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RESPONSE OF MAMMALS TO ECOTOURISM, CATTLE FARMING, AND HABITAT STRUCTURE IN THE NORTHERN AND SOUTHERN BRAZILIAN PANTANAL

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ABSTRACT. The Pantanal, the world's largest wetland, is a biodiversity hotspot and home to several threatened species. The growth and transition of the local economy are a major threat to the ecosystem, and sustainable income sectors need to be established. The local economy is based mainly on cattle farming, while ecotourism has recently become important. Our study was conducted in two subregions of the Brazilian Pantanal, the northern subregion Poconé in Mato Grosso and the southern subregion Nhecolândia in Mato Grosso do Sul. Our results indicate that the two main economic sectors, cattle farming and ecotourism, can support sustainable development when operated at a small scale. Traditional cattle farming had no negative effect on mammalian wildlife richness or abundance in either of our study areas, whereas ecotourism did not affect species abundance but did affect species richness in a few cases. These results are derived from a ten-month camera-trap study (middle of July to middle of October 2010, end of December 2012 to beginning of March 2013, and middle of August to end of November 2013) conducted in both subregions. The habitats at both of our study sites consisted of a mix of forest and grassland savanna, the most important factor to support high species diversity. Our study is part of an ongoing long-term Pantanal mammal monitoring project aiming to introduce sustainable management practices.

RESUMO. Resposta dos mamíferos ao ecoturismo, pecuária e estrutura do habitat no Pantanal norte e sul do Brasil. O Pantanal, a maior área úmida do mundo, é um centro de biodiversidade e local onde vivem várias espécies ameaçadas. O crescimento e a transição da economia local são uma grande ameaça para esse ecossistema, portanto, é necessário estabelecer setores de renda sustentável. A economia local é baseada, principalmente, na pecuária, enquanto o ecoturismo se tornou importante recentemente. Este estudo, desenvolvido em duas sub-regiões do Pantanal brasileiro, a sub-região norte de Poconé, em Mato Grosso, e a sub-região sul de Nhecolândia, em Mato Grosso do Sul, demonstrou que esses dois setores econômicos podem apoiar o desenvolvimento sustentável quando conduzidos em pequena escala. A pecuária tradicional não demonstrou um efeito negativo sobre a riqueza ou abundância de espécies de mamíferos selvagens em nenhuma das áreas estudadas. Embora o ecoturismo, também não tenha afetado a abundância de espécies, observa-se, em poucos casos, que a riqueza de espécies foi afetada. Esses resultados são parte de um estudo de dez meses empregando câmeras trap (meio de julho a meio de outubro de 2010, fim de dezembro de 2012 a início de março de 2013 e agosto a novembro de 2013) em ambas sub-regiões. A estrutura do habitat, composta por florestas e pastagens, é o vetor mais importante para suportar a alta diversidade de espécies

desse ecossistema. Esse estudo está inserido em um projeto de longo prazo de monitoramento de mamíferos silvestres do Pantanal, com o objetivo de introduzir práticas de manejo sustentável.

Key words: wetlands, anthropogenic impact, camera-trap, habitat use, species richness.

Palavras-chaves: áreas úmidas, impacto antrópico, câmera trap, uso de habitat, riqueza de espécies.

INTRODUCTION

Situated in the Neotropical floodplains of the upper Paraguay River and its tributaries, the Pantanal is one of the largest freshwater ecosystems in the world. The region of the Pantanal contains approximately 250 000 km² of high plateaus surrounding approximately 150 000 km² of seasonally inundated savanna wetlands (Coutinho et al. 1994). Adjacent biomes such as the Cerrado (dry savanna in the east), Amazonia (north), Atlantic Forest (southeast), and Chaco (wet savanna in the west) contribute to the high biodiversity of this ecosystem (Harris et al. 2005; Mittermeier et al. 2005; Alho & Silva 2012).

Eighty percent of the Pantanal basin is periodically flooded during the rainy season from October to April, with unique patterns of seasonal and interannual variation in flooded areas in the different subregions of the Pantanal (Junk & Silva 1995; Hamilton et al. 1996; Hamilton 1999; Alho et al. 2011). The annual and multiannual cycles of changing hydrological conditions, combined with differences in topography, result in a unique biome (Nunes Da Cunha et al. 2007; Alho et al. 2011). The fauna includes over 170 species of mammals, of which 14 are currently listed as endangered (Alho et al. 2011). Most of the Pantanal (95%) is privately owned, and approximately 80% (118 000 km²) of this land is used for cattle farming (Seidl et al. 2001), which has been the dominant land-use activity for the last two centuries (Seidl et al. 2001) and is regarded as having an overall low environmental impact in this region (Santos et al. 2002, 2004).

In recent decades, the environment has been threatened by increased cattle-stocking rates, flood control, improvements to infrastructure, and conversion and simplification of habitats (Seidl et al. 2001; Padovani et al. 2004; Harris et al. 2005; Alho 2008; Abreu et al. 2010). This trend is especially critical in elevated forested areas that are a crucial refuge for animals during seasonal flooding (Santos 2001; Desbiez et al. 2009a). Forested areas originally accounted for only 30% of the Pantanal area (Silva et al. 1999) but are the main target of deforestation (Desbiez et al. 2009a). Overall, the conversion of native vegetation to human-use areas within the

floodplain increased from 0.64% to 16.04% between 1976 and 2017 and could reach 29% by 2050 if the trend continues (Padovani 2017). This scenario highlights the importance of studies that estimate the influence of different land management strategies on this ecosystem to introduce urgently needed sustainable management. Increasing concerns related to the future of this ecosystem has led to a variety of conservation activities. Today, the Pantanal is a National Heritage Site as designated by the Brazilian Constitution and is a UNESCO Biosphere Reserve. Approximately 403 500 ha are protected within the Pantanal National Park (Parque Nacional do Pantanal Matogrossense) and Natural Heritage Private Reserves (RPPN, Reservas Particulares do Patrimônio Natural; ICMBIO 2018; Pegas & Castley 2014).

Recently, ecotourism is supplementing and replacing traditional cattle ranching as an alternative economic income in the Pantanal region (Alho & Sabino 2011). This kind of tourism has been seen as a contribution to protecting biodiversity and ecosystem functions in developing countries (Gössling 1999; Higginbottom 2004). Worldwide, ecotourism has become one of the fastest-growing sectors (Miller 2007), and studies indicate its potential for habitat preservation, species conservation and local community support (e.g., Krüger 2005; Salvador et al. 2011; Mossaz et al. 2015; Buckley et al. 2016).

Nevertheless, recent research has also highlighted that wildlife-focused ecotourism can have a negative impact on both conservation and animal welfare (Moorhouse et al. 2015, 2016), especially where the type and intensity of the tourist activity is as unregulated as in the Pantanal. Despite self-implemented regulations on privately owned ecotourism farms, only jaguar-related tourism activities are generally controlled by law (Diário Oficial de Mato Grosso, 19 de Agosto de 2011, Resolução CONSEMA-85/11).

The use of ecotourism as a conservation tool and the possible consequences for Pantanal wildlife need to be assessed to ensure sustainable growth of the industry. Estimating population abundances and richness and identifying potential negative impacts

are important for the evaluation of protection efforts and future plans for wildlife conservation.

Here, we present a comparative analysis of two wildlife camera-trap studies conducted in the northern subregion Poconé in Mato Grosso and the southern subregion Nhecolândia in Mato Grosso do Sul between 2010 and 2013. The objective of this study was (1) to provide an overview of the biodiversity of medium to large terrestrial mammals in the Pantanal; (2) to estimate the potential impact of cattle farming and ecotourism on species richness and abundance; and (3) to evaluate the importance of the natural habitat structure in this unique ecosystem. To evaluate the potential differences between the two subregions, mammal species composition, richness, and abundance were compared between the study areas.

MATERIALS AND METHODS

Study areas

The study was conducted at two privately managed ecotourism and traditional cattle farms in two regions of the Brazilian Pantanal. In the northern Pantanal (hereafter NP) of Mato Grosso, we worked at Fazenda Hotel Pouso Alegre, located in the Poconé subregion (16° 32' 31" S, 56° 43' 21" W; 8 000 ha). In the southern Pantanal (hereafter SP) of Mato Grosso do Sul, we sampled at Fazenda Barranco Alto, located in the Nhecolândia subregion (19° 34' 40" S, 56° 09' 08" W; 10 000 ha). Both farms formerly exclusively bred cattle. At present, they keep approximately 700 (NP) and 2 000 (SP) Nelore beef cattle (*Bos taurus indicus*) on native pastures. Today, the main income of both farms is ecotourism based on observing wildlife, and the owners of both areas are cautious about preserving the natural habitat mosaic. Our study areas receive approximately 2 000 (NP) and 800 (SP) visitors each year.

Camera trapping

In total, we established 147 different trap stations within our two study areas, resulting in a trapping effort (hereafter TE) of 1 141 trap nights (hereafter TN). At each station, a single camera-trap was active for seven consecutive nights and days. In the NP study area, 57 different trap stations were established, resulting in a total of 511 TN (Fig. 1). Data were collected between December 2012 and March 2013 (16 trap stations) and from August to November 2013 (57 trap stations). In the SP study area, we established 90 different trap stations, resulting in a total of 630 TN. In SP, camera-traps were active between July and October 2010.

In both study areas, the trap stations were established in a regular grid, maintaining 1 km distance (\pm 30 m, depending on vegetation structure and landscape conditions) between each station. The grid was generated using the Hawth Tools® (Beyer 2004; vers. 3.27) extension of Arc Map® (ESRI 2005; vers. 9.1). The camera-traps were installed 60 cm above the ground on a stable tree, tree trunk, pole, or tripod. Where trails or dirt roads were present, camera-traps were placed at a right angle to the

track. In the NP, we used six camera-traps (RECONYX HyperFire™ Professional PC800), and in the SP, ten camera-traps (RECONYX HyperFire™ HC500). All camera-traps were operated using a passive infrared-triggered system.

To estimate the possible influence of human activities and habitat structure within the study areas, camera-trap stations were categorized as (1) used/not used by cattle (based on camera trap records); (2) located in an area accessible/inaccessible by tourists (as described by the farm owners); and (3) according to general habitat structure. We defined two habitat structures: open (pasture areas, savannas and grasslands with small vegetation islands) and closed (dense shrublands, riverine and semideciduous forests).

Image analyses

All camera-trap images were analyzed using RECONYX software MapView™ Professional. Species with a smaller than 25 cm head-body length on average were excluded from the analysis because our methods were not suitable for small mammals (Rowcliffe et al. 2008; Tobler et al. 2008; Glen et al. 2013; Harrison 2015). Mammal species were identified using Eisenberg and Redford's Mammals of the Neotropics (1999). Nomenclature followed Wilson and Reeder's Mammal Species of the World, 3rd Edition (2005). Only independent records of a particular species were counted as valid. Following O'Brien et al. (2003), an independent record was defined as (1) consecutive images of different individuals of the same or different species; (2) consecutive images of individuals of the same species taken more than 0.5 h apart; and (3) nonconsecutive images of individuals of the same species.

Statistical analyses

Species richness

The observed species richness (S_{obs}) was estimated at each camera-trap station and then accumulated per study area, habitat structure, and for all stations located in areas used or not used by cattle or tourists. Species richness was then compared between the different categories using the pooled and separated data sets of both study areas. Analyses were performed using Estimate S 9.1.0.

To address the sensitivity of species richness counts to number, size, and spatial arrangement of samples and to allow a fair comparison of equivalent numbers of samples, we calculated sample-based rarefaction curves showing the statistical expectation of the species richness (S_{est}) and its accumulation curve. The accumulation curves were rescaled to the number of individuals and were used to evaluate sampling adequacy, with the curves that reached an asymptote suggesting that all present species were registered (Gotelli & Colwell 2001, 2011). Each accumulation curve was randomized 1000 times (Tobler et al. 2008).

Following Payton et al. (2003) and MacGregor-Fors & Payton (2013), we calculated the 84% confidence intervals of S_{est} and considered S_{est} to be significantly different with a $P(\alpha)=0.05$ if the confidence intervals did not overlap. We used the nonparametric abundance-based Chao1 estimator to estimate the number of species present in our study areas (S_{Chao1}) (Chao 1984; Colwell & Coddington 1994). The classic Chao1 procedure was applied where advised. In all other cases, the bias-corrected formula was preferred.

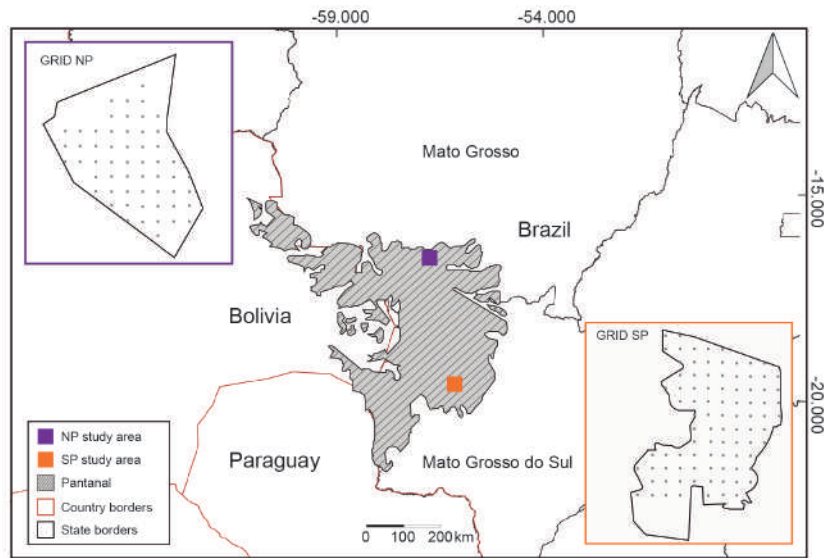


Fig. 1. Geographical location of study areas in the northern (NP) and southern (SP) Pantanal with grid shapes and camera-trap stations (dots) (NP= 57, SP= 90). Map source: GGIS 3.12.1; Pantanal shape file source: Bioscience, An Ecoregions-Based Approach to Protecting Half the Terrestrial Realm.

Abundance

Following O'Brien et al. (2003), we used the number of independent records of a species obtained at each trap station as a measure of species abundance. To infer which factor (study area, cattle, tourists, or habitat structure) most influenced the abundance of each species, we performed general linear mixed models (GLMMs) using the glmmTMB package (Bolker et al. 2009; Brooks et al. 2017) in R (R Core Team 2018, vers. 3.5.1 "Feather Spray"), which fits the models through a maximum likelihood estimation via a template model builder. The analyses were performed in two steps: (1) five different distributions were tested to find the best fit for our data set; and (2) the importance of the four different factors habitat structure, tourists, cattle, and study area was evaluated. We tested the negative binomial (types I and II), Conway-Maxwell-Poisson, generalized Poisson, and the Tweedie (log-link) families. Families causing errors were excluded. The models were then ranked based on the Akaike (1974) information criterion (hereafter AIC), the most widely used model selection criterion among ecologists (Aho et al. 2014). Because of the small sample sizes, we used a variant of the AIC, the AICc, which is more suitable in this case (Sugiura 1978). Following Burnham & Anderson (2002), we calculated the AICc differences ($\Delta AICc$) between the models to judge the five different distributions. A $\Delta AICc$ of 0 to 2 gives substantial support to a model, a $\Delta AICc$ of 4 to 7, considerably less support, and a $\Delta AICc > 10$, essentially no support. Thus, for each species, we kept the model with the lowest $\Delta AICc$ for further analysis.

In the second step, the chosen model was compared against four submodels, each missing one of the four factors. Following the $\Delta AICc$ rules described above, here, the

model with the highest $\Delta AICc$ indicates a high importance of the missing factor.

Only species with a minimum of 10 records in one of our study areas were considered to ensure valid sample sizes. Only samples from the local dry seasons ($n=147$) were used for the GLMMs.

RESULTS

Trapping success and species richness

In total, 23 different mammal species (on 1 378 images) were identified, 21 in the NP and 22 in the SP (Table 1). Records of the South American red brocket (*Mazama americana*) and brown brocket (*Mazama gouazoubira*), which are both known to occur in the area, were pooled due to identification problems, especially for black and white night shots. The most common species was the white-lipped peccary (*Tayassu pecari*), followed by the capybara (*Hydrochoerus hydrochaeris*). The least common species were the bush dog (*Speothos venaticus*) and pampas deer (*Ozotoceros bezoarticus*), which only occurred in the SP. The nine-banded armadillo (*Dasypus novemcinctus*), six-banded armadillo (*Euphractus sexcinctus*), gray four-eyed opossum (*Philander opossum*), giant anteater (*Myrmecophaga tridactyla*), cougar (*Puma concolor*), and marsh deer (*Blastocerus dichotomus*) were the rarest species in both study areas.

Table 1

List of species recorded at camera-trap stations in the Northern Pantanal (NP) and the Southern Pantanal (SP) with corresponding number of independent records (REC), number of trap stations at which the species were recorded (TS) and IUCN red list status (downloaded June 17, 2019). Nomenclature follow Wilson & Reeder 2005 (downloaded June 17, 2019). South American red and brown brocket were treated as one species due to identification problems on infrared night shots.

Order/Family	Scientific Name	Common Name	NP		SP		IUCN ¹
			REC	TS	REC	TS	
Didelphimorphia							
Didelphidae	<i>Philander opossum</i>	gray four-eyed opossum	3	3	9	4	LC
Pilosa							
Myrmecophagidae	<i>Myrmecophaga tridactyla</i>	giant anteater	8	4	7	7	VU
	<i>Tamandua tetradactyla</i>	southern tamandua	7	7	16	14	LC
Cingulata							
Dasyopodidae	<i>Dasyus novemcinctus</i>	nine-banded armadillo	3	3	9	6	LC
	<i>Euphractus sexcinctus</i>	six-banded armadillo	3	3	6	3	LC
Primates							
Cebidae	<i>Cebus apella</i>	tufted capuchin	1	1	-	-	EN
Carnivora							
Canidae	<i>Cerdocyon thous</i>	crab-eating fox	40	20	83	31	LC
	<i>Speothos venaticus</i>	bush dog	-	-	2	1	NT
Procyonidae	<i>Nasua nasua</i>	South American coati	40	13	24	15	LC
	<i>Procyon cancrivorus</i>	crab-eating raccoon	23	13	25	14	LC
Felidae	<i>Leopardus pardalis</i>	ocelot	12	10	17	14	LC
	<i>Puma concolor</i>	cougar	8	7	4	4	LC
Mustelidae	<i>Eira barbara</i>	tayra	5	4	10	8	LC
Perissodactyla							
Tapiridae	<i>Tapirus terrestris</i>	South American tapir	34	23	22	13	VU
Artiodactyla							
Cervidae	<i>Mazama</i> spp.	South American red/brown brocket	53	26	58	24	DD/LC
	<i>Blastocerus dichotomus</i>	marsh deer	9	5	1	1	VU
	<i>Ozotoceros bezoarticus</i>	pampas deer	-	-	3	3	NT
Tayassuidae	<i>Pecari tajacu</i>	collared peccary	39	10	38	13	LC
	<i>Tayassu pecari</i>	white-lipped peccary	60	7	269	39	VU
Suidae	<i>Sus scrofa</i>	wild boar	17	5	111	36	LC
Rodentia							
Dasyproctidae	<i>Dasyprocta azarae</i>	Azara's agouti	44	21	60	20	DD
Caviidae	<i>Hydrochoerus hydrochaeris</i>	capibara	56	6	114	8	LC
Lagomorpha							
Leporidae	<i>Sylvilagus brasiliensis</i>	tapeti	12	8	13	4	LC
No. of records			477		901		
No. of species			21		22		

¹ Status January 2019

The sample adequacy in both study areas and in the pooled data set were good. S_{chao1} suggested similar species richness, as observed (S_{obs}). S_{est} did not significantly vary between the different areas (Fig. 2a, Table 2).

Tourists

Sampling adequacy was good in the pooled data set, and S_{est} was significantly higher at camera-trap sites

inaccessible by tourists than at sites located in areas used by tourists (Fig. 2b). No significant results were observed when comparing only within the NP or the SP, but TE was sufficient only in areas not visited by tourists in the SP (Fig. 2c). S_{chao1} suggested similar species richness as observed for the pooled data set and for areas not visited by tourists in the SP. For the remaining areas, S_{chao1} indicated that there were more species present than we captured (Table 2).

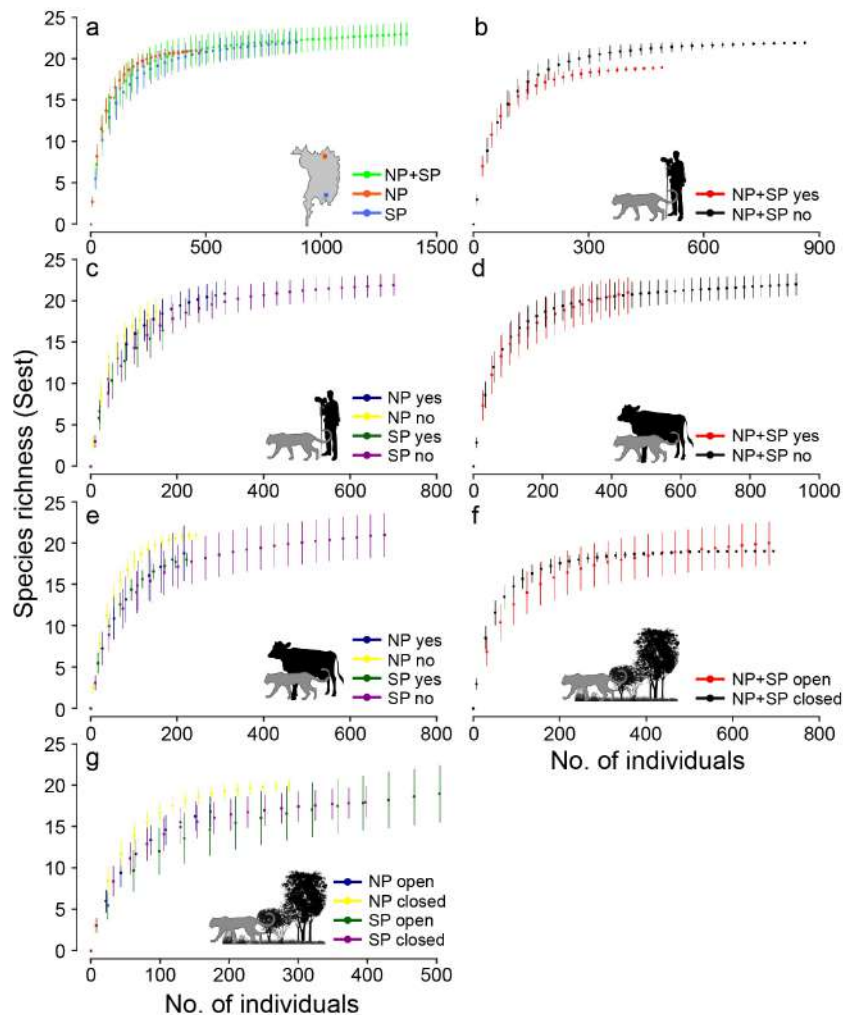


Fig. 2. Sample-based rarefaction curves of estimated species richness (S_{est}) and corresponding 84% confidence intervals re-scaled to individuals. Data were analyzed for the pooled and separated data sets of our two study areas in the Northern Pantanal (NP) and the Southern Pantanal (SP). (a) S_{est} in the NP+SP, the NP and the SP; (b) S_{est} at trap stations accessible and inaccessible by tourists in the NP+SP; (c) S_{est} at trap stations accessible and inaccessible by tourists in the NP and the SP; (d) S_{est} at trap stations used and not used by cattle in the NP+SP; (e) S_{est} at trap stations used and not used by cattle in the NP and the SP; (f) S_{est} at trap stations in open or closed habitat structures in the NP+SP; and (g) S_{est} at trap stations in open or closed habitat structures in the NP and the SP. Data were analyzed using EstimateS 9.1.0 (Colwell 2013).

Cattle

When data were pooled, sampling adequacy was good at stations not used by cattle. S_{est} did not significantly differ between stations with or without cattle (Fig. 2d). In each study area, more sampling was needed at the stations used by cattle. S_{est} did not significantly differ between stations with or without cattle in either the NP or the SP (Fig. 2e). S_{chao1}

suggested high species richness in all cases, with extremely high estimations for camera sites used by cattle in the NP (Table 2).

Habitat

When data were pooled, sampling effort was sufficient in the closed habitat structure but was too low in the open habitats. S_{est} did not significantly vary between the two habitat structures (Fig. 2f). The

same results were found for the separated study area analysis (Fig. 2g). S_{chao1} suggested similar species richness for both habitat structures for the pooled data set and the NP, but there were more species detected in open and closed habitats in the SP than in the NP (Table 2).

Table 2

Observed species richness (S_{obs}), species richness estimator Chao 1 (S_{chao1}), and rarefied species richness (S_{est}) based on the smallest common trapping effort (TE), with corresponding 84% confidence intervals (CI) at the trap stations in our study areas in the Northern Pantanal (NP) and the Southern Pantanal (SP) (a); at trap stations accessible and in-accessible by tourists (b); at trap stations used (Y) and not used (N) by cattle (c); and at trap stations in open (O) or closed (C) habitat structures (d). Data were pooled (NP+SP) and analyzed separately for each study area using EstimateS 9.1.0 (Colwell 2013).

		S_{obs}	S_{chao1}	S_{est}	84% CI	TE
(a) Study area						
NP + SP		23	23	21.66	± 1.63	163
NP		21	21.11	21	± 0	73
SP		22	22	21.61	± 1.36	90
(b) Tourists						
NP + SP	Y	19	19.02	19	± 0	65
	N	22	22	21.58	± 0.45	98
NP	Y	21	22.72	19.03	± 1.70	46
	N	19	20.49	19	± 1.59	27
SP	Y	17	17.75	17	± 2.46	19
	N	22	22	17.91	± 1.80	71
(c) Cattle						
NP + SP	Y	21	23.32	21	± 2.50	51
	N	22	23	20.65	± 1.61	112
NP	Y	19	33.93	19	± 3.35	25
	N	21	23.59	19.26	± 0.88	48
SP	Y	18	18.5	18	± 0.77	26
	N	21	21.59	18.35	± 2.63	64
(d) Habitat structure						
NP + SP	O	20	20	20	± 2.61	66
	C	19	19	18.87	± 0.14	97
NP	O	17	17	17	± 1.80	25
	C	20	20.1	18.62	± 0.95	48
SP	O	19	21	19	± 3.48	41
	C	18	19	17.64	± 1.81	49

Abundance

A total of 1 218 independent records of 14 species ($n \geq 10$) were used for the GLMMs. All 14 species were recorded at trap stations situated in areas accessible and inaccessible by tourists or used and not used by cattle. Thirteen species used both habitat

structures. Capybaras were exclusively recorded in open habitat.

Based on the ΔAICc values, none of the 14 species responded to the presence or absence of tourists. Three species showed a reaction towards the factor study area, one species to the factor cattle, and six species to the factor habitat. Four species did not react to any of the factors. The GLMM analyses of the ocelot yielded no informative results, thus this species was omitted from further discussions (Table 3).

For the South American brocket, Azara's agouti, tayra, crab-eating fox, and crab-eating raccoon, habitat structure was the most important factor. South American brocket ($\Delta\text{AICc}=12.93$, $n=85$) and Azaras agouti ($\Delta\text{AICc}=18.33$, $n=91$) were clearly more frequent in closed habitats. Tayras ($\Delta\text{AICc}=5.43$, $n=14$) showed a minor preference for closed habitats, and crab-eating raccoons for open habitat structure ($\Delta\text{AICc}=6.79$, $n=36$).

Crab-eating foxes were much more abundant in open habitats ($\Delta\text{AICc}=17.43$, $n=98$) and were the only species showing a marginal reaction towards cattle with more individuals trapped at stations used by cattle as well ($\Delta\text{AICc}=2.44$, $n=66$). For the South American tapir, white-lipped peccary, and wild boar, study area was the most important factor. Tapirs showed a small preference for the NP ($\Delta\text{AICc}=2.58$, $n=25$), and white-lipped peccaries ($\Delta\text{AICc}=17.80$, $n=269$) and wild boars ($\Delta\text{AICc}=16.71$, $n=111$) occurred in much larger numbers in the SP study area.

DISCUSSION

Previous camera-trap studies with varying TE in different regions of the Pantanal have indicated the presence of 17 to 29 mammal species (Trolle 2003; Trolle & Kéry 2003; Bastazini 2011; Porfirio et al. 2014), which is in line with our findings. In a comparably short study period of 1 141 TN, we recorded 23 species, of which six are of global conservation concern and are listed as vulnerable or near threatened (IUCN 2019). Species such as the giant armadillo (*Priodontes maximus*), jaguar (*Panthera onca*), jaguarundi (*Puma yagouaroundi*) or lowland paca (*Cuniculus paca*) were not recorded during our studies but have been reported for the Northern or Southern Pantanal before (Trolle 2003; Bastazini 2011). They might avoid these particular areas or occur naturally at low population densities, or the study design, with its comparably short period of sampling, was unlikely to capture them (Voss & Emmons 1996).

When comparing species composition, richness and abundance between the two study areas, only small variances were documented. Bush dogs and pampas deer occurred in small numbers and only in the SP. Although the bush dog is known to occur in the NP as well, the low population density, large home range sizes and extensive foraging behavior of this species might have resulted in decreased chances to gather information in a short sample period (Beisiegel & Ades 2004; Beisiegel & Zuercher 2005; DeMatteo & Loiselle 2008; Lima et al. 2009, 2012; Michalski 2010). Previous studies on pampas deer have shown that this species tends to avoid forested habitats and prefers open grasslands and savannas (Merino et al. 1997; Tomás et al. 2001). This species is more common in the Central Pantanal, where these habitat types dominate (Mourão et al. 2000); thus, it might be rare in our study regions.

Differences in the abundance of the South American tapir might have resulted from its frequent use of habitats with water and its ability to adapt to extreme flooding, which provides an advantage over other mammal species sharing similar food sources (Bodmer 1990). In the NP, the flood regime and fluctuations are greater than those in other regions of the Pantanal (Gonçalves et al. 2011), and a higher proportion of floodable and swampy habitats can be found in the NP than in the SP (Evans et al. 2014). These differences were also observed in our study areas and might favor the semiaquatic nature of the South American tapir.

To date, studies on the white-lipped peccary have focused mainly on the SP (e.g., Desbiez et al. 2009b; Keuroghlian et al. 2009, 2015), and little is known about the species' behavior in the NP (Hofmann 2013). The results of our study indicated that the species is much less common in the NP than in the SP, which might result from a lower proportion of its favored forest in the NP (Keuroghlian et al. 2009; Desbiez et al. 2009b; Evans et al. 2014).

Wild boar were abundant in the SP but were very rarely trapped in the NP study area. This introduced species is a main hunting target and effectively acts as a replacement species for hunting of native wildlife within the SP (Desbiez et al. 2011b). The small number of wild boars found in the NP might have resulted from hunting pressure on neighboring farms, but this factor was not evaluated here. A comparison during varying water levels could reveal further adaptations to the different flood patterns and local variations at both study areas.

A considerable number of studies have noted the potential negative impacts of tourist encounters on habitat use, feeding and breeding patterns, parent-offspring bonds, and increased vulnerability to competitors and predators for a wide range of species (e.g., Roe et al. 1997; Treves & Brandon 2005; Lemon et al. 2006; Geffroy et al. 2015; Meissner et al. 2015; Cecchetti et al. 2018). However, low-intensity ecotourism reserves have also been shown to act as effective faunal refuges with similar species richness and composition as found in adjacent pristine areas (Salvador et al. 2011).

Our results suggest that while tourism, as conducted in our study areas, did not impact species abundance, it had a negative impact on species richness. However, data should be interpreted with caution because this assumption was only met for the pooled data set of both study areas. Considering the study areas separately, the limited access of tourists to the area and the presence of undisturbed refuges within each study area might still provide a chance to preserve natural species abundance and richness and could be an alternative to intensive land use.

Stocking rates, livestock grazing, associated habitat degradation and food competition have been proven to affect mammal abundance, richness and behavior worldwide (e.g., Keesing 1998; Moser & Witmer 2000; Shepherd & Ditgen 2005; Chaikina & Ruckstuhl 2006; Elliott & Barrett 2007; Kinnaird & O'Brien 2012). However, low cattle densities have been shown to have little impact on mammal diversity (McLaughlin & Mineau 1995; Ceballos et al. 2010; Lipson et al. 2011), and low-intensity farming might even promote mammalian biodiversity (Bignal & McCracken 1996; Tscharnkte et al. 2005).

In Latin America, of the activities that affect wildlife, cattle ranching is generally considered to be least disturbing to wildlife (Hoogesteijn & Hoogesteijn 2010), although findings from Vila et al. (2008) and Quintana (2003) suggest that herbivorous species such as the capybara and pampas deer can be subject to grazing competition and tend to avoid areas with cattle. Following Desbiez et al. (2011a), the competition and diet overlap in the Pantanal are not as pronounced as suggested by these examples from Argentina. The similarities in resource use and reduction of the height of forage resource might even be beneficial to the capybara. Junk et al. (2006) further suggest that in the Pantanal, cattle can help to maintain the unique landscape by controlling the regrowth of shrubs and trees.

Table 3

Statistical results of the generalized linear mixed models (GLMMs) of each species with $n \geq 10$. Analysis was performed in two steps: (a) the evaluation of the different families and (b) the exploration of the importance of the four factors habitat structure, tourists, cattle or site. Model estimation was based on $\Delta AICc$ with (a) the $\Delta AICc=0$ indicating the best fitting model and (b) the highest $\Delta AICc$ indicating the most important factor. Analysis was performed in R (R Core Team 2018). Species' common names follow (Wilson & Reeder 2005). Abbreviations: K= number of parameters, AICc=Akaike information criterion with a correction for small sample sizes, $\Delta AICc$ = difference between model of interest and most parsimonious one, AICcWt= Akaike weight, Cum.Wt= cumulative weight, LL= Log-likelihood.

Species		K	AICc	$\Delta AICc$	AICcWt	Cum.Wt	LL
Azara's agouti	(a) genpois(link = log)	6	272.36	0.00	0.55	0.55	-129.88
	nbinom1(link = log)	6	272.99	0.63	0.40	0.95	-130.19
	nbinom2(link = log)	6	277.07	4.71	0.05	1.00	-132.24
	compois(link = log)	6	285.86	13.49	0.00	1.00	-136.63
	tweedie(link = log)	7	288.86	16.50	0.00	1.00	-137.03
	(b) without habitat structure	5	290.69	18.33	0.00	1.00	-140.13
	without tourists	5	272.80	0.44	0.45	1.00	-131.19
	without cattle	5	272.73	0.36	0.45	1.00	-131.15
	without study area	5	270.19	0.00	1.00	0.75	-129.88
capybara	(a) nbinom2(link = log)	6	160.66	0.00	0.58	0.58	-74.03
	nbinom1(link = log)	6	161.75	1.09	0.33	0.91	-74.57
	genpois(link = log)	6	165.19	4.53	0.06	0.97	-76.29
	tweedie(link = log)	7	166.57	5.91	0.03	1.00	-75.88
	compois(link = log)	6	256.32	95.66	0.00	1.00	-121.86
	(b) without habitat structure	5	183.11	22.45	0.00	1.00	-86.34
	without tourists	5	160.66	0.00	0.57	0.57	-74.03
	without cattle	5	160.21	0.00	0.56	0.56	-74.89
	without study area	5	159.49	0.00	0.64	0.64	-74.53
collared peccary	(a) nbinom1(link = log)	6	212.58	0.00	0.42	0.42	-99.99
	nbinom2(link = log)	6	213.29	0.70	0.29	0.71	-100.34
	tweedie(link = log)	7	214.20	1.61	0.19	0.90	-99.70
	genpois(link = log)	6	215.39	2.80	0.10	1.00	-101.39
	compois(link = log)	6	275.39	62.81	0.00	1.00	-131.40
	(b) without habitat structure	5	210.66	0.00	0.72	0.72	-100.12
	without tourists	5	210.88	0.00	0.70	0.70	-100.23
	without cattle	5	210.69	0.00	0.72	0.72	-100.13
	without study area	5	210.74	0.00	0.72	0.72	-100.16
crab-eating fox	(a) nbinom1(link = log)	6	314.85	0.00	0.34	0.34	-151.12
	tweedie(link = log)	7	315.67	0.82	0.22	0.56	-150.43
	genpois(link = log)	6	315.68	0.83	0.22	0.78	-151.54
	nbinom2(link = log)	6	316.69	1.84	0.13	0.92	-152.04
	compois(link = log)	6	317.68	2.83	0.08	1.00	-152.54
	(b) without habitat structure	5	332.28	17.43	0.00	1.00	-160.93
	without cattle	5	317.29	2.44	0.23	1.00	-153.43
	without study area	5	314.59	0.00	0.53	0.53	-152.08
	without tourists	5	312.77	0.00	0.74	0.74	-151.17

Table 3: Continued.

Species		K	AICc	Δ AICc	AICcWt	Cum.Wt	LL
crab-eating raccoon	(a)	genpois(link = log)	6	195.61	0.00	0.53	-91.51
		nbinom1(link = log)	6	196.15	0.53	0.41	-91.77
		nbinom2(link = log)	6	200.16	4.55	0.05	-93.78
		tweedie(link = log)	7	207.57	11.95	0.00	-96.38
		compois(link = log)	6	207.76	12.15	0.00	-97.58
	(b)	without habitat structure	5	202.40	6.79	0.03	1.00
		without cattle	5	194.10	0.00	0.68	-91.84
		without study area	5	193.93	0.00	0.70	-91.75
		without tourists	5	193.45	0.00	0.75	-91.51
ocelot	(a)	tweedie(link = log)	7	-339.01	0.00	1.00	176.91
		compois(link = log)	6	155.39	494.41	0.00	-71.40
		nbinom2(link = log)	6	155.41	494.43	0.00	-71.41
		genpois(link = log)	6	155.54	494.55	0.00	-71.47
		nbinom1(link = log)	6	155.58	494.59	0.00	-71.49
	(b)	without study area	6	-290.44	43.58	0.00	1.00
		without tourists	6	-457.66	0.00	1.00	235.13
		without habitat structure	6
		without cattle	6
South American brown/ red brocket	(a)	nbinom1(link = log)	6	315.10	0.00	0.50	-151.25
		genpois(link = log)	6	315.39	0.29	0.43	-151.40
		nbinom2(link = log)	6	319.17	4.07	0.07	-153.29
		tweedie(link = log)	7	327.65	12.55	0.00	-156.42
		compois(link = log)	6	329.23	14.13	0.00	-158.31
	(b)	without habitat structure	5	328.03	12.93	0.00	-158.80
		without cattle	5	315.08	0.00	0.50	-152.33
		without study area	5	313.69	0.00	0.67	-151.63
		without tourists	5	313.30	0.00	0.71	-151.44
South American coati	(a)	nbinom2(link = log)	6	228.90	0.00	0.35	-108.15
		genpois(link = log)	6	228.93	0.03	0.34	-108.16
		nbinom1(link = log)	6	229.13	0.24	0.31	-108.27
		tweedie(link = log)	7	238.70	9.81	0.00	-111.95
		compois(link = log)	6	249.18	20.29	0.00	-118.29
	(b)	without habitat structure	5	229.39	0.50	0.44	1.00
		without study area	5	229.11	0.21	0.47	1.00
		without cattle	5	228.62	0.00	0.53	-109.10
		without tourists	5	226.81	0.00	0.26	-108.15
South American tapir	(a)	genpois(link = log)	6	216.68	0.00	0.42	-102.04
		nbinom1(link = log)	6	217.13	0.45	0.34	-102.27
		nbinom2(link = log)	6	219.03	2.34	0.13	-103.21
		tweedie(link = log)	7	219.82	3.13	0.09	-102.51
		compois(link = log)	6	223.08	6.39	0.02	-105.24
	(b)	without study area	5	219.27	2.58	0.22	1.00
		without tourists	5	214.63	0.00	0.74	-102.10
		without cattle	5	214.62	0.00	0.74	-102.10
		without habitat structure	5	214.52	0.00	0.75	-102.05

Table 3: Continued.

Species		K	AICc	Δ AICc	AICcWt	Cum.Wt	LL
southern tamandua	(a) nbinom1(link = log)	6	140.72	0.00	0.25	0.25	-64.06
	genpois(link = log)	6	140.72	0.00	0.25	0.50	-64.06
	compois(link = log)	6	140.72	0.01	0.25	0.75	-64.06
	nbinom2(link = log)	6	140.73	0.02	0.25	1.00	-64.07
	(b) without habitat structure	5	139.29	0.00	0.67	0.67	-64.43
	without study area	5	139.18	0.00	0.68	0.68	-64.37
	without cattle	5	139.06	0.00	0.70	0.70	-64.32
	without tourists	5	138.54	0.00	0.75	0.75	-64.06
tapeti	(a) nbinom2(link = log)	6	105.82	0.00	0.44	0.44	-46.61
	genpois(link = log)	6	106.53	0.71	0.31	0.75	-46.97
	nbinom1(link = log)	6	107.10	1.28	0.23	0.99	-47.25
	tweedie(link = log)	7	113.20	7.38	0.01	1.00	-49.20
	compois(link = log)	6	121.33	15.52	0.00	1.00	-54.37
	(b) without cattle	5	106.25	0.44	0.45	1.00	-47.91
	without habitat structure	5	105.38	0.00	0.55	0.55	-47.48
	without tourists	5	105.06	0.00	0.59	0.59	-47.32
tayra	(a) nbinom2(link = log)	6	102.48	0.00	0.28	0.28	-44.94
	nbinom1(link = log)	6	102.76	0.27	0.25	0.53	-45.08
	genpois(link = log)	6	102.85	0.36	0.24	0.77	-45.12
	compois(link = log)	6	102.87	0.38	0.23	1.00	-45.13
	(b) without habitat structure	5	107.92	5.43	0.06	1.00	-48.75
	without study area	5	100.65	0.00	0.71	0.71	-45.11
	without cattle	5	100.34	0.00	0.74	0.74	-44.96
	without tourists	5	100.31	0.00	0.75	0.75	-44.94
wild boar	(a) nbinom1(link = log)	6	318.38	0.00	0.67	0.67	-152.89
	genpois(link = log)	6	319.82	1.44	0.32	0.99	-153.61
	nbinom2(link = log)	6	326.92	8.54	0.01	1.00	-157.16
	tweedie(link = log)	7	330.49	12.11	0.00	1.00	-157.84
	compois(link = log)	6	352.46	34.09	0.00	1.00	-169.93
	(b) without study area	5	335.09	16.71	0.00	1.00	-162.33
	without cattle	5	316.64	0.00	0.70	0.70	-153.11
	without tourists	5	316.23	0.00	0.75	0.75	-152.90
white-lipped peccary	(a) genpois(link = log)	6	403.22	0.00	0.57	0.57	-195.31
	nbinom2(link = log)	6	421.62	18.40	0.00	1.00	-204.51
	tweedie(link = log)	7	441.19	37.97	0.00	1.00	-213.19
	compois(link = log)	6	554.96	151.74	0.00	1.00	-271.18
	nbinom1(link = log)	6	403.77	0.55	0.43	1.00	-195.59
	(b) without study area	5	421.02	17.80	0.00	1.00	-205.30
	without tourists	5	401.33	0.00	0.72	0.72	-195.45
	without cattle	5	401.18	0.00	0.74	0.74	-195.37
white-lipped peccary	without habitat structure	5	401.07	0.00	0.75	0.75	-195.32

Recent studies, however, indicate negative consequences for the diversity and behavior of frugivorous mammals. The home range size of white-lipped peccary can be affected by the indirect effects of cattle due to deforestation and habitat conversion to exotic grass pasture (Keuroghlian et al. 2015). Eaton et al. (2017) argue that faunal composition and diversity in the Pantanal are affected by interference from cattle and related forest vegetation alterations, such as a decrease in fruiting-tree diversity.

Our results suggest that small-scale cattle ranching on natural pastures, as conducted in our study areas, has no negative impact on species richness or abundance. Within our study areas, the limited access of the cattle may represent a low impact on the available vegetation and might provide an opportunity for wild mammals to avoid encounters with cattle. Unfortunately, the traditional cattle production in the Pantanal is under threat and being replaced by an intensive cattle farming system (Abreu et al. 2010), which needs to be evaluated separately.

Previous studies have shown that mammal diversity and composition in the Pantanal are highly associated with intact forest. Forests or forest edges are the most selected habitat of mammal species (Desbiez et al. 2009b), and areas adjacent to large fragments of forest can support native species, while highly converted and developed areas have shown considerably reduced diversity (De Souza et al. 2018). During our study, both habitat structures, open and closed, supported a similar species richness and composition. When looking at the abundance data, habitat is the most decisive factor for the highest number of species and therefore must be seen as a priority before the presence or absence of tourists or cattle.

During the dry season, the majority of the species used open and closed habitat structures equally. In this period, the expansion of terrestrial habitats not only simplifies the movements between forest patches but also enables the intensive use of floodable grassland habitats (Mamede & Alho 2006; Alho 2008). Comparing our results to those of previous studies in the Pantanal, the South American brocket, Azara's agouti, and tayra showed a similar preference for forested habitats, while the capybara was only present in grasslands. The southern tamandua, white-lipped peccary, and South American coati were less selective towards forested areas than that documented in the literature (Desbiez et al. 2009b; Keuroghlian et al. 2009; Desbiez & Medri 2010).

The habitat use of the crab-eating fox is known to be diverse. De Almeida Jácomo et al. (2004) describe

a similar use of grasslands, cerrados, and forests, while (Desbiez et al. 2009a) observed its selection of open grassland and scrub grassland, which is supported by our study. The crab-eating raccoon occupies a variety of habitats but is known to be highly associated with water (Emmons & Feer 1990). Its preference for open habitats might result from the seasonal flooding of these sites and their proximity to lakes or ponds.

CONSERVATION IMPLICATIONS AND PERSPECTIVES

The key to the conservation of the mammal diversity in the Pantanal is the sustainable use of its resources and the protection of the unique habitat mosaic of the floodplain.

Little is known about the potential impact of ecotourism and cattle ranching in the Pantanal, and the present study only provides an initial insight into the responses of mammal species. To aid a more robust outcome and to gather information about the complete assemblage of species, including those with large home ranges, the number of trap nights should be increased in both study areas. We also recommend a more accurate classification of habitats and equal sampling during both local seasons to investigate the full habitat use of all species. To be able to make more differentiated statements concerning the influence of modern cattle farming and tourism on species composition, abundance and richness, areas with more intense land use as well as strictly protected areas should be included while also considering local differences, limitations and interactions of environmental factors.

Low-intensity tourism based on wildlife observation could be a promising factor in the sustainable economic use of the Pantanal in the long run. While tourism creates additional income for cattle ranchers, it could promote the protection of natural heritage and wildlife research (Hoogesteijn & Hoogesteijn 2010) and could be a rare opportunity for conservation outside strictly protected areas. However, although ecotourists could be considered environmentally sensitive, a high number of people and related habitat modification, impacts from associated infrastructure, pollution, and disturbance of species' natural behaviors are among the main negative effects (Roe et al. 1997; Krüger 2005). To guarantee a sustainable future and to preserve the unique wildlife the sector depends on, selecting effective management practices to control the scale and concept of ecotourism in the Pantanal is recommended.

Of other activities that affect wildlife, the traditional method of cattle ranching in the Pantanal has been shown to be the least disturbing to wild mammal species. However, the conversion of natural habitats to increase cattle capacity is an ongoing threat in the region. For example, (De Souza et al. 2018) found that intensive habitat conversion resulted in smaller subsets of the original diversity and composition, marked by the absence of apex predators. The maintenance of forest refuges within a pasture is essential for biodiversity, as we showed in our habitat preference analysis. Preserving and strengthening the “old way” of cattle farming could be essential to balance biodiversity conservation with productive land uses (Bignal & McCracken 1996; Abreu et al. 2001; Tscharnkte et al. 2005; Eaton et al. 2011). When establishing conservation plans for the Pantanal, involving private landowners in conservation planning could yield considerable benefits (Mann et al. 2015). Future studies should address not only species welfare but also livestock and pasture management practices.

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