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Environmental patterns and daily activity of dung beetles (Coleoptera: Scarabaeidae) in the Atlantic Rainforest of Brazil

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Abstract

Iannuzzi L, Salomão RP, Costa FC, Liberal CN. 2016. Environmental patterns and daily activity of dung beetles (Coleoptera: Scarabaeidae) in the Atlantic Rainforest of Brazil. Entomotropica 31(23): 196-207.

The aim of the present study was to evaluate the daily activity and habitat associations of dung beetles, to examine their seasonal variation and to determine which species are dominant in a region of Brazilian Atlantic Forest. Sampling was performed with pitfall traps baited with carrion and human excrement. Dung beetles were more abundant in open habitat during the day, and in closed habitat at dusk. No difference was found in the abundance and period of activity between seasons. Species richness varied with seasonality in different habitats. Greatest species richness was found at dusk. No significant association was found between body size and period of activity. Segregation of the dung beetle community was found to be associated with the period of activity.

Additional key words: Habitat type, Scarabaeinae, segregation, temporal activity.

Resumen

Iannuzzi L, Salomão RP, Costa FC, Liberal CN. 2016. Variaciones estacionales y actividad diaria de los escarabajos del estiércol (Coleoptera: Scarabaeidae) en una región de la selva Atlántica brasileña. Entomotropica 31(23): 196-207.

El objetivo de este estudio fue evaluar la actividad diaria de los escarabajos del estiércol y su asociación con el hábitat, así como investigar las variaciones estacionales y determinar cuáles son las especies dominantes en una región de la selva atlántica brasileña. El muestreo se realizó con trampas de caída cebadas con carroña y excremento humano. Los escarabajos del estiércol fueron más abundantes en hábitats abiertos durante el día y en hábitats de selva cerrada durante el periodo crepuscular. No hubo diferencias estadísticamente significativas en la abundancia y el periodo de actividad de los escarabajos del estiércol entre las temporadas. La riqueza de especies cambió de acuerdo a la temporada en los hábitats evaluados. La mayor riqueza fue observada en el periodo crepuscular y no fue observada asociación entre el tamaño corporal de los escarabajos del estiércol y el período de actividad. Así mismo, se observó segregación de la comunidad de escarabajos del estiércol asociada al periodo de actividad.

Palabras clave adicionales: Periodo de actividad, Scarabaeinae, segregación, tipo de hábitat.

Introduction

Insects are good models for the exemplification of segregation along different ecological gradients (Schowalter 2006). In tropical forests, where there is a high degree of insect richness and competition, spatial complexity and the variety of resources available allow the coexistence of species from the same guild (Wilson 1992, Davis 1999, Tokeshi 1999, Feer and Pincebourne 2005). Habitat type also plays a role in the segregation of insect communities, clearly observed in dung beetles (Scarabaeidae: Scarabaeinae), as a large number of species effectively inhabit open habitat, in which the influence of abiotic factors is greater (Nichols et al. 2007, Costa et al. 2009, Rodrigues et al. 2013). On the other hand, a portion of the dung beetle community in tropical forests exhibits a preference for closed forests (Costa et al. 2009, Rodrigues et al. 2013).

Temporal variation and habitat specialization in dung beetle activity constitutes one of the main mechanisms for the avoidance of competition (Hanski and Cambefort 1991, Hernández 2002, 2007; Feer and Pincebourne 2005, Lopes et al. 2011). There is a clear shift in species composition of dung beetle from disturbed to undisturbed areas, being this shift followed by a pattern of higher abundances in diurnal dung beetles of disturbed areas (Nichols et al. 2007, Lopes et al. 2011). The period of activity of a given species corresponds to the time interval used for foraging and sexual activity and is defined based on the incidence (presence and permanence) of sunlight (Pianka 1973, Mañosa et al. 2004, Hernández 2007, González-Maya et al. 2009). Peak activity is generally classified as diurnal, nocturnal or crepuscular and is regulated by a number of different factors (Hernández 2002, 2007; Feer and Pincebourne 2005, Gillet et al. 2010, Gerber et al. 2012), such as the presence of predators and the availability of food resources (Dawkings and Krebs 1979, Overdorff 1988, Pianka 1973, González-Maya et al. 2009). Indeed, adaptations to different periods of the day contribute to the success and survival of organisms (Gill 1991, Halffter and Halffter 2009, Valera et al. 2011). Throughout their evolution, dung beetles have undergone a number of changes in body size and tegument color which are thought to be related to the period of daily activity (Hernández 2002, Feer and Pincebourne 2005).

Dung beetles exhibit strong competitive behavior for food resources and are therefore commonly united in functional guilds based on diet and way of resource allocation (Halffter and Edmonds 1982, Hanski and Cambefort 1991). Moreover, dung beetle activities are segregated throughout different periods of the day and year due to factors such as temperature, humidity, season and amount of sunlight (Landin 1968, Hanski and Cambefort 1991, Caveney et al. 1995, Liberal et al. 2011). In tropical environments, dung beetles are more active during the rainy season due to the greater availability and preservation of resources used for feeding and nesting (Gill 1991, Davis 1996, Neves et al. 2010, Liberal et al. 2011). The availability of food resources, which consist mainly of excrement from vertebrates, exerts a regulatory pressure on the activity period of these insects (Hanski and Cambefort 1991, Scholtz et al. 2009). The period of activity is also an important factor for mating, with some dung beetles exhibiting iridescence that may be related to intraspecific signaling and to avoid predators (Vullinec 1997). Moreover, studies have shown that the coloration of dung beetles bodies is related to their activity, with diurnal species generally colorful and nocturnal species darker, suggesting an association with thermal regulation (Hernández 2002, Scholtz et al. 2009). Higher temperatures and greater luminosity during the day lead to a more rapid desiccation rate of this ephemeral resource. Thus, environments of closed habitats, as tropical forests, preserve resources for a longer

period of time in comparison to open habitat, which exhibits rapid desiccation (Spector and Ayzama 2003).

The aims of the present study were 1) to determine the influence of habitat and season on the diel flight activity of dung beetles in open and closed forests in a region of the Atlantic Forest in northeastern Brazil; 2) to evaluate the association between functional groups (roller, tunneler, dweller) according to the periods of activity of dung beetles; 3) to evaluate the association between body size and activity period of dung beetles; and 4) to analyze species dominance at different times of the day. Based on knowledge that different species carry out their activities during different periods of day, the following hypotheses were tested regarding the temporal period of dung beetle activity: 1) greater abundance and species richness are found in closed forest habitat during the rainy season and nocturnal period; 2) the roller guild of dung beetles will occur mainly during the diurnal period, tunnelers will occur mainly during the nocturnal period, and dwellers will not exhibit preference among the periods of the day; 3) small beetles are generally diurnal and large beetles are nocturnal; and 4) species that dominate the dung beetle community do not have strong circadian barriers to their period of activity due to successful adaptations to the habitat and therefore occupy a larger temporal period.

Materials and Methods

The present study was conducted at the Campo de Instrução Marechal Newton Cavalcanti (CIMNC) located in the state of Pernambuco in northeastern Brazil (lat 07° 50' 00" S, long 35° 06' 00" W). The CIMNC is used for the training of military troops (Andrade 2004) and is considered one of the largest continuous patches of Atlantic Forest north of the São Francisco River, with dense lowland rainforest (IBGE 1992). This area was previously used for sugarcane cultivation. The cessation of monoculture activities following the expropriation of the land by the Brazilian Army in 1944 has led to its current state of secondary regeneration succession (Rego et al. 2004). The CIMNC is located at 42 km from the city of Recife (state capital of Pernambuco) and spreads through the cities of Abreu e Lima, Araçoiaba, Igarassu, Paulista, Paudalho and Tracunhaém, with 7 324 ha covering both forested and urbanized areas. Average annual minimum and maximum temperatures are 20.4 °C and 30.4 °C, respectively. Average annual precipitation is 2 010 mm. The region has a rainy tropical climate with a dry summer with mean precipitation of 343 mm and rainfall concentrated between March and September, with mean precipitation of 1 667 mm (LAMEPE 2010, APAC 2015). The soil is composed of latosols and podzolics on the top of plateaus and residual tops; podzolics with fragipan, plinthic podzolics and podzols on the small depressions of the tableland; concretionary podzolics in dry areas and on cliffs; and gleysol and alluvial soils in meadow areas (Beltrão et al. 2005).

Data collection

Sampling was performed using pitfall traps baited with human excrement (30 g) and carrion (30 g), consisting of bovine spleen that was rotten in plastic recipient during 48 h (see Filgueiras et al. 2011, Costa et al. 2013). Each sampling unit consisted of two traps (1 with excrement and 1 with carrion). In each habitat, the traps were distributed in two sets spaced 20 m apart, each with two types of bait (3 m between traps), being kept in field during 24 hours without bait replacement. Beetles were collected from six areas (three open and three closed habitats) of the CIMNC spacing at least 1 000 m apart (Figure 1). Open habitats were characterized by sparse vegetation cover composed essentially of grasses and no canopy. These habitats were within the forest of CIMNC and had areas around 60 m^2 and the traps were installed near

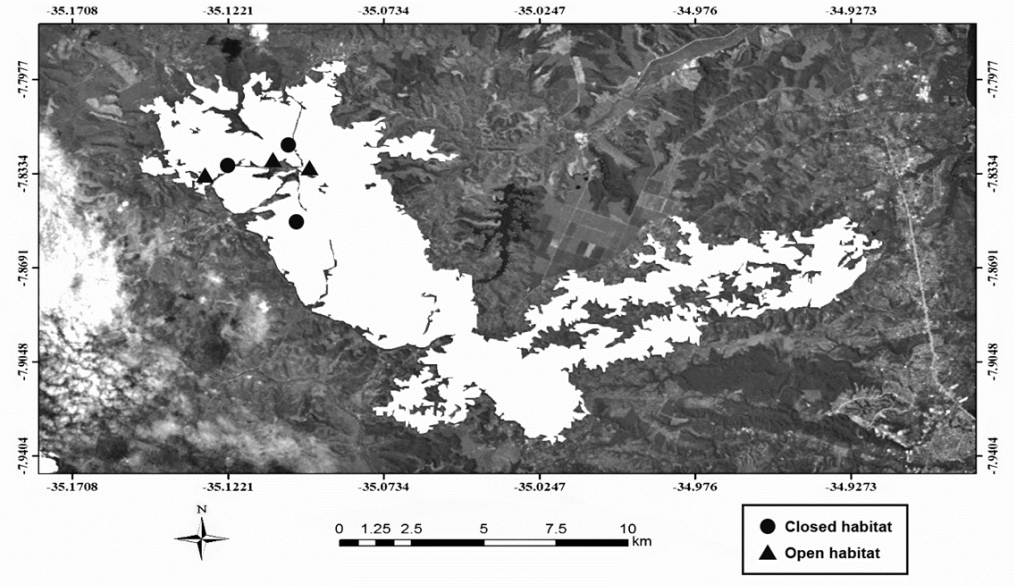

Figure 1. Campo de Instrução Marechal Newton Cavalcante (CIMNC) – Pernambuco, Brasil (lat 07° 50' 00" S, long 35° 06' 00" W).

the center of them. Closed habitats had canopy coverage ranging from 7 to 10 m and more closed vegetation coverage than open habitat. Sampling was performed once per month from April to June (rainy season) and October to December (dry season) during 2010. For the determination of the periods of activity, the traps were deployed during daylight hours (08 :00 hours to 17:00 hours) as well as at dusk (17:00 hours to 19:00 hours) and night (19:00 hours to 05:00 hours).

Ten specimens of each species were randomly selected for the measurement of mean body length (apex of the clypeus to the apex of the pygidium) with the aid of a digital caliper. The species *Dichotomius* sp. was not measured due to the structural damage on the only individual obtained in the study. Specimens with a body length larger than 20 mm were classified as large, those with a body length between 10 and 20 mm were classified as medium-sized and those with a body length less than 10 mm were classified as small.

The entomological collection of Universidade Federal de Pernambuco was used as reference for dung beetle identification. Also, Dr. Fernando Zagury Vaz-de-Mello (Universidade Federal do Mato Grosso) assisted with the identification of the material. The classification of functional guilds (roller, tunneler, dweller) followed Halffter and Edmonds (1982).

Data analysis

Factorial ANOVA with Tukey's post hoc test was used to compare the abundance and richness of dung beetles in different seasons (dry and rainy), habitats (closed and open), and periods of the day (diurnal, crepuscular and nocturnal). One-way ANOVA was used to determine whether body size was associated with the period of activity. The assumptions of both ANOVA were tested. For One-way ANOVA abundance data were log-transformed. These analyses were carried out using the STATISTICA 7.0 software program (Statsoft 2004).

Non-metric multidimensional scaling (NMDS) was used to search for overall differences in species abundance and composition between

periods of activity (diurnal, crepuscular and nocturnal). Two analyses were performed – one using type of habitat and one using season as data samples, with period of the day as the factor in both analyses. Ordination was undertaken for abundance and composition using the Bray-Curtis index. Analysis of similarities (ANOSIM) was used to test the differences in species abundance and composition between periods of activity. Also, to evaluate the dung beetle functional groups (roller, tunneler, dweller) according to the periods of activity, we performed an ANOSIM in which the periods of the day were the factors. For this, the data was forth root transformed to avoid the discrepancy among very abundant and very rare species. Each period of the day of each month was considered one sampling unit. These analyses were performed using the PRIMER 6 software program (Clarke and Gorley 2006).

The Pielou evenness index (J') was calculated to determine the existence of homogeneity in the distribution of species abundance among the different periods of activity. For such, the R software program was used. Abundance ranking with log-transformed data was used in the comparison of dominance patterns among the different periods of activity to minimize the influence of rare species on the analysis. A graph for each habitat was also created to allow the visualization of the findings.

Results

A total of 860 individuals representing 24 species of dung beetles were collected in both habitats. The most abundant species were *Dichotomius* aff. *sericeus* (Harold, 1867) (402 individuals), *Canthon staigi* (Pereira, 1953) (252 individuals) and *Canthon* aff. *simulans* (Martínez, 1950) (76 individuals). Together, these three species accounted for 84.8 % of the overall sample (Table 1).

The majority of genera had species with a preference for more than one period of the day. *Coprophanaeus* Olsoufieff, 1924 was an exception, as the species of this genus were exclusively crepuscular (Table 1). Five species of three genera were distributed over all three daily activity periods: *Canthon staigi*, *Deltochilum* sp., *D.* aff. *sericeus*, *Eurysternus caribaeus* (Herbst, 1789) and *Eurysternus hirtellus* Dalman, 1824.

Habitat abundance was highly significant ($F = 36.56$; $df = 1, 96$; $p < 0.05$) being more than three times as high in closed habitat (n = 665) as in open habitat (n = 195) (Figure 2A). *Ateuchus* sp.1 (n = 11) was exclusive to closed habitat , while *C.* aff. *simulans* (n = 76) was exclusive to open habitat. The period of activity for each species was not affected by season ($F = 0.2$; $df = 1, 96$; $p = 0.65$), independent of type of environment (Figure 2A).

Three hundred forty-eight individuals (40.5 % of the total) were collected at dusk, 313 (36.4 %) were collected in the diurnal period,and 199 (23.1 %) were collected during the nocturnal period. The variation in abundance throughout the day was dependent on the type of habitat, with greater abundance during diurnal period in the open habitat (121 individuals) and at dusk in the closed habitat (287 individuals). Abundance was greatest in closed habitat at dusk ($p = 0.0004$) and at night ($p = 0.0001$).

Eighteen species were reported in the crepuscular period, 12 in the diurnal period and 11 in the nocturnal period. Species richness was significantly distinct between environments ($F = 17.57$; $df = 1, 96$; $p < 0.05$) (Figure 2B). The greatest difference between habitats occurred in the nocturnal period, with the closed habitat (s= 11) exhibiting fivefold greater richness in comparison to the open habitat (s = 2) ($p = 0.02$) (Figure 2B). There was interaction between the factors period of activity and environment, in relation to species richness ($F = 5.2$; $df = 2, 96$; $p < 0.05$) (Figure 2B). In the closed habitat, richness was lowest during the diurnal period, with eight

Table 1. Abundance, species richness and mean size of dung beetle species collected in open and closed forests of CIMNC during different dial periods (crepuscular [C], diurnal [D] and nocturnal [N]), seasons and environments.

		Dry season						Rainy season					
		Open habitat			Closed habitat			Open habitat			Closed habitat		
Taxa	Mean size (mm)	D	C	N	D	C	N	D	C	N	D	C	N
Ateuchus aff. *ovalis*	5											1	
Ateuchus sp.1	4.6					4	6					1	
Ateuchus sp.2	6.5					1	1						
Canthidium aff. *manni*	6.3								1				
Canthidium sp.1	4.9	1			1			2					1
Canthidium sp.2	4							1					
Canthidium sp.3	4										1		
Canthon staigi	9.3		1		60	2	21	26			108	32	2
Canthon nigripennis	5.8	2	3			1		1					
Canthon aff. *simulans*	4	26						40	10				
Canthon sp.	5.5							7			1	1	
Canthonella silphoides	3.6					5	2						
Coprophanaeus acrisius	26.3								2				
Coprophanaeus dardanus	21.4											1	
Coprophanaeus aff. *ensifer*	39.4								1				
Deltochilum sp.	10		5			3		6	3	2	3	11	4
Deltochilum aff. *irroratum*	13		1									1	
Dichotomius depressicolis	21												2
Dichotomius nisus	21.5		1										
Dichotomius aff. *sericeus*	127		21	8	1	131	94		10	3	1	83	50
Dichotomius sp.	-							1					
Eurysternus hirtellus	6.1	1			10		1	6	1		2	1	
Eurysternus caribaeus	13.8	1	1		4	8	1						
Sylvicanthon sp.	7.5						1						
Abundance		31	33	8	76	155	127	90	28	5	116	132	59
Richness		5	7	1	5	8	8	9	7	2	7	10	5

species (Figure 2B); in contrast, species richness ranged from 13 and 11 species in the crepuscular and nocturnal periods, respectively. In the open habitat, species richness was at least fourfold greater in the diurnal (s = 9) and crepuscular (s = 12) periods in comparison to the nocturnal (s = 2) period.

The period of activity was a determinant factor for the segregation of the dung beetle community in relation to season of the year (Global R: 0.651; $p < 0.05$). Two clusters were formed – one made up of diurnal dung beetles and another uniting both crepuscular and nocturnal dung beetles. Moreover, internal segregation in each group was found based on season (Figure 3). When habitat was the

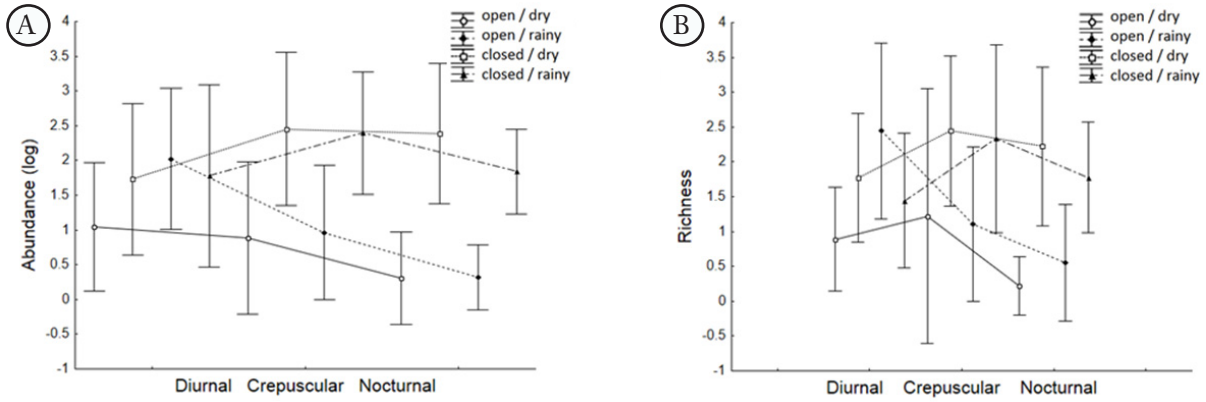

Figure 2. Abundance (A) and richness (B) of dung beetles collected in open and closed forests of CIMNC during diurnal, crepuscular and nocturnal activity periods, wet and dry seasons and open and closed habitats. Bars indicate Standad Error.

sampling unit, segregation of the dung beetle community also occurred in relation to period of the day, with the crepuscular and nocturnal periods grouped together and the diurnal period separated from the other two periods (Global R: 0.316; $p < 0.05$) (Figure 4). The dung beetle functional groups (roller, dweller, tunneler) were segregated according to periods of the day (tunneler – Global R: 0.61; $p < 0.05$; roller – Global R: 0.343; $p < 0.05$; dweller – Global R: 0.239; $p < 0.05$).

Evenness was equilibrated with regard to period of activity in open environment (diurnal J'= 0.63; crepuscular J'= 0.66; nocturnal J' = 0.62). However, evenness was low during diurnal (J' = 0.27) and nocturnal (J'= 0.37) periods in closed environments, indicating the dominance of one or more species per daily activity period. In closed habitat, *Canthon staigi* was the most abundant diurnal species, *Dichotomius* aff. *sericeus* was dominant at dusk, and at night (Figure 5A). In open habitat, *C.* aff. *simulans* and *Canthon staigi* were dominant at day, *D.* aff. *sericeus*, was dominant at dusk. During the nocturnal period in open habitat, *D.* aff. *sericeus* and *Deltochilum* sp. were the only species caught (Figure 5B).

Five species were classified as large (> 20 mm), four were classified as medium-sized (10-20 mm) and 14 were classified as small (<10 mm) (Table 1). No significant association was found between body size and period of activity (MS = 601.7; F = 1.25; df = 2; p = 0.31).

Discussion

In the present study, the dung beetle community exhibited temporal segregation, with some species only occurring at a certain time of the day and others distributed throughout all three-activity periods. A strong degree of competition is one of the main explanations for restricted occupation (Peck and Forsyth 1982, Hanski and Cambefort 1991, Horgan and Fuentes 2005, Scholtz et al. 2009). Due to the ephemeral nature and relative scarcity of the resources used by dung beetles in Neotropical habitats, carrying out activities at different times of the day is a strategy employed to diminish competition (Gill 1991, Hernández 2002, Feer and Pincebourne 2005, Hernández 2007).

The findings for the majority of species analyzed herein are similar to results obtained in previous studies, with greater abundance and species richness in closed habitats and different species composition in comparison to open habitats (Nichols et al. 2007). Therefore, as stated by Lopes et al. (2011), there are situations where the richness and abundance

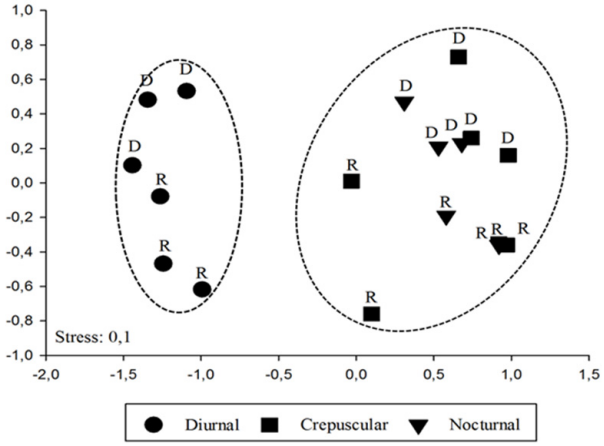

Figure 3. Non-metric multidimensional scaling (NMDS) ordination of the dung beetle abundance in three diel periods with month as the sampling unit. R – rainy period; D – dry period. Groupings exhibited with 45 % similarity.

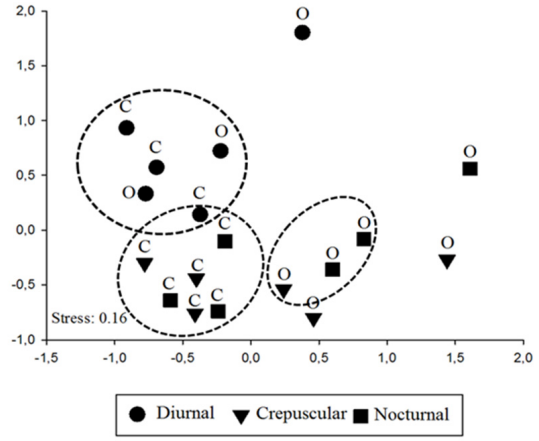

Figure 4. Non-metric multidimensional scaling (NMDS) ordination of the dung beetle abundance in three diael periods with environment as the sampling unit. O – open habitat; C – closed habitat. Groupings exhibited with 45 % similarity.

do not exhibit differences among disturbed and preserved habitats due to opportunistic species that are well adapted to disturbances, although the species composition exhibited a clear shift between habitat structures. Moreover, different species exhibit different periods of activity (Hernández 2002, Feer and Pincebourne 2005). The genus *Coprophanaeus* Olsoufieff, 1924 occurred exclusively during the crepuscular period, which is reported to be the period of greatest activity of species for this genus (Hernández 2007, Edmonds and Zidek 2010). *Dichotomius* Hope, 1838 is recognized as a typically crepuscular and nocturnal genus, which was confirmed in the present study (Hernández 2002, Feer and Pincebourne 2005, Hernández 2007). In agreement with Feer and Pincebourne (2005) data for French Guyana, *Eurysternus* Dalman, 1824 species from this study were restricted to diurnal activity. However, in the southern Atlantic Forest, *Eurysternus caribaeus* is classified as diurnal and nocturnal, differing from our study (Lopes et al. 2011). This pattern could be a result of the non-segregation of the crepuscular period from the diurnal and nocturnal period in the study of Lopes et al. (2011). Thus, even when exposed to different local environmental conditions, the majority of species demonstrated specific patterns regarding the period of activity due to the physiology of the individuals, with some exceptions as observed in *E. caribaeus* (Caveney et al. 1995, Lopes et al. 2011).

Greatest dung beetle abundance and species richness in closed forests were found during the crepuscular period, while the lowest were found during the diurnal period. In open habitats, the greatest abundance and richness were found during the diurnal periods, while during the nocturnal period we found the lowest abundance and richness. Our data is in disagreement with that of Hernández (2002), and Feer and Pincebourne (2005), both of which reported that dung beetles in other regions of tropical rainforest exhibit greater activity during the day. The differences found in the period of activity between these studies may be related to the regional distinction on species composition, which favoured a more diurnal activity of the dung beetles species, as observed in Hernández

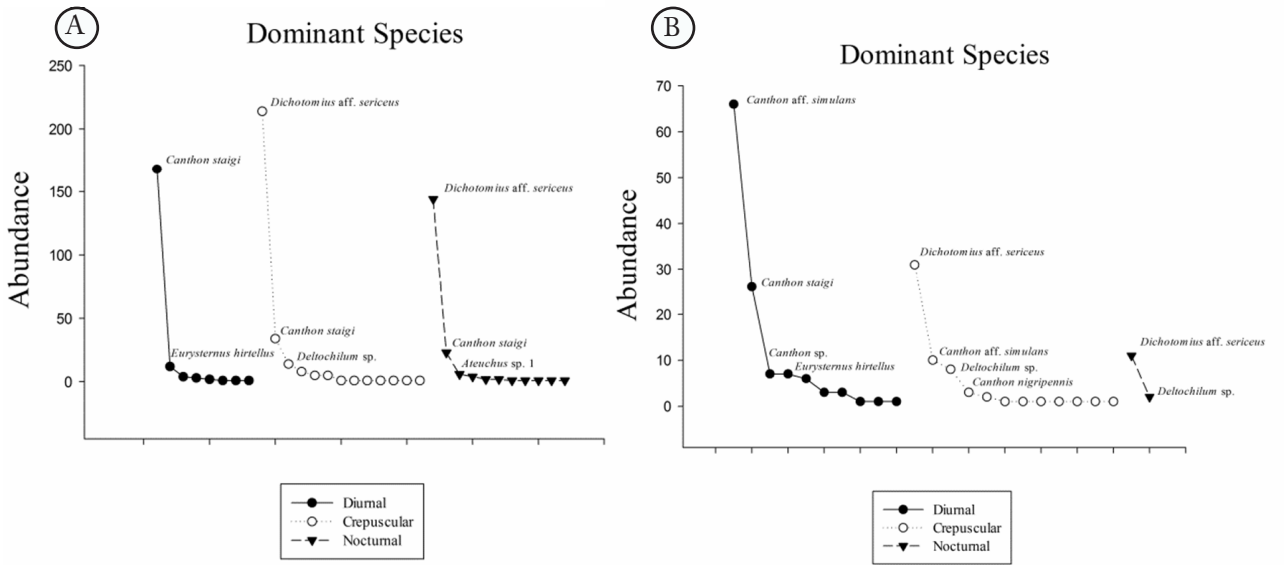

Figure 5. Species rank abundance of dung beetles during the diel activity periods in closed (A) and open (B) habitats of CIMNC.

(2002) and Feer and Pincebourne (2005). Also, the high abundance of diurnal species on Serra do Japi, as *Canthidium trinodosum* (Bohenann, 1858) and *Eurysternus cyanescens* Balthasar, 1939, which represented about 40 % of the total dial activity of the study, favored a higher abundance of dung beetles during the day in the study of Hernández (2002). Besides the competition for resources, temperature and luminosity are also limiting factors with regard to the activity of dung beetles (Davis et al. 2002, Hernández 2002, Neves et al. 2010). In our study area, where temperatures during the day are high (mean: 30 °C), the lower temperatures of the crepuscular period favor greater dung beetle richness and abundance. Furthermore, mammals generally defecate at the beginning and end of their activity period, leading to a greater availability of resources for dung beetles during these times (Vaz-de-Mello and Louzada 1997, Feer and Pincebourne 2005).

Diurnal dung beetles tend to exhibit adaptations that favor the occupation of warmer periods of the day (Hernández 2002, Scholtz et al. 2009). As most dung beetles are ectothermic, the small body size assists in physiological regulation during the day, favoring the exchange of heat with the environment (Feer and Pincebourne 2005, Scholtz 2009). Despite this adaptation, low dung beetles diversity has previously been found in open habitats of the Neotropics. These habitats, however, are also subjected to the greater action of wind, temperature and luminosity, which are more intensive in comparison to closed forests (Feer and Pincebourne 2005, Costa et al. 2009). Nonetheless, species that use resources quickly, such as dung rollers, can overcome these constraints (Krell et al. 2003), which may explain our findings. The dominance of species from the genus *Canthon* Hoffmannsegg, 1817 during the day in open habitats may be explained by the rapid resource exploitation exhibited by roller dung beetles. In contrast, *Dichotomius* aff. *sericeus* was more abundant in the closed habitat at dusk and at night. Such environments do not experience many abrupt oscillations and may therefore be more favorable to the occurrence of dung beetles (Caveney 1995), unlike the open habitat of the study area, which undergoes a mean reduction in temperature of approximately 10 °C (Albuquerque 2013).

Unlike semi-arid tropical forests, the Atlantic Forest does not experience a strong reduction in dung beetles activity in the dry season (Filgueiras et al. 2009, Hernández and Vaz-de-Mello 2009, Neves et al. 2010, Liberal et al. 2011). In our study area within the Atlantic Forest of Brazil, there were no abrupt changes between seasons that occurred regarding the presence of mammals or vegetal coverage (Barros-Batesti et al. 2000, Pereira 2008). Although some species exhibited uniform distribution throughout the year, a lower degree of species richness was found in the open habitat during the dry season. As such, environments often become even more adverse during periods with low rainfall, causing a large portion of species to aggregate in closed habitat (Feer and Pincebourne 2005). Thus, species that occur in the open habitat throughout the year likely have greater distribution at times in which there is less competition with other species.

In conclusion, the daily activity of dung beetles in the CIMNC was dependent on the type of habitat, with diurnal species being more active in open habitat and both crepuscular and nocturnal species more active in closed habitat. Dusk proved to be the period of greatest dung beetles activity. The specificity of species for a given period of the day and differences in composition between habitats demonstrate the importance of environmental heterogeneity for the maintenance of dung beetles diversity.

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