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Original Research Article

Forest matters: Use of water reservoirs by mammal communities in cattle ranch landscapes in the Paraguayan Dry Chaco

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A B S T R A C T

Cattle ranching has led to a significant decrease in forest cover in the Neotropic. In this study we evaluate how medium- and large-sized mammals cope in these human-modified landscapes in the Paraguayan Dry Chaco, where by state law at least 25% of forest cover must be preserved. Using a camera-trap approach, we studied how the surrounding vegetation matrix and season (dry or rainy) influence the pattern of occurrence and detectability of species around artificial water reservoirs for cattle supply. We registered 26 mammal species, and the responses of 14 different species were modelled. Five species (*Tayassu pecari*, *Leopardus pardalis*, *Pecari tajacu*, *Mazama gouazoubira* and *Myrmecophaga tridactyla*) showed a positive response to forest cover, with *T. pecari* and *L. pardalis* being extremely sensitive to deforestation. Also, forest cover showed a positive effect on the detectability of *Tapirus terrestris* and *Puma concolor*. By contrast, for two generalist canids, *Lycalopex gymnocercus* and *Cerdocyon thous*, and the semiaquatic *Hydrochoerus hydrochaeris* forest cover negatively influenced species detectability. Cattle ranches have the potential to maintain a substantial part of the original chacoan fauna, with forest cover being a main factor in structuring the mammal assemblages found around water reservoirs. Additionally, in ten species there was a moderate to strong increase in the probability of detection around water reservoirs during the dry season. The conservation of large forest tracts combined with strict compliance with poaching bans are key management strategies for the conservation of mammal diversity in the human-altered landscapes of the Chaco.

1. Introduction

Human society is built on biodiversity. However, environmental change from local to global scale to sustain a growing human population has led to a decline in biodiversity, and this trend is likely to continue in the future. (Vitousek et al., 1997; Díaz et al., 2006; Rockström et al., 2009; Cardinale et al., 2012). The loss of biodiversity is usually linked to several interrelated causes such as overhunting, invasive species, population isolation and climate change among others. But changes in land use leading to habitat destruction and degradation exert the most significant impact (Pimm and Raven, 2000; Rockström et al.,

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2009; Laurance, 2010; Romero-Muñoz et al., 2020). Within this context, South America has suffered from a net loss of around 4 million ha of forest between 2000 and 2010, with agriculture and livestock expansion as the main causes of deforestation (FAO, 2016). Owing to the potential loss of biodiversity due to deforestation, the establishment of good management practices in these modified and anthropized landscapes is a priority for biodiversity conservation (Grau et al., 2008; Núñez-Regueiro et al., 2015; Periago et al., 2015; Galetti et al., 2017; Bogoni et al., 2018).

In recent decades, the drivers of deforestation have shifted in the tropics as a consequence of globalized financial markets and an increasing demand for commodities, which has attracted the interest of the private sector (Butler and Laurance, 2008). Nowadays, deforestation is substantially driven by large-scale agriculture and cattle ranching, as opposed to causes related to small-scale farming and local communities (Butler and Laurance, 2008; Laurance, 2010; Caldas et al., 2013). This is, in fact, the case of the Gran Chaco, which is distributed throughout Argentina, Bolivia, and Paraguay, and is the second largest forest in the neotropics after the Amazon rainforest. The Gran Chaco presents a pronounced east–west gradient in precipitation, with the most mesic areas lying closer to the Rio Paraguay in Paraguay and Argentina. Aridity progressively increases to the west, culminating in the driest areas where the Chaco shifts to the Andean foothills. This gradient results in a division of the Chaco into two main climatic subregions: the humid Chaco (from 1000 to 1100 to 1600 mm of rainfall per year) and the dry Chaco (from 400 to 1000–1100 mm of rainfall per year). In the Paraguayan dry Chaco, the annual rate of land transformation is the highest of the region since 2009 (Vallejos et al., 2015), with a loss of around 400 000 ha of forest per year between 2010 and 2014 (Arévalos et al., 2015). Whereas soybean cultivation is the main driver of deforestation in other areas of the dry Chaco, the most significant driver in Paraguay is large-scale cattle ranching (Caldas et al., 2013), causing the greatest mean size of deforested patches in the region (Vallejos et al., 2015). In an effort to conserve the Chaco forest in Paraguay and to preserve its biodiversity, landowners in the Chaco (with at least 2000 ha) are obliged by law to preserve at least 25% of their properties covered with natural forests (Article 42 of Forestry Law 422/73).

Mammals, especially medium- and large-sized species (i.e. adult body mass >1 kg), are usually strongly affected by habitat destruction and degradation in all of the neotropics (Periago et al., 2015; Galetti et al., 2017; Bogoni et al., 2018). The diversity of these types of mammals in the Gran Chaco competes with the tropical forests of South America, showing high level of endemic and vulnerable mammal species (Redford et al., 1990; Mares, 1992). Medium- and large-sized mammals are key components for the adequate functioning of ecosystem processes, and carry out unique ecological roles in the Gran Chaco. This involves mainly regulating plant recruitment and chacoan biodiversity through long-distance seed dispersion, seedling and seed consumption, and controlling the populations of granivore and herbivorous species (Silman et al., 2003; Beck, 2005; Weckel et al., 2006; Keuroghlian and Eaton, 2009; Jorge et al., 2013; Periago et al., 2015; Galetti et al., 2015; Sarasola et al., 2016). Additionally, hunting greatly interacts with land conversion, as increased accessibility to the previous so-called impenetrable chacoan forests goes hand in hand with the increased risk of the extinction of native species (Peres, 2001; Altrichter and Boaglio, 2004; Altrichter, 2006; Periago et al., 2015; Benítez-López et al., 2017). Subsistence hunting using traditional methods by indigenous communities is regulated by law in some natural areas (Hill et al., 1997; Hill and Padwe, 2000), but prohibited and un-regulated commercial and sport poaching is a common activity in the country which threatens the conservation status of several mammal species (Jacquet et al., 2008; Weiler and Nuñez, 2012; Asociación Paraguaya de Mastozoología and Secretaría del Ambiente, 2017).

Deforestation, linked to the expansion of cattle ranching, and increased illegal hunting are not the only factors that can potentially affect mammal diversity in the dry Chaco. Due to the seasonal dry climate, different systems for harvesting rainwater have been designed to secure water supplies for the livestock along the dry Chaco. These systems range from being very primitive and inexpensive to very complex and highly sophisticated (Magliano et al., 2015). As a result, permanent bodies of water are increasingly available throughout the landscape. Subsequently, some key species, like the semi-aquatic capybara *Hydrochoerus hydrochaeris*, are expanding their range to the west, migrating from humid areas to the previously uninhabitable Paraguay dry Chaco (Campos-Krauer and Wisely, 2011). Additionally, permanent artificial bodies of water provide a critical resource for the native fauna in seasonally dry climates where natural water bodies are scarce (Valeix et al., 2008; Astete et al., 2017; Dias et al., 2019).

In this study, we used a camera trapping to assess how medium- and large-sized mammals (adult body mass >1 kg, Nuñez-Regueiro et al., 2015; Bogoni et al., 2018) cope in these human-modified landscapes dominated by large cattle ranches in the Paraguayan dry Chaco (mean size of deforested patches is around 3500 ha, Vallejos et al., 2015). To this end, we established the following objectives: (1) to analyze how the surrounding vegetation matrix influences the use of water reservoirs by medium- and large-sized mammals (our hypothesis is that the sites with the greatest forest cover around water reservoirs will show mammal assemblages that most closely resemble the original community, with the presence of generalist and forest specialist species); and (2) to investigate the seasonal use of water reservoirs during the dry and rainy season. As water availability is a limiting resource in these seasonally dry environments, we assume there will be a more intense use of water reservoirs by mammals during the dry season, which would equate to an increase in the probability of detecting mammals.

2. Material and methods

2.1. Study area

The study area was located in Estancia Montania (21°57′48″ S, 60°04′19″ W), Department of Boquerón, in the dry Chaco ecoregion of west Paraguay. Estancia Montania is a cattle ranch extending over a total of 37 000 ha and it raised approximately of 23 000 heads of cattle of the Brangus breed during the study period. Extensive cattle ranches like Estancia Montania are common in the Paraguayan dry Chaco. Forest clearing began in 1987, and the extension of pastures gradually increased until 2014, when deforestation in the ranch ceased and the current landscape configuration was reached. A total of 10 500 ha (28% of the property) currently remains uncleared, as stipulated by Article 42 of the Forestry Law 422/73, and is covered by continuous primary dry forest. *Aspidosperma triternatum*, *Bulnesia sarmientoi*, *Ceiba chodatii*, *Prosopis kuntzei* and *Schinopsis balansae* are the dominant tree species in the primary dry forests, and the palm *Copernicia alba* is the most dominant species growing in seasonally flooded soils. 3443 ha (9%) is also covered by forest vegetation distributed in 100-m-wide strips with a dirt road running along the middle. Vegetation strips act as windbreakers surrounding the 100 ha patches of managed pastures. 22 360 ha (60%) are covered by pastures, organized in units of 100 ha patches (1 $\times$ 1 km) for the purpose of managing the cattle. Pastures are dominated by the introduced guinea grass *Panicum maximum* cv. Gatton (Poaceae). Initially (between 1987 and 2007) all trees and shrubs were cut down during land clearing, although a sparse cover of recruiting *Prosopis nigra* and *P. alba* trees still remain, providing the cattle with shade and forage. The most recent clearings, between 2008 and 2014, left a density of 30% of the remaining trees per ha (Resolución INFONA, 1915/2013).

The study area is located at 150 m asl., and the region is a large alluvial plain with Haplic Luvisol - Eutrical Cambisol as the most abundant soils (FAO/UNESCO 1990). The annual precipitation recorded at the ranch was 905 mm in 2015 and 1001 mm in 2016. There is a high level of seasonal variation, including a rainy season from October to April (mean 813 mm) and a dry season from May to September (mean 140 mm). The mean annual temperature ranges from 18 to 24 °C in winter (the dry season) and from 25 to 29° in summer (the rainy season) (DGEEC, 2016).

Hunting is an activity that is controlled by the Paraguayan Wildlife Law (Law 96/92), although permits are not granted for sport or subsistence hunting. However, poaching is a common problem in the country (Jacquet et al., 2008; Weiler and Nuñez, 2012; Asociación Paraguaya de Mastozoología and Secretaría del Ambiente, 2017). Strict compliance with the law is overseen by the ranch manager and owners and, as a result, the impact of hunting in Estancia Montania is quite low.

2.2. Data collection

We selected 12 of the 32 water reservoirs artificially established in Estancia Montania. To maximize the range of the predictive variable (Gotelli and Ellison, 2012), i.e. the forest cover around water reservoirs, we selected the only two water reservoirs surrounded by primary continuous forest whereas the other 10 sites were randomly chosen. Water reservoirs comprised a rectangular pond (80 m long, 40 m wide, and 2–6 m deep) and a circular tank. The circular tanks were elevated 4–14 m above the ground surface. Runoff water was captured by the rectangular pond and water was pumped into the circular tank where it was stored and delivered to livestock wells through gravity. The livestock did not have direct access to these water reservoirs and the distance between them was 8.3 ± 3.9 km (mean ± s.d.).

For each reservoir, a camera trap (Bushnell Trophy/Velleman) was located in a wildlife trail placed on the path leading toward the reservoir at approximately 50 cm above the ground, and no bait was used. Stations were examined monthly between July 2015 and July 2016, and the memory cards and batteries were changed when necessary. The camera traps were programmed to operate for 24 h day^{-1}, taking three pictures with a time interval of 1 s, followed by a 10-s-long video. The sampling effort totaled 2877 trap-nights, as camera/batterie malfunctioning and full memory cards after windy periods reduced the maximum potential sampling effort.

Percentage of forest cover was measured in a 1 km-buffer area centered in each camera trap using the Arc Gis 10.5. software. Forest cover was 28.5% ± 27.4 (mean ± s.d.) and ranged from 10 to 12% of the total cover near the water reservoirs surrounded by pastures, and up to 98% near water reservoirs surrounded by primary dry forests (Fig. 1). There was a significant inverse correlation between forest and pasture covers ($r = -0.998$, Pearson coefficient, Fig. S1).

2.3. Statistical analysis

We merged the camera-trapping data using 5-day intervals (84 occasions). We used an occupancy modelling approach, as described by Mackenzie et al. (2006), to estimate individual species occupancy (Ψ) and detection probabilities (p). For occupancy modeling, we considered the species that appeared at least ten times (14 presences were the minimum for *Leopardus pardalis*) in their detection record. Thus, we were able to evaluate a total of 14 species. For each species, a set of eight candidate models (Table S1) were selected using the following *a priori* hypotheses: 1) forest cover will influence the probability of occupancy at the water reservoirs; 2) forest cover will influence the probability of detection; and 3) season (rainy or dry season) will influence the probability of detection. We fitted the detection histories and the matrix/season covariates into a single-season occupancy model, since the occupancy status of the mammal species was considered to be constant throughout the study year (Mackenzie et al., 2006). The candidate models were assessed based on the Akaike Information Criterion corrected for a small sample size (AIC_c) and Akaike weights (ω_i). Occupancy and detection probabilities were calculated using model averaging by multiplying each parameter estimate by the AIC weight of each of the top models with delta AICc <2 units ($\sum AIC_c$ weights $= 1$). Occupancy modelling was performed with the PRESENCE 12.24 software (Hines, 2006). Overdispersion parameter ($\hat{c}$) was estimated by bootstrap resampling (1000 times), and were significant overdispersion was found (Table S2), the models were adjusted by the Quasi-AIC_c (MacKenzie and Bailey, 2004). *Puma concolor* was modelled using Royle and Nichols (2003) heterogeneous detection probabilities, due to the absence of convergence in parameter estimation under homogeneous detection assumptions (Mackenzie et al., 2006).

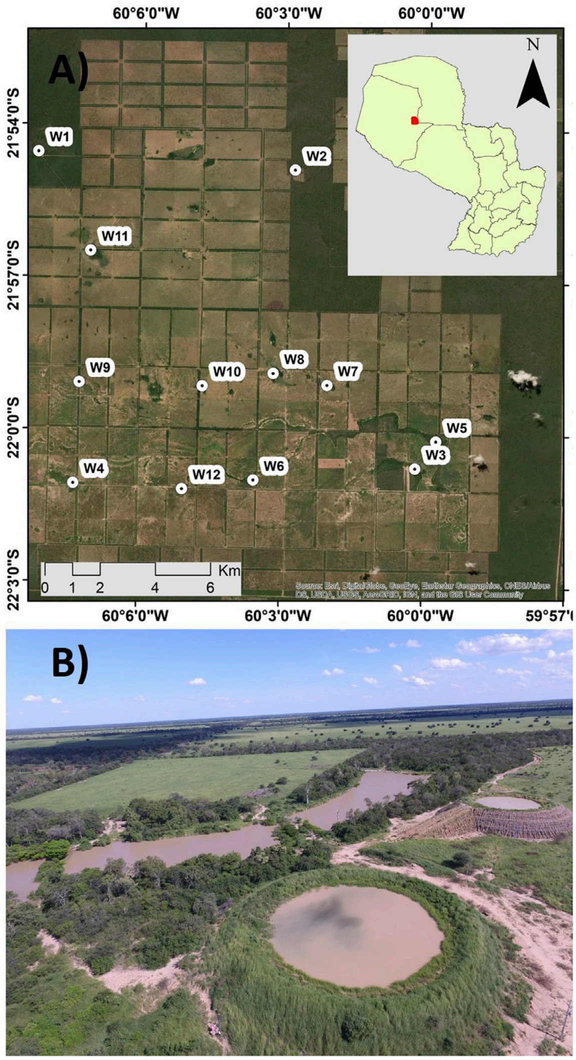

Fig. 1. A) Aerial photograph of the Estancia Montania cattle ranch. Locations of the sampled water reservoirs are indicated by code sites. Inset shows cattle ranch location in Paraguay. B) Water reservoir system at the study area. Runoff water is collected by rectangular ponds and pumped into circular tanks that are elevated above the ground surface. Cattle pastures are depicted at the bottom of the image. The forest cover surrounding each water reservoir varies between sites.

We also used a Principal Coordinate Analysis (PCoA) to visualize the differences in the use of water reservoirs by mammal communities in relation to the surrounding matrix (pastures or primary forests). The intensity of the use at each site by each mammal species was calculated as the proportion of weeks with detections in relation to the total number of weeks. Data was transformed using the Hellinger transformation. PCoA was analyzed using the *cmdscale* function and Bray-Curtis as dissimilarity distance (Borcard et al., 2018) and forest cover (%) was projected using the *ordisurf* function. This analysis was performed with the *vegan* library (Oksanen et al., 2018) under the R environment (R Development Core Team, 2018).

3. Results

We recorded 26 species mammals of medium to large size belonging to 13 families (Table 1). 22 and 24 species were detected in the dry and the rainy season, respectively. Species that appeared exclusively in the dry or rainy season were species recorded only with 1 or 2 presences. In total, 22 817 photographs showed positive sightings of native fauna that were subsequently identified at the species level. *Hydrochoerus hydrochaeris* (capybara) was the most prominent animal around the water reservoirs, appearing in 74.1% of the pictures, followed by *Pecari tayacu* (collared peccary, 5.9%), *Tayassu pecari* (white-lipped peccary, 3.7%), *Mazama gouazoubira,* (gray brocket, 3.2%) and *Tapirus terrestris* (tapir, 3.2%; Table 1).

In relation to occupancy probability, *T. pecari* and *Leopardus pardalis* (ocelot) were the species with the strongest response to forest cover (Fig 2ab, Table S1). *Tayassu pecari* showed an extremely low probability of occupancy when forest cover was below 30%, and *L. pardalis* only showed high occupancy probabilities when forest cover was high (beyond 70%). Additionally, forest cover had a strong positive effect on the detectability of *T. pecari* (Fig. 2a). Forest cover also showed a positive effect,

Table 1
List of medium- and large-sized mammal species potentially encountered in the dry Chaco forests. National and global conservation status of the species is shown based on UICN criteria.

Family	Species (Species code)	N° of sites with presences (n° of pictures)	MADES Res. 632/2017 [a]	UICN [b]
Dasypodidae	*Dasypus novemcinctus*	1 (3)	LC	LC
Chlamyphoridae	*Cabassous chacoensis*	0	LC	NT
	Calyptophractus retusus	0	LC	DD
	Chaetophractus vellerosus	1 (1)	LC	LC
	Chaetophractus villosus	3 (14)	LC	LC
	Euphractus sexcinctus	1 (9)	LC	LC
	Priodontes maximus	1 (1)	EN	VU
	Tolypeutes matacus	8 (172)	LC	NT
Myrmecophagidae	*Myrmecophaga tridactyla*	5 (41)	VU	VU
	Tamandua tetradactyla	3 (10)	LC	LC
Tapiridae	*Tapirus terrestres*	8 (722)	VU	VU
Cervidae	*Mazama gouazoubira*	9 (728)	LC	LC
	Mazama americana	0	LC	DD
Tayassuidae	*Tayassu pecari*	4 (845)	VU	VU
	Pecari tajacu	7 (1339)	LC	LC
	Parachoerus wagneri	2 (178)	EN	EN
Canidae	*Cerdocyon thous*	12 (501)	LC	LC
	Chrysocyon brachyurus	0	VU	NT
	Lycalopex gymnocercus	11 (200)	LC	LC
Felidae	*Leopardus pardalis*	3 (43)	NT	LC
	Leopardus geoffroyi	10 (434)	LC	LC
	Puma yaguaroundi	1 (4)	LC	LC
	Puma concolor	9 (85)	LC	LC
	Panthera onca	3 (18)	CR	NT
Mephitidae	*Conepatus chinga*	10 (123)	LC	LC
Mustelidae	*Eira barbara*	1 (3)	LC	LC
	Lontra longicaudis	0	LC	NT
	Galictis cuja (GalCuj)	3 (7)	LC	LC
Procyonidae	*Procyon cancrivorus* (ProCan)	12 (417)	LC	LC
	Nasua nasua	0	LC	LC
Hydrochaeridae	*Hydrochoerus hydrochaeris* (HydHyd)	12 (16908)	LC	LC
Caviidae	*Dolichotis salinicola*	0	LC	LC
Myocastoridae	*Myocastor coypus*	0	LC	LC
Leporidae	*Sylvilagus brasiliensis* (SylBra)	3 (11)	NE	LC

[a] Asociación Paraguaya de Mastozoología y Secretaría del Ambiente (2017)
[b] IUCN (2019).

although weaker, on the occupancy probability of *P. tajacu*, *M. gouazoubira* and *Myrmecophaga tridactyla* (giant anteater) (Fig 2cde, Table S1). Forest cover did not show a clear effect on the occupancy probability around the water reservoirs with respect to *Tapirus terrestris*, but had a very strong and positive effect on its detection probability (Fig. 2f, Table S1). *Puma concolor* (puma) showed a high probability of occupancy that was independent of forest cover, but also showed a positive increase in detection probability in relation to forest cover (Fig. 2g, Table S1). Forest cover did not show any clear effect on the occupancy and detection probabilities of *Tolypeutes matacus* (southern three-banded armadillo), *Leopardus geoffroyi* (Geoffroy's cat), *Conepatus chinga* (Molina's hog-nosed skunk) and *Procyon cancrivorus* (crab-eating raccoon) (Fig 2hijm, Table S1). Lastly, *H. hydrochaeris, Cerdocyon thous* (crab-eating fox) and *Lycalopex gymnocercus* (pampas fox) showed occupancy probabilities approaching 1.0, being independent of forest cover, but showed higher detection probabilities when the percentage of forest cover was low (Fig 2kln, Table S1).

Seven species, *Procyon cancrivorus*, *M. gouazoubira*, *Leopardus geoffroyi*, *C. thous*, *Conepatus chinga*, *L. pardalis* and *T. pecari*, exhibited a higher detection probability during the dry season rather than the rainy season ($\omega_i > 0.80$, Fig. 3, Table S1). Additionally, the results obtained for three species, *H. hydrochaeris*, *P. tajacu* and *P. concolor*, weakly supported the hypothesis that detection is higher during the dry season ($\omega_i > 0.50$, Fig. 3, Table S1). For the remaining species, the detection probabilities were similar throughout the year (Fig. 3, Table S1).

The PCoA analysis showed the dissimilarities between sites in the two first axes of ordination (which explained 63.9 percent of the variation, Fig. 4). The sites with water reservoirs surrounded by high forest cover showed high-intensity use by *T. terrestris*, *T. pecari*, *P. tajacu*, *L. pardalis*, *M. gouazoubira*, *P. concolor*, *Myrmecophaga tridactyla* and *Tamandua tetradactyla*. In contrast, the sites with water reservoirs surrounded by pastures and low forest cover were characterized by high-intensity use by *Hydrochoerus hydrochaeris*, *Cerdocyon thous* and *Lycalopex gymnocercus*.

4. Discussion

Although extensive land-use change and deforestation is a current problem, our study shows that cattle ranches have the potential to maintain a substantial part of mammal diversity. Around 75–80% of the medium- and large-sized mammals previously cited as being present in our study area were in fact detected (Table 1). Of the potential eight non-detected species

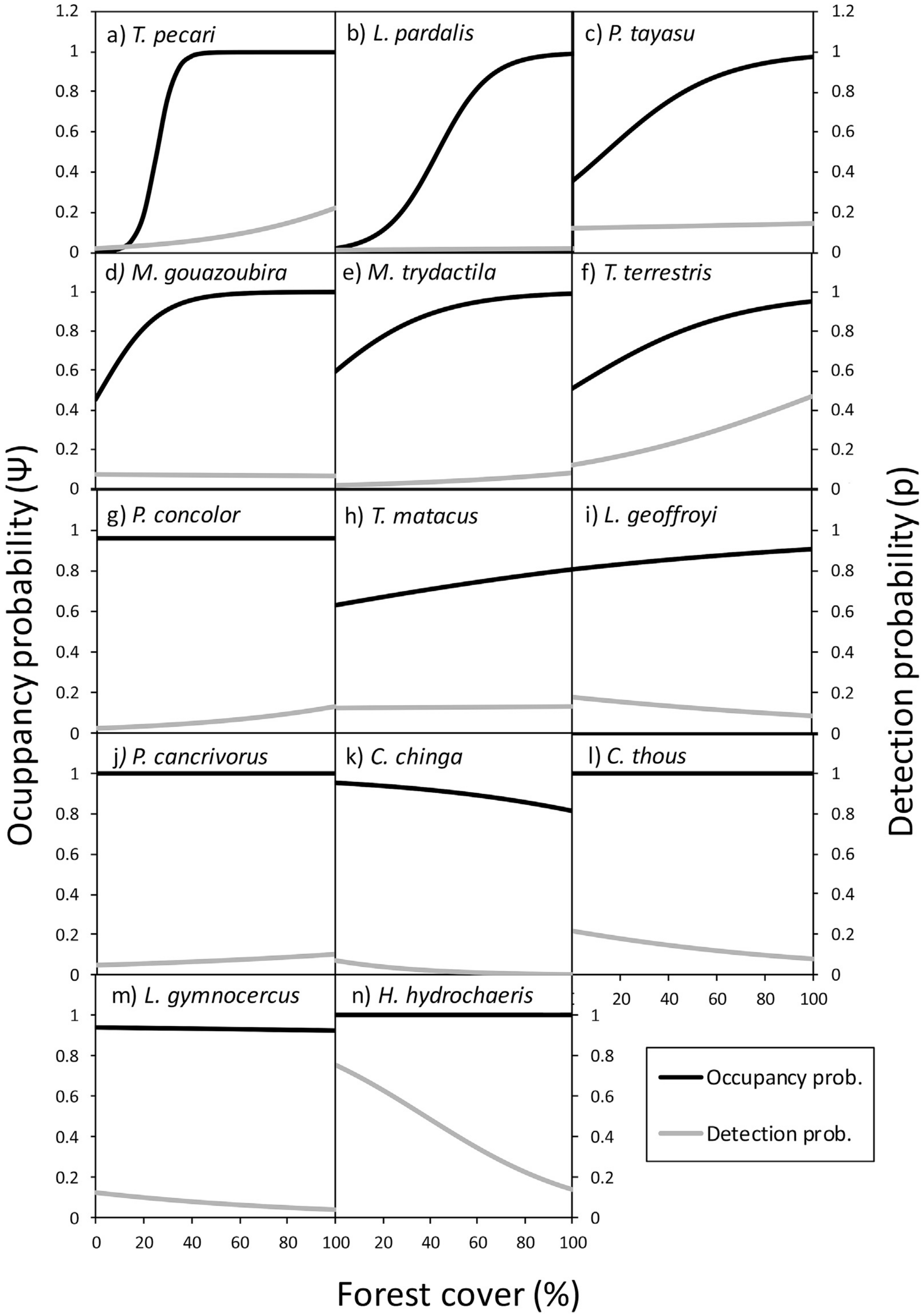

Fig. 2. Occupancy (black line) and detection (gray line) probabilities of the selected mammal species in relation to forest cover (%).

(Table 1), two of them, the coati (*Nasua nasua*) and the chacoan mara (*Dolichotis salinicola*), were detected during later camera trap studies in Estancia Montania (data not shown). The semiaquatic species *Lontra longicaudis* and *Myocastor coypus* were not detected, most probably due to their strong preference for water bodies. Also, armadillos *Cabassous chacoensis* and *Calyptophractus retusus*, of which little is known, are mainly fossorial species, and are likely to have a extremely low

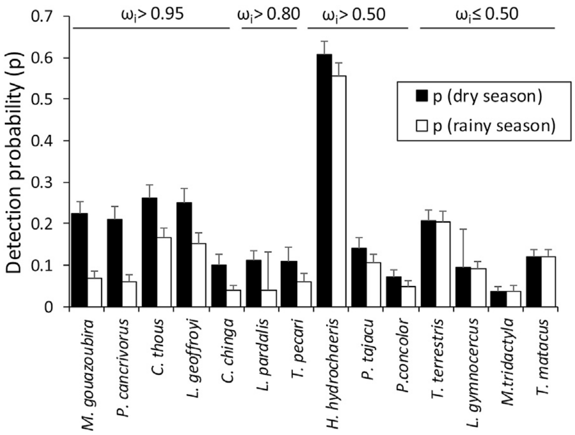

Fig. 3. Detection probabilities (±SE) of the selected mammal species during the dry (black) bars) and wet seasons (black bars). Species are ordered from left to right according to stronger evidence of higher detection probabilities during the dry season. Combined weighs (ωi) of the models where detection probability is affected by season are shown.

detectability using the camera-trap approach. Furthermore, our study site is located in the outer limits of the distribution range of the maned wolf *Chrysocyon brachyurus*, although the expansion of its range in Brazil, associated with deforestation and the conversion to grasslands, has recently been reported (Queirolo et al., 2011). *M. gouazoubira*, on the other hand, was commonly found and easily detected. However, the related red brocket deer *M. americana* was not detected. Some studies have suggested that *M. gouazoubira* and *M. americana* generally inhabit separate areas; *M. americana* tends to choose moister habitats in the Chaco (Rumiz, 2002; Rivero et al., 2005) and are rarely detected in drier sites (Rumiz, 2002; Deem et al., 2004).

We were able to detect a relatively complete mammal assemblage in these human-modified landscapes. Also, all the species listed in the three categories of higher threat ("Critical", "Endangered" and "Vulnerable") at the global (UICN, 2019) and regional levels (Asociación Paraguaya de Mastozoología and Secretaría del Ambiente, 2017) were present; some of which, such as the "Vulnerable" species *Tapirus terretris* and *Tajassu peccary,* had a relatively high probability of detection. Very few studies have addressed the conservation potential of large farmlands in the Chaco, despite their increase over the past few decades. The mammal communities found in agricultural fields with a landscape configuration similar to that of the Argentinian Chaco (Núñez-Regueiro et al., 2015) are known to be more impoverished than in our study area, especially the threatened species (Núñez-Regueiro et al., 2015). There could be two possible reasons that explain the rich diversity of mammals found in Estancia Montania. First, extensive deforestation in the Paraguayan dry Chaco started later than in other chacoan regions, although it has accelerated dramatically in the last two decades (Caldas et al., 2013; Arévalos et al., 2015; Vallejos et al., 2015). Thus, although these species have initially survived habitat change, they could eventually become extirpated without any further habitat modification, a process known as extinction debt (Tilman et al., 1994; Kuussaari et al., 2009). Therefore, it is imperative to continue monitoring these sites; however, the presence of several females with offspring registered by the camera-traps (data not shown) supports the potential of cattle ranches to conserve biodiversity in the long term. The second explanation, and most likely the most critical, is that the pressure associated with hunting is low within our study site. Although these water reservoirs are usually the places preferred by illegal poachers to stalk their prey, we only detected one poacher in one single day throughout the entire study period (data not shown). Hunting is explicitly and strictly prohibited for all workers in Estancia Montania, and the single poacher detected was an intruder unassociated with the cattle ranch. Although hunting pressure usually interacts synergistically with habitat conversion and fragmentation, this activity is undoubtedly one of the main drivers of defaunation in neotropical forests (Altrichter et al., 2012; Laurance et al., 2012; Periago et al., 2015; Galetti et al., 2017; Bogoni et al., 2018; Romero-Muñoz et al., 2020). Moreover, strict compliance with hunting bans is likely to be an important issue related to the management of the conservation of mammal diversity in human-altered landscapes.

Of the species analyzed, 71% showed a moderate to strong increase in probability detection around water reservoirs during the dry season. Since many neotropical mammals have a stronger preference toward habitats closer to water sources, due to the availability of water itself and the associated prey (Goulart et al., 2009; Astete et al., 2017; Regolin et al., 2017; Dias et al., 2019), it is not surprising there was a higher frequency of use around artificial water reservoirs during the dry season. Natural bodies of standing water are abundant during the rainy season but become greatly reduced or disappear entirely during the dry season (Eidt, 1968; Magliano et al., 2005). Therefore, permanent man-made water reservoirs are likely to be essential resources for mammal communities in the cattle ranches located within the dry Chaco. In fact, in other extreme habitats like the Caatinga of northwestern Brazil, artificial water sources are managed infrastructures in protected areas that explain the spatial distribution of herbivore/frugivore species, such as *M. gouazoubira* and *P. tajacu*, and the large carnivores that prey on them like *P. concolor* (Astete et al., 2017).

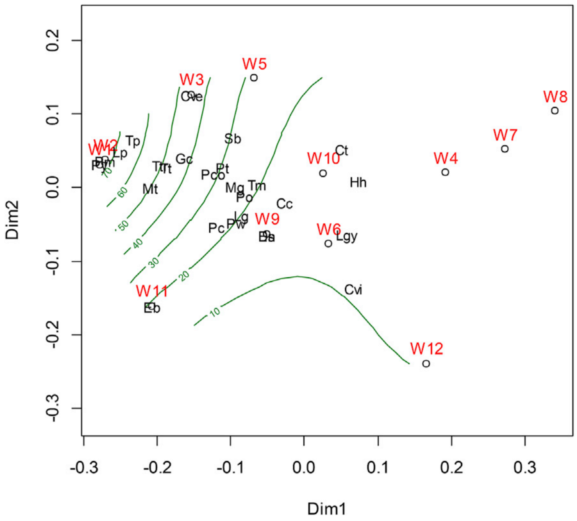

Fig. 4. Principal Coordinate Analysis (PCoA) showing differences in the use of water reservoirs by mammal communities in relation to the surrounding forest matrix. Sites were consecutively numbered from the highest forest cover (W1) to the lowest forest cover (W12). Green lines show variation in forest cover (%) in the ordination space. Species codes are: Cc: *C. chinga*, Ct: *C. thous*, Cve: *C. vellerosus*, Cvi: *C. villosus*, Dn: *D. novemcinctus*, Eb: *E. barbara*, Es: *E. sexcintus*, Gc: *G. cuja*, Hh: *H. hydrochaeris*, Lg: *L. geoffroyi*, Lgy: *L. gymnocercus*, Lp: *L. pardalis*, Mg: *M. gouazoubira*, Mt: *M. tridactyla*, Pc: *P. cancrivorus*, Pco: *P. concolor*, Pm: *P. maximus*, Po: *P. onca*, Pt: *P. tajacu*, Pw: *P. wagneri*, Py: *P. yaguaroundi*, Sb: *S. brasiliensis*, Tm: *T. matacus*, Tp: *T. pecari*, Tt: *T. terrestris*; Ttr: *T. tetradactyla*. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Although the time of year influenced the probability detection of most of our species, forest cover was a critical factor in determining the composition of mammal communities detected around water reservoirs. The species most affected by the lack of forest cover were the white-lipped peccary, *Tayassu pecari*, and the ocelot *Leopardus pardalis*. In the case of *T. peccary*, this species is considered vital for maintaining ecosystem processes, and is important for seed predation and dispersion, plant demography and diversity, as well as being prey for jaguars and pumas (Silman et al., 2003; Beck, 2005; Keuroghlian and Eaton, 2009; Altrichter et al., 2012), and have been proposed as surrogate to monitor ecosystem functioning (Jorge et al., 2013). Forest lost and hunting pose the most significant threat to this species, and, as in other biomes, are driving the steep decline in the number of white-lipped peccary in the Chaco region (Altrichter and Boaglio, 2004; Sowls, 2013; Núñez-Regueiro et al., 2015; Reyna-Hurtado et al., 2016). In our site, the low hunting pressure suggests that forest loss can be enough to cause an irreversible decline in the white-lipped peccary populations if connectivity for this species becomes seriously compromised in the absence of adequate forest corridors between suitable patches. White-lipped peccary consumes a large amount of food consisting mainly of fruits and large seeds of tree and palm species (Beck, 2005) and so it requires large and ecologically intact forest to maintain viable populations (Altrichter et al., 2012). Additionally, *T. pecari* was more commonly detected around water reservoirs during the dry season than during the rainy season. Water is a limiting factor responsible for the high level of mortality observed during the dry season which affects herd size (Reyna-Hurtado et al., 2009, 2016). But again, although artificial water reservoirs provide a key resource for this species, the lack of enough forest cover precluded its use in most of our study sites during the dry season. The other species most affected by the loss of forest cover was the ocelot *Leopardus pardalis,* which is classified within the "Least Concern" category by the IUCN. Its populations show a range-wide decrease (Paviolo et al., 2015), and in Paraguay is now considered as a "Near Threatened" species (Asociación Paraguaya de Mastozoología and Secretaría del Ambiente, 2017). The importance of forest cover for this species is well established (Harveson et al., 2005; Lyra-Jorge et al., 2010; Regolin et al., 2017; Paolino et al., 2018), but its sensitivity to the loss of forest cover varies among studies. Although some authors describe the ocelot as a species tolerant of intermediate-cover sites (Goulart et al., 2009), our results are in accordance with the reports that stress the ocelot is extremely sensitive and only occupies densely forested areas (Harveson et al., 2004; Regolin et al., 2017; Cruz et al., 2019). Strong preference of ocelot for dense vegetation has been related with prey availability (Wang, 2002; Cruz et al., 2019), avoidance of large predators in open areas (Harvenson et al., 2004) and susceptibility to human activity (Cruz et al., 2019). Other mammals with a strong preference toward habitats with high forest cover were *Pecari tajacu*, *Mazama gouazoubira*, *Tapirus terrestris* and *Myrmecophaga tridactyla*. The higher occupation of forested water sources by anteaters is consistent with the results found in wetlands in Argentina (Di Blanco et al., 2017) and differ from the results obtained for Brazil's Pantanal (Mourão and Medri, 2007). Water sources also drove habitat selection for *P. tajacu*, *M. gouazoubira* and *T. terrestris* (Norris, 2014; Astete et al., 2017; Ferreguetti et al., 2017) and *M. gouazubira* was the species with the most significant difference regarding detectability between seasons. This is most likely related to being less dependent on water sources during the wet season and more dependent during the dry season, since importance of distance to water as a predictor variable of occupancy has been only observed in dry environments (Ferreguetti et al., 2015; Astete et al., 2017; Rodrigues et al., 2017). However, these species showed occupancy probabilities of around 0.4–0.6 when the forest cover was between 15 and 20%. This suggests *M. gouazubira* is more tolerant to deforestation than *T. pecari* and *L. pardalis*, or at least shows the potential of using forest strips for a few kilometers encouraging the animals to use the water reservoirs (Nuñez-Regueiro et al., 2015).

Furthermore, the mammal assemblages around the water reservoirs surrounded by a higher cover of cattle pastures were dominated by two canid species, the Pampas fox *Lycalopex gymnocercus* and the crab-eating fox *Cerdocyon thous*, as well as the semiaquatic capybara *Hydrochoerus hydrochaeris* (Fig. 4). Although the forest cover did not affect the occupancy probability of these species, it did have a negative effect on the detection probability, findings which indicate a high-intensity use of areas dominated by open pastures. Both canids are generalist species with similar diets, and are tolerant of anthropogenic impact (Di Bitteti et al. 2009; Dias and Bocchiglieri, 2016; Bossi et al., 2019). In the case of *L. gymnocercus*, this species is usually described as inhabiting grasslands, but can also be found in wooded savannas, deserts, and open forests. *C. thous*, on the other hand, has been described as a habitat generalist. However, both species are known to have a strong preference toward grazed areas occupied by cattle, which is likely related to predator avoidance and prey consumption (Di Bitteti et al. 2009; Dias et al., 2019). The capybara, *Hydrochoerus hydrochaeris*, was the most commonly detected species in our study area, and in all sites the presence of capybara herds was recorded. Capybara is a semi-aquatic species that requires permanent bodies of standing water, and their populations over the past decades have been continuously expanding westwards toward the Paraguayan dry Chaco due to deforestation and land conversion. Also, the increase in the number of cattle ranches has been the primary driver for the expansion of its range (Campos-Krauer and Wisely, 2011). The detection probability of capybara was greater in areas surrounded by the high cover of pastures, since this species is an efficient grazing herbivore that preferably feed on grasses (Quintana, 2003; Desbiez et al., 2011). However, increasing populations of *H. hydrochaeris* has led to some negative effects. *H. hydrochaeris* compete with livestock for pastures (Quintana, 2003; Desbiez et al., 2011) and during the dry season, the scarcity of grasses can alter its habitat use by intensifying its movement, which in turn reduces selectivity and increases the trampling of and the damage caused to tree seedlings (Fleury et al., 2015). In addition, *H. hydrochaeris* has the potential to infect cattle, wildlife and humans with pathogens and parasites (Labruna et al., 2004; Herrera et al., 2005). On the other hand, *H. hydrochaeris* is one of the main types of prey for jaguars and pumas, and their abundance helps to reduce conflicts between big cats and cattle (Polisar et al., 2003).

5. Conclusions

Cattle ranches have the potential for maintaining a substantial part of the original chacoan fauna, where forest cover is a main component in the structuring of the mammal assemblages found around water reservoirs. High forest cover favors the occurrence and/or detectability of several threatened and non-threatened mammal species. This is especially the case for vulnerable *T. pecari* and *L. pardalis*, species that have been recognized as having roles in the functioning of ecosystems (Silman et al., 2003; Beck, 2005; Jorge et al., 2013; Periago et al., 2015; Galetti et al., 2015; Sarasola et al., 2016). In sites with high grassland cover and low forest cover the generalist canid species *L. gymnocercus* and *C. thous* were quite common, indicating their ability to thrive in these anthropized habitats. The semiaquatic, *H. hydrochaeris* was by far the most commonly encountered species around water reservoirs. This observation confirms the expansion of its range toward the dry Chaco, which is linked to the proliferation of cattle ranches. (Campos-Krauer and Wisely, 2011). Higher detection probabilities for most of the species during the dry season indicates that artificial water reservoirs in cattle ranches are important infrastructures for wildlife when most of the natural bodies of water are ephemeral in the dry Chaco. The conservation of large forest tracts and strict compliance with poaching bans are key management strategies for the conservation of mammal diversity in the increasingly predominant human-altered landscapes of the Chaco.

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Credit author statement

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Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

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