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Original Investigation

Forage use in domestic cattle (*Bos indicus*), capybara (*Hydrochoerus hydrochaeris*) and pampas deer (*Ozotoceros bezoarticus*) in a seasonal Neotropical wetland

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ABSTRACT

The impact of livestock grazing on native wildlife remains a topic for considerable debate. In the Brazilian Pantanal extensive cattle ranching has been practised since the mid-18th century and cattle live alongside a diverse group of medium to large sized terrestrial mammalian herbivores. This study examined the use, similarity and selection of forage resources among cattle (*Bos indicus*), pampas deer (*Ozotoceros bezoarticus*) and capybara (*Hydrochoerus hydrochaeris*) in a paddock in the central region of the Brazilian Pantanal. Plants consumed were identified through micro-histological analysis of faecal samples collected from three species over several seasons, and quadrats (0.5 m × 0.5 m) were allocated to patches within each of the main landscapes to measure availability of resources. Overall, cattle were classified as grazers, capybara as mixed feeders, pampas deer as browsers. 126 plants were identified in faecal samples of the three species. Similarity indices were highest between domestic cattle and the capybara and lowest between these two species and the deer. Diets were more similar between the species during the wet season (period of resource abundance) than during the dry season (period of resource scarcity). Overall animals selected different forage species *H. amplexicaulis* and *L. hexandra* were the only plants selected by all three herbivores. In this study, the presence of cattle does not appear to be as detrimental to wild herbivores as suggested by other examples in the literature.

Introduction

Extensive cattle ranching started in the Brazilian Pantanal in the mid-18th century. It is considered one of the very few examples of sustainable management of a tropical biome. Until recently this wetland was considered quite pristine (Seidl et al., 2001; Junk et al., 2006). Private ranches, whose main economic activity is beef production, occupy approximately 95% of the Brazilian Pantanal (Seidl et al., 2001). Under traditional management practices, consisting of the seasonal movement of herds among patches of native savannas, cattle ranching is considered to have a low environmental impact (Santos et al., 2010) because it relies on the use of renewable resources (Takahashi et al., 2009). The key to safeguarding the Pantanal is to optimise the use of natural resources while respecting the environment's natural limits, ensuring the maintenance of biodiversity and the ecosystem's resilience (Santos et al., 2010). One of the main natural resources in the Pantanal is native forage species. According to Pott and Pott (1999) of the 1860 species of plants found in the Pantanal, the most numerous families include Fabaceae (240), Poaceae (212) and Cyperaceae (91). Sustainable use of natural resources in the Pantanal implies that the various actors within the trophic guilds are not significantly impacted by the introduction of cattle. Among the primary consumers of the trophic chain in the Pantanal are a diversity of medium to large sized terrestrial mammalian herbivores which live alongside cattle (*Bos indicus*) and include: pampas deer (*Ozotoceros bezoarticus*); capybara (*Hydrochoerus hydrochaeris*); tapir (*Tapirus terrestris*); marsh deer (*Blastocerus dichotomus*); red brocket deer (*Mazama americana*) and grey brocket deer (*Mazama goazoubira*). An important question that needs to be examined is whether or not there is forage overlap between cattle and these native herbivores, as well as the implications of such overlap for native species.

Cattle introduced in the Pantanal have been shaping the landscape units with a relatively low impact since the basis of their diet is native forage resources. Areas of the Pantanal without cattle accumulate a large amount of highly inflammable vegetation biomass especially at the end of the dry season (August and September). According to Pott and Pott (1994) cattle can be considered as "the fire fighters of the Pantanal" since they consume a large part of this inflammable vegetation. However, the addition of a new species to an ecosystem can change the structure of the community

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assemblage particularly within similar guilds (Shea and Chesson, 2002; Patterson et al., 2003). The global introduction of domestic livestock into grasslands ranging from lowland tropical savannahs to high altitude mountain grasslands has been considered a serious threat to ecosystems throughout the world. A wide range of negative impacts are associated with the introduction of livestock, one of which is their effect on sympatric native herbivores. In the Indian Trans-Himalaya of the Tibetan Plateau, livestock competes with wild bharal (*Pseudois nayau*) (Mishra et al., 2004). Cattle and zebra (*Equus quagga* sp.) as well as cattle and elephant (*Loxodonta africana*) competition has been documented in the grasslands of Kenya (Young et al., 2005). In Tanzania during the wet season, cattle showed overlap in resource use with both zebra and wildebeest (*Connochaetes taurinus*) (Voeten and Prins, 1999). In Patagonia, livestock competes with guanaco (*Lama guanicoe*) (Baldi et al., 2004). Many authors have voiced concern regarding the impact of livestock grazing on native wildlife and this issue remains a matter for considerable debate (Fleischner, 1994; Baldi et al., 2004; Lamprey and Reid, 2004; Chaikina and Ruckstuhl, 2006; Vila et al., 2008).

Consequences of overlap in the use of plant material would be greatest during periods of limited food resources like droughts and floods, when availability of forage resources is lowest (Santos et al., 2010). Overlap in resource use during periods of food scarcity may lead to competition for resources (Ives et al., 1999; Keddy, 2001; Shea and Chesson, 2002). Competition between cattle and native herbivores in some areas has been found to occur only when resources are limited (Gordon and Illius, 1989; Voeten and Prins, 1999; Mishra et al., 2004). Even if overlap in resource use does not occur year round, it is still possible that high overlap during periods of resource scarcity will have a negative effect on the co-existence between native and exotic wildlife and can change the competitive interactions between them and is thus of conservation concern (Shea and Chesson, 2002).

In the central Pantanal, pampas deer and capybara were found to be among those native herbivores with the highest densities and metabolic biomass (Desbiez et al., 2010a). Use of forage resources between cattle, capybara and pampas deer was examined in a representative paddock in the central Pantanal during both the wet and dry season. The objective of the study was to determine potential similarity in resource use and selection and hypothesise on potential competitive interactions between native herbivores and domestic cattle in the Brazilian Pantanal.

Methods

Study area

The study area was a 151 ha paddock located in the Nhumirim ranch (lat. 19°04′S, long. 56 36′W, alt. 98 m) in the Nhecolândia sub-region of the Pantanal. This sub-region is one of the most important areas for extensive cattle ranching in the floodplain. The vegetation is characteristic of the relatively higher areas in the sub-region and presents a complex mosaic of habitats that include permanent and temporary ponds, seasonally flooded and scrub grasslands, forest patches and scrub forests. Details of the study area are provided in Santos (2001). The study area is subjected to small floods which generally occur due to heavy rain. Cattle are maintained year round in the area as opposed to other areas of the Pantanal where floods are of mainly fluvial origin and cattle sometimes need to be removed or managed during such floods.

The climate is classified as Aw de Koeppen: tropical climate, megathermic with a dry winter and rains in the summer (Cadavid Garcia, 1986). During the study period the average temperatures were 25.6 °C and 25.5 °C and the total rainfall was 1125.7 mm and 895.9 mm for the years 1997/1998 (October/1997 to September/1998) and 1998/1999 (October/1998 and September/1999) respectively. Landscape units were classified as: (1) semi-deciduous forest; (2) scrub forest; (3) scrub grassland; (4) open grassland dominated by *Axonopus purpusii* and *Andropogon* spp.; (5) open grasslands dominated by *Elyonurus muticus*; (6) permanent ponds and temporary ponds that dry up during the dry season and (7) floodable grasslands.

Sampling

Forty-six Nelore cows (*Bos indicus*), and their calves were maintained in the paddock throughout the study. The stock rate (3.3 ha/cow) was considered low to moderate when compared to the traditional average in the region (3.6 ha/cow) (Silva et al., 2001). This means that cattle was able to conduct selective grazing throughout the study period. A group of 12 capybara also resided year round in the paddock and a pair of adult pampas deer and two sub-adults frequently visited the paddock. The dietary estimation for the pampas deer was therefore affected by the inclusion in their faeces of food located outside the paddock. Between October 1997 and September 1999, faecal samples were collected monthly from cattle and capybara while samples for pampas deer were collected when they were inside the paddock. Faecal samples were stored in 70% alcohol. At least one sample was collected per species per month although for the Pampas deer this was not always possible. An interactive key based on the Delta software provided an easy to use reference collection of epidermal cells of all forage species present in the study (Desbiez et al., 2010b). Each faecal sample was separately ground in a blender and a microscope slide was prepared using Hoyer's mounting solution. Slides were then air-dried for two weeks before being analysed. Twenty fields were examined on each slide under 100× magnification to identify plant composition for each sample. A total of 726 slides were prepared for cattle, 29 for pampas deer and 67 for capybara. Cumulative curves for capybara and pampas deer were made to test if data collection was sufficient. The faecal analysis assumed equal digestibility between the different plants species and no correction factors were applied. Species frequency data were converted to relative percentages of plant dry weight in the diet of each species (Sparks and Malecheck, 1968; Holechek and Gross, 1982). Relative percentages of plant dry weight results from each sample were then pooled to determine overall diet in both the wet (October to March) and dry season (April to September). Plant species were considered key forage species when they occurred in at least 2% or more of the dry weight of the diet in a season.

Forage plants were sampled in the main landscape units used by animals, classified as open grasslands (dominated by *A. purpusii*), lowlands (including permanent ponds edges, temporary ponds floodable grasslands) and scrub grasslands. Thirty quadrats (0.5 m × 0.5 m) were allocated to patches within each of the three main landscape to estimate botanical composition according to the method proposed by Mannetje and Haydock (1963). Forested areas were not considered since forage availability in them is very low. Botanical composition of key plant species available was then corrected by area of each landscape units' open grassland (45 ha), lowlands (24 ha) and scrub grassland (35.4 ha) to obtain an estimate of resource availability in the study area. However for capybaras which used a limited area around two ponds (10.6 ha lowland and 15.5 ha open grassland) only part of the study area was used to calculate resource availability. Although for cattle and pampas deer we considered similar resource availability, the deer had access to resources beyond the paddock which escaped our control. Resource availability results were pooled into two seasons: wet and dry.

Specific plant species selection was quantified using Manly's selectivity index (SI) α (Chesson, 1978). This index varies between 0 and 1.0 with values above 0.5 indicating preference for the

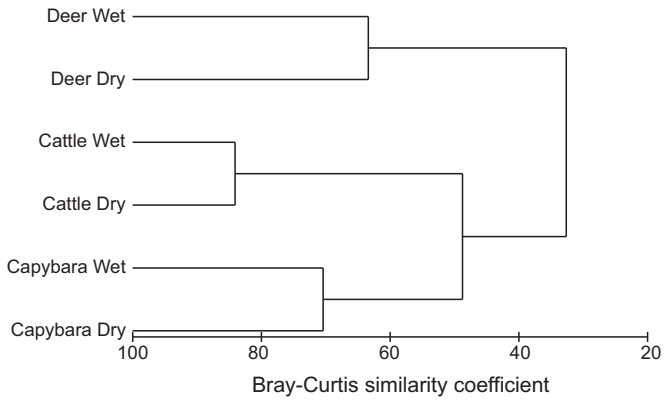

Fig. 1. Cluster analysis of Bray-Curtis similarity indices of cattle, capybara and pampas deer diet during the wet and dry season in Nhecolândia, Pantanal between October 1997 and September 1999.

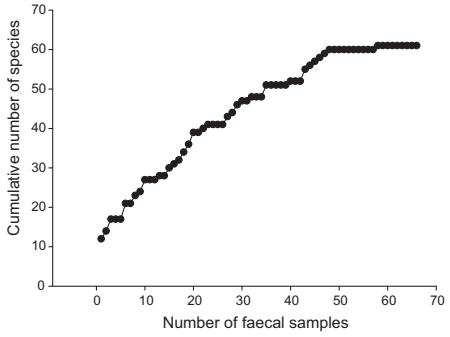

Fig. 2. Cumulative number of plant species in faecal samples determined by micro-histological analysis and number of capybara faecal samples in Nhecolândia, Pantanal between October 1997 and September 1999.

resource while values below 0.5 indicate discrimination against the resource. A value near 0.5 indicates non-selective feeding towards the resource.

Herbivores were classified into feeding types according to the proportion of grasses (Poaceae) in their diets. Grazers were defined as species in which grasses represent >75% of their diets. Browsers were defined as species consuming <25% of grass in their diets, and mixed-feeders were those animals that consumed between 25% and 75% of grasses in their diets (Mendoza et al., 2002). Niche breadth for each species and for each season was also calculated using the index proposed by Levins (Krebs, 1998). Levin's index is minimal when all the samples occur in only one resource state, indicating minimum niche breadth or maximum specialisation (Krebs, 1998). Relative percentage dry weight of dicotyledons, monocotyledon and three most numerous plant families (Fabaceae, Poaceae and Cyperaceae) was determined.

The Bray-Curtis similarity coefficient using the PRIMER software (Clarke and Gorley, 2006) was used to examine resemblance between species and seasons. Square root transformation was used for Bray-Curtis, to prevent over-dominance. Species with exactly the same frequency of plants identified in their faecal samples have a Bray-Curtis similarity coefficient of 1. A hierarchical cluster analysis using PRIMER software (Clarke and Gorley, 2006) was used to recognise similarities as well as the variations in similarities between the wet and dry season between the three species.

Results

A total of 126 different plant species were identified in the faecal samples of the three species. Overall 30 species represented 2% or more of the dry weight of the diet of one of the herbivores in either season. A total of 95 plant species from 23 families were identified in the cattle faecal samples. Over 75% of plant dry weight in the diet of cattle belonged to the Poaceae family, classifying cattle as grazers (Table 1). Although similarity indices between diet during the wet and dry season were high (Bray-Curtis similarity 84.07) (Fig. 1), cattle consumed less than 75% Poaceae during the dry season (Table 1). While cattle can be classified as gazers in the wet season they are classified as mixed feeders in the dry season. *A. purpusii*, *Mesosetum chaseae*, *Hymenachne amplexicaulis*, *Panicum laxum* and *Eleocharis mínima* were the species with the highest dry weight in the diet (Supplementary Table 1). However, only *H. amplexicaulis* and *Leersia hexandra* were selected throughout the year, while *E. minima* was selected only in the wet season and *Attalea phalerata* in the dry season (Table 2). Manly's selectivity index indicated non-selective feeding of *A. purpusii*, *M. chaseae* and *P. laxum* (Table 2).

A total of 61 plant species from 22 families were identified in the capybara faecal samples. 35% of plant dry weight in the diet of capybara belonged to the Poaceae family, classifying capybara as mixed-feeders (Table 1). Cyperaceae were the most consumed family of plants and capybaras were classified as mixed feeders in both the wet and dry season. During the dry season the number and proportion of dry weight of dicotyledon plants in the diet increased. The Bray-Curtis similarity index between wet and dry season diet was 70.38 (Fig. 1). The cumulative number of species consumed by capybara indicate that sample size was probably adequate to capture the full range and diversity of plants consumed by capybaras (Fig. 2). Overall *E. mínima*, *Diodia kuntzei*, *Panicum laxum*, unidentified *Cyperus* spp., *L. hexandra* and *A. purpusii* were the species with the highest dry weight in the diet of capybaras (Supplementary Table 2). Manly's selectivity index indicated selection of *Caperonia castaneifolia*, *Cyperus* spp., *Digitaria* spp., *Diodia kuntzei*, *Eleocharis acutangula*, *Eleoacharis interstincta*, *E. mínima*, *Hydrocleys* sp., *H. amplexicaulis*, *L. hexandra*, *P. laxum*, *Pontederia* spp., and *Reimarochloa brasiliensis* (Table 2). While *Bacopa salzmanii* was selected only in the dry season (Table 2). Manly's selectivity index indicated non-selective feeding of *A. purpusii* (Table 2). All of the species selected are aquatic or semi-aquatic.

A total of 45 plant species from 22 families were identified in the pampas deer faecal samples. Less than 25% of plant dry weight in the diet of pampas deer belonged to the Poaceae family, classifying pampas deer as browsers (Table 1). However during the wet season, 35% of their diet was composed of Poaceae classifying them as mixed-feeders during that period (Table 1). In fact the Bray-Curtis similarity index between wet and dry season diet was the lowest of the three species considered (63.35%) (Fig. 1). The cumulative number of species consumed by pampas deer indicate that sample size was probably too low to capture the full range and diversity of plants consumed (Fig. 3). Results indicate that *Melochia simplex*, *Nymphoides grayana*, *Ludwigia* spp., *L. hexandra*, *Aeschynomene* spp. and *Byrsonima orbignyana* were the species with the highest dry weight in the diet (Supplementary Table 3). Manly's selectivity index indicated selection of *Aeschynomene fluminensis*, *Byrsonima orbigniana*, *Ludwigia* spp., *Melochia simplex*, *Nymphoides grayana* and *Thalia geniculata* (Table 2). In the wet season *Cynodon dactylon*, *H. amplexicaulis* and *L. hexandra* were selected while *Diospyrus hispida* and *Richardia grandiflora* were selected in the dry season (Table 2).

Bray-Curtis similarity indices were highest between domestic cattle and the capybara and lowest between these two species and the deer (Table 3). Diets were more similar among all the species during the wet season than during the dry season (Table 3). Over-

Table 1
Number of species, niche breadth, relative percentage dry weight of plants and feeding type classification of cattle, capybaras and pampas deer during the wet and dry season in Nhecolândia, Pantanal between October 1997 and September 1999.

		Total	Wet season	Dry season
Cattle	Number of species	95	84	86
	Niche breadth	40.5	34.2	41.9
	Dry weight dicotyledons (%)	7.9	4.4	11.1
	Dry weight Fabaceae (%)	0.6	0.3	1.0
	Dry weight monocotyledons (%)	92.1	95.6	88.9
	Dry weight Cyperaceae (%)	12.7	13.3	12.1
	Dry weight Poaceae (%)	76.5	80.4	72.8
	Feeding type classification	Grazer	Grazer	Mixed-feeder
Capybara	Number of species	61	42	50
	Niche breadth	29.1	22.6	26.9
	Dry weight dicotyledons (%)	27.0	11.1	35.5
	Dry weight Fabaceae (%)	0.8	0.4	1.1
	Dry weight monocotyledons (%)	73.0	88.9	64.5
	Dry weight Cyperaceae (%)	37.8	39.2	37.3
	Dry weight Poaceae (%)	35.1	49.6	27.2
	Feeding type classification	Mixed-feeder	Mixed-feeder	Mixed-feeder
Pampas deer	Number of species	45	33	34
	Niche breadth	27.3	24.6	21.6
	Dry weight dicotyledons (%)	77.8	64.0	81.7
	Dry weight Fabaceae (%)	8.6	9.2	8.9
	Dry weight monocotyledons (%)	22.2	36.0	18.3
	Dry weight Cyperaceae (%)	1.0	2.1	0.7
	Dry weight Poaceae (%)	21.5	34.9	17.7
	Feeding type classification	Browser	Mixed-feeder	Browser

Table 2
Manly's selectivity index for key forage species consumed by cattle, capybara and pampas deer in Nhecolândia, Pantanal between October 1997 and September 1999.

Forage species/family	Cattle		Capybara		Deer	
	Rainy	Dry	Rainy	Dry	Rainy	Dry
Aeschynomene fluminensis Vell, Fabaceae	<0.01	<0.01	0.00	0.00	0.97	0.97
Andropogon bicornis L., Poaceae	0.49	0.51	0.00	0.00	<0.01	<0.01
Andropogon hypogynus Hackel, Poaceae	0.49	0.55	0.00	0.00	<0.01	<0.01
Andropogon selloanus (Hackel) Hackel, Poaceae	0.37	0.03	<0.01	<0.01	<0.01	<0.01
Axonopus purpusii (Mez) Chase, Poaceae	0.52	0.56	0.42	0.01	0.12	0.01
Bacopa salzmanii (Benth.) Wettst. ex Edwall, Scrophulariaceae	0.00	0.00	0.69	**0.88**	0.00	0.00
Byrsonima orbigniana A. Juss., Malpighiaceae	<0.01	<0.01	0.00	0.00	**0.72**	**0.83**
Caperonia castaneifolia (L.) A.St.-Hil., Euphorbiaceae	<0.01	<0.01	**0.84**	**0.99**	<0.01	<0.01
Cynodon dactylon (L.) Pers, Poaceae	<0.01	<0.01	<0.01	<0.01	**0.83**	0.25
Cyperus spp., Cyperaceae	<0.01	<0.01	**0.95**	**0.98**	0.00	0.00
Digitaria spp., Poaceae	<0.01	<0.01	**0.97**	**0.98**	0.00	0.00
Diospyrus hispida DC., Ebenaceae	<0.01	<0.01	0.00	0.00	0.50	**0.97**
Diodia kuntzei, K., Rubiaceae	<0.01	<0.01	**0.94**	**0.98**	0.42	0.03
Eleocharis acutangula (Roxb.) Steud., Cyperaceae	<0.01	<0.01	**0.87**	**0.94**	0.00	0.00
Eleoacharis interstincta (Vahl) Roem. & Schult., Cyperaceae	<0.01	<0.01	**1.00**	**1.00**	0.00	0.00
Eleocharis minima Kunth, Cyperaceae	0.75	0.62	**0.99**	**0.99**	0.00	0.00
Hydrocleys sp., Limnocharitaceae	0.00	0.00	**1.00**	**0.99**	0.70	0.09
Hymenachene amplexicaulis (Rudge) Nees, Poaceae	**0.87**	**0.79**	**0.99**	**0.99**	**0.93**	0.09
Leersia hexandra Sw., Poaceae	**0.86**	**0.75**	**0.99**	**0.99**	**0.89**	0.42
Ludwigia spp., Onagraceae	0.00	0.00	0.00	0.00	**0.92**	**0.95**
Mesosetum chaseae Luces, Poaceae	0.36	0.33	0.00	0.00	0.12	0.01
Melochia simplex A. St.-Hil., Poaceae	0.00	0.00	<0.01	<0.01	**0.83**	**0.75**
Nymphoides grayana (Griseb.) Kuntze, Menynthaceae	0.00	0.00	<0.01	<0.01	**0.92**	**0.95**
Panicum laxum Sw., Poaceae	0.46	0.40	**0.87**	**0.81**	<0.01	<0.01
Pontederia spp., Pontederiaceae	0.00	0.00	**0.90**	**0.99**	0.00	0.00
Reimarochloa brasiliensis (Spr.) Hitchc., Poaceae	<0.01	<0.01	**0.99**	**0.97**	0.00	0.00
Richardia grandiflora (Cham. & Schltdl.) Steud., Rubiaceae	<0.01	<0.01	0.00	0.00	0.03	**0.96**
Sida cerradoensis Krap., Malvaceae	0.06	0.66	0.00	0.00	<0.01	<0.01
Attalea phalerata(Mart.) Bur., Arecaceae	0.33	**0.88**	0.00	0.00	0.00	0.00
Thalia geniculata L. Marantaceae	<0.01	<0.01	0.00	0.00	**0.89**	**0.81**

Values in bold indicate the plant is highly selected.

all animals selected different forage species *H. amplexicaulis* and *L. hexandra* were the only plants selected by all three herbivores.

Discussion

Sample size accounted for differences in the diversity of species consumed by the three species. While the number of samples collected was sufficient for cattle and capybara, more samples need to be collected to fully capture the diversity of plants consumed by the pampas deer. In addition, the pampas deer consumed forage resources from outside the paddock, therefore the selectivity index for plants could be biased as more resources are available outside the paddock. However, this study does enable us to make a preliminary assessment of potential similarity of forage resource

Table 3
Similarity indices based on Bray-Curtis analysis of similarity for diets of cattle, capybara and pampas deer in Nhecolândia, Pantanal between October 1997 and September 1999. On the top right the similarity indices for the total diet are presented and on the bottom left similarity indices for the wet and dry season are presented.

	Cattle	Capybara	Deer
Cattle	X	52.43	38.71
Capybara	51.62 wet season 48.60 dry season	X	38.52
Deer	38.69 wet season 32.39 dry season	33.66 wet season 27.16 dry season	X

use and selection among domestic cattle, capybara and pampas deer.

The limits between browser, mixed-feeder and grazer are arbitrary separations in a continuum, and different authors use different limits. For example, Pérez-Barbería et al. (2001) have used 10% and 90% of Poaceae in the diet as their limit. In this case the limits of 25% and 75% (Mendoza et al., 2002) were thought to be adequate as they reflected seasonal changes in the diet of cattle and pampas deer. Data presented in this paper illustrates how forage use for a given species can vary temporally and how the classification of a species as grazer or browser can vary between seasons. For this reason, and due to examples where plant species consumed by given species of herbivore change depending on the environment and forage available, some authors (Demment and Longhurst, 1987; Hoffmann, 1988) argue that herbivores should be classified as concentrate selectors or roughage eaters. Furthermore, different parts of the same plant species may provide forage to both concentrate selectors or roughage eaters.

Although cattle consumed the highest variety of species, in reality five species made up most of their diet. Four of these species are Poaceae and can be considered as key species for the nutritional management of cattle in native pastures (Santos et al., 2010). These forage species were also the plants species with the highest availability in grazed areas and three were even considered as non-selected (Table 3). Observations of cattle show that they spent most their time grazing in areas where these key species are most abundant, maximising their consumption and selecting the most nutritious parts of these forage species (Santos et al., 2003). For this reason management strategies of pastures (rotation, fallow) that favour the maintenance of these key species in their growth stage are important. According to Hofmann (1989) cattle are classified as non-selective roughage grazers but can change categories depending on the pasture conditions and availability. This study illustrated this, and in the dry season cattle consumed a higher diversity of plant species. Results from this study illustrate the importance of maintaining a high diversity of native pasture species especially for periods of lower forage availability such as droughts. Native forage species are dynamic and their occurrence and growth will vary across time and climatic conditions (Santos et al., 2010). It is important to understand these dynamics to implement adaptive management strategies for native grasses (Santos et al., 2010).

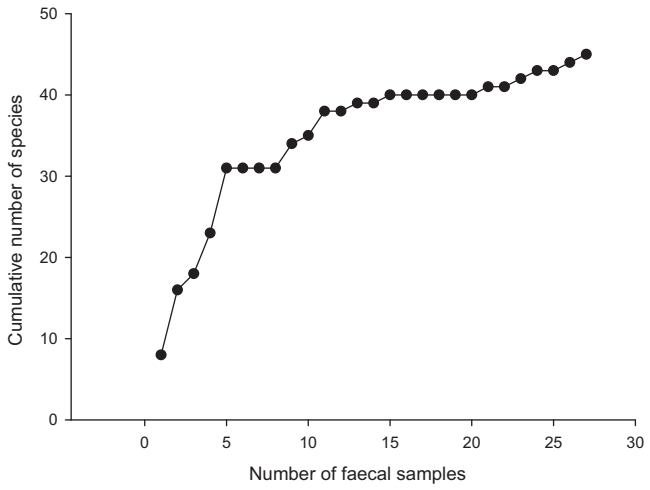

Fig. 3. Cumulative number of plant species in faecal samples determined by microhistological analysis and number of pampas deer faecal samples in Nhecolândia, Pantanal between October 1997 and September 1999.

The capybara is a hindgut fermenter and its digestive efficiency is comparable to that of ruminants due to copophragy and several adaptations to grazing (Borges et al., 1996). Capybaras are selective grazers and in this study six species represented 64% of total capybara diet. Most species consumed were selected and were not the most abundant species in the paddock. In Argentina, Quintana et al. (1998) report that four species of Poaceae and one species of Cyperaceae represented over 60% of the capybaras diet. In Colombia Forero-Montana et al. (2003) also report that six species of Poaceae and one species of Cyperaceae represented over 60% of capybara diet. The Poaceae family is one of the most common family in all capybara diet studies, classifying them as grazers or mixed feeders (Barreto and Herrera, 1998; Forero-Montana et al., 2003; Herrera and Macdonald, 1989; Quintana, 2003; Quintana et al., 1998). In this study, as in previous studies by Forero-Montana et al. (2003) in Colômbia and Escobar and Gónzalez-Jiménez (1976) in Venezuela Cyperaceas are very important in their diet throughout the year. Seasonal variations in diet have also been observed for capybara living in areas subject to climatic variations (Barreto and Herrera, 1998; Forero-Montana et al., 2003). In this study during the wet season, an increase in available resources (Santos et al., 2010) allows the animals to be more selective thus choosing the more profitable food items while in the dry season niche breadth increases as pastures around the pond dry out and more dicotyledons are consumed.

Except in the central San Luis Province of Argentina where 80% of the pampas deer diet was composed of Poaceae (Jackson and Giulietti, 1988), most studies have classified pampas deer as selective browsers (Costa et al., 2006; Lacerda, 2008; Pinder, 1997; Rodrigues and Monteiro-Filho, 1999). In this study pampas deer were classified as browsers, but during the wet season they might be considered as mix feeders. Lacerda (2008) also reports on the seasonal variation in the diet of the pampas deer and she hypothesises that it may be due to changes in the quality of forage resources between both seasons. During the wet season, palatable fresh shoots of Poaceae species are growing and available (Santos et al., 2010). Even though the sample size in this study was low, pampas deer do appear to feed preferentially on shrubs and herbs rather than grasses like capybara and cattle. Similarity of forage resource use was lowest between the pampas deer and the two other herbivores. However in a study in the Argentinean pampas Vila et al. (2008) showed that habitat selection by pampas deer was affected by cattle presence, and pampas deer were usually encountered in areas without cattle. In this study pampas deer were observed to use similar areas as cattle and generally fed nearby. However the pampas deer consumed many forage species that cattle did not such

as *Ludwigia* spp., *Melochia simplex e Nymphoides grayana* which predominate in lowland grasslands. Even though similarity of the diets of pampas deer and cattle appear to be low, poorly managed cattle at high stock rates which degrades pastures may affect pampas deer diet as well as in other dimensions of their niche not examined in this study.

Similarity in resource use is not sufficient evidence of competition (Keddy, 2001; Schoener, 1983). A high similarity may indicate shared resource utilisation and lack of competition, or that resources are super-abundant or it may imply strong competition that has not yet led to divergence in resource use. Similarity between the three species was highest during the wet season, the period of highest forage availability (Santos et al., 2010) and lowest during the dry season, the period of lowest forage availability (Santos et al., 2010). The three herbivores selected different forage species, however *H. amplexicaulis* and *L. hexandra* were selected by all three herbivores. Santos et al. (2002) verified that *H. amplexicaulis* and *L. hexandra* have 17.9 and 11.5% of crude protein, respectively. These grasses are classified as C3 photosyinthetic pathway species and often have higher quality and less bulk than C4 photosyinthetic pathway species. This probably explains the selection of these species by pampas deer, considered a concentrate selector or browser. Land management strategies persevering native pasture and these species in particular will benefit both wild and domestic herbivores.

The highest similarity in diet was found between capybara and cattle. Grazing competition between capybara and livestock was found in Entre Rios Provence in Argentina (Quintana, 2003). Overlap between capybara and two species of livestock (cattle and sheep) was always higher than 50% throughout the year reaching up to 77% between capybara and sheep in the winter (Quintana, 2003). It is possible however, that similarity in resource use between capybaras and cattle may be beneficial to the capybara. Cattle grazing reduces the height of forage resources and increases the abundance of sprouting grass (Santos et al., 2010) which is much more nutritious, palatable and within reach for capybaras. Cattle grazing reduce the growth of invasive shrubs and plants maintaining the parkland landscape of the Pantanal from which the capybaras benefit (Junk et al., 2006). Capybara was found to prefer open grasslands and lowlands instead of scrub grasslands (Desbiez et al., 2009) which would dominates without continuous cattle grazing. Out of all the forage species consumed by the two herbivores, one species Poaceae stands out: *Axonopus purpusii*. This grass was one of the few species available throughout the different seasons. The presence of cattle favours the occurrence and even dominance of *A. purpusii* in native pastures (Santos et al., 2008) and although not selected it was certainly an important item in the diet of both cattle and capybara.

This study shows that the presence of cattle under traditional extensive ranching practices on native pasture and under moderate stocking rates may not be as detrimental to wild herbivores as suggested by other examples in the literature. However, in the Pantanal, cattle ranching is becoming increasingly competitive and many land owners are now intensifying ranching practices (Seidl et al., 2001). Since the early 1970s, ranchers have been clearing land and planting pastures of exotic grasses to increase the carrying capacity for livestock. Selection by the three herbivore species of *H. amplexicaulis* and *L. hexandra* illustrate the importance of developing management strategies for some native forage species. High stocking rate which cause overgrazing (Santos et al., 2010) and the introduction of exotic species as *Brachiaria humidicola* and *Panicum repens* (C4 species) is eliminating native forages species which are important to both domestic and native herbivores. By removing the available plant diversity and converting native grasslands into uniform cultivated pastures, interactions between domestic and wild herbivores will be altered.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.mambio.2010.10.008.

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