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Article

Anteaters on the edge: giant and lesser anteaters (*Myrmecophaga tridactyla* and *Tamandua tetradactyla*) at their geographic distributional limits in Paraguay

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ABSTRACT. Species tend to be less abundant at the limits of their geographic distribution. Giant and lesser anteaters have their southernmost limits in Argentina and Paraguay, where scarce information exists regarding their ecology and conservation. We present a study carried out in the Paraguay River floodplain, in an area dedicated to cattle rearing using native grasses in a subtropical flooded savanna associated with naturally occurring forest islets, wetlands and palm groves. Using camera-traps within three different forest types, we estimated parameters related to habitat preference, social behavior and activity patterns of both species. Results show that capture success was greater in the Floodable sub-humid forest islets (FSF), compared to other types of forests: Riparian forests associated with wetlands (W-RF) and Mesoxerophytic semi-deciduous forests dominated by *Schinopsis balansae* (MXF). Most detections corresponded to solitary anteaters, although mother-young pairs were occasionally observed during summer. Both species showed a nocturnal and crepuscular activity pattern with a peak of records around midnight. *Myrmecophaga tridactyla* was detected between 11°C and 26°C, while *Tamandua tetradactyla* occurred between 15°C and 23°C. Future research that incorporates systematically taken data in other different habitats, including grasslands and shrublands, during all seasons of the year is recommended.

KEYWORDS. Camera-traps, Humid Chaco, floodable forest.

RESUMEN. Osos en el borde: oso hormiguero gigante y oso melero (*Myrmecophaga tridactyla* y *Tamandua tetradactyla*) en sus límites de distribución geográfica en Paraguay. Las especies tienden a ser menos abundantes en los límites de su distribución geográfica. El oso hormiguero y el oso melero tienen su límite de distribución al Sur en Argentina y Paraguay, donde existe escasa información sobre su ecología y conservación. Presentamos un estudio realizado en la planicie de inundación del Río Paraguay, en un área dedicada a la ganadería sobre pasturas nativas en sabanas subtropicales inundables asociadas con isletas de bosques naturales, humedales y palmares. Estimamos parámetros referentes a preferencia de hábitat, comportamiento social y patrones de actividad de ambas especies a través del uso de cámaras trampa en tres tipos de bosques. Los resultados indican que el éxito de captura fue mayor en las islas de bosques subhúmedos inundables, comparado con los otros tipos de boques: bosques riparios asociados a humedales y bosques semicaducifolios mesoxerofíticos dominados por *Schinopsis balansae*. La mayoría de las capturas corresponde a osos solitarios, aunque ocasionalmente fueron observadas hembras cargando a sus crías durante el verano. Ambas especies mostraron un patrón de actividad nocturno y crepuscular con un pico de registros alrededor de la medianoche. *Myrmecophaga tridactyla* fue detectado entre 11°C y 26°C, mientras que *Tamandua tetradactyla* apareció entre 15°C y 23°C. Se recomiendan futuras investigaciones que incorporen datos tomados sistemáticamente en otros tipos de hábitats, incluyendo pasturas y matorrales, durante todas las estaciones del año.

PALABRAS CLAVE. Cámaras trampa, Chaco Húmedo, bosque inundable.

The giant anteater (*Myrmecophaga tridactyla* Linnaeus, 1758) is distributed from Honduras, through Paraguay and Argentina (Miranda *et al.*, 2014a); while the lesser anteater (*Tamandua tetradactyla* Linnaeus, 1758) occurs only in South America (Miranda *et al.*, 2014b). Both species occur sympatrically throughout most of their geographic distribution (Fonseca *et al.*, 1996; Paglia *et al.*, 2012). However, very little information exists on the population status of the giant anteater across its range (Quiroga *et al.*, 2016), especially in Paraguay (De La Sancha *et al.*, 2017).

Myrmecophaga tridactyla is listed as Vulnerable by national (APM & SEAM, 2017) and global (IUCN, 2014a) assessments. The species is considered the most threatened mammal of Central America, apparently extirpated from Belize and Guatemala, and has disappeared from parts of Costa Rica (Miranda *et al.*, 2018). In addition, the national status for *M. tridactyla* in Uruguay is Extinct (Fonseca &

Rylands, 2004; Fallabrino & Castiñeira, 2006), locally extinct in some parts of Brazil (Chiarello *et al.*, 2007; Miranda *et al.*, 2018) and eastern Paraguay (Smith, 2012).

The main causes of decline of the giant anteater populations are the reduction, deterioration and fragmentation of habitats (Rodrigues *et al.*, 2008; De Matos *et al.*, 2019). There is considerable uncertainty regarding how fast the species responds to habitat loss, and how time-delayed responses vary in space (Semper-Pascual *et al.*, 2018). Habitat loss may lead to a decrease in population size and isolation among remnant populations; for instance, Collevatti *et al.* (2007) showed that the population of *M. tridactyla* in Emas National Park (Brazil) has a low level of genetic diversity and a high level of inbreeding.

Tamandua tetradactyla is listed as Least Concern at national (APM & SEAM, 2017) and global (IUCN, 2014b) levels. The species is widespread in Paraguay, but local extinction has occurred in large areas of eastern Paraguay, remaining common in the Humid Chaco but less so in the Dry Chaco (Smith, 2007). In Uruguay, *T. tetradactyla* is considered threatened or insufficiently known (Fallabrino & Castiñeira, 2006).

The distribution of anteaters is poorly known, there is no information regarding the abundance of individuals and there is little data available for wild populations especially outside Brazil (Smith, 2007; Alzate-Gaviria *et al.*, 2016; Miranda *et al.*, 2018). Even recently, some unexpected records of *M. tridactyla* outside the range of the known distribution for the species have also been reported (e.g. in an interandean zone of Colombia, Figel *et al.*, 2015).

Habitat preference in giant and lesser anteaters varies among regions. In the Brazilian Pantanal, for instance, *M. tridactyla* was recorded mostly in open grasslands, scrub grasslands and forest edges, while *T. tetradactyla* was found mainly in forests and forest edges (Desbiez & Medri, 2010).

Although giant anteater studies can be found in Brazil (Miretzki & Goss Braga, 2014; Passos *et al.*, 2016; Mamalis *et al.*, 2018) and the North of Argentina (Perez Jimeno & Llarin Amaya, 2009; Quiroga *et al.*, 2016), data of these species in Paraguay is still scarce or even absent (De La Sancha *et al.*, 2017;Smith & Rios, 2018). Most of the Paraguayan Chaco (a convergence of Pantanal, Cerrado, Dry and Humid Chaco ecoregions) is located within the area of the *M. tridactyla* geographic distribution, however, our study area is located a few kilometers from the possibly extinct zone towards the southern limit (Miranda *et al.*, 2014a).

The aim of this research was to study the giant and the lesser anteaters in the Paraguayan Humid Chaco using camera-traps in order to estimate parameters related with habitat preference, social behavior and activity patterns of both species in this poorly known region of their distribution.

MATERIALS AND METHODS

Study area. The study was performed in a cattle ranch of the Humid Chaco Ecoregion in Paraguay (Fig. 1). The property is located in the floodplain of the Paraguay River and is mainly dedicated to extensive free-range cattle ranching since at least 1904, however, no evidence of drastic forest clearings was found in the last 114 years (visual comparative of a drawn map from 1904 signed by E. Dominguez and vegetation map elaborated by Z. El Raiss), maintaining its original vegetation cover, except for selective extraction of wood used for cattle ranching infrastructure (*i.e.*, cabin construction, fencing and bridges mostly from *Schinopsis balansae* Engler, *Copernicia alba* Morong and *Prosopis* spp.) (Laino *et al.*, 2017). Predominant ecosystems of the area include wetlands and natural vegetation formations conditioned by topography and frequent flooding (Ginzburg & Adamoli, 2006) creating a mosaic of subtropical forests, grasslands and marshes (Mereles *et al.*, 2013). Rainfall averages 1,200 mm per year, and the temperature means 15°C in the coldest periods (June-August) and 28°C in the hottest months (December-February) (Mereles *et al.*, 2013; DMH, 2018). The total ranch area is 4,000 ha, however the sampling site covered 500 ha non-randomly selected according to accessibility and flooding conditions during the time of the sampling.

The study was conducted in three vegetation types: i) Riparian forests associated to wetlands (W-RF), ii) Mesoxerophytic semi-deciduous forests dominated by *Schinopsis balansae* (MXF), and iii) Floodable sub-humid forest islets (FSF) (Fig. 1). Wetlands are low floodable areas which vary with the rainy season, where vegetation is represented by emergent stands of *Typha*, *Cyperus* and *Thalia*; in open waters, also including floating stands of *Pistia*, *Eichornia*, *Victoria* among others (Peña-Chocarro *et al.*, 2006). W-RF in our study site are usually associated to a ~50-100 m riparian forest strip linked to periods of flooding (Maturo *et al.*, 2005; Peña-Chocarro *et al.*, 2006); common tree species for our study site are *Peltophorum dubium* (Spreng.) Taub., *Ocotea diospyrifolia* (Meisn.) Mez, *Nectandra angustifolia* (Schrad.) Nees, *Inga vera* Willd, and *Genipa americana* L., with lower presence of *Vitex megapotamica* (Spreng.) Moldenke and *Terminalia trifolia* Spreng. MXF or *quebrachales* are dominated by *Schinopsis balansae* and *Libidibia paraguariensis* (D. Parodi) Burkart and occasionally *Aspidosperma quebracho-blanco* Schltdl. (Mereles, 2005; Peña-Chocarro *et al.*, 2006). FSF are present in the Paraguay River floodplain and are associated with palm groves of *Copernicia alba* (Perez de Molas, 2016). Some tree species of the FSF are common with the riparian forest, however, these forests occur in well-defined islets, usually surrounded by savannas rather than following the course of streams or wetlands; some species common to this type of forest and our study site include: *Peltophorum dubium*, *Enterolobium contortisiliquum* (Vell.)

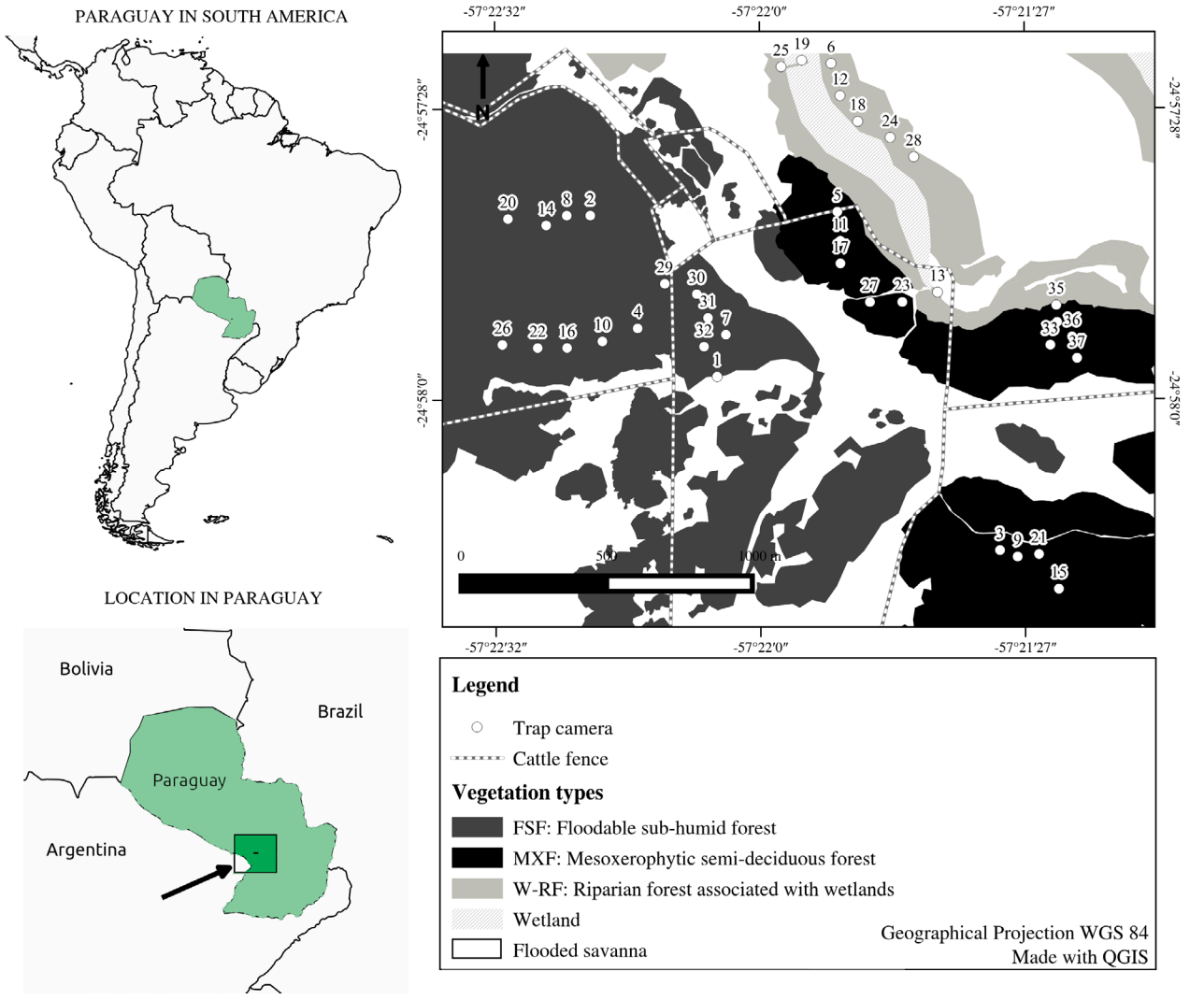

Fig. 1. Location of the study area in the Humid Chaco Ecoregion in Paraguay (left) and camera-trap ubications from November 2016 to March 2018. The numbers of the amplified area (right) indicate the date and season in which the trap cameras were placed in the different forests types (see Tab. I).

Morong, *Ficus enormis* (Miq.) Miq., *Ocotea diospyrifolia, Sapium haematospermum* Müll.Arg., *Gleditsia amorphoides* (Griseb.) Taub., *Guazuma ulmifolia* Lam., *Chloroleucon tenuiflorum* (Benth.) Barneby & J.W.Grimes, *Handroanthus heptaphyllus* (Vell.) Mattos, *Syagrus romanzoffiana* (Cham.) Glassman and *Copernicia alba*.

Methods. We used five Bushnell Trophy Cam HD Essential camera-traps from November 2016 to March 2018. Cameras were installed 45 cm above the ground and were programmed to operate 24h00 per day, reaching a total sampling effort of 1,268 camera-days. Camera-traps were rotated in the three forest types previously described: i) Riparian forests associated to wetlands (W-RF), ii) Mesoxerophytic semi-deciduous forests dominated by *Schinopsis balansae* (MXF), and iii) Floodable sub-humid forest islets (FSF) (Tab. I, Fig. 1). Cameras were rotated to standardize sampling efforts across habitat types.

Photographs and videos taken by camera-traps were considered records (see two records of this research in Figs 2, 3). Only the first record was considered when more than one photograph or video of the same species was taken at the same camera-trap within a 1 hr interval. Between 1 and 21 photos and 0 and 3 videos were obtained for each record for this study. Sampling effort and capture success were calculated according to SRBEK-ARAUJO & GARCIA CHIARELLO (2005) (Tab. II). Social behavior was described through the patterns of activity and number of individuals in each record.

Tab. I. Forest type, camera-trap locations from November 2016 to March 2018 (date and season) and sampling effort (camera-days) for the study of giant anteater (*Myrmecophaga tridactyla* Linnaeus, 1758) and lesser anteater (*Tamandua tetradactyla* Linnaeus, 1758) in the Humid Chaco Ecoregion in Paraguay (W-RF, Riparian forests associated to wetlands; MXF, Mesoxerophytic semi-deciduous forests dominated by *Schinopsis balansae*; FSF, Floodable sub-humid forest islets).

Forest type	Camera-trap locations*	Study period (dates)	Season of the year	Sampling effort (camera-days)
W-RF	13-19-25	November 18, 2016 to January 19, 2017	Spring-summer	180
	6-12-18-24-28	September 21 to November 7, 2017	Spring	235
MXF	3-9-15-21	April 1 to 30, 2017	Autumn	120
	5-11-17-23-27	August 18 to Septermber 20, 2017	Winter	160
	33, 34, 35, 36 y 37	February 7 to March 7, 2018	Summer	140
FSF	1-7	November 18, 2016 to January 19, 2017	Spring-summer	108
	2-8-14-20	March 16 to 31, 2017	Summer-autumn	60
	4-10-16-22-26	July 18 to August 16, 2017	Winter	133
	29, 30, 31 y 32	November 9 to December 12, 2017	Spring	132
Total camera-days				1,268

* See camera-trap geographic locations in Fig. 1.

Figs 2, 3. Photos taken by trap cameras in the Humid Chaco Ecoregion in Paraguay: 2) Giant anteater (*Myrmecophaga tridactyla* Linnaeus, 1758) on March 20th, 2017; 3) Lesser anteater (*Tamandua tetradactyla* Linnaeus, 1758) on November 28th, 2017.

Tab. II. Sampling effort (camera-days), number of records and capture success (%) of giant anteater (*Myrmecophaga tridactyla* Linnaeus, 1758) and lesser anteater (*Tamandua tetradactyla* Linnaeus, 1758) by forest type and season of the year in the Humid Chaco Ecoregion in Paraguay using camera-traps from November 2016 to March 2018 (W-RF, Riparian forests associated to wetlands; MXF, Mesoxerophytic semi-deciduous forests dominated by *Schinopsis balansae*; FSF, Floodable sub-humid forest islets).

	Sampling effort (camera-days)	Number of records of *M. tridactyla*	Capture success (%) of *M. tridactyla*	Number of records of *T. tetradactyla*	Capture success (%) of *T. tetradactyla*
By forest type					
W-RF	415	5	1.20	1	0.24
MXF	420	2	0.48	3	0.71
FSF	433	10	2.31	5	1.15
By season					
Spring	513	10	1.95	6	1.17
Summer	302	3	0.99	1	0.33
Autumn	160	1	0.63	1	0.63
Winter	293	3	1.02	1	0.34

RESULTS

Habitat preference. Mean capture success for *T. tetradactyla* was 0.7% and 1.3% for *M. tridactyla* (Fig. 4). In both species, capture success was greater in Floodable sub-humid forest islets (FSF). *T. tetradactyla* appeared more frequently in FSF (1.2%), followed by Mesoxerophytic semi-deciduous forests dominated by *Schinopsis balansae* (MXF) and Riparian forests associated to wetlands (W-RF), with 0.7% and 0.2%, respectively. While, *M. tridactyla* capture success was greater in FSF (2.3%), followed by W-RF (1.2%) and MXF (0.5%).

Social behavior. Most detections consisted of individual anteaters for both species (Figs 2, 3), for *M. tridactyla,* 88% (n=15) records were of solitary giant anteaters and 12% (n=2) were mother-young pairs; juvenile giant anteaters transported on their mother's back were observed only during summer (December 2016 and November 2017). For *T. tetradactyla,* 89% (n=8) of the records were of solitary individuals, while only one detection included a female with offspring, observed in November 2017.

Activity patterns. Both species showed a pattern of crepuscular and nocturnal activity with a peak of records around midnight (Fig. 5). *M. tridactyla* was recorded between 17h00 and 09h00, with the highest frequency of detection between 21h00 and 01h00 (58.8%). Meanwhile, *T. tetradactyla* was recorded between 18h00 and 02h00, with the highest period of activity between 22h00 and 01h00 (55.4%). *M. tridactyla* was always detected between 11°C and 26°C, while *T. tetradactyla* was always detected between 15°C and 23°C.

Both species capture success was greater during spring time: 2% for *M. tridactyla* and 1.2% for *T. tetradactyla* (Tab. II), however, it should be noted that sampling was not evenly distributed for all seasons in all vegetation types due to floods caused by heavy rain. Sampling was conducted in all seasons of the year for FSF, in spring and summer for W-RF, and in autumn, winter and summer for MXF (Tab. I).

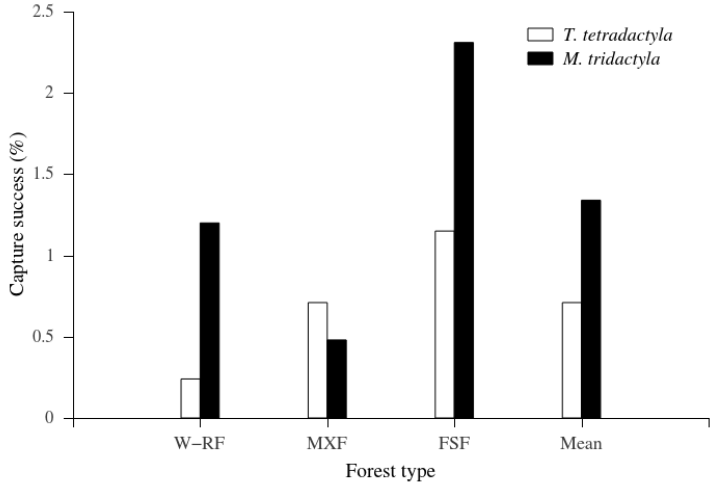

Fig. 4. Capture success (%) of lesser anteater (*Tamandua tetradactyla* Linnaeus, 1758) and giant anteater (*Myrmecophaga tridactyla* Linnaeus, 1758) in the Humid Chaco Ecoregion in Paraguay using trap-cameras from November 2016 to March 2018 by forest types: W-RF, Riparian forests associated to wetlands; MXF, Mesoxerophytic semi-deciduous forests dominated by *Schinopsis balansae*; FSF, Floodable sub-humid forest islets.

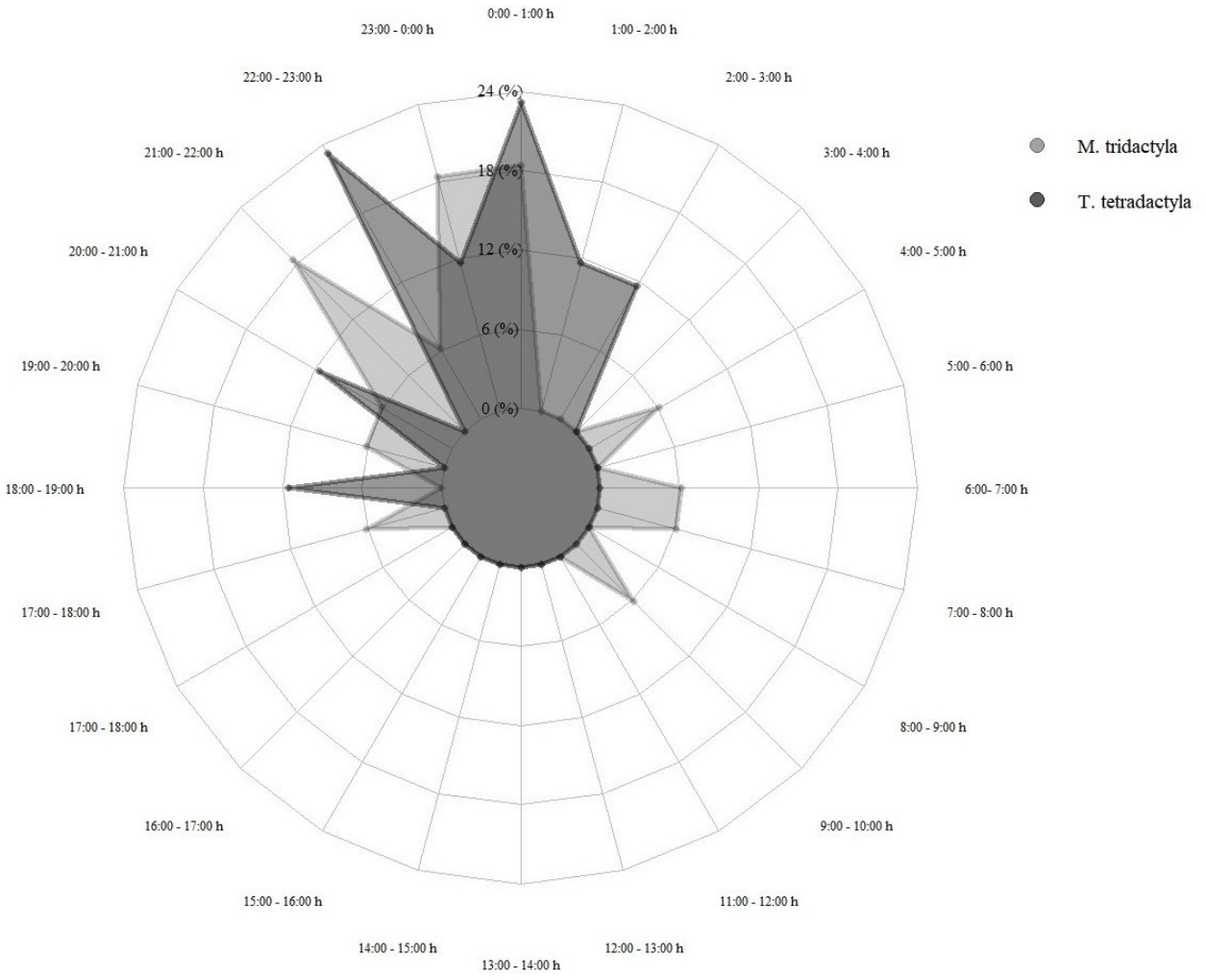

Fig. 5. Records (%) by hour of the day of giant anteater (*Myrmecophaga tridactyla* Linnaeus, 1758) and lesser anteater (*Tamandua tetradactyla* Linnaeus, 1758) in the Humid Chaco Ecoregion in Paraguay using trap-cameras from November 2016 to March 2018.

DISCUSSION

Our results showed a preference of anteaters for the Floodable sub-humid forest islets (FSF), however, both species also appeared in other forest types. At a continental scale, giant anteaters are more frequently recorded in dry forests than in moist forests (Quiroga *et al.*, 2016). Lesser anteaters are climbers and inhabit mainly forested environments and giant anteaters live in forested areas and in open areas, where they are more abundant due to their limited ability to climb (Rodrigues *et al.*, 2008). However, a study carried out in the central region of the Pantanal (Brazil) reported the highest densities of *M. tridactyla* and *T. tetradactyla* in forest landscapes compared to open grasslands and scrubs, where they also were detected (Desbiez & Medri, 2010).

Our sampling site covered 500 ha in three forest types, grasslands and shrublands were not considered for this study. Studied forests islets are immersed in flood-prone savannas, however, camera-traps were only placed inside arboreal vegetation. Anteaters generally use a mosaic of habitats (*e.g.*, forest islets for shelter and rest and savannas for foraging and daytime rest) (Desbiez & Medri, 2010; Quiroga *et al.*, 2016), therefore, we recommend further research that also includes other plant formations. Size and shape of forest islets were not considered in this study because of their variability, while FSFs and the MXFs are larger and develop naturally in circular, oval or irregular shapes in slightly elevated areas of the floodplain; W-RFs are sinuous formations extending along wetlands and rivers.

Both species were usually detected alone, but occasionally females were observed carrying pups on their back, as reported by Desbiez & Medri (2010), Figel *et al.* (2015) and Passos *et al.* (2016). Anteaters are usually nocturnal, although they occasionally engage in diurnal activity (Rodrigues *et al.*, 2008). According to our results, both species showed a pattern of crepuscular and nocturnal activity with a peak of records around midnight. Giant and lesser anteaters display both nocturnal and diurnal activity as part of a thermoregulatory behavior to avoid exposure during

the hottest or coldest hours of the day (Desbiez & Medri, 2010). Giant anteaters spend more hours active and are more nocturnal during summer, and wild-reared individuals are more nocturnal than captive-reared ones (Di Blanco *et al.*, 2016). In some regions and during some periods, they display much more diurnal than nocturnal activity (Rodrigues *et al.*, 2008). Activity patterns can be especially distinct in the southernmost limit of their geographic distribution which is characterized by marked thermal seasonality (Di Blanco *et al.*, 2016) as in the Humid Chaco.

Important limitations of this study are the small sampling size and limited number of camera-traps and the lack of systematic sampling during the four seasons of the year in the three analyzed forest types and in other plant formations of the study area, however, there are few published studies regarding anteaters in Paraguay and errors and contradictions persist in literature (Smith, 2007, 2012; Smith & Rios, 2018). This research provides preliminary data on the species in the Humid Chaco, which is a key step for the design of conservation strategies for *M. tridactyla* and *T. tetradactyla* and as basis for further studies.

In addition to cattle and anteaters, camera-traps also recorded 43 species of wild animals of which three are threatened or near threatened: bare-faced curassow (*Crax fasciolata*), greater rhea (*Rhea americana*) and neotropical otter (*Lontra longicaudis*). Results suggest that cattle ranching activities developed in low-altered ecosystems, where low densities of cattle are maintained on native pastures (savannas) and the different types of forests are conserved, allow, so far, coexistence with anteaters and other wild animals.

Anteater populations are threatened by highway road kills and fire, which is the most common cause of *M. tridactyla* death in Brazil (Silveira *et al.*, 1999; Fonseca & Rylands, 2004). Fire is an ecological component in the design of the vegetation of the Humid Chaco due to the high productivity of the herbaceous stratum and an insufficient level of herbivory to assimilate all the production of herbaceous biomass (Ginzburg & Adamoli, 2006). In savannas, the presence of cattle along with the conservation of the forest islets could be a key combination for anteater conservation, highlighting the importance of conserving wetlands and their associated riparian forests in the region as natural refuges for wild animal species.

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