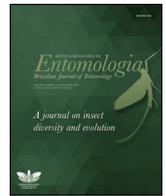




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Daily activity of *Dichotomius geminatus* (Arrow, 1913) and *Deltochilum verruciferum* Felsche, 1911 (Coleoptera: Scarabaeinae) facing carrion: from resource perception to feeding



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ABSTRACT

Dung beetles (Scarabaeinae) interact with resources in different ways and are classified according to resource relocation guilds. *Dichotomius geminatus* (Coprini) and *Deltochilum verruciferum* (Canthonini) are two of the most abundant and ecologically important species of the semi-arid region of Brazil, and understanding their behaviour may facilitate the comprehension of strategies associated to competition for resources. The aim of the present study was to investigate the behavioural repertoire of *D. geminatus* (tunneler) and *D. verruciferum* (roller), in isolation and controlled setting in the Brazilian semi-arid biome, using carrion as a food resource. Our hypothesis was that, due to the distinct food relocation strategies presented by these species, distinct behaviours would occur involving resource utilization. We also compared the behaviour of the two species and investigated the period of diel activity. Both species were more active during the night, but *D. geminatus* presented a shorter peak of nocturnal activity when compared to *D. verruciferum*. Although there was activity during the day, feeding was only observed during the night, for both species. During the periods of inactivity, *D. verruciferum* commonly went underneath the carrion, remaining still. As the target species of the study are very abundant, the differences in behaviour associated with the distinct relocation guilds may indicate a strategy to avoid direct competition.

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Introduction

Arid and semi-arid environments are strongly restrictive due to its scarce resource availability for both plants and animals (Dayton and Fitzgerald, 2006; Ma et al., 2008; Holter et al., 2009; Valera et al., 2011). To cope with such limitations, animals may adopt different behavioural strategies (Leal et al., 2003; Ocampo and Philips, 2005; Liberal et al., 2011; Nobre et al., 2012). Dung beetles (Coleoptera: Scarabaeinae), for example, exhibit temporal variation in behaviours, which constitutes one of the main mechanisms to avoid unfavourable habitat conditions, contributing to their ecological success (Hanski and Cambefort, 1991; Hernández, 2002; Feer and Pincebourne, 2005; Hernández, 2007; Halffter and Halffter, 2009; Lopes et al., 2011; Valera et al., 2011). The daily activity of dung beetles is generally classified as either diurnal, nocturnal or crepuscular, and is regulated by a number of factors (Hernández, 2002; Feer and Pincebourne, 2005; Hernández, 2007; Gillett et al.,

2010), such as the presence of predators and the availability of food resources (Young, 1982; Hanski and Cambefort, 1991; Scholtz et al., 2009).

The Caatinga forest is a semi-arid biome restricted to Brazil (Andrade-Lima, 1981; Leal et al., 2003). This region has very high temperatures throughout the year and low irregularly distributed annual rainfalls, concentrated within few months, presenting years of drought during months commonly classified as rainy (Leal et al., 2003; Prado, 2003). In Caatinga areas, as in many tropical regions of the world, necrophagy is a common habit among dung beetles, and many species are known to be copro-necrophagous (Hernández, 2007; Neves et al., 2010; Medina and Lopes, 2014). Overall, dung beetles rely on animal faeces, mainly of mammals, for food and reproduction (i.e. coprophagy). However, the coprophagous behaviour could be replaced or supplemented by other resources including dead animals (i.e. necrophagy) or decaying material (i.e. saprophagy) (Gill, 1991; Halffter and Halffter, 2009; Scholtz et al., 2009). The relatively low species richness of the native mammals of Caatinga (Mares et al., 1985; but see Albuquerque et al., 2012) is one of the factors reflecting the poor diversity of the dung beetles in this biome, which may be explained by the low availability of different

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resources. Furthermore, the Caatinga's high temperatures and dry climate (Leal et al., 2003) presents a limiting factor for dung beetles, since they depend on ephemeral resources that become unusable when desiccated (Theuerkauf et al., 2009). The use of carrion seems to be an attractive alternative in the Caatinga, as it stays attractive for long periods when compared to faeces (Theuerkauf et al., 2009; Mayer and Vasconcelos, 2013).

Deltochilum verruciferum, and *Dichotomius geminatus*, are two of the most common and abundant dung beetles in Caatinga forests (Hernández, 2007; Liberal et al., 2011; Medina and Lopes, 2014). The high abundance of some dung beetle species are usually correlated with essential ecological services, since they remove large portions of excrement, consequently dispersing seeds and improving the soil quality (Nichols et al., 2008). Species of *Deltochilum* Eschscholtz, 1822 are usually associated with copro-necrophagy, but there are also active predators within the genus (Hanski and Cambefort, 1991; Cano, 1998). They have anatomical adaptations such as clypeal teeth and well-developed tibiae, which help them to catch and process active preys. *Deltochilum* species are telecoprids or rollers – they roll dung balls taking it away from the original site (Halffter and Edmonds, 1982; Scholtz et al., 2009). They are characterized by having strong posterior legs (Scholtz et al., 2009), and travel relatively long distances (from many centimetres to a few metres) to store their resources, spending a great deal of energy in the process (Krell et al., 2003; Krell-Westerwalbesloh et al., 2004). On the other hand, members of *Dichotomius* Hope, 1838 are associated with copro-necrophagy and saprophagy (Hanski and Cambefort, 1991; Halffter and Halffter, 2009). They are paracoprids (tunnellers group), which bury directly underneath the pile of dung. They have strong and well-developed anterior legs to help with the digging of galleries close to food resources (Hanski and Cambefort, 1991; Scholtz et al., 2009).

Species that share the same resource and dwell at the same sites, as *D. geminatus* and *D. verruciferum*, may exhibit adaptive strategies to avoid excessive competition for resources (Medina and Lopes, 2014). Microhabitat specialization, specific period of activity and distinct foraging behaviours may result from competitive scenarios (Larsen et al., 2006; Hernández, 2007). Dung beetles, for example, exhibit specific behaviours encompassing the resource exploitation that appears as result of the intensive competition of these insects for decaying matter (Hanski and Cambefort, 1991; Halffter and Halffter, 2009; Vaz-de-Mello and Génier, 2009). The guilds of resource relocation among dung beetles are a clear response to competition for the scarce and ephemeral food that these beetles feed on (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991; Scholtz et al., 2009).

The aim of the present study was to investigate the behavioural activity repertoire of *D. geminatus* and *D. verruciferum*, focusing in their foraging strategies associated with carrion. Considering the differences in morphology and foraging strategies associated to these species guilds (i.e. *Deltochilum* – roller; *Dichotomius* – tunneler), we expected that their activity repertoire and the specific foraging strategies would differ between them. For instance, high locomotion rates would be expected for *D. verruciferum*, whereas high rates of gallery-related activities would be expected for *D. geminatus*. Due to the higher locomotion expected for *D. verruciferum*, and consequently higher energetic costs, we expected that this species would present higher number of feeding events. Despite the current knowledge on resource relocation for the target genera (e.g. Halffter and Edmonds, 1982), the strategy used by these animals from the initial resource identification to actual relocation is poorly known. Due to the high temperatures on Caatinga, and the relative large size and dark colouration of the studied species (morphological characteristic usually associated to nocturnal insects, see Hernández (2007) and Scholtz et al. (2009)), we expected them to show nocturnal activity, to cope with the environment conditions.

The data presented in our study provides comparative information on the behavioural ecology of two species of dung beetles and may bring insights into evolutionary aspects of their foraging strategies.

Material and methods

Study area and trapping method

The study was conducted in two fragments of Caatinga scrub forest situated in northeastern Brazil: Area-1: located at “Boqueirão da Onça” (10.9048°S, 41.2111°W), North of Bahia, Brazil; and Area-2: located at Parnamirim city (8.5026°S, 39.3442°W), Pernambuco, Brazil. Both fragments are well-preserved, thus presenting a dung beetle fauna with reduced environmental stressors. Both areas have hot semi-arid climate (type “BSh”), according to the Köppen climate classification (Velloso et al., 2002), presenting low variation on the temperature throughout the year. The average annual temperature in Boqueirão da Onça is $30 \pm 0.68^\circ\text{C}$, whereas in Parnamirim the average annual temperature is $26 \pm 1.20^\circ\text{C}$ (Velloso et al., 2002; IBGE, 2013; Climate-Data, 2016). The average annual rainfall is 650 mm and 431 mm in Boqueirão da Onça and Parnamirim, respectively. The rainy period occurs irregularly from October to April, and the rainfall usually is distributed on a few months of this season (Velloso et al., 2002; Beltrão et al., 2005). Dung beetle sampling and observation were conducted in February and March 2013 in Area-1, and April 2013 in Area-2, periods in which the studied species (*D. geminatus* and *D. verruciferum*) are known to be active in these regions (Hernández, 2007; Liberal et al., 2011).

To capture the dung beetles, we used pitfall traps with two bait types: human faeces and carrion (rotten bovine spleen). In total, we used 120 baited pitfall traps and, in each area, we used 60 pitfall traps, 30 baited with carrion (50 g) and 30 baited with human faeces (50 g). For each trap, we suspended the bait beneath a lid directly above the pitfall. The lid was used to stop the rain from getting into the traps. Inside the traps we added some of the local soil to allow the beetles to dig and hide, in an attempt to reduce stress to the individuals. Traps were left on the site for 24 h and the beetles were collected and kept in cylindrical plastic bottles (10 cm × 6 cm) also containing soil taken from the campsites. Those beetles were taken to observational studies in arenas on the site. After the samplings, 20 individuals of *D. verruciferum* and 25 of *D. geminatus* were randomly selected for the arena observations. Due to logistical limitations, the number of individuals per species could not be standardized. The identification of both species was done based on the reference material of the “Coleção Entomológica da UFPE” (Entomological Collection of the Federal University of Pernambuco; CE-UFPE) that was determined by the specialist Dr. Fernando Zagury Vaz-de-Mello. After the observational studies, vouchers of *D. verruciferum* and *D. geminatus* specimens were incorporated to the CE-UFPE.

All the individuals of *D. geminatus* were obtained from Parnamirim city; while 17 individuals of *D. verruciferum* were obtained from Boqueirão da Onça, and the remaining three from Parnamirim. The individuals were not sexed and were selected randomly from the traps.

Arena observations

We placed each beetle in a separate arena to observe their behavioural activity pattern individually. The arenas consisted of 45 cm × 20 cm × 10 cm plastic trays, with a layer of 3 cm of local Caatinga soil, 50 g of carrion (rotten bovine spleen) and one individual dung beetle (Bertone et al., 2006; Dormont et al., 2010). Roller dung beetles such as *D. verruciferum* can move long distances

Table 1
Ethogram of *Deltochilum verruciferum* and *Dichotomius geminatus* facing the offer of carrion.

Category	Behaviour	Description	Species on which the behaviour was observed
Leg-body rub	Head rub	Rubbing anterior legs in circular movements around the head and antenna	Both
	Leg rub	Rubbing anterior legs on extended middle legs, or rubbing middle legs on the posterior legs	Both
Ground stop	Elytra rub	Rubbing posterior and middle legs around the elytra	<i>D. verruciferum</i>
	Pygidium rub	Rubbing posterior legs on the pygidium in circular movements	Both
	Close to resource stop	On the ground, not moving, near a food resource with retracted antennae	Both
	Far from resource stop	On the ground, not moving, at least 5 cm away from the resource, with motionless extended antennae, motionless retracted antennae or with antennae moving up and down (retracting and extending)	Both
Flight	Head tuck	On the ground, not moving, with head pushed into the sand, close to the food resource	<i>D. verruciferum</i>
	Flight preparation 1	Middle legs moving in the air, body supported on the anterior and posterior legs	<i>D. verruciferum</i>
	Flight preparation 2	Elytra opened, with posterior wings extended for several seconds	<i>D. verruciferum</i>
Body movement	Flight	Flying with extended legs, elytra and wings wide open	Both
	Turning	Turning the body around, through approximately 180°, and occasionally turning it back again	<i>D. verruciferum</i>
Gallery-related activities	Head movement	Moving the head from side to side	<i>D. geminatus</i>
	Body shake	Moving the body repeatedly backwards and forwards	<i>D. geminatus</i>
	Antenna movement	Supporting the body on the anterior legs, with middle and posterior legs motionless in the air and antennae moving up and down	<i>D. geminatus</i>
	Gallery stop	Remaining motionless at the entrance of the gallery; or supporting the body on the anterior legs, with middle and posterior legs retracted and antennae moving up and down	<i>D. geminatus</i>
Locomotion	Gallery movement	Locomotion in front of the gallery (side to side orientation); entering or leaving the gallery	<i>D. geminatus</i>
	Ground locomotion	Walking on the ground or on top of the resource, with stretched or retracted antennae (both species); Going under the resource and pushing the soil with the head during locomotion (Exclusive on <i>D. verruciferum</i>)	Both
Digging	Slow motion	Moving in a lethargic manner on the ground with antennae straight up.	Both
	Head dig	Burrowing a hole in the ground (or the food resource) using the head	Both
	Leg dig	Burrowing a hole in the ground (or the food resource) using anterior and middle legs.	Both
Feeding Resource manipulation	Feeding on the resource, sometimes moving body, legs and head.		Both
	Manipulation of the resource without feeding.	Pushing the resource using the head or anterior legs; Touching the resource with the antennae.	<i>D. geminatus</i> Both
Underground	Staying under the resource or under the ground		Both

with their food; however, the aim of this study was to evaluate behaviours related to feeding activity. We believe the size of the arena was adequate for this purpose and did not influence our results. As this species did not perform rolling behaviour, which could implicate on the displacement through long distances, we considered that there was no direct interference of the arena size in the observed behaviours. The arenas were covered with clean film to prevent the beetles from escape. The arenas were built in the sampling sites where individuals were collected. Temperature, humidity and luminosity in the arenas were, thus, similar to natural conditions (i.e. on both sampling sites: average temperature 26 ± 0.8 °C, average relative humidity 40% and 12 h photoperiod, from 05:30 to 17:30).

The arena observations started at 07:00, approximately 60 min after the beetle sampling from the pitfall traps in the field. A piece of carrion was placed in each arena before the beetle. Systematic observations started 30 min after the individual was placed in the arena to allow habituation. We used the focal sampling method (Altmann, 1974) to observe the individuals. We recorded the frequency of each type of behaviours performed by the animals (see Table 1 in the Results section) to establish and compare the behavioural activity repertoire of the both studied species when facing carrion availability. When there is no food in the surroundings, dung beetles usually display activities to find food, and once found, the activities are focused on resource exploitation (Hanski

and Cambefort, 1991; Scholtz et al., 2009). Thus, we gave special attention to feeding-related behaviours associated with the carrion. Feeding occurred when the animals manipulated and ingested carrion using their mouthparts. Observations were conducted for 24 continuous hours, and a 5-min focal session was conducted per hour per animal, at the beginning of each hour. In overnight we used an infrared light to facilitate the observations, as this light source does not affect the behaviour of insects (Allema et al., 2012; Kamenova et al., 2015). A digital video recorder (Sony DSC-HX5) and direct observations were used to record the beetles' behaviours.

Data analysis

For a visual and explorative evaluation of the similarities of the periods of activity among the studied species, we performed a non-metric multidimensional scaling (NMDS) analysis based on Jaccard matrix of similarity. Each individual was considered as a sampling unit, the beetle active hours of the day were considered as variables, and the species were considered as factors. The Jaccard matrix of similarity was constructed based on data of activity ("1") and inactivity ("0") of the specimens. The NMDS ordination was performed with 2500 repetitions. For a statistical analysis of the segregation of the period of activity of *D. verruciferum* and *D. geminatus*, we performed analysis of similarities (ANOSIM). For both NMDS and ANOSIM, we used Primer 6.0 software (Prime-E).

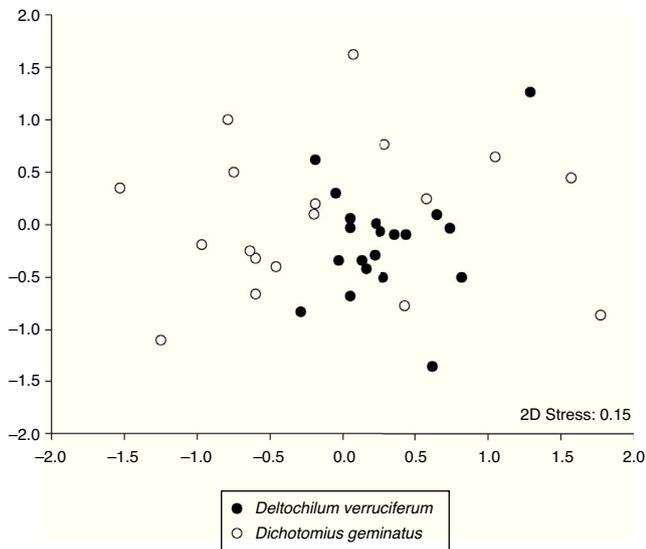


Fig. 1. NMDS ordination for the period of activity of *Deltochilum verruciferum* and *Dichotomius geminatus*.

A general linear model was used to verify whether the distribution of behaviours of both species differed from an even distribution, and to investigate whether the diurnal behaviours (observations from 05:00 to 17:59) exhibited by the beetles differed from the nocturnal ones (observations from 18:00 to 04:59). For pairwise post hoc evaluation, a Tukey test was conducted. Each individual was considered one sampling unit, and the number of records of each category was compared between the other categories and the periods of the day. A binomial Z score test was used to compare the frequency of foraging-related behaviours between the two species. The behaviours were classified in main categories according to the general patterns of activities observed on dung beetle on other studies (Otronen, 1988; Hanski and Cambefort, 1991; Favila et al., 2012). As certain behaviours had small number of records in the study, we analyzed the behaviours among categories, to exhibit clearer responses. For these analyses, we used SPSS 21 (IBM corp) and Statistica 10 (Statsoft corp).

Results

The behavioural repertoire of *D. verruciferum* consisted of 18 behaviours distributed into nine categories, whereas the repertoire of *D. geminatus* had 18 behaviours distributed into 10 categories (Table 1). Three categories were considered as behavioural states: “underground”, “gallery-related activities” and “ground stop”. All other categories were considered to be events. A total of 13 behaviours were common to both species. “Gallery-related activities” was a category only observed in *D. geminatus*. Five behaviours were exclusive to *D. verruciferum* (i.e. elytra rub; head tuck; flight preparation 1 and 2 and turning), and five behaviours were exclusive to *D. geminatus* (i.e. head movement; body shake; antenna movement; gallery stop and gallery movement).

The majority of the activities occurred overnight. Between 10:00 and 17:00, both species remained inactive underground. The period of activity of the studied species presented a significant segregation (R -global = 0.001; p = 0.001), and the NMDS ordination exhibited a grouped distribution of the period of activity of *D. verruciferum*, while *D. geminatus* presented a spread distribution (Figure 1). Overall, in *D. verruciferum*, activity peaks occurred between 19:00–22:00, 02:00–04:00 and 07:00–08:00 (Figure 2a). *D. geminatus* activity peak occurred between 02:00–05:00 (Figure 2b). There was a difference in the frequency of use of the different behavioural

categories in both species: *D. verruciferum* (F = 20.07; p < 0.05) and *D. geminatus* (F = 6.63; p < 0.05). In *D. verruciferum*, “Leg-body rub” and “Locomotion” were the most commonly seen behavioural categories. In *D. geminatus*, the category “Locomotion” was the most common one.

There was a significant difference in the frequency of occurrence of three out of seven behavioural categories between the day and night periods in *D. verruciferum* (Table 2). The categories “Leg-body rub” and “Locomotion” were most frequently seen during the night (Table 2). In *D. geminatus*, the categories “Body movement” and “Locomotion” were mostly observed during the night (Table 2). For both species, feeding activities were recorded exclusively during the nocturnal period (Table 2).

The activities related to carrion were perception of resource and feeding. While individuals of *D. verruciferum* utilized their anterior legs, making movements that indicate the ripping of the resource, individuals of *D. geminatus* fed only positioning their head and mouthpart on resources. Some behaviours were only observed in one of the species. Only *D. verruciferum* went underneath the carrion. Only *D. geminatus* remained still in front of the gallery entrance. A difference in the number of recorded activities between *D. verruciferum* and *D. geminatus* was observed in all the behavioural categories (Table 3). “Locomotion” was the category in which both species exhibited the highest mean number of records; however, *D. verruciferum* presented a much higher mean number of records (6.65 ± 3.52) than *D. geminatus* (1.80 ± 1.84). There was also a strikingly distinction in the mean number of records between the species for the following categories, respectively for *D. verruciferum* and *D. geminatus*: “Leg-body rub” (2.95 ± 2.50 and 0.20 ± 0.50); “Flight” (1.10 ± 1.97 and 0.12 ± 0.36); “Body movement” (0.05 ± 0.22 and 0.80 ± 1.35) and “Feeding” (1.30 ± 1.49 and 0.12 ± 0.33) (Table 3).

Discussion

The activities performed by *D. geminatus* and *D. verruciferum* were related to locomotion, feeding, communication and gallery building, but neither species built feeding balls with the carrion. These behaviours are commonly observed in dung beetles, usually associated with resource location and mating-related activities (Hanski and Cambefort, 1991; Scholtz et al., 2009; Vaz-de-Mello and Génier, 2009). The establishment of necrophagy by dung beetles of the Neotropical region is a result of the scarcity of medium and large mammals, which results in a relative lack of dung resources (Halffter and Matthews, 1966). Despite the high richness of dung beetles in the Neotropics, a relative small number of species use carcasses for feeding and breeding balls when compared to excrement (Gill, 1991; Favila, 1993; Endres et al., 2005). For example, species of *Coprophanæus* Olsoufieff (1924) relocate carrion masses underground that can be used for both shelter and food for their larvae (Halffter et al., 1974; Halffter and Edmonds, 1982; Otronen, 1988; Endres et al., 2005). Some species of dung beetles that nest on carcass are also attracted by other resources, but their occurrence is more abundant when the nest resource is easily available (Favila, 1993; Vaz-de-Mello et al., 1998; Avendaño-Mendoza et al., 2005; Silveira et al., 2006; Amézquita and Favila, 2011).

The behaviour “Leg-body rub” was often observed in both studied species. This behaviour can have different meanings depending on the body part that the leg touches. We observed the animals touching the elytra, the pygidium and the mouthparts. When the leg touches the elytra or the pygidium, the behaviour is usually associated with hormonal release for mating (Vaz-de-Mello and Génier, 2009; Favila et al., 2012; Souza, 2013) and is performed when the individual is close to their nesting galleries or food resources (Vaz-de-Mello and Génier, 2009; Favila et al., 2012). We

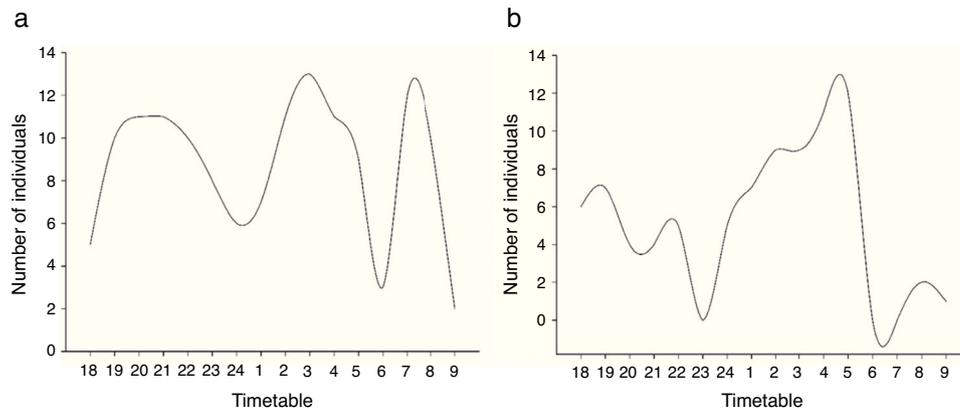


Fig. 2. Numbers of individuals of *Deltotichilum verruciferum* (a) and *Dichotomius geminatus* (b) that performed some behaviour during the observations. The active and inactive individuals are not necessarily the same during the periods of activity. * From 10:00 to 17:00 no activity was observed for both species.

Table 2
Comparison between diurnal and nocturnal activity patterns of *Deltotichilum verruciferum* and *Dichotomius geminatus*. Bold indicates a significant difference (Tukey test).

Species	Category of behaviour	Mean \pm SD		p
		Diurnal	Nocturnal	
<i>Deltotichilum verruciferum</i>	Leg-body rub	0.50 \pm 0.76	2.45 \pm 2.01	0.001
	Flying	0.3 \pm 0.57	0.8 \pm 1.64	0.999
	Body movement	0.05 \pm 0.22	0	1.000
	Locomotion	2.05 \pm 1.79	4.6 \pm 3.42	0.000
	Digging	0.45 \pm 0.75	0.2 \pm 0.41	0.988
	Feeding	0	1.3 \pm 1.49	0.036
	Resource manipulation	0.05 \pm 0.22	0.05 \pm 0.22	1.000
	<i>Dichotomius geminatus</i>	Leg-body rub	0	0.2 \pm 0.5
Flying		0.08 \pm 0.27	0.04 \pm 0.2	1.000
Body movement		0	0.8 \pm 1.35	0.006
Locomotion		0.48 \pm 0.58	1.32 \pm 1.77	0.003
Digging		0.24 \pm 0.43	0.44 \pm 0.58	0.472
Feeding		0	0.12 \pm 0.33	0.999
Resource manipulation		0.04 \pm 0.2	0.16 \pm 0.47	0.999

Table 3
Binomial Z score comparing the frequency of use of the different behavioural categories between *Deltotichilum verruciferum* and *Dichotomius geminatus*.

Category of behaviour	Mean n of records \pm SP		Z	p
	<i>Deltotichilum verruciferum</i>	<i>Dichotomius geminatus</i>		
Leg-body rub	2.95 \pm 2.50	0.20 \pm 0.50	141.69	<0.05
Flying	1.10 \pm 1.97	0.12 \pm 0.36	199.85	<0.05
Body movement	0.05 \pm 0.22	0.80 \pm 1.35	18.20	<0.05
Locomotion	6.65 \pm 3.52	1.80 \pm 1.84	27.83	<0.05
Digging	0.65 \pm 0.87	0.68 \pm 0.74	58.11	<0.05
Feeding	1.30 \pm 1.49	0.12 \pm 0.33	199.53	<0.05
Resource manipulation	0.10 \pm 0.30	0.20 \pm 0.65	92.51	<0.05

observed the leg touching the mouthparts just before or just after feeding; suggesting that this behaviour is a foraging related activity.

The studied dung beetles were most active during night-time. Several factors may control the activity period of dung beetles in the Caatinga, including temperature and direct sunlight (Davis et al., 2002; Feer and Pincebourne, 2005). Furthermore, animals under elevated predation risk may also adapt their behaviour to avoid encounters with predators (Young, 1982; Brook et al., 2012). Nocturnal dung beetles are usually larger and are dark coloured (Hernández, 2002; Scholtz et al., 2009) favouring the maintenance of the body temperature (Hernández, 2002; Feer and Pincebourne, 2005; Scholtz et al., 2009; Medina and Lopes, 2014). The dark colouration is a camouflaged pattern often associated with the avoidance of night-time predators (Hernández, 2002; Scholtz et al., 2009). The studied dung beetles follow this pattern to some extent: i.e. they are dark coloured, relatively large (mean size: *D. verruciferum* – 18 mm; *D. geminatus* – 14 mm) when compared to other

dung beetles of the Caatinga (Hernández, 2007) and showed a nocturnal habit; these characteristics could reduce encounters with night-time predators, such as some nocturnal staphylinid beetles (Young, 1982).

Although both species were mainly nocturnal, there was a significant segregation in the period of activity of *D. verruciferum* and *D. geminatus*. Studies evaluating the period of activity in dung beetles usually subdivide the 24 h daily cycles in diurnal, nocturnal and crepuscular (Krell et al., 2003; Feer and Pincebourne, 2005; Iannuzzi et al., 2016). Notwithstanding, according to our data, we can infer that even though the study species are currently classified as nocturnal (Hernández, 2007), there were actually distinct periods of the night where the organisms of each species are more active. Due to the ephemeral and random distribution of feeding resources of dung beetles, there is an intense competition for food among these insects, what may result in different feeding strategies, microhabitat distribution and periods of activity (Hanski and

Cambeftor, 1991; Larsen et al., 2006; Scholtz et al., 2009). Considering that both *D. verruciferum* and *D. geminatus* are large-bodied and abundant species, which competes for similar resources and co-occur during the nocturnal period in the Caatinga (Hernández, 2007), it seems reasonable and strategic that they present peaks of activity in different periods of the night.

D. verruciferum used carrion more often than *D. geminatus*, which would be expected considering that the former species is larger and may demand a greater energy intake (Doube, 1990). Locomotion was more often observed in *D. verruciferum* than in *D. geminatus*, which may also be related to a larger requirement for food (Krell et al., 2003). Telecoprid species, like *D. verruciferum*, may expend a lot of energy, because of their typical behaviour of rolling food resources on the ground (Halffter and Edmonds, 1982; Krell et al., 2003). Gallery-related behaviours were exclusive to *D. geminatus*, which explain its sedentary and energetically less costly behavioural pattern. Among the dung beetles, some species are commonly observed motionless at gallery entrances, a behaviour usually associated with hormonal release for the attraction of mates (Vaz-de-Mello and Génier, 2009; Favila et al., 2012). Moreover, considering that *D. geminatus* is a paracoprid species, gallery-related behaviour would be expected to occur more often than locomotion-related behaviour (Halffter and Edmonds, 1982). The resource relocation behaviour is usually grouped according to tribes in Scarabaeinae (Halffter and Edmonds, 1982; Scholtz et al., 2009). However, these behaviours apparently do not have a phylogenetical relationship, since in certain genera defined as rollers, there are subgroups of species that show tunneler behaviours, and vice versa (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991; Scholtz et al., 2009). The environmental conditions might influence the resource relocation behaviours on relatively short time spans, promoting shifts to alternative nesting strategies among dung beetle species (Scholtz et al., 2009). Species such as *D. verruciferum* and *D. geminatus* follow the behavioural pattern established for the tribes that they belong (i.e. Canthonini and Coprini, respectively) (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991). However, it is difficult to predict if, and how, the environmental condition observed on Caatinga could have led to a shift of these species behaviour. Comparisons on behaviour of species that are distributed on both Caatinga and more mesic ecosystems (e.g. Atlantic Rainforest) could clarify possible strategies adopted according to different habitat conditions.

With regards to perceiving and interacting with the resource, we observed that when the beetles were exhibiting locomotion behaviour, they kept their antennal lamellae extended. Also, when they were close to the resource, the antennae moved. This gives us some evidence of the importance of the antenna in the foraging process. In fact, after finding a resource, dung beetles usually move their antenna around it to aid chemical/odour perception (Gill, 1991; Scholtz et al., 2009). When interacting with the carrion in the arena, both species used their anterior legs to remove small particles of it before ingestion. Microorganisms and leftover food in the resources are the most nutritious parts of the dung beetles diet, but non-nutritious parts can also be ingested (Halffter and Matthews, 1966; Holter et al., 2002; Halffter and Halffter, 2009). Although both dung beetle species investigated went under the soil surface, only *D. verruciferum* went underneath the carrion. In the wild, when there is a high level of competition for a portion of the resource, it is common to see *D. verruciferum* performing aggressive displays (Salomão pers. obs.). Going underneath the resource to feed or to rest may help reducing the need for costly aggressive behaviours, as it reduces direct contact with competitors (and potential predators) on the top of the food.

Through this study, we could verify different patterns of activity for two abundant Caatinga dung beetle species. The differences seem to be related to their adaptation for interaction with food

resources. Overall, *D. verruciferum* performed activities mostly related to displacement and this can be an important factor associated with the higher food intake when compared to tunneller species such as *D. geminatus*. The latter, on the other hand, performed more gallery-related activities as expected for species belonging to the same nesting guild. Behavioural categories such as “Leg-body rub” (exclusive to *D. verruciferum*) and “Gallery-related activities” (exclusive to *D. geminatus*) are related to inter-specific communication, which is a common pre-requisite to resource relocation (Otronen, 1988; Favila et al., 2012). Resource use in dung beetles usually shows differences when the animals are grouped together, because it may lead to competitive or cooperative scenarios (Otronen, 1988; Hanski and Cambefort, 1991; Vaz-de-Mello and Génier, 2009; Favila et al., 2012). Thus, future studies should focus on investigating these animals in pairs or groups to evaluate further details of resource allocation in the wild.

Conflicts of interest

The authors declare no conflicts of interest.

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