

Original article

Activity patterns of medium and large mammals in two savanna ecosystems in the Colombian Llanos

Patrones de actividad de mamíferos medianos y grandes en dos ecosistemas de sabana de los Llanos colombianos

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Abstract

Neotropical savannas have undergone continuous processes of landscape transformation (e.g., agriculture, oil, gas, and hydrocarbon industry) and very little is known about the ecology and natural history of key biological groups such as terrestrial mammals while the information on behavioral aspects of mammalian species in these ecosystems is very scarce. Here, we aimed to describe the activity patterns of medium and large mammals in two savanna ecosystems in the Colombian Llanos. A set of 60 camera traps was installed in the two ecosystems for 35 days (2100 camera days). We described the activity patterns of nine predominantly nocturnal species. We found no difference in circadian distributions of mammals between ecosystems. *Cuniculus paca* Linnaeus 1758 and *Dasyprocta fuliginosa* Wagler 1832 showed patterns of exclusion probably due to competition whereas other species like *Tamandua tetradactyla* Linnaeus 1758 and *Myrmecophaga tridactyla* Linnaeus 1758 displayed similar activity patterns. We highlight the importance of savannas for the conservation of these species and discuss the relevance of studies on activity patterns for mammal ecology and conservation in Neotropical savannas.

Keywords: Activity periods; Behavioural strategies; Camera traps; Neotropical mammals; Niche overlap; Orinoco basin; Savanna regions.

Resumen

A pesar de que las sabanas neotropicales han sido sometidas a procesos continuos de transformación del paisaje (por ejemplo, la agricultura, la industria de petróleo, gas e hidrocarburos), muy poco se sabe sobre la ecología e historia natural de grupos biológicos importantes como los mamíferos terrestres, y la información asociada con los aspectos comportamentales de las especies de mamíferos que habitan estos ecosistemas es especialmente escasa. El objetivo del estudio fue describir los patrones de actividad de mamíferos medianos y grandes en dos ecosistemas de sabana de los Llanos colombianos. Se instalaron 60 cámaras trampa en los dos ecosistemas durante 35 días (2100 días-cámara). Se describieron los patrones de actividad de nueve especies predominantemente nocturnas. No se encontraron diferencias en las distribuciones circadianas de mamíferos entre ecosistemas. *Cuniculus paca* Linnaeus 1758 y *Dasyprocta fuliginosa* Wagler 1832 mostraron patrones de exclusión explicados probablemente por la competencia, en tanto que otras especies como *Tamandua tetradactyla* Linnaeus 1758 y *Myrmecophaga tridactyla* Linnaeus 1758 mostraron patrones de actividad similares. Se destaca la importancia de las sabanas para la conservación de estas especies y se discute la relevancia de los estudios sobre patrones de actividad para la ecología y conservación de mamíferos en las sabanas neotropicales.

Palabras clave: Periodos de actividad; Estrategias conductuales; Cámaras trampa; Mamíferos neotropicales; Solapamiento de nicho; Cuenca del Orinoco; Regiones de sabana.

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Introduction

The balance of time between activity and resting periods is critical to satisfying the biological needs of animal individuals (Downes, 2001). Since activity periods represent higher energetic costs of mobility (Dunbar, 1988), foraging effort (Weckel, *et al.*, 2006), predation risk (Suselbeek, *et al.*, 2014), and thermal stress (Owen-Smith, 1998), optimization of the time that individuals are active become essential for their survival (Di Blanco, *et al.*, 2017). Mammalian activity patterns reflect physiological and ecological traits of species within a community (Tobler, *et al.*, 2009; Blake, *et al.*, 2012). Typically, the regulation of circadian rhythms is associated with the daily light-dark cycle and some mammals can specialize in a particular period of the day (Mistlberger & Antle, 2011), which allows classification as diurnal, nocturnal, crepuscular, or even cathemeral (Gómez, *et al.*, 2005; Leuchtenberger, *et al.*, 2018). However, mammals can change their activity patterns due to extrinsic (abiotic) and intrinsic (biotic) factors, which are reflected in inter- and intra-specific variations (Di Blanco, *et al.*, 2017).

In mammal communities, activity patterns also reflect interactions between coexisting species, for example, predator-prey relationships (Foster, *et al.*, 2013), or niche differentiation by resource partitioning in species with similar ecological traits such as diet and habitat use (Schoener, 1974; Tobler, *et al.*, 2009; Ferregueti, *et al.*, 2018). Variations in activity patterns among mammal populations may exhibit individuals' strategies to overcome local factors including ecological interactions with other species (Leuchtenberger, *et al.*, 2018). Consequently, mammal species can behave differently depending on their ecological context, which is determined by land use, environmental conditions, and coexisting species (Di Blanco, *et al.*, 2017; Grotta-Neto, *et al.*, 2019). Information on species' niche overlap is therefore important to understand the potential of species to coexist and interact in a community (Estes, *et al.*, 2011).

Throughout more than 3,000,000 km² of Neotropical savannas (Sarmiento, 1983, 1984), there is an important variability of habitats that promotes richness and turnover of mammal species (Morales-Martínez, *et al.*, 2018; Castillo-Figueroa, *et al.*, 2019; Cely-Gómez, *et al.*, 2021). However, little is known about the behavioral patterns of mammals in different savanna types. Particularly, in the savanna ecosystems of the Colombian Llanos, several anthropogenic activities such as livestock raising and oil industry may influence activity periods because of the noise caused by the employment of heavy machinery, the habitat alteration probably increasing competition between species, and the formation of roads to allow human hunting (Payán & Boron, 2019). Regrettably, the current government plans may increase these pressures in the coming years (Departamento Nacional de Planeación-DNP, 2019). Indeed, according to the Colombian government, 70% of the Llanos region has potential for land-use conversion to agricultural systems (rice fields, oil palm, soy), and silvopastoral production (Consejo Nacional de Política Económica y Social-CONPES, 2014; López-Ricaurte, *et al.*, 2017). However, mammal surveys in the Colombian Llanos are limited (Ferrer-Pérez, *et al.*, 2009; Mosquera-Guerra, *et al.*, 2017; Castillo-Figueroa, *et al.*, 2019; Boron, *et al.*, 2019; Aya-Cuero *et al.*, 2019), especially regarding mammalian ecology and activity patterns (Mosquera-Guerra, *et al.*, 2018).

Given that little is known about mammals' activity patterns in the Colombian Llanos and the importance of this information for an in-depth understanding of mammal behavior over human-dominated landscapes, the objectives of this study were to describe the activity patterns of medium- and large-sized mammals in two savanna ecosystems in the Colombian Llanos.

Materials and methods

Study area

The Colombian Llanos occupies around 30.4% of the country and extends from the Colombian Andes Piedmont to the Venezuelan border between 2.5° to 7°N and 74° to 67.5°E

(Romero-Ruiz, *et al.*, 2011), and its high ecosystem and landscape diversity includes a mixture of biogeographic Andean, Amazonian, and Guyanese elements (Romero, *et al.*, 2004; Correa, *et al.*, 2006; Minorta-Cely & Rangel, 2014).

The annual precipitation fluctuates between 667 mm in the driest places and 3,766 mm in the most humid ones. The regional climate has a unimodal rainfall pattern with a dry season between December and March and a rainy season between April and November, June being the wettest month and January the driest one (Minorta-Cely & Rangel, 2014). The altitude ranges between 200- and 1,200-m and the vegetal communities vary depending on flood levels and the topography (Mora-Fernandez, *et al.*, 2011).

The study area localities comprised two savanna ecosystems: Locality 1 (SE-1) corresponded to a floodplain savanna ecosystem in Tame municipality, department of Arauca, in the villages of San Salvador and San Joaquin within the Casanare River basin (6.2398° -71.5863°; 172 m) (Figure 1), characterized by a mosaic of floodplain savannas (74%), riparian stratified forest (16.6%), and exotic pastures (9.4%) (Castillo-Figueroa, *et al.*, 2019), currently facing anthropogenic landscape-scale transformations due to oil and gas industry activities. Farmers also use the highly fertile flooded savannas to grow different crops (Baptiste & Ariza, 2008) and, therefore, the forests are partially fragmented (30%) (Castillo-Figueroa, *et al.*, 2019). Locality 2 (SE-2) corresponded to an aeolian savanna ecosystem in the locality of Altagracia, Trinidad municipality,

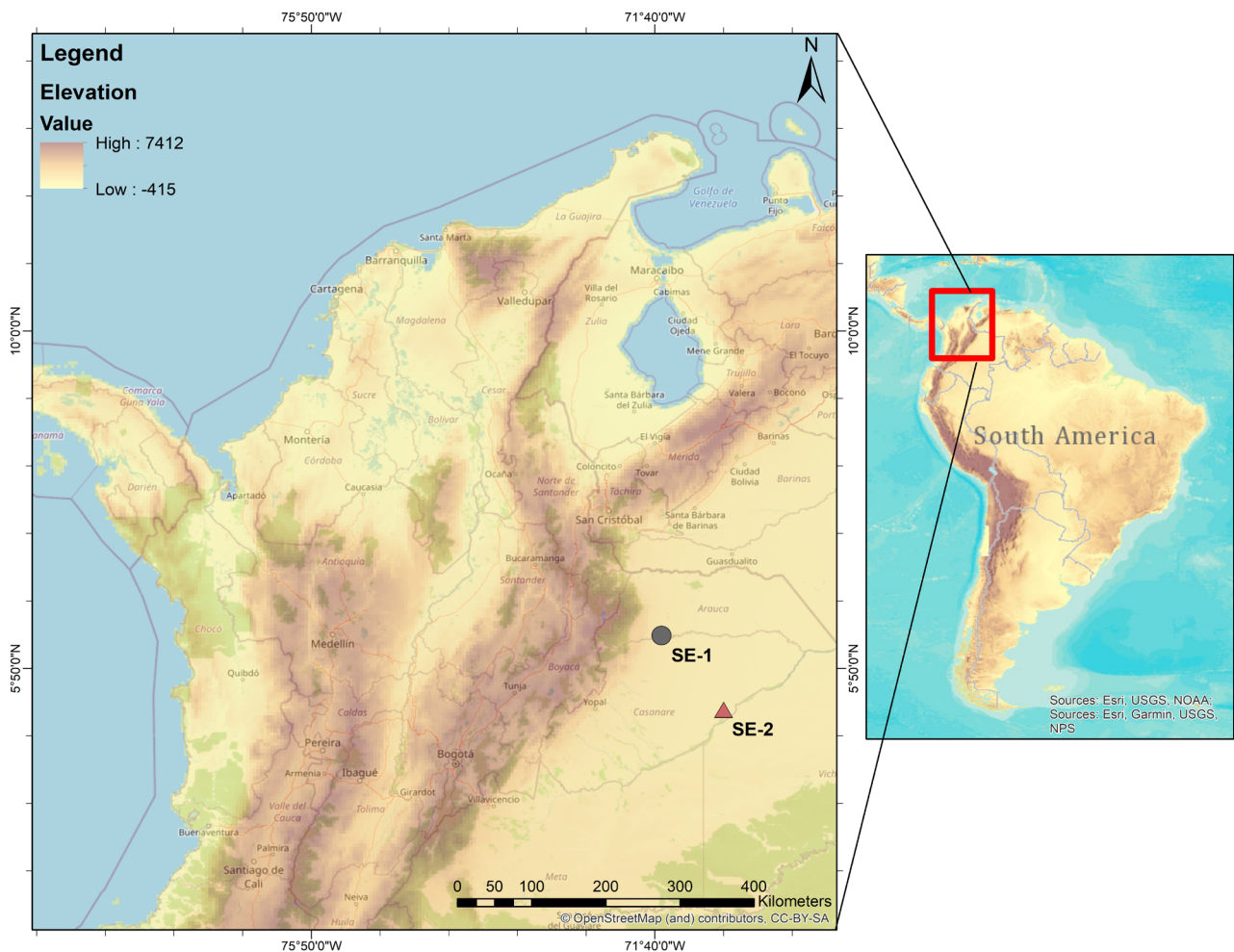


Figure 1. Savanna ecosystems in Colombian Llanos. Gray circle correspond to floodplains savanna in Arauca department (SE-1) and pink triangle to aeolian savannas in Casanare department (SE-2)

department of Casanare, in the private reserves of San Cristobal and Santa Marta, within the Pauto, Caños Yatea, and Garcero River basins (5.3204° -70.8310°; 119 m) (**Figure 1**) characterized by a mosaic of aeolian floodplain savannas (71.1%), floodplain forests (14.2%), grasslands (0.6%), exotic pastures (9.8%), and crops (4.3%) transformed by human activities including hydrocarbon projects, livestock raising, improved pastures, and rice crops (**Castillo-Figueroa, et al., 2019**).

Medium and large-sized mammal sampling

We sampled medium (1-15 kg) and large-sized terrestrial mammals (>15 kg) and carried out the fieldwork simultaneously in the two localities (SE-1, SE-2) at the end of the wet season (October to November 2017). We situated cameras using a 1 km grid to ensure sufficient spacing between them considering each camera as an independent site (**O'Brien, et al., 2003**) for a total of 30 camera traps in each ecosystem during 35 days (**Table 1**). All camera traps (Bushnell Trophy Cam) were set at an average height of 40 cm above the ground and programmed to take three pictures per trigger one-second intervals. Cameras operated 24h/day recording the moon phase, date, and time of each photograph. We did not use bait to attract mammals.

Although the sample size was small, it was very representative (>90%) of each savanna ecosystem according to Chao 2 estimator (**Castillo-Figueroa, et al., 2019**) (**Table 1**). We determined the differences between the two mammal assemblages by using an analysis of similarity (ANOSIM) (**Castillo-Figueroa, et al., 2019**), a non-parametric permutation test based on 9,999 permutations, to evaluate the difference between two or more sampling units with R values between +1 (total dissimilarity) and -1 (total similarity) (**Clarke, 1993**).

Data analysis

For the taxonomic identification of species, we used the guides by **Ramírez-Chaves, et al. (2016)** and **Solari, et al. (2013)** directly from the pictures with no automated identification software. To obtain the metadata from the images (hour, date, moon phase, temperature) we used the NAIRA software (**Pulido-Castelblanco, et al., 2017**). Photographs of the same species in the same place after an hour interval were considered as independent events (**O'Brien, et al., 2003**; **Cruz, et al., 2014**).

We described the activity patterns of all the species detected but we only analyzed those with a minimum of 20 independent events in each locality to then categorize them according to their activity patterns. We classified each species record as diurnal, nocturnal, or crepuscular (1h before and after sunrise and sunset) following **Gómez, et al. (2005)**. Crepuscular hours were calculated using the Moonrise 3.5 software (**Sidell, 2002**) estimating sunset and sunrise to make data comparable (**Porfirio, et al., 2016**). Then, we categorized species following **Gómez, et al. (2005)** based on the percentage of records in the different periods: 1) Diurnal ($\geq 70\%$ of records occurring during the day); 2) nocturnal ($\geq 70\%$ of records during the night); 3) crepuscular (from 50 to 60% of records during crepuscular periods); 4) crepuscular/diurnal (from 60 to 70% of records during the day and crepuscular periods); 5) crepuscular/nocturnal (from 60 to 70% of records during the night and crepuscular periods); 6) cathemeral, when records were randomly distributed along the day cycle.

Table 1. Species sampling of medium and large-sized mammals from SE-1 (Arauca) and SE-2 (Casanare)

Species sampling	SE-1	SE-2
Sampling effort	1050 trap-days	1050 trap-days
Species representativeness	90.38%	97.32%
Chao 2 estimator mean \pm SD	15.49 \pm 0.5	12.33 \pm 0.16

To parse out activity overlaps between species sharing the same trophic resources in each locality (i.e., frugivorous rodents and anteaters), we applied the Morisita-Horn test (Horn, 1966) using Past 3.0 (Hammer, *et al.*, 2001). Finally, for the activity patterns of species present in both ecosystems, we compared them using the Mardia-Watson-Wheeler W test, a non-parametric test that assesses if there is a difference in the distribution of two or more circular samples (Batschelet, 1981; Mardia & Jup, 2000) with the null hypothesis posing that both samples come from the same population and, therefore, a p-value over 0.05 means there is no difference between the two activity patterns analyzed. The p-value is calculated assuming that the statistical value of W follows a Chi-squared distribution (Di Blanco, *et al.*, 2017). For these analyses, we used the Oriana 4.01 software (Kovach, 2011).

Results

We recorded 16 mammalian species, 14 in SE-1 and 12 in SE-2, but we analyzed only nine (six species in SE-1 and seven in SE-2) as the others did not comply with the minimum number of independent events required (20 events or more) (Table 2). Four of the species

Table 2. Activity patterns of medium and large-sized mammals from SE-1 (Arauca) and SE-2 (Casanare). Crep/Noc corresponds to the species showing a crepuscular/nocturnal behavior

Site	Taxa	Number of events	Percentage of records (%)			Activity pattern
			Diurnal	Nocturnal	Crepuscular	
Arauca (SE-1)	<i>Didelphis marsupialis</i>	18	5.5	94.5	0	Nocturnal
	<i>Dasypus novemcinctus</i>	22	22.7	68.2	9.1	Crep/Noct
	<i>Tamandua tetradactyla</i>	29	20.7	69	10.3	Crep/Noct
	<i>Myrmecophaga tridactyla</i>	45	24.4	69	6.6	Crep/Noct
	<i>Hydrochoerus hydrochaeris</i>	1	100	0	0	Diurnal
	<i>Cuniculus paca</i>	48	16.6	79	4.4	Nocturnal
	<i>Dasyprocta fuliginosa</i>	132	75.8	22.8	1.4	Diurnal
	<i>Cerdocyon thous</i>	10	50	40	10	Cathemeral
	<i>Puma yagouaroundi</i>	3	66.7	0	33.3	Crep/Day
	<i>Leopardus pardalis</i>	13	23.1	61.5	15.4	Crep/Noct
	<i>Eira barbara</i>	14	35.8	50	14.2	Cathemeral
	<i>Mazama gouazoubira</i>	6	66.6	16.7	16.7	Crep/Day
	<i>Odocoileus cariacou</i>	36	41.6	55.6	2.8	Cathemeral
	<i>Pecari tajacu</i>	139	34.8	39.1	26.1	Cathemeral
Casanare (SE-2)	<i>Didelphis marsupialis</i>	28	3.6	85.7	10.7	Nocturnal
	<i>Dasypus novemcinctus</i>	6	0	100	0	Nocturnal
	<i>Tamandua tetradactyla</i>	20	20	70	10	Nocturnal
	<i>Myrmecophaga tridactyla</i>	28	14.3	78.5	7.2	Nocturnal
	<i>Hydrochoerus hydrochaeris</i>	26	65.4	26.9	7.7	Crep/Day
	<i>Cuniculus paca</i>	25	4.3	87	8.7	Nocturnal
	<i>Dasyprocta fuliginosa</i>	54	92.6	3.7	3.7	Diurnal
	<i>Cerdocyon thous</i>	3	0	100	0	Nocturnal
	<i>Puma concolor</i>	5	60	40	0	Cathemeral
	<i>Leopardus pardalis</i>	6	33.3	66.7	0	Cathemeral
	<i>Odocoileus cariacou</i>	50	80	6	14	Diurnal
	<i>Pecari tajacu</i>	7	85.8	14.2	0	Diurnal

with > 20 records were present in the two localities: the southern tamandua (*Tamandua tetradactyla* Linnaeus 1758), the giant anteater (*Myrmecophaga tridactyla* Linnaeus 1758), the paca (*Cuniculus paca* Linnaeus 1766), and the black agouti (*Dasyprocta fuliginosa* Wagler 1832).

Activity patterns of mammal species

In SE-1, pacas had the highest proportion of nocturnal activity (79%) whereas the black agoutis had the most daytime events (75.8%) (**Figure 2**). Nine-banded armadillos (*Dasypus novemcinctus* Linnaeus 1758), southern tamanduas, and giant anteaters showed a crepuscular/nocturnal behavior (**Table 2**), and collared peccaries (*Pecari tajacu* Linnaeus 1758) were detected all day long with similar activity proportions.

In SE-2, black-eared opossums (*Didelphis marsupialis* Linnaeus 1758) had the highest proportion of nocturnal activity (85.7%) while black agoutis had the greatest proportion of diurnal activity (92.6%) followed by white-tailed deer (*Odocoileus cariacou* Boddaert 1784) with 80% (**Figure 3**). The capybaras appeared to show a crepuscular/diurnal behavior while southern tamandua (70%) and giant anteater (78.5%) photos were taken mostly at night (**Table 2**).

Activity pattern overlaps and comparison between ecosystems

In both ecosystems, pacas and black agoutis showed little overlapping (SE-1: 0.26, SE-2: 0.04) compared to giant anteaters and southern tamanduas, both with high values in each ecosystem (SE-1: 0.73, SE-2: 0.62). The W tests showed non-significant within-species differences in their 24-hour cycles between the two localities (**Table 1S**, <https://www.raccefyn.co/index.php/raccefyn/article/view/1461/3136>).

Discussion

Although ecological and environmental differences across the Llanos influence mammal communities' structure (Castillo-Figueroa, *et al.*, 2019), our results show that this is not necessarily reflected in species activity patterns. The comparison of medium and large-sized terrestrial mammals activity patterns in the two savanna ecosystems under study may

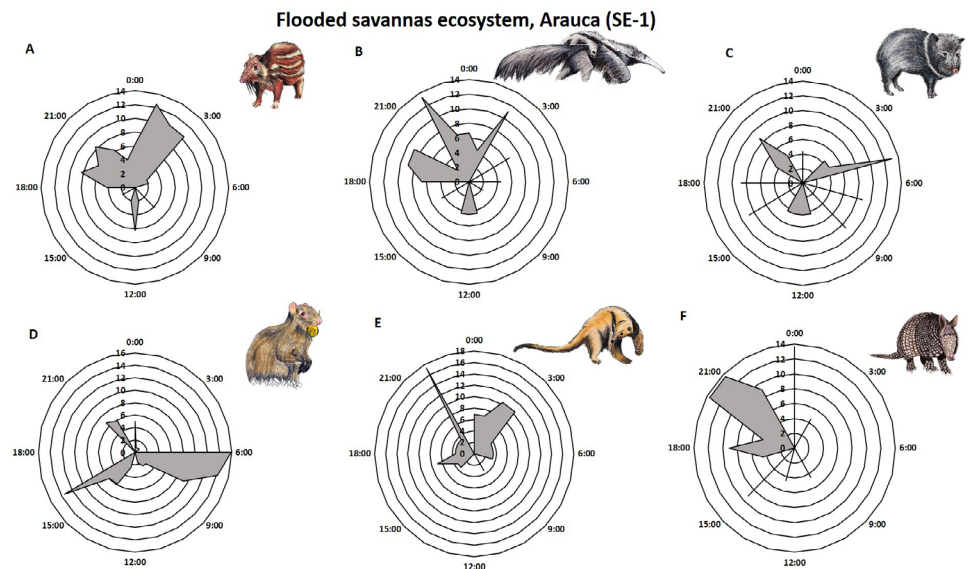


Figure 2. Activity patterns of medium- and large-sized mammals in SE-1 (Arauca). (A) *Cuniculus paca*. (B) *Myrmecophaga tridactyla*. (C) *Pecari tajacu*. (D) *Dasyprocta fuliginosa*. (E) *Tamandua tetradactyla*. (F) *Dasypus novemcinctus*. Gray bars represent the number of independent events (n) per hour

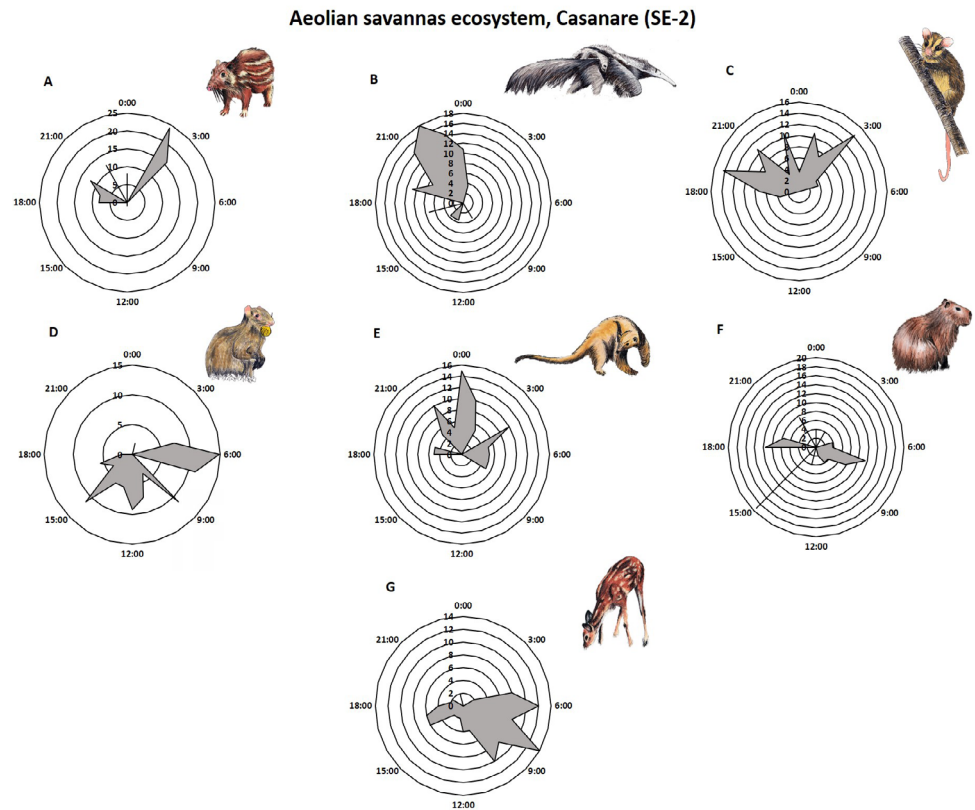


Figure 3. Activity patterns of medium- and large-sized mammals from SE-2 (Casanare). (A) *Cuniculus paca*. (B) *Myrmecophaga tridactyla*. (C) *Didelphis marsupialis*. (D) *Dasyprocta fuliginosa*. (E) *Tamandua tetradactyla*. (F) *Hydrochoerus hydrochaeris*. (G) *Odocoileus cariacou*. Gray bars represent the number of independent events (n) per hour

have been influenced by detectability and abundance differences among species in the two sites (Castillo-Figueroa, *et al.*, 2019) as from the 16 species recorded in both sites, only four were shared in both localities. We found no differences in mammals activity patterns between the two savanna ecosystems, but the activity patterns of each species showed variations compared to those reported in studies conducted in other regions and climatic seasons (Gómez, *et al.*, 2005; Blake, *et al.*, 2011; Foster, *et al.*, 2013; Albanesi, *et al.*, 2016; Dias, *et al.*, 2019).

Species activity patterns

Pacas exhibited nocturnal activity as reported in previous studies (Gómez, *et al.*, 2005; Blake, *et al.*, 2012; Huck, *et al.*, 2013; Leuchtenberger, *et al.*, 2018; Dias, *et al.*, 2019), and in both savanna ecosystems (Figures 2A and 3A), the 0h-3h period was their most active. However, there may be a regional variation as in the Brazilian pampa the highest activity was recorded between 1h-05h period (Leuchtenberger, *et al.*, 2018) while in México's Pacific Coastal Plain, the highest peak of activity was registered between 20h and 22h (Hernández-Hernández, *et al.*, 2018).

The nine-banded armadillo was nocturnal with a peak of activity between 18h and 0h (Figure 2F), however, some studies have reported variations in peak activity, with the highest activity between 0h and 6h, suggesting changes in response to habitat perturbation (Ramírez-Mejía & Sánchez, 2016) and habitat patch size, with peaks in crepuscular hours (Norris, *et al.*, 2010). Possibly, temperatures also influence this species' activity pattern during daytime (McBee & Baker, 1982; Reis, *et al.*, 2006).

The white-tailed deer was diurnal with the highest peak between 6h and 11h (**Figure 3G**), similar to that reported for this species by **López-Tello, et al.** (2015) with the most active periods from 9h to 11:59h. Previous studies have shown variations in this species' activity patterns depending on environmental conditions (ambient temperature and seasonality). For example, in the mountain cloud forest of the Peruvian Andes, the white-tailed deer has been described as a cathemeral species (**Jiménez, et al.**, 2010).

Capybaras showed a crepuscular-diurnal activity with the highest peaks during the early day (7h) and before sunset (16h) (**Figure 3F**). This behavior possibly reduces the risk of nocturnal predators as reported in similar ecosystems in the Brazilian Pantanal (**Foster, et al.**, 2013). Typically, capybaras have nocturnal and cathemeral activity (**Gómez, et al.**, 2005; **Foster, et al.**, 2013; **Rodríguez, 2013**; **Rinaldi, 2014**; **Leuchtenberger, et al.**, 2018) meaning they may be more nocturnal in areas with high human contact during the day (**Rodríguez, 2013**), but with activity peaks also during the day and dusk to prevent encounters with nocturnal predators such as jaguars (*Panthera onca* Linnaeus 1758) and pumas (*Puma concolor* Linnaeus 1771) (**Foster, et al.**, 2013).

The collared peccary exhibited a cathemeral pattern with the maximum number of events at 5h but many small peaks during the day and night (**Figure 2C**). Some studies have reported this species as strictly diurnal in the Peruvian Amazon (**Tobler, et al.**, 2009) and Bolivia's Chaco (**Maffei, et al.**, 2004), while others have reported the same cathemeral pattern in the Yungas piedmont forest in Argentina (**Albanesi, et al.**, 2016). The flexibility of this pattern allows mammals to adjust their activity time to reduce encounters with predators and competitors, or to reduce the energetic cost of thermoregulation (**Donati & Borgognini-Tarli, 2006**).

The black-eared opossum had two activity periods: between 18h-23h and 0h-3h (**Figure 3C**), which is considered mainly nocturnal (**Arroyo-Arce, et al.**, 2017). In Costa Rica, this species highest activity period goes from 21h-23h and 0h-2h (**Vaughan & Hawkins, 1999**). On the other hand, the black agouti was diurnal with two peaks (**Figure 2D and 3D**), one in the early morning (6h-9h) and the other in the late afternoon (14h-16h) as has been also reported in the lowland forest of Ecuador (**Blake, et al.**, 2011).

Giant anteaters and southern tamanduas were nocturnal in the aeolian savanna, with higher peaks between 21h-3h (**Figures 2B and E**), and crepuscular-nocturnal in the floodplain savanna, with peaks before sunset and dawn (**Figures 3B and E**). Some studies have reported giant anteaters cathemeral activity as it helps for thermoregulation, which is particularly important in insectivorous mammals with low metabolic rate as is the case of this species (**McNab, 1984**; **Camilo-Alves & Mourão, 2006**). To minimize energetic costs, nocturnal activity should be limited when nighttime temperatures are low (**Gerkema, et al.**, 2013; **Bennie, et al.**, 2014) and it would be more efficient in crepuscular hours.

Activity patterns overlap and comparison between ecosystems

Resource partitioning was clear between pacas and black agoutis since their activity pattern overlap was among the lowest in the two ecosystems. Both rodents feed on fallen fruits and seeds (**Emmons & Feer, 1997**) and perhaps there is a time division, as suggested by **Blake, et al.** (2011) and **Tobler, et al.** (2009). Besides, the difference in size between pacas (6-12 kg) and black agoutis (3.5-6 kg) (**Pérez, 1992**; **Emmons & Feer, 1997**) may contribute to niche partitioning in these rodents considering that the size is related to the demand for trophic resources and energy expenditure (**Gómez-Ortiz & Moreno, 2017**). However, it is important to assess other niche dimensions such as habitat use.

On the other hand, giant anteaters and southern tamanduas activity patterns greatly overlapped. Although both species are obligate insectivores, giant anteaters feed mainly on terrestrial ants and southern tamanduas on arboreal ants and termites (**Sandoval-Gómez, et al.**, 2012; **Gallo, et al.**, 2016) and, therefore, they can forage at the same time as there is no resource overlap.

No differences were found in the circadian distribution of mammals between the two savanna ecosystems (**Table 1S**, <https://www.raccefyn.co/index.php/raccefyn/article/view/1461/3136>), probably due to three main hypotheses: 1) local factors influencing activity periods such as climate, temperature, and daylight hours (**Di Blanco, et al., 2017**) may be similar in the two places; 2) hunting pressure and other anthropogenic disturbances (**Lendrum, et al., 2017; Gaynor, et al., 2018**) could be similar in the two sites, and 3) considering that shifts in circadian distributions can impose high fitness costs (**Kronfeld-Schor & Dayan, 2003**), mammals' endogenous clock constraints tend to limit activity pattern plasticity in the different sites (phylogenetic constraints) (**Gaynor, et al., 2018**), which would explain why activity pattern variation of medium and large mammals at the intraspecific level may be less than that at the interspecific level (**Romero-Muñoz, et al., 2010**) as in our results.

Bearing in mind that human disturbances such as crops and oil industry are present in both ecosystems, medium and large-sized mammals' activity patterns in them may be related not only to daily light-dark cycles, but also to anthropogenic pressures probably affecting species interspecific relationships (**Lendrum, et al., 2017**). Although we did not quantify human disturbance, we acknowledged the potential importance of anthropogenic impacts on activity patterns in both ecosystems. Moreover, as **Dias, et al. (2019)** have pointed out, the availability of food resources may be related to climatic seasons depending on the mammal guild since species tend to display behavioral adjustments to environmental conditions (**Ferreguetti, et al., 2017**). Here, however, we sampled a specific climatic season (transition between the rainy season and the dry season), so future studies should compare changes in the activity patterns in different climatic seasons and level of human disturbance to understand how changes in resources due to natural and human-made conditions can affect species behavior.

Given the differences in mammal diversity across the savanna ecosystems, understanding how species interact within and between savanna types is crucial as each ecosystem harbors a highly distinct mammal assemblage (ANOSIM $R = 0.23$, $p < 0.01$) (**Castillo-Figueroa, et al., 2019**). This information is crucial to adequately manage human disturbances that may affect species' behavior and their ecological interactions in the region. For example, some studies have suggested that certain species can adapt to activity periods with minimum human disturbance and noise (**Payán & Boron, 2019**), yet this has not been extensively tested in Neotropical savannas, which are highly transformed ecosystems. In fact, considering the intensity of agricultural activities that threaten the mammal diversity of this region, and taking into account the national government plans (**DNP, 2019**) oriented to expand productive lands for agriculture almost tenfold from 40 km² to 3,000 km² in the Colombian Llanos, it is urgent to further study mammals and their needs to design effective conservation plans and protect savanna ecosystems.

Final considerations

Activity patterns constitute an important component of the natural history and ecology of mammals. However, the knowledge on mammal activity across Neotropical savannas is scarce and further studies are required for an in-depth understanding of interactions between biotic, abiotic, and human factors. Here we described the activity patterns of nine species with little overlapping for frugivorous rodents and high for anteaters, which may reflect temporal partitioning to avoid competition between pacas and black agoutis and the fact that ecological features other than temporality likely allow the coexistence of giant anteaters and southern tamanduas (e.g., dietary composition and spatial dimension). We found no differences in the circadian distribution of the four species sharing the two savanna ecosystems, possibly because of phylogenetic restrictions associated with endogenous clock constraints, as well as similar local factors and human disturbances in both of them. Considering the accelerating transformations in savanna regions, it is urgent to keep studying their ecological characteristics as they may contribute important information for conservation and management plans of mammalian species in the future.

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Supplementary Information

Table 1S. Comparisons of circadian distributions of four species present in the two savanna ecosystems. Mardia-Watson-Wheeler tests (W), and statistical probability value ($P < 0.05$ as significant). See the table 1S in <https://www.raccefyn.co/index.php/raccefyn/article/view/1461/3136>

Author contributions

DCF: analyzed the data, contributed to the theoretical and conceptual framework, wrote the paper, prepared figures, and tables, and reviewed the drafts of the paper; DMM: wrote the paper, contributed to materials and methods, prepared the figures, and reviewed the drafts of the paper; MERP wrote the paper, contributed to the theoretical and conceptual framework, designed the mammal sampling, and reviewed the drafts of the paper.

Conflicts of interest

The authors declare no conflicts of interest.

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