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Seasonal and Daily Variations in Dung Beetle Assemblages (Coleoptera: Scarabaeidae) in Two Contrasting Habitats in a Livestock Ranch in Central Uruguay: Implications for Habitat Management and Species Conservation

Cecilia Canziani[1,§] and Patricia González-Vainer[2,§,*]

[1]*Centro Regional de Profesores del Centro, Consejo de Formación en Educación, Administración Nacional de Educación Pública. Florida, Uruguay. E-mail: cecilia.canziani@docente.ceibal.edu.uy (Canziani)*

[2]*Sección Entomología, Facultad de Ciencias, Universidad de la República. Iguá 4225, Montevideo 11400, Uruguay. *Correspondence: E-mail: vainer@fcien.edu.uy (González-Vainer)*

[§]*CC and PG contributed equally to this work.*

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ORCiD

Cecilia Canziani: https://orcid.org/0000-0002-4993-4029

Patricia González-Vainer: https://orcid.org/0000-0001-6206-3646.

Dung beetles play a vital role in the functioning and sustainability of agroecosystems. The temporal niche partitioning facilitates species coexistence by minimizing interspecific competition. Temporal activity patterns of dung beetles are influenced by various biotic and abiotic factors. Changes in land use by humans may alter activity patterns and spatial distribution. In this study we analyzed a) the seasonal variations in abundance and richness of dung beetle assemblages in two contrasting habitats within a ranch in Uruguay and their relationship with environmental factors; b) the influence of the habitat on daily patterns of flight activity of dung beetles and assessed seasonal and daily species composition changes; c) the seasonal variations of daily activity patterns of the most abundant species. We sampled dung beetles every two weeks for a year with pitfall traps baited with carrion and cow and horse excrements in an open grazed pasture and a *Eucalyptus* plantation, used as a shelter for livestock. Each 24-hour sampling was divided into 5 intervals: morning, noon, afternoon, evening, and night. The seasonal variations of abundance and species richness of Scarabaeidae in both habitats were similar from mid-spring to mid-autumn, without activity in the winter season; temperature influenced these patterns. Diurnal dung beetles were more abundant than crepuscular and nocturnal in the open habitat but not clearly in the *Eucalyptus* plantation. However, the abundance and richness of nocturnal species were similar in both habitats. The daily activity period significantly influenced the segregation of dung beetles in both habitats. Species composition differed markedly between diurnal and crepuscular/nocturnal species without changes across seasons. Scarabaeinae species were mostly diurnal in grassland, while a nocturnal species was predominant in *Eucalyptus* plantation. Aphodiinae species were mainly active at dusk and night. We concluded that the daily activity of the species depends on the habitat, which should be considered when designing conservation measures for dung beetles in this region.

Key words: Scarabaeinae, Aphodiinae, Daily flight activity, Grassland, *Eucalyptus* plantation

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BACKGROUND

Dung beetles of the subfamilies Scarabaeinae and Aphodiinae (Scarabaeidae), both in the larval and adult stages, feed mainly on mammalian excrement, but some species may also feed on carrion, seeds, decomposing fruits and fungi, and vegetable detritus (Cambefort 1991; Halffter and Halffter 2009). These insects are involved in important ecosystem functions, such as nutrient recycling (Yokoyama et al. 1991), soil hydration and aeration (Brown et al. 2010), secondary seed dispersal (Urrea-Galeano et al. 2019), and natural control of organisms that develop in mammalian feces (Gregory et al. 2015).

It has been postulated that because of the patchy and ephemeral nature of the food resources exploited by dung beetles, strong competition between co-occurring species is highly probable and it likely plays an important role in structuring communities (Hanski and Cambefort 1991). Several previous studies have demonstrated that dung beetles exhibit niche partitioning along several ecological axes (*e.g.*, Hanski and Cambefort 1991; Doube and Wardhaugh 1991; Chao et al. 2013), including macro- and micro-habitats (*e.g.*, Ahuatzin et al. 2023; Reis et al. 2023), dung food type (*e.g.*, Araújo et al. 2022), foraging and nesting strategies (Doube 1990), as well as colonization times (*e.g.*, Noriega et al. 2008; Verdú et al. 2022) and seasonality (*e.g.*, Niino 2014). Temporal activity patterns show when animal species exploit the environment and represent a key niche dimension, as the activity period of a given species corresponds to the time interval used to perform sexual and foraging behaviors (Pianka 2011). As adult insect flight patterns are influenced by various abiotic and biotic factors (Hanski and Cambefort 1991; Vebrová et al. 2018; Franzén 2022), temporal niche partitioning is a primary question for both ecological research and biodiversity conservation (Frey et al. 2017). There is evidence that human impacts on the landscape, including land use change and human activity, can alter species activity patterns as well as affect their spatial distribution (Knop et al. 2023).

Temporal niche partitioning is an important strategy for enabling the coexistence of ecologically similar species (Frey et al. 2017; Franzén et al. 2022). In particular, differences in the yearly activity peaks as well as differences in the diel flight activity patterns of dung beetles, tend to decrease interespecific competition while allowing the coexistent of different species and the possibility of being the first colonizers of the resource (Montes de Oca and Halffter 1995; Caveney et al. 1995; Palmer 1995; Sowig 1997; Hernández 2002; Krell-Westerwalbesloh et al. 2004; Feer and Pincebourne 2005). Each dung beetle species has specific hours of activity and they can be divided into diurnal, nocturnal, or crepuscular (Krell-Westerwalbesloh et al. 2004, Feer and Pincebourne 2005; Giménez et al. 2017). A number of different factors may be driven the daily activity patterns, such as the avoidance of predators and the availability of food resources (Hanski and Cambefort 1991; Martín-Piera et al. 1994; Davis 1999; Byrne and Dacke 2011); the thermal tolerance of the species and air temperature (Bartholomew and Heinrich 1978; Byrne and Dacke 2011; Giménez-Gómez et al. 2017); the body size, eye size and morphology, and light intensity (Feer and Pincebourne 2005; Verdú et al. 2006; Chown and Klok 2011; Byrne and Dacke 2011). Studies on diel dung beetle activities have also shown that patterns of flight activity of the assemblages may depend both on the climatic region and the habitat (*e.g.*, Mena et al. 1989; Cambefort 1991; Gill 1991; Larsen et al. 2008; Chown and Klok 2011; Nichols et al 2013; Iannuzzi et al. 2016). In addition to this, seasonal and diel temporal dimensions would be able to interact with each other in dung beetles. Some studies have note that some species with a crepuscular or nocturnal activity during summer change to a diurnal activity during spring and autumn (Koskela 1979; Fincher et al. 1986; Mena et al. 1989; Gill 1991; Kohlmann 1991; Davis 1996).

Seasonal activity of dung beetles is influenced mainly by temperature and precipitation, jointly or separately according to the climatic region (Hanski and Cambefort 1991; Hernández 2007; Hernández and Vaz de Mello 2009; Liberal et al. 2011; Agoglitta et al. 2012; Sánchez-Hernández et al. 2021), and also by the seasonal variation in quality and quantity of the available trophic resources (Edwards 1991; Martín-Piera and Lobo 1996). The seasonal variability of dung beetle assemblages has been extensively studied in tropical and subtropical regions (*e.g.*, Hernández and Vaz-de-Mello 2009; Abot et al. 2012; Medina and Lopes 2014; Barreto et al. 2019; Cassenote et al. 2019; Touroult et al. 2017; Casas et al. 2021; Sánchez-Hernández et al. 2021); in Mediterranean region (e.g. Errouissi et al. 2011; Agoglitta et al. 2012; Senyüz et al. 2019; Lobo and Cuesta 2021; Cuesta et al. 2021), and also in temperate and northern temperate-cold regions of Europe (Landin 1961; Hanski 1980; Holter 1982; Wassmer 1994; Palestrini et al. 1995; Tocco and Villet 2016). Seasonality of dung beetles has been less researched in temperate region of South America

(González-Vainer and Morelli 1998 1999; Morelli et al. 2002; Ranz et al. 2017). A previous study in Uruguay about seasonal patterns of dung beetles assemblages in native grassland, has shown the occurrence of higher richness and abundance during the warm seasons (since mid-spring to early autumn) (Morelli et al. 2002), but seasonal variation of the species composition or daily activity patterns of the species have not been analyzed.

Therefore, the aims of our current study were: i) assess the patterns of seasonal variation in the abundance and richness of Scarabaeidae in an open pasture and *Eucalyptus* plantation, and their relationship with environmental factors (air temperature and rainfall); ii) examine the influence of the habitat on daily patterns of flight activity of the assemblages; iii) analyze changes in species composition along different seasons and at daily time scale, and iv) examine the interaction between seasonal and daily patterns of the most abundant species.

MATERIAL AND METHODS

Study site

Uruguay is located entirely in the temperate zone (30º–5º south latitude), and the four seasons are clearly defined. The average annual maximum temperature is 22.6°C and the average annual minimum is 12.9°C. The highest temperatures (mean maximum temperature, 29.2°C) occur in the summer months (December to February) and the lowest (mean minimum temperature, 7.5°C) in winter (June to August). The average values of annual accumulated rainfall over the country are between 1200 and 1600 mm, with more or less regular rains throughout the year (Severova 1997, Inumet 2010).

The study was performed in a private ranch in Puntas de Sauce de Maciel, Florida, Uruguay (33°45'47.6"S, 56°19'15.5"W, 161 m.a.s.l.). The farm has a total area of 122 ha, of which 82 ha are used for cattle grazing on native pastures, and a total of 3 ha are occupied by exotic *Eucalyptus* forests used as a shelter for livestock. Two experimental plots were placed in the open pastures and the *Eucalyptus* plantation.

Dung Beetle Sampling

Scarabaeinae and Aphodiinae dung beetles were sampled using baited pitfall traps. Each trap consisted of a buried plastic bucket (12,5 cm diameter and 15 cm depth) with the rim at ground level and filled with 250 cc of a solution of formaldehyde (10%) and a drop of detergent. The bait wrapped in a nylon stocking was placed on a 5 cm mesh wire rack. Three kinds of bait were used: cow dung (CD), horse dung (HD) and rotting lamb meat as carrion (Ca). A total of nine traps (three of each kind of bait) were placed alternately every 25 meters, in each sampling area. The traps were placed simultaneously at the two sites every forthnigth during a year, and remained in the field for 24 h. To study the daily flight activity patterns of every species, each 24-hour sampling was divided into 5 intervals: morning, noon, afternoon, evening, and night. The duration of these sampling periods varied throughout the year depending on the photoperiod (See Table 1). The traps were emptied at the end of each interval and the baits were replaced. The beetle species collected were counted and classified into diurnal, crepuscular and nocturnal.

Table 1. Schedule of sampling periods during the 24 hours according to the photoperiod in each season

	Morning	Noon	Afternoon	Evening	Night
Summer	5:30-11:00	11:00-14:00	14:00-19:30	19:30-20:30	20:30-5:30
Autumn	6:40-11:30	11:30-13:30	13:30-18:00	18:00-19:00	19:00-6:40
Winter	7:40-12:00	12:00-13:00	13:00-17:30	17:30-18:30	18:30-7:40
Spring	6:40-11:30	11:30-13:30	13:30-18:00	18:00-19:00	19:00-6:40

Statistical analysis

The climatological records of the study period were provided by the Durazno Meteorological Station, located approximately 40 km from the work area. Spearman Rank correlations among abundances and species richness of dung beetles and air temperatures (mean, maxima and minimun) and monthly rainfall were performed.

Seasonal and daily activity differences in abundance, and species richness, were evaluated through two-way ANOVA using habitat and month of the year, and habitat and daily activity as main factors respectively.

Changes in community composition of dung beetles between seasons, and diel periods, were assessed by one-way Permutational Multivariate Analysis of Variance (PERMANOVA) and the group dispersion were evaluated by PERMDISP on a similarity matrix of species based on the Bray-Curtis index. Species which contributed at least 1% of the total abundance, and root-root transformed data were used. The results were graphically illustrated with Non-metric Multidimensional Scaling (nMDS) to show the seasonal and daily activity similarity of samples. These analyses were performed with Primer 7.0 software package (Clarke and Gorley 2015).

RESULTS

Seasonal variation in species abundance and richness

Climatological recordings are represented in figure 1. The mean air temperatures of summer (December-February), autumn (March-May), winter (June-August) and spring (September-November) were 23.1°C, 17.1°C, 11.4°C and 16.9°C respectively. The annual rainfall was 863 mm in 2010; an atypical period of deficient rainfall occured since October 2010 to January 2011 (spring/summer).

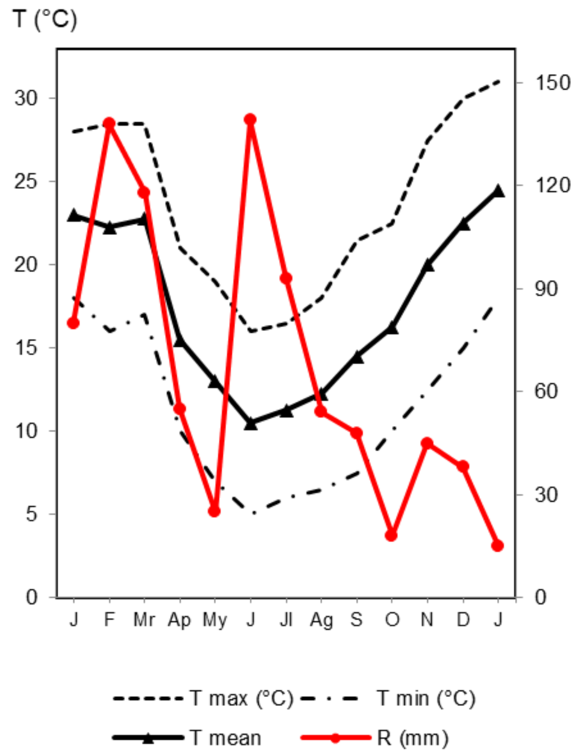

Fig. 1. Climatological recordings at Puntas de Sauce Maciel, Florida (Uruguay), from January 2010 − January 2011.

A total of 2416 individuals representing 17 species of Scarabaeinae and Aphodiinae were collected in both habitats (Table 1). Seasonal variation in the total abundance of Scarabaeidae in both habitats showed, in general, a similar continuous pattern of occurrence from mid-spring (October) to mid-autumn (April). Flight activity declined sharply in May (late autumn) and it was null during all winter (Fig. 2). No significant differences were detected in the abundances, in the month x habitat interaction ($F_{(9, 160)} = 0.95$; $P = 0.50$). Notwithstanding this, flight activity showed more marked fluctuations in the *Eucalyptus* plantation, with two noticeable peaks in April (middle-autumn) and November (last-spring); the activity in these months was significantly higher than those recorded in the immediately preceding and following months, respectively (LSD tests, P <0.05 in all cases) (Fig. 2). In open pasture there were not significant differences in abundances between the months of flight activity.

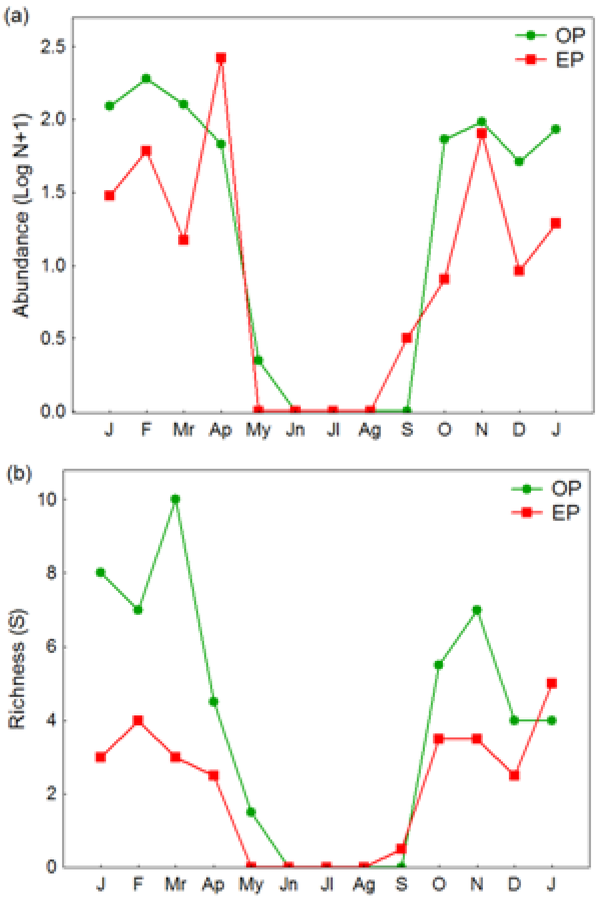

Fig. 2. Monthly variations (mean/trap) in abundance of Scarabaeidae in pitfall traps located in open pasture (OP) and *Eucalyptus* plantation (EP) in Puntas de Sauce Maciel (Florida, Uruguay).

In contrast to abundance, the patterns of seasonal variation in species richness were different between the pasture and the *Eucalyptus* plantation (interaction month x habitat ($F_{(9,160)} = 11.31$; $P < 0.0001$). Species richness in pasture was highest in the period January-March 2010 (summer - early autumn), with a marked peak in March; a minor peak in species richness was observed in November (mid-spring) (Fig. 3). It is interesting to note that species richness in open pasture in January 2011 was significantly lower than the respective in January of previous year. Comparatively, seasonal variation of species richness was less fluctuant within the period of flight activity in the *Eucalyptus* plantation, although it was slightly higher in summer (Fig. 3).

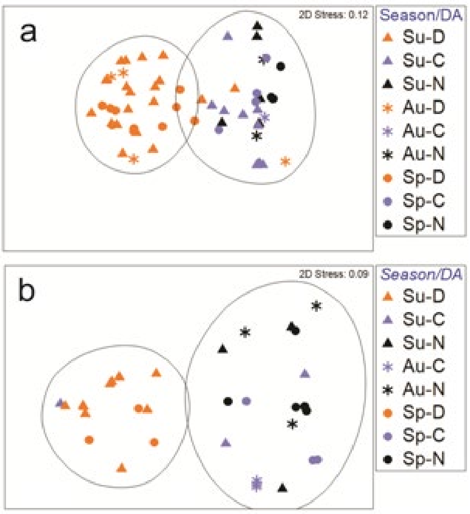

Fig. 3. Monthly variations (mean/trap) in species richness of Scarabaeidae in pitfall traps located in open pasture (OP) and *Eucalyptus* plantation (EP) in Puntas de Sauce Maciel (Florida, Uruguay).

Fluctuations in abundance and species number were positively correlated with air temperatures (mean, maxima and minimun) in both habitats (Table 2); both parameters were drastically reduced or nule when mean and minimal temperatures decreased below 16°C and 10°C respectively, since late-autumn (May) to early spring (September). No correlations were found between monthly rainfall through the whole year and abundance and species richness; however, in pasture, species richness was positively correlated with precipitation when only the months with flight activity were considered (Table 2).

Table 2. Results of Spearman Rank correlations among abundances and species richness of dung beetles and some environmental variables (T: temperature; R_1: monthly rainfall January 2010/January 2011; $R_{2:}$ monthly rainfall excluding winter's months)

	Open pasture (n = 24)		*Eucalyptus* plantation (n = 24)
	Abundance	Richness	Abundance
T mean	0.76 ***	0.77***	0.67***
T max	0.68 ***	0.70***	0.58**
T min	0.79***	0.81***	0.72***
R_1 mm	-0.01	-0.002	0.04
R_s mm	0.41	0.56***	0.48

**P < 0.01; ***P < 0.001.

Daily variation in species abundance and richness

The variation in abundance of dung beetles throughout the day was dependent on the type of habitat (interaction daily activity x habitat: $F_{(2, 90)} = 3.93$, $P = 0.02$). In grasslands, diurnal flight activity was significantly greater than those of dusk and nighttime (LSD test, $P < 0.001$ in both cases). In *Eucalyptus* plantation there was a significant reduction in diurnal flight activity compared to that of the grassland (LSD test, $P < 0.01$); it was also lower, although not significantly different, than those at dusk and night, which were similar to each other and slightly higher than those in the grassland (Table 3).

The pattern of variation in species richness during the day was also habitat-dependent (interaction, $F_{(2, 90)} = 6.87$, $P < 0.01$). In the open pasture, mean species richness per trap was significantly higher during the diurnal period than in the crepuscular and nocturnal periods (LSD test, $P < 0.001$ in both cases). However, in *Eucalyptus* plantation the mean number of species in the diurnal period decreased significantly in comparison to the pasture (LSD test, $P < 0.0001$), being similar to those of crepuscular and nocturnal periods. These two last were similar to those respective of the pasture (Table 3). Table 4 shows dial activity of each species.

Table 3. Mean (± SE) values of abundance and species richness of dung beetles in diurnal (D), crepuscular (C) and nocturnal (N) baited pitfall traps located in open pastures (OP), and *Eucalyptus* plantation (EP). Different letters indicate significant differences ($P < 0.01$)

	Daily activity	Habitat	
		OP	EP
Abundance (n° ind / trap)	D	85.6 ± 15.90 ^{a}	24.1 ± 7.43 ^{b}
	C	23.9 ± 11.00 ^{b}	32.2 ± 19.28 ^{b}
	N	16.2 ± 5.83 ^{b}	38.4 ± 26.50 ^{b}
Richness (n° spp / trap)	D	4.56 ± 0.70 ^{a}	1.56 ± 0.32 ^{b}
	C	2.13 ± 0.38 ^{b}	1.44 ± 0.34 ^{b}
	N	1.31 ± 0.34 ^{b}	1.20 ± 0.22 ^{b}

Table 4. Abundance of dung beetle species collected in an open pasture (OP) and in a *Eucalyptus* plantation (EP) in Puntas de Sauce Maciel (Florida) during different dial periods

Species	OP			EP		
	D	C	N	D	C	N
Large Telecoprid						
Malagoniella bicolor Guérin-Méneville	-	-	1	-	-	-
Medium Telecoprid						
Canthon bispinus Germar	60	2		3	1	
Canthon lividum Blanchard	14	-	-	2	-	-
Canthon curvipes Harold	1	-	-	-	-	-
Canthon muticus Harold	16	-	-	-	-	-
Canthon latipes Blanchard	1	-	-	-	-	-
Large Paracoprid						
Gromphas lacordairii (Oken)	105	-	-	-	-	-
Onterus sulcator Fabricius	3	1	8	8	12	111
Medium Paracoprid						
Ateuchus breve Harold	6	-	-	-	-	-
Canthidium breve Germar	29	-	-	-	-	-
Small Paracoprid						
Onthophagus hircus Mannerheim	694	3	-	291	7	1
Endocoprid						
Ataenius platensis (Blanchard)	140	298	29	4	10	2
Ataenius perforatus Harold			5	17	413	320
Ataenius opatroides Blanchard	-	1	-	-	-	-
Aphodius nigrita Fabricius	4	2	25	-	-	6
Aphodius pseudolividus Balthasar	22	42	83	12	12	35
Parataenius simulator Harold	1	-	-	-	-	-
Total number	946	140	86	321	455	468
Richness	14	5	5	8	6	4

(D: diurnal; C: crepuscular; N: nocturnal).

Seasonal and daily variation of species composition in dung beetle assemblages

Permanova analyses showed that season was not a crucial factor for predicting the assemblage composition of dung beetles neither in pasture (Pseudo-F = 1.83; *P* = 0.10) nor in EP (Pseudo-F = 2.03; *P* = 0.08). nMDS showed that samples of autumn, spring, and summer, group each other in the two habitats (Figs. 4 and 5). SIMPER procedure for the two habitats showed that most of species of the dung beetle assemblages are typifying of the three seasons (from spring to autumn) or typifying of two seasons: spring and summer or spring and autumn (Table 5).

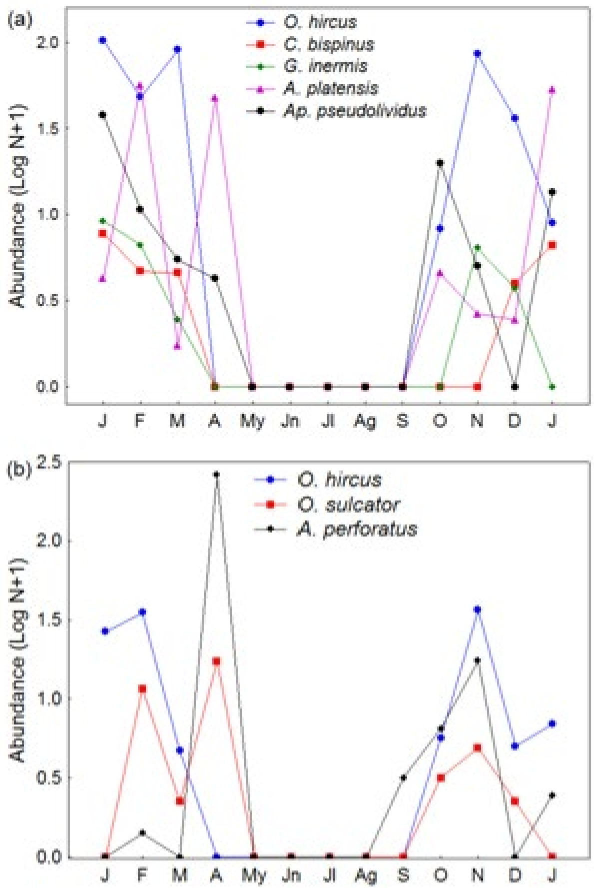

Fig. 4. Non-metric multidimensional scaling of diurnal (D), crepuscular (C) and nocturnal samples (N) of dung beetles in autumn (Au), spring (Sp) and summer (Su) in the open pasture in Puntas de Sauce Maciel (Florida, Uruguay).

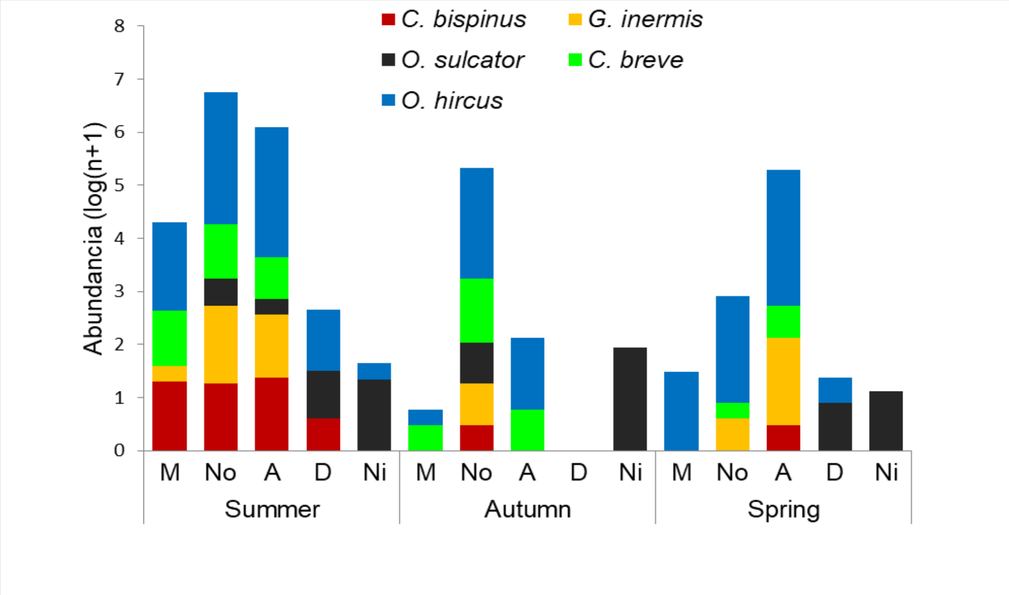

Fig. 5. Non-metric multidimensional scaling of diurnal (D), crepuscular (C) and nocturnal samples (N) of dung beetles in autumn (Au), spring (Sp) and summer (Su) in the *Eucalypus* plantation in Puntas de Sauce Maciel (Florida, Uruguay).

Table 5. Similarity percentages of typifying (>10%) species in the average similarity (within-group), identified by the SIMPER procedure for the dung beetle assemblages analyzed in Puntas de Sauce Maciel (Florida, Uruguay)

	Su	Au	Sp
Open pasture			
O. aff. hircus	42.20	17.71	47.55
G. lacordairii	5.58		6.21
C. bispinus	10.00		
A. pseudolividus	15.91	18.08	31.36
A. platensis	24.42	21.84	10.38
C. breve		16.35	
Average Similarity	**42.45**	**41.66**	**47.63**
Eucalyptus plantatio			
Ataenius perforatus	8.25	83.80	59.10
Onterus sulcator		11.03	26.52
O. aff. hircus	83.06		10.68
Average Similarity	**40.20**	**44.7**	**46.74**

(Sp: spring; Su: summer; Au: autumn).

On the contrary, the daily period of activity was a determinant factor for the segregation of the dung beetle assemblage both in the pasture (Pseudo-F = 26.12; $P = 0.001$) and in the *Eucalyptus* plantation (Pseudo-F = 17.48; $P = 0.001$). There were no difference in dispersion within groups (PERMDISP: F = 3.1889; $P = 0.06$ in open pasture; F = 2.96, $P = 0.08$ in *Eucalyptus* plantation). Particularly, species composition of diurnal samples was markedly different of those of crepuscular and nocturnal respectively in both habitat (Permanova Pair-wise tests, $P = 0.001$ in all cases). Species composition was similar between crepuscular and nocturnal samples (Permanova Pair-wise tests, $P \geq 0.05$) in both habitats. Both nMDS also indicated high degree of overlapping between crepuscular and nocturnal samples, but not between these and diurnal's (Fig. 4 and 5).

Seasonal and daily activity patterns of species

Seasonal variations of the most abundant species show their different monthly fluctuations but also their overlapping through seasons (Figs. 6 and 7).

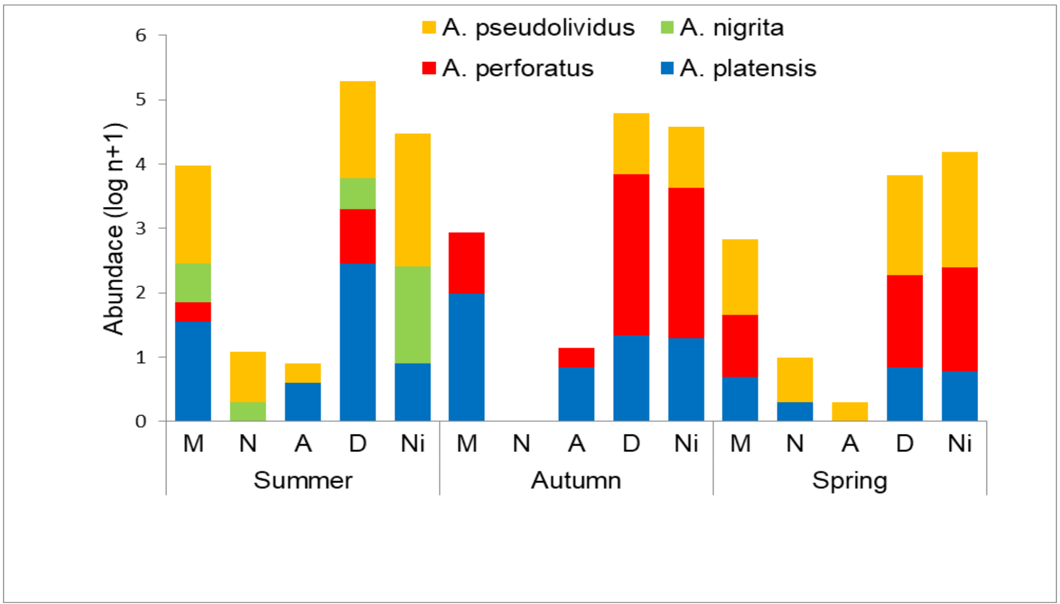

Fig. 6. Monthly flight activity of dung beetle species sampled during 2010 in open pasture in Puntas de Sauce Maciel (Florida, Uruguay).

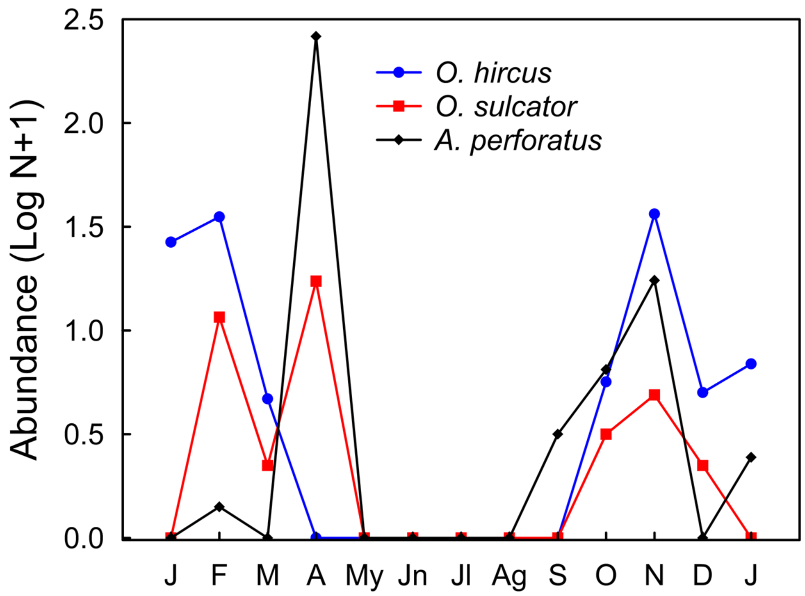

Fig. 7. Monthly flight activity of dung beetle species sampled during 2010 in *Eucalyptus* plantation in Puntas de Sauce Maciel (Florida, Uruguay).

The species' diurnal or crepuscular and nocturnal activity preferences did not change seasonally (Figs. 8 and 9). The vast majority of paracoprid and telecoprid Scarabaeinae species, which predominated in the grassland, were diurnal and their flight activity was concentrated at noon and afternoon in the three seasons (Fig. 8). *Onthophagus hircus* can also extend its activity into the morning and slightly into the twilight in summer and spring. *Canthidium breve* is also active in the morning in summer. In the case of the roller species *Canthon bispinus*, its activity predominates from morning to afternoon during its period of greatest abundance in summer, while in autumn and spring its scarce activity is restricted to midday or afternoon (Fig. 8). Only the large paracoprid *Ontherus sulcator*, which predominated in *Eucalyptus* plantation, showed mainly nocturnal activity during the three seasons (Fig. 8).

In general, non-nester dweller species predominated at dusk and at night in the three seasons of the year, with the exception of *Aphodius pseudolividus* and *Ataenius platensis*, whose flight activity also occurred in the morning within their seasonal periods of greatest activity in summer/spring and in summer/autumn respectively (Fig. 9). It is likely that the morning flight activity of these species occurs at dawn or in the early hours but these time periods were not discriminated in the sampling.

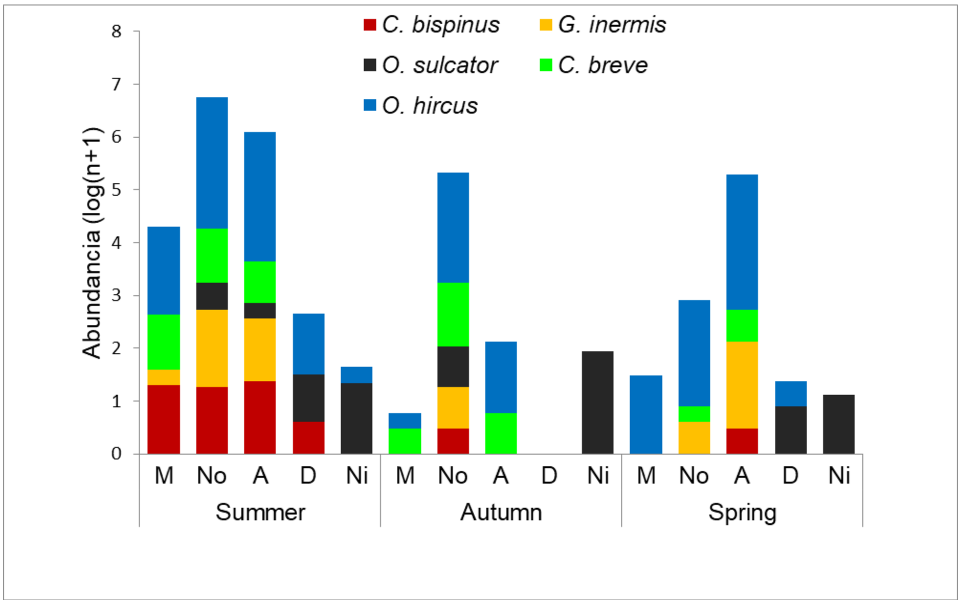

Fig. 8. Seasonal variation of daily flight activity of Scarabaeinae species in a livestock ranch at Puntas de Sauce Maciel, Florida (Uruguay). (M: moorning; N: noon; A: afternoon; D: dusk; Ni: night).

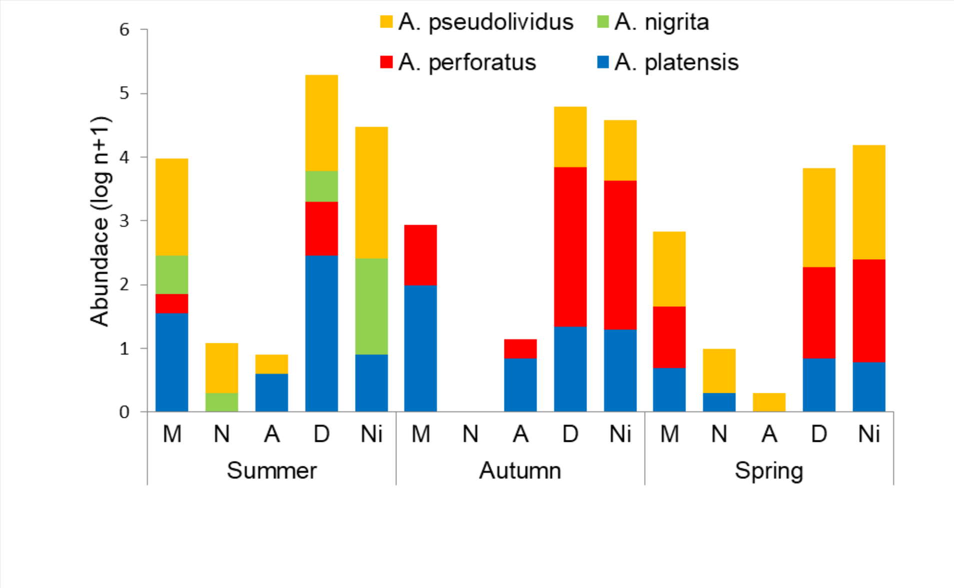

Fig. 9. Seasonal variation of daily flight activity of Aphodiinae species in a livestock ranch at Puntas de Sauce Maciel, Florida (Uruguay). (M: moorning; N: noon; A: afternoon; D: dusk; Ni: night).

DISCUSSION

The seasonal activity of dung beetles was largely determined by air temperature. The continuous activity pattern of the dung beetle assemblage from mid-spring to early autumn is consistent with that already recorded for Scarabaeidae assemblages in grasslands of Uruguay in a previous study (Morelli et al. 2002), and also in subtropical and temperate areas in southern Brazil (da Silva et al. 2013; Cassenote et al. 2019). A similar pattern occurs in northern temperate region, where temperature is also the key factor restricting dung beetle activity (Hanski and Cambefort 1991; Lobo and Cuesta 2021). The studied species were characterized by a wide variety of seasonal patterns: bimodal (spring-summer or sprig-autumn), multimodal (spring-summer-autumn) and unimodal concentrated in summer period. Despite this, the seasonal activity of the species did not represent a key factor in the segregation of them within the community, due to the high overlap of species in similar seasons.

Rainfall was not an important agent determining dung beetle seasonal activity. This is probably due to the fact that the rains are distributed regularly during the year, which is a feature of the temperate climate in Uruguay. Same result was found by the other mentioned studies in Uruguay and southern Brazil (Morelli et al. 2002; da Silva et al. 2013; da Silva and Cassenote 2019). On the contrary, precipitations play a fundamental role driving dung beetle temporal distribution in tropical and subtropical regions where two seasons, dry and wet are clearly differentiated, and temperature values do not show great variation. In those regions, seasonality of rainfall affects the assemblages of dung beetles, which present greater richness and abundance during rainy periods (Neves et al. 2010; Andrade et al. 2011; Abot et al. 2012; Caballero and León-Cortéz 2012; Novais et al. 2016). A detail to note in our study is that species richness in the pasture was positively correlated with precipitation when only those months with beetle activity were considered. This was reflected in the significant reduction in species richness in the last summer months, December/2010 and January/2011, when a period of drought was recorded. Possibly some species in open grasslands were negatively affected by the combination of high temperatures and low levels of precipitation in that period. Although more data are needed, it could be predicted that drier summers negatively influence the activity of some species in grasslands, as occurs during the summer in the Mediterranean region, where the combination of high temperatures and lack of rain usually reduces the number of species (Lumaret and Kirk 1987). Doube (1991) also found that dung beetles are more active during the wet summer months in South Africa, and that dry periods during that season cause a temporary reduction in dung beetle activity.

The daily activity of dung beetles was dependent on the type of habitat, with diurnal species predominating in the open habitat. Diurnal species demonstrated a significantly more negative response than nocturnal species to the conversion of grassland into a forested area. This was reflected in the drastic decrease in the abundance and richness of diurnal species in the *Eucalyptus* plantation. The observed decline of diurnal species in the forest plantation suggests that the abiotic conditions in this area penalize these species because of their requirements of light or temperature to carry out their activities. This pattern was similar to that found by Iannuzzi et al. (2016) in open and closed habitats in the Atlantic rain forest in Brazil.

Our results also indicated that the daily period of activity was a key factor for the segregation of the two main groups which make up the dung beetle assemblage: Scarabaeinae y Aphodiinae. The guild of diurnal species was dominated by the Scarabaeinae species, which they preferred midday and afternoon to search for food. This pattern is analogous to that commonly occurring in Mediterranean regions (Lobo and Cuesta 2021). On the contrary, the crepuscular/nocturnal guild was dominated in abundance and richness by the small species of Aphodiinae both in the open pasture and in the *Eucalyptus* plantation. This is consistent with what happens in temperate regions (or continental climate) of the northern hemisphere (Koskela 1979; Hanski and Cambefort 1991; Kaminski et al. 2015). This might be the method for dwellers to avoid interpecific competition with diurnal tunnelers and rollers.

It is known that daily activity of dung beetles is related, at least partly in endothermic species, to certain physiological characteristics, such us mechanisms of thermoregulation (Verdú et al. 2012), and that it could be closely associated to tolerance to maximum and minimum temperatures, and to the thermal range of each species (Verdú et al. 2006 2007; Giménez et al 2017). Species active in the grassland at midday and afternoon in summer, such as the roller *Canthon bispinus* and the paracoprids *Gromphas lacordairii* and *Onthophagus hircus* would be the most tolerant to high temperatures. These species could probably have active mechanisms of thermoregulation that allow them to dissipate excess body heat (Verdú et al 2012). On the contrary, crepuscular / nocturnal species which avoid high temperatures, such as the big paracoprid *O. sulcator*, would have adaptive thermoregulatory mechanisms to retain heat in order to obtain a prolonged flight performance, as has been demonstrated for other beetle species (Verdú et al. 2012). Overall, no drastic seasonal changes were observed in the species' daily activity preferences. However, it was observed that diurnal species such as *O. hircus* and *Canthidium breve*, whose activities extend from morning to afternoon in spring and summer, are restricted to the warmest hours of midday during autumn, which would be related with their thermal ranges (Verdú et al 2006 2007; Giménez et al 2017).

In addition to this, it has been postulated that diel flight activity might be largely determined by phylogenetic constraints (Niino et al. 2014), *e.g.*, species in the Coprini tribe like *O. sulcator*, are almost all nocturnal, whereas those in Atheuchini, Onthophagini, Phanaeini and Deltochilini are mostly diurnal, as proven by several studies (Montes de Oca and Halffter 1995; Davis 1999; Feer and Pincebourne 2005; Niino et al. 2014; Lobo and Cuesta 2021).

In this study we confirm that dung beetles show well-defined seasonality in southern South America, where temperature, rather than precipitation, is the main factor driving annual seasonal variation in dung beetle species richness and abundance. However, it is very likely that changes in rainfall patterns, with periods of drought in the warmer seasons, could have a negative effect on some dung beetle species, as we barely observed. Taking into account the climate change scenario in which changes in rainfall patterns are predicted with increases in the intensity and duration of droughts (Dai 2013), associated negative effects could be expected on the dung beetle communities in the region and on the ecosystem services they provide. Long-term studies should be carried out to corroborate this question.

We also corroborated that the daily period of activity was a key factor for the segregation of dung beetle assemblages and that it depended on the habitat. Therefore, human impacts on the landscape, such as the replacement of grasslands by forest plantations, can alter the spatial distribution of dung beetle species, especially those with diurnal activity. This basic knowledge is crucial and must be taken into account to design effective long-term conservation measures for this group of insects, especially because of the notable increasing development of forestry and silvopastoral systems in Uruguay in the last 20 years (Bussoni et al. 2017).

CONCLUSIONS

This work conducted on dung beetle assemblages in two different habitats, open pasture and *Eucalyptus* plantation, yielded several conclusions. Firstly, the study documented seasonal variations in abundance and species richness of dung beetles, primarily influenced by air temperature rather than rainfall. Dung beetle activity spanned from mid-spring to early autumn, with marked declines during winter months. In general, rainfall was not a significant factor influencing the seasonal activity of dung beetles, probably due to the regular distribution of rainfall throughout the year in the temperate climate of Uruguay. However, it should be noted that the lack of rain during the period of beetle activity could negatively affect species richness in open habitats.

Species showed a wide variety of seasonal patterns, including bimodal, multimodal, and unimodal distributions across seasons. Despite seasonal fluctuations, species composition within the community showed significant overlap across similar seasons.

Daily activity patterns of dung beetles varied between habitats, with diurnal species predominating in open pasture and crepuscular/nocturnal species dominant in *Eucalyptus* plantation. This habitat-dependent activity suggests that landscape alterations, such as forestation, can impact dung beetle populations, particularly those with diurnal habits.

The study highlighted the role of daily activity in segregating dung beetle assemblages, with diurnal species mainly comprising Scarabaeinae and crepuscular/nocturnal species dominated by Aphodiinae. Daily activity preferences were not drastically influenced by seasonal changes. These findings suggest that physiological traits of species, such as thermoregulation mechanisms, and phylogenetic constraints may influence daily activity patterns.

Understanding the influence of habitat alterations on dung beetle activity is crucial for effective conservation strategies, especially with increasing land use changes.

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