Bull. 60:315–324.
- Lobo JM, Hortal J, Cabrero-Sañudo FJ. 2006. Regional and local influence of grazing activity on the diversity of a semi-arid dung beetle community. Divers Distrib. 12:111–123.
- Lobo JM, Lumaret JP, Jay-Robert P. 1998. Sampling dung beetles in the French Mediterranean area: effects of abiotic factors and farm practices. Pedobiologie. 42:252–266.
- Lopes J, Korasaki V, Catelli LL, Marçal VVM, Nunes, MPBP. 2011. A comparison of dung beetle assemblage structure (Coleoptera: Scarabaeidae: Scarabaeinae) between an Atlantic forest fragment and adjacent abandoned pasture in Paraná, Brazil. Zoologia. 18:72–79.
- Louzada JNC, Silva PRC. 2009. Utilisation of introduced Brazilian pastures ecosystems by native dung beetles: diversity patterns and resource use. Insect Conserv Divers. 2:45–52.
- Marchiori CH, Caldas ER, Almeida KGS. 2003. Succession of Scarabaeidae on bovine dung in Itumbiara, Goiás, Brazil. Neotrop Entomol. 32:173–176.
- Marchiori CH, Oliveira ÂT, Linhares AX. 2001. Artrópodes associados a massas fecais bovinas no sul do estado de Goiás. Neotrop Entomol. 30:19–24.
- Martínez-Garza C, González-Montagut R. 1999. Seed rain from forest fragments into tropical pastures in Los Tuxtlas, Mexico. Plant Ecol. 145:255–265.
- Medri ÍM, Lopes J. 2001. Scarabaeidae (Coleoptera) do Parque Estadual Mata dos Godoy e de área de pastagem, no norte do Paraná, Brasil. Rev Bras Zool. 18:135–141.
- Milhomem MS, Vaz-de-Mello FZ, Diniz IR. 2003. Técnicas de coleta de besouros copronecrófagos no Cerrado. Pesqui Agropecu Bras. 38:1249–1256.
- Novelo RE, Delfín-González H, Morón MÁ. 2007. Copronecrophagous beetle (Coleoptera: Scarabaeidae) diversity in an agroecosystem in Yucatan, Mexico. Rev Biol Trop. 55:83–99.
- Nyeko P. 2009. Dung beetle assemblanges and seasonality in primary forest and forest fragments on agricultural landscapes in Budongo, Uganda. Biotropica. 41:476–484.
- Ridsdill-Smith J, Matthiessen JN. 1981. Controlling cattle dung and the bush fly. J Agr West Aust. 22:76–77.

- Ridsdill-Smith TJ, Hayles L, Palmer MJ. 1987. Mortality of eggs and larvae of the bush fly, *Musca vetustissima* Walker (Diptera: Muscidae), caused by scarabaeine dung beetles (Coleoptera: Scarabaeidae) in favourable cattle dung. Bull Ent Res. 77: 731–736.
- Rodrigues MM. 2008. Besouros coprófagos (Coleoptera: Scarabaeoidea) em três diferentes usos do solo no sul de Mato Grosso do Sul, Brasil [master thesis]. Dourados (Brazil): Universidade Federal da Grande Dourados.
- Rodrigues SR, Barros ATM, Puker A, Taira TL. 2010. Diversidade de besouros coprófagos (Coleoptera, Scarabaeidae) coletados com armadilha de interceptação de vôo no Pantanal Sul-Mato-Grossense, Brasil. Biota Neotrop. 10:123–127.
- Rodrigues SR, Marchini LC. 2000. Ocorrência de besouros coprófagos em dois diferentes ambientes. Rev Bras Entomol. 44: 35–38.
- Ronqui DC, Lopes J. 2006. Composição e diversidade de Scarabaeoidea (Coleoptera) atraídos por armadilha de luz em área rural no norte do Paraná, Brasil. Iheringia, Sér Zool. 96:103–108.
- Roslin T. 2000. Dung beetle movements at two spatial scales. Oikos. 91:323–335.
- Silva FAB, Hernández MIM, Ide S, Moura RC. 2007. Comunidade de escarabeíneos (Coleoptera, Scarabaeidae) copro-necrófagos da região de Brejo Novo, Caruaru, Pernambuco, Brasil. Rev Bras Entomol. 51:228–233.
- Silva FAB, Costa CMQ, Moura RC, Farias AI. 2010. Study of the dung beetle (Coleoptera: Scarabaeidae) community at two sites: Atlantic forest and clear-cut, Pernambuco, Brazil. Environ Entomol. 29:359–367.
- Silva RJ, Diniz S, Vaz-de-Mello FZ. 2010. Heterogeneidade do habitat, riqueza e estrutura da assembléia de besouros rola-bostas (Scarabaeidae: Scarabaeinae) em áreas de cerrado na Chapada dos Parecis, MT. Neotrop Entomol. 39:934–940.
- Smith ABT, Skelley PE. 2007. A review of the Aphodiinae (Coleoptera: Scarabaeidae) of southern South America. Zootaxa. 1458:1–80.
- Vaz-de-Mello FZ. 2000. Estado atual de conhecimento dos Scarabaeidae s. str. (Coleoptera: Scarabaeoidea) do Brasil. In: Martín-Piera F, Morrone JJ, Melic A (editors). Hacia un proyecto CYTED para el inventario y estimación de la diversidad entomológica en Iberoamérica. Zaragoza: Sociedad Entomológica Aragonesa. pp. 181–195.
- Verdú JR, Galante E. 1997. Aphodius brasiliensis Castelnau (Coleoptera: Aphodiidae): larval morphology and notes on biology. Coleopt Bull. 51:378–383.
- Verdú JR, Galante E. 2000. Larval morphology and biology of two species of *Aphodius (Plagiogonus)* from the Iberian Peninsula (Coleoptera: Scarabaeidae: Aphodiinae). Eur J Entomol. 97: 395–401.
- Verdú JR, Moreno CE, Sánchez-Rojas G, Numa C, Galante E, Halffter G. 2007. Grazing promotes dung beetle diversity in the xeric landscape of a Mexican Biosphere Reserve. Biol Conserv. 40:308–317.
- Yamada D, Imura OO, Shi K, Shibuya T. 2007. Effect of tunneler dung beetles on cattle dung decomposition, soil nutrients and herbage growth grassland. Grassl Sci. 53:121–129.
- Yokoyama K, Kai H, Tsuchiyama H. 1991. Paracoprid dung beetles and gaseous loss of nitrogen from cow dung. Soil Biol Biochem. 23:643–647.
- Waterhouse DF. 1974. The biological control of dung. Sci Am. 230:100–109.
- Wegner GS, Niemczyk HD. 1981. Bionomics and phenology of *Ataenius spretulus*. Ann Entomol Soc Am.74:374–384.