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Full Length Research Paper

The response of a landscape species, white-lipped peccaries, to seasonal resource fluctuations in a tropical wetland, the Brazilian pantanal

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Local extinctions of white-lipped peccary, due to habitat fragmentation and hunting, have been reported throughout its vast geographical range. Recent studies have shown that their role as fruit predators and dispersers affects the biodiversity of certain forest habitats. Fruits may be reduced in deforested habitats, so documenting fruit availability and use is critical to peccary conservation efforts and forest biodiversity. Our 5 year research was based in the lower- middle Rio Negro, southern Pantanal of Brazil, a well-preserved region where cattle-related impacts are minimal. We have been investigating the habitat and feeding requirements of white-lipped, while surveying resource availability. Based on monthly fruit surveys in different habitats, we know that spatial and temporal variability of fruits is high. Marked periods of fruit scarcity occur during the year and gallery forest fruit counts were the highest. Habitat use trends indicated that there is a strong association between white-lipped peccaries and forested areas, especially gallery forest. White-lipped peccaries depended less on single dominant fruits, and their diets showed greater seasonal variation, i.e. they consumed a much greater diversity of fruits in the wet season. Fruit richness and quantity was higher during the wet season, (65 spp. - wet; 33 spp. - dry). The dry season could be considered a period of fruit scarcity in terms diversity and quantity. We expect these periods to affect peccary movements and range requirements. The non random use of habitats observed for white-lipped, illustrate the importance of habitat diversity, especially diversity of forest types and their associated fruiting species. Preventing further deforestation of an already naturally patchy habitat are priorities for conservation in the pantanal.

Key words: Landscape species, pantanal, seasonal frugivory, white-lipped peccary, fruit scarcity, conservation.

INTRODUCTION

Fruit eating animals are a major component of the vertebrate community biomass in Neotropical forests, and act as important seed dispersers or predators (Terborgh 1983, 1986). Frugivores contribute to the dynamics and structure of forests as predators of some tropical fruits, effectively thinning plant populations, and as dispersers of others, establishing new populations of tropical tree species. In addition to trophic effects, their impacts on soil, litter, and subsequent seedling dynamics could be considered ecosystem engineering (Jones et al. 1994; Keuroghlian and Eaton, 2009). Therefore, the maintenance of vertebrate frugivores must be considered a priority in conservation projects.

White-lipped peccaries (*Tayassu pecari*) are abundant and widespread fruit-eating (frugivorous/omnivorous) mammals in Neotropical rain forests (Bodmer 1990).

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Recent studies have shown that their role as fruit predators and dispersers affects the biodiversity of neotropical forest habitats (Painter, 1998; Altrichter et al., 1999; Silman et al., 2003; Keuroghlian and Eaton, 2008; Keuroghlian and Eaton, 2009). The white-lipped peccaries (WLP) are the only rain forest ungulates, which form large herds (50 - 300 individuals), so their effects on forest habitats can be dramatic. Extirpation of WLP from a rain forest area will cause habitat alterations and additional biodiversity losses (Painter, 1998; Altrichter et al., 2001; Silman et al., 2003; Keuroghlian and Eaton, 2008a; Keuroghlian and Eaton, 2008b). Local extinctions of the white-lipped peccary have been reported throughout its vast geographical range (Ditt, 2002; Cullen Jr., 2001; Glanz, 1990; Janson and Emmons, 1990; Leigh and Wright, 1990; Peres, 1996; Wilson, 1990; Kiltie and Terborgh, 1983; Azevedo and Conforti, 2008) and the species has recently been upgraded to near threatened (IUCN, 2009). There is evidence that the availability of fruits in small forest fragments is decreased in comparison to continuous tracts of tropical forest (Terborgh, 1986). Area reduction is generally accompanied by a loss of habitat diversity, which will in turn affect fruit diversity. These events may intensify naturally occurring periods of fruit scarcity (Terborgh, 1986). Some fruit-eating mammals will emigrate from these areas during periods of fruit scarcity, while others may alter their diets (Terborgh, 1986; Desbiez et al., 2009). Because fruits are major components of peccary diets (Bodmer, 1990), we investigated the availability of fruits and peccary frugivory in the Brazilian Pantanal: a naturally patchy ecosystem that is undergoing environmental threats.

The Pantanal is a huge sedimentary basin dominated by seasonal wetlands, meandering rivers, and a diverse assortment of tropical forest and savanna types (Willink et al., 2001). While extensive flooding produces high quality seasonally-available pastures for grazers, it also limits large-scale development of the region (Junk, 2005). The region is threatened by a variety of environmentally unsound human activities that have intensified over the last 30 years, e.g. large-scale agriculture on the plateaus encircling the Pantanal, gold mining, heavy fishing pressure, and environmentally disastrous development schemes for increasing barge traffic on the Rio Paraguay (Willink et al., 2001; Gottgens et al., 2001; Junk, 2005). Due to economic pressures, many large ranches in the Pantanal have been sold and divided into smaller, less viable properties (Gomes and Villela, 1999). To make smaller properties economically viable, ranchers have clear-cut native forests and planted exotic grasses to increase grazing area and productivity (Seidl, 2001). More than half the biomass of the community of medium to large sized mammals in the Pantanal are frugivorous species (Desbiez and Bodmer, in press), and their conservation is directly linked to the preservation of fruit resources. White-lipped peccaries were one of five "landscape species" chosen during a December, 2003 workshop sponsored by WCS and Embrapa-Pantanal. Conservation efforts targeting landscape species help maintain regional biodiversity and ecological integrity, because the species chosen use large, diverse areas, have significant impacts on ecosystem structure and function, and are vulnerable to human-related environ-mental threats (WCS Living Landscapes Bulletin, 2001). Baseline data on the main resources used by a landscape species is important to evaluate potential threats that can cause the decline of WLP in the region. Our specific objectives were to:

1. Document and compare seasonal availability of fruit resources; and
2. Describe seasonal diets and fruit consumption by peccaries. These baseline data will identify periods of fruit scarcity, as well as changes in the abundance and distribution of fruit resources that would be expected to impact fruit consumers, including the highly frugivorous WLP.

METHODS

Study site

Our study occurred at Fazenda Rio Negro (FRN), (19°30' S, 56°12.5' W), a 7647 ha area of the lower-middle Rio Negro of the Brazilian the southern Pantanal. Approximately 89% of the Fazenda (7000 ha) is a private reserve designated for research and ecotourism, while the remaining 11% is used for cattle. The average rainfall during the study period was 1200 mm most of which fell between October and March.

The region is characterized by forests, some open grasslands associated with flooded grasslands (*vazantes*); and many lakes (Eaton, 2006). Seasonal fruit availability was sampled in each of 5 habitats listed below:

Gallery or riparian forests: This habitat covers the higher banks along the Rio Negro. Large portions of the forest become flooded as river water level rises (Eaton, 2006) and spills over banks, or fills seasonal channels, called *corixos* that penetrate laterally from the river into the gallery forest. Dominant plant species in this habitat are Tucum (*Bactris glaucescens*), *Ficus* sp., Pimentinhas (*Licania Parvifolia* and *Couepia uiti*), Inga (*Inga uruguensis*), Bacupari (*Rheedia brasiliensis*), and Acuri (*Attalea phalerata*).

Baias **and bordering vegetation:** *Baias* are permanent to temporary shallow lakes with low to medium salinities; typically with productive and diverse aquatic plants zones; substrates of silt and aquatic plant detritus. The borders of *baias* are characterized by transitional vegetation, 5 - 50 m wide. Distinct vegetation zones follow a seasonally fluctuating moisture gradient and a slight (0.5 - 1 m) rise in elevation. The wetter zones consist of flood-tolerant herbaceous plants and bushes, while the higher drier zones consist of grasslands (*campo sujo* and *caronal*) or *cordilheira* forest (see description below). Examples of fruiting tree species that border *baias* are Espinheiro (*Chomelia obtuse*) and Araca *(Psidium guineense).*

Salinas **and bordering vegetation:** *Salinas* are shallow alkaline soda lakes with high salinities; typically with few types of aquatic plants and no fish, but productive algal and invertebrate communities. The borders of *salinas* are also characterized by transitional vegetation, 5 - 50 m wide. The vegetation zones follow moisture and alkalinity gradients, as well as a slight (0.5 - 1 m) rise in eleva-tion. Depending on the season, the wetter zones consist of a few herbaceous species that are tolerant of moisture and alkaline con-ditions (high water periods), or bare sand (low-water periods). The higher drier zones almost always consist of *cordilheira* forest (see description below). Caranda palms (*Copernicia alba*) are characteristic of *salina* borders.

Cordilheira (cerrado, cerradão,* and semi deciduous forest*): This habitat is a mixture of savanna forest formations (*cerrado*, *cerradão*, and semi deciduous forest) that are typical of the Nhecolândia ecoregion of the Pantanal. These forests are not inundated during the wet season, because they are formed on sandy elevations 1 - 2 meters higher than the surrounding landscape. Typical species encountered are: Pequi (*Caryocar brasiliense*); Lixeira (*Curatella americana*); Taruman (*Vitex cymosa*); Acuri (*Attalea phalerata*); Ximbuva (*Enterolobium contortisiliquu*); Paratudo (*Tabebuia aurea*); Canjiqueira (*Coccoloba cajubensis*); Bocaiuva (*Acrocomia aculeata*); Manduvi (*Sterculia apetala*); and Marmelo (*Alibertia edulis*).

Grasslands *(campo sujo, caronal,* and *vazantes):* Grassland habitat varies substantially in the Rio Negro region, ranging from areas with scattered trees, *campo sujo*, to open savannas with no trees. Of the latter, one of the most extensive types, *caronal*, is dominated by the grass, *Elyonurus muticus*. Seasonally flooded grasslands that frequently link *baias* during high-water periods are called *vazantes*

Fruit availability

Seasonal fruit availability for ground-dwelling frugivores was documented from 2000 - 2004 to determine if and when periods of fruit scarcity occurred in the Pantanal and to compare fruit use by peccaries to fruit availability. Each year, we sampled fruits on a monthly schedule and ensured that an equal number of surveys were conducted in the dry and wet seasons. We stratified our sampling by habitat types, so that fruits from rare habitats would not be overlooked. Census trails, numbered every 50 m, approximately 2000 m long, and 500 - 800 m apart, were established so that sampled habitat types in proportion to their availability were represented at the study site. For each habitat type, we collected samples of fresh fruits on the forest floor within 10 randomly chosen 50 m^2 plots (Blake et al., 1990; (Keuroghlian and Eaton, 2008a).

The ten plots chosen within habitat categories were different each sampling period. Fruits in the plots that were desiccated or overgrown with fungus were not considered palatable, so were not included in the samples. The fruits from each 50 m^2 sample were identified to species, counted, dried at 50°C, and weighed to the nearest 0.1 g. We repeatedly weighed the samples until constant dry weights were obtained. Numbers and dry weights from the ten plots were averaged for individual months and habitats.

For seasonal comparisons, we categorized months as dry or wet based on rainfall data collected since 2000, and then we averaged numbers and dry weights of fruits from individual months within the dry and wet categories. To combine monthly numbers and dry weights (over all years) from the different habitats into estimates of overall fruit availability for the study site, we averaged habitat values and weighted them by habitat area (Keuroghlian et al 2009). We used the monthly weighted averages of numbers and dry weights of samples, to calculate monthly availability proportions for individual fruit species. To examine whether fruit abundance was related to rainfall, we regressed the monthly number of fruits sampled on monthly rainfall values.

We discontinued surveys in grassland habitats after the first year, because fruits were never found. Seasonal proportions for numbers and dry weights were obtained by averaging the monthly proportions within each season (as above, months were categorized as dry or wet based on local rainfall data). Finally, we used the seasonal proportions to calculate and compare richness, diversity, and evenness indices based on numbers and dry weights of fruit species (Ludwig and Reynolds, 1988). These indices in combination with seasonal relative abundance distribution were used to interpret fruit availability and scarcity. Our estimates of fruit availability for Fazenda Rio Negro are weighted averages of samples from the different habitats described above.

Diet analysis

For WLP, we were able to estimate fruit use by following fresh foraging trails and quantifying feeding bouts. Since WLP move in herds of 40 or more individuals, they leave well-defined foraging trails. From 2000 - 2004, we followed fresh foraging trails and documented the number of feeding bouts and the fruit species eaten at each bout. Signs that a feeding bout had occurred included pieces of un-eaten fruits, tracks concentrated near fruiting trees, and diggings in the soil and litter. To calculate proportional use of individual fruit species along a white-lipped foraging trail, we summed the number of bout locations for the species and divided the sums by the total number of bout locations observed on a trail. For each sampling month, we averaged the proportions from 3 to 7 different foraging trails. Seasonal proportions were obtained by averaging monthly proportions within seasons. We used the same richness, diversity, and evenness indices that were used for fruit availability (Ludwig and Reynolds 1988) to compare seasonal fruit use by WLP (Keuroghlian and Eaton 2008a).

RESULTS

Fruit availability

During 37 fruit surveys conducted from 2000 - 2004, we collected 65 different species from the forest floor. Gallery forest fruit counts were the highest and *Salina* fruit counts were the lowest, 0.40 fruits/m^2/month and 0 .12 fruits/m^2/month respectively. Both monthly fruit abundance (r^2 = 0.35) and monthly dry weight (r^2 = 0.13), weighted by habitat area Keuroghlian (et al., 2009), had significant positive linear relationships with monthly rainfall (Figure 1). *T*-tests to determine whether the regression slopes were different from zero were both significant (fruit abundance t = 3.874, df = 28, P = 0.005; dry weight t = 2.042; df = 28; P = 0.05) (Figure 1).

Relative-abundance distributions based on fruit dry weights showed that the availability of fruits differed dramatically between seasons (Figure 2). We collected 65 fruit species from the forest floor in the wet season compared to only 35 species in the dry season (Table 1). The relative flatness of the wet season curve indicated that fruit biomass was distributed more evenly among a greater number of medium-abundance species. In contrast, the steeper dry season curve showed that the samples were dominated by a few very abundant species. Total

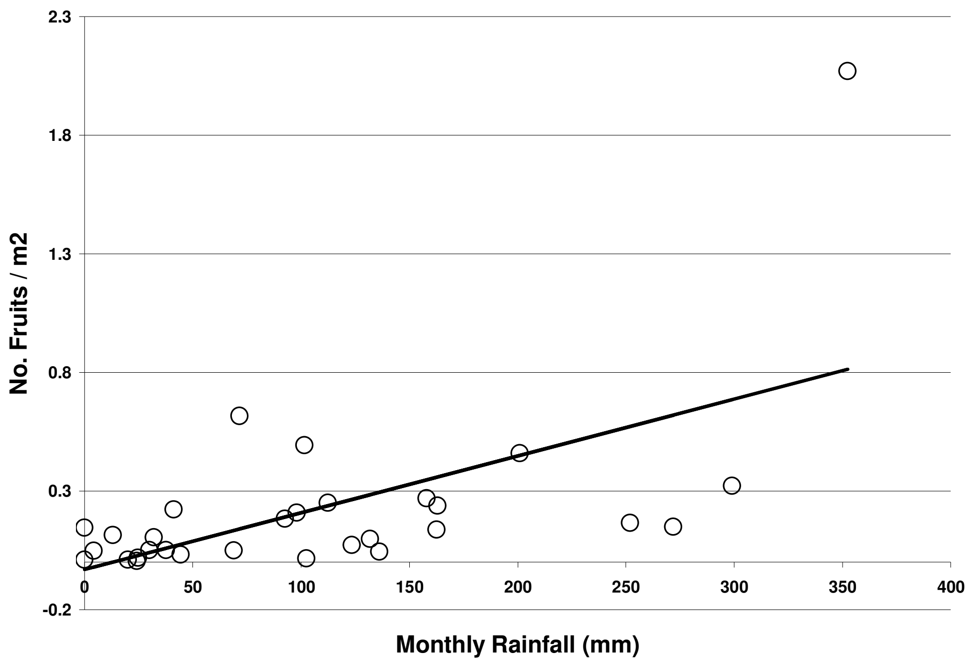

Figure 1. Regression of monthly fruit numbers weighted by habitat area on monthly rainfall at Fazenda Rio Negro, Aquidauana, Mato Grosso do Sul, Brazil (2000 - 2004) (N = 37, $r^2 = 0.35$).

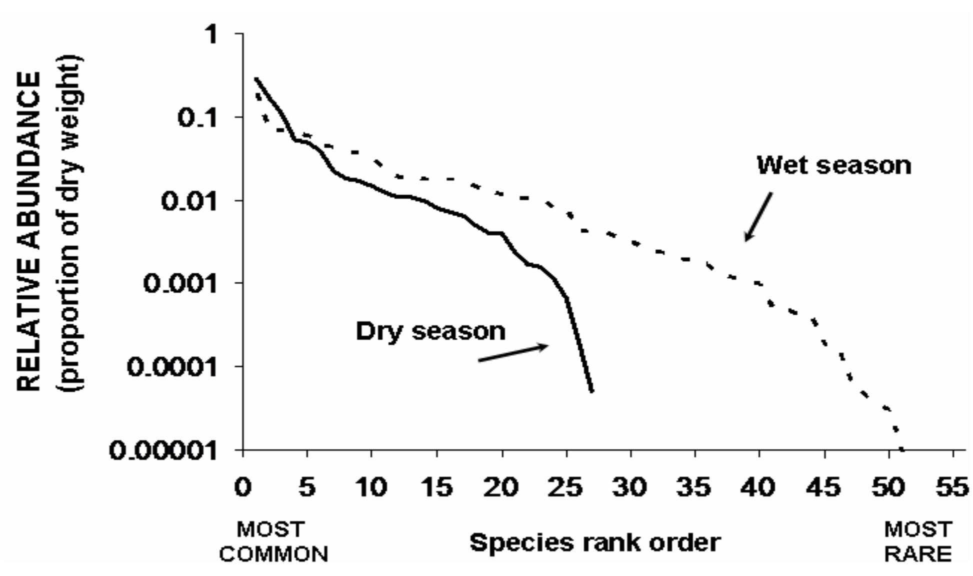

Figure 2. Relative abundance distributions for fruit based on dry weight (g) for the dry and wet season fruit censuses (2000 - 2004) at Fazenda Rio Negro, Mato Grosso do Sul, Brazil

fruit mass (dry weight) was lower, that is 1.57 g/m^2/month in the dry season vs. 8.37 g/m^2/month in the wet season. Fruit counts were also lower, averaging 4.97 fruits/m^2/ month in the dry season compared with 5.42 fruits/m^2/ month in the wet season. The quantity of fruits available for the dry season was due primarily to two palms, acuri (*A. phalerata)* and bocaiuva (*Acrocomia aculeata*).

The mean proportions of fruits in the dry and wet seasons, based on numbers (Table 1) and dry weights (Table 2), respectively, are shown for all species making up more than 0.1% of the seasonal totals. Acuri palm fruits (*A. phalerata*), Taruman (*Vitex cymosa*), Canjiqueira

Table 1. Wet and dry season fruit availability expressed as mean proportions of fruit numbers . Data are from monthly census plots collected from 2000 to 2004 at Fazenda Rio Negro, Aquidauana, Mato Grosso do Sul, Brazil. Proportions for species that are < 0.1% of monthly totals are not shown. Numbers in parenthesis rank the top ten most abundant fruits in terms of dry weights (number 1 being the most abundant).

			Fruit numbers			
			Wet		Dry	
Family	***Genus***	***Species***	**Prop.**	**Rank**	**Prop.**	**Rank**
Annonaceae	*Annona*	*dioica*	0.002			
Apocynaceae	*Harcornia*	*speciosa*	0.001		0.004	
Arecaceae	*Acrocomia*	*aculeata*	0.020		0.176	(2)
Arecaceae	*Bactris*	*glaucescens*	0.083	(3)	0.035	(7)
Arecaceae)	*Attalea*	*phalerata*	0.126	(1)	0.217	(1)
Arecaceae	*Copernicia*	*alba*	0.040	(8)		
Bromeliaceae	*Bromelia*	*balansae*	0.006		0.035	(6)
Burseraceae	*Protium*	*heptaphyllum*	0.049	(6)		
Caryocaraceae	*Caryocar*	*brasiliense*	0.011			
Chrysobalanaceae	*Licania*	*parvivolia*	0.001			
Chrysobalanaceae	*Couepia*	*Uiti*	0.006			
Combretaceae	*Buchenavia*	*tomentosa*	0.005			
Combretaceae	*Combretum*	*discolor*	0.013			
Dilleniaceae	*Davilla*	*elliptica*	0.001			
Ebenaceae	*Diospyros*	*hispida*	0.035	(9)		
Euphorb	*Sapium*	*Sp.*	0.001			
Euphorbiaceae			0.017		0.001	
Guttiferae	*Rheedia*	*brasiliensis*	0.034	(10)	0.052	(5)
Lauraceae	*Ocateae*	*diospyrifolia*	0.006		0.003	
Leguminosae			0.004			
Leg.-Faboideae	*Dipteryx*	*alata*	0.001		0.102	(3)
Leg.-Mimosoideae	*Inga*	*uruguensis*	0.008		0.033	(7)
Loranthaceae	*Strychnos*	*pseudoquina*	0.014		0.005	
Malpighiaceae	*Byrsonima*	*orbignyana*	0.069	(5)		
Melastomataceae	*Mouriri*	*elliptica*	0.004			
Melastomataceae			0.003			
Moraceae	*Ficus*	*Sp.*	0.044	(7)	0.019	
Myrtaceae	*Psidium*	*guineense*	0.018			
Myrtaceae	*Eugenia*	*desynterica*	0.004		0.002	
Myrtaceae	*Ukwn*	*Sp.*	0.080	(4)	0.031	(8)
Opiliaceae	*Agonandra*	*brasiliensis*	0.001		0.006	
Olacaceae	*Dulacea*	*egleri*	0.002			
Rhamnaceae	*Rhamnidium*	*elaeocarpum*	0.001			
Rubiaceae	*Alibertia*	*edulis*	0.033		0.009	
Rubiaceae			0.006		0.011	
Rubiaceae	*Chomelia*	*obtusa*	0.007			
Rubiaceae	*Genipa*	*americana*	0.002			
Sapindaceae	*Paulina*	*pinnata*	0.003			
Sapindaceae	*Sapindus*	*saponaria*	0.023		0.006	
Sapotaceae	*Chrysophyllum*	*marginatum*	0.006			

(*Byrsonima orbignyana*), a Myrtaceae species, and Tucum (*Bactris glaucescens*) represented 45% of the fruits counted during the wet season (Table 1). In terms of dry weight in the wet season, *A. phalerata*, *V. cymosa*, *B.*

Table 1 contd.

				Fruit numbers			
				Wet	Dry	Wet	Dry
Family	***Genus***	***Species***	**Prop.**	**Rank**	**Prop.**	**Rank**	**Family**
Sapotaceae	*Pouteria*	*sp*	0.001				Sapotaceae
Simacaceae	*Smilax*	*fluminensis*	0.003		0.026	(10)	Simacaceae
Sterculiaceae	*Guazuma*	*ulmifolia*	0.019		0.030	(9)	Sterculiaceae
Sterculiceae	*Sterculia*	*apetala*	0.001		0.001		Sterculiceae
Verbenaceae	*Vitex*	*cymosa*	0.090	(2)	0.063	(4)	Verbenaceae
	Species 1		0.002		0.003		
	Species 2		0.002				
	Species 3		0.002				

Table 2. Wet and dry season fruit availability expressed as mean proportions of dry weight. Data are from monthly census plots collected from 2000 to 2004 at Fazenda Rio Negro, Aquidauana, Mato Grosso do Sul, Brazil. Proportions for species that are < 0.1% of monthly totals are not shown. Numbers in parenthesis rank the top ten most abundant fruits in terms of dry weights (number 1 being the most abundant).

			Fruit dry weights			
			Wet		Dry	
Family	**Genus**	**Species**	**Prop.**	**Rank**	**Prop.**	**Rank**
Annonaceae	*Annona*	*dioica*	0.002			
Apocynaceae	*Harcornia*	*speciosa*	0.008		0.004	
Arecaceae	*Acrocomia*	*aculeata*	0.068	(3)	0.071	(2)
Arecaceae	*Bactris*	*glaucescens*	0.059	(5)	0.012	
Arecaceae	*Attalea*	*phalerata*	0.190	(1)	0.287	(1)
Arecaceae	*Copernicia*	*alba*	0.037	(8)		
Bromeliaceae	*Bromelia*	*balansae*	0.019		0.022	(7)
Burseraceae	*Protium*	*heptaphyllum*	0.011		0.002	
Caryocaraceae	*Caryocar*	*Brasiliense*	0.036	(9)		
Chrysobalanaceae	*Licania*	*parvivolia*	0.001			
Chrysobalanaceae	*Couepia*	*uiti*	0.018			
Combretaceae	*Buchenavia*	*Tomentosa*	0.008			
Combretaceae	*Combretum*	*discolor*	0.011		0.011	
Euphorbiaceae			0.017			
Guttiferae	*Rheedia*	*Brasiliensis*	0.066	(4)	0.054	(4)
Lauraceae	*Ocateae*	*diospyrifolia*	0.012		0.010	
Leguminosae			0.003			
Leg.-Caesalpinioideae	*Hymenaea*	*stigonocarpa*	0.002			
Leg.-Faboideae	*Dipteryx*	*alata*	0.050	(6)	0.109	(3)
Leg.-Mimosoideae	*Inga*	*Uruguensis*	0.012		0.039	(6)
Leg.-Mimosoideae	*Anadenanthera*	*colubrina*			0.011	
Loranthaceae	*Strychnos*	*pseudoquina*	0.004		0.001	
Malpighiaceae	*Byrsonima*	*Orbignyana*	0.017			
Melastomataceae	*Mouriri*	*elliptica*	0.003			
Melastomat.						
Moraceae	*Ficus*	*Sp.*	0.010		0.008	
Myrtaceae	*Psidium*	*Guineense*	0.019			
Myrtaceae	*Eugenia*	*Desynterica*	0.025			
Myrtaceae	*Ukwn*	*Sp.*	0.033	(10)	0.018	(8)
Piperaceae	*Piper*	*Sp.*			0.002	

Table 2. Contd.

			Fruit dry weights			
			Wet		Wet	
Family	**Genus**	**Species**	**Prop.**	**Rank**	**Prop.**	**Rank**
Rhamnaceae	*Rhamnidium*	*elaeocarpum*	*elaeocarpum*			
Rubiaceae	*Alibertia*	*edulis*	*edulis*	(7)	0.002	
Rubiaceae						
Rubiaceae	*Chomelia*	*obtusa*	*obtusa*			
Rubiaceae	*Genipa*	*Americana*	0.004			
Sapindaceae	*Sapindus*	*Saponaria*	0.015		0.015	(10)
Sapotaceae	*Pouteria*	*Sp*	0.001			
Sapotaceae	*Pouteria*	*ramiflora*	0.001			
Sapotaceae	*Chrysophyllum*	*marginatum*	0.002			
Simacaceae	*Smilax*	*fluminensis*			0.007	
Sterculiaceae	*Guazuma*	*ulmifolia*	0.018		0.017	(9)
Sterculiceae	*Sterculia*	*apetala*	0.001		0.005	
Verbenaceae	*Vitex*	*cymosa*	0.069	(2)	0.049	(5)

glaucescens, and *Rheedia brasiliensis* were the most available fruits (45% combined) (Table 2).

Fruits of the Acuri palm (*A. phalerata)* were abundant during both seasons but their availability was slightly higher during the dry season (19% dry weight in the wet season vs. 29% dry weight during the dry season) when including transitional seasonal months. Transitional months (September, October, April and May) could be considered wet season or dry season months depending on rainfall that particular year.

A. phalerata (29%) combined with the second and third most available fruits in the dry season, Bocaiuva (*A. aculeata*) (17%) and Cumbaru (*Dypteryx alata*) (11%), made up 57% of the total fruit dry weight. The top three fruits in terms of numbers during the dry season were *A. phalerata* (22%), followed by *A. aculeata* (18%), and *D. alata* (10%). They comprised 50% of the fruits counted (Table 1).

When seasonal transitional months were removed, *A. phalerata* was actually more abundant during the wet season, 0.94 fruits/m^2/month, versus 0.79 fruits/m^2/ month during the dry season. The fruiting period of *A. phalerata* was asynchronous, spanning throughout the year with peak availability, average of four years of census, in November (1.9 fruits/ m^2/month).

Hill's diversity numbers, N0, N1, and N2, Hill's modified evenness ratio, E5, and the Simpson and Shannon indices of diversity (Ludwig and Reynolds 1988) confirmed the seasonal patterns shown in the species-area curves (Figure 2). N0, the number of all species collected, N1, the number of abundant species, and N2, the number of very abundant species were all greater in the wet season than in the dry season. Hill's modified evenness ratio, E5, which gets closer to one as fruit numbers or dry weights are partitioned more evenly among species, was the same during the dry and wet seasons (Table 4). Simpson's and Shannon's indices, which are presented for comparisons with other studies, also showed greater diversity during the wet season.

Diet analysis

From 2000 - 2004, we followed over 100 white-lipped peccary foraging trails and documented feeding bouts during 23 months of sampling (8 dry season and 15 wet season months). The length of foraging trails ranged between approximately 500 and 1000m. Based on the data from trails and direct observations, we documented a total of 65 fruit species eaten by white-lipped, peccaries, 65 species in the wet season and 32 species in the dry season (Table 3). Seasonal trends of richness and diversity for fruit use by WLP were similar to those observed for fruit availability. The greater diversity of fruits in the wet season corresponded to a greater diversity of fruits consumed by WLP (Table 4, Figures 2 and 3). WLP ate a greater number of different species in the wet season compared to the dry season. Fruits of the Acuri palm (*A. phalerata)* were by far the most consumed (Table 3). Three other palm species, *A. aculeata*, *B. glaucescens*, and *Copernicia alba*, were also among the top ten most consumed fruits. WLP chew and spit both *A. phalerata* and *A. Aculeata*, and predate both *B. glaucescens* and *C alba* seeds.

Table 3. Percents (>1%, wet and dry seasons combined) of fruits consumed by white-lipped peccaries, based on surveys of foraging trails conducted from 2000 to 2004 at Fazenda Rio Negro, Aquidauana, Mato Grosso do Sul, Brazil. Species are listed from highest to lowest percent consumed.

Family	Common name	Genus	Species	Percent consumed
Arecaceae (Palmae)	Acuri	*Attalea*	*Phalerata*	24.64
Arecaceae	Bocaiuva	*Acrocomia*	*aculeate*	6.72
Sterculiaceae	Chico magro	*Guazuma*	*Ulmifolia*	6.56
Arecaceae	Tucum	*Bactris*	*Glaucescens*	6.18
Loranthaceae	Erva	*Strychnos*	*Pseudoquina*	5.74
Malpighiaceae	Canjiqueira	*Byrsonima*	*orbignyana*	4.29
Olacaceae	Laranjinha	*Dulacea*	*Egleri*	4.54
Arecaceae	Caranda	*Copernicia*	*Alba*	4.10
Guttiferae	Bacupari	*Rheedia*	*Brasiliensis*	3.85
Arecaceae	Tucum seeds	*Bactris*	*Glaucescens*	3.16
Sapotaceae		*Pouteria*	*Sp*	3.08
Leg.-Caesalpinioideae	Jatoba	*Hymenaea*	*Stigonocarpa*	2.95
Rubiaceae	Espinheiro	*Chomelia*	*obtuse*	2.61
Myrtaceae		*Eugenia*	*Jambolana*	2.56
Caryocaraceae	Pequi	*Caryocar*	*Brasiliense*	2.43
Verbenaceae	Taruman	*Vitex*	*Cymosa*	1.96
Myrtaceae	Araca	*Psidium*	*Guayava*	1.90
Lauraceae	Canela	*Ocateae*	*Diospyrifolia*	1.87
Leg.-Mimosoideae	Farinha seca	*Albizia*	*Saman*	1.86
Chrysobalanaceae	Pimenteira	*Licania*	*Parvivolia*	1.82
Rubiaceae	Marmelo preto	*Alibertia*	*Edulis*	1.78
Ebenaceae	Olho de boi	*Diospyros*	*Hispida*	1.73
Sapindaceae	Saboneteiro	*Sapindus*	*Saponaria*	1.64
Leg.- Mimosoideae	Ximbuva	*Enterolobium*	*contortisiliquum*	1.61
Sapindaceae	Justa conta	Talisia	Esculenta	1.36
Bromeliaceae	Gravateiro	*Bromelia*	*Balansae*	1.19
Myrtaceae	Uvaia	*Eugenia*	*Desynterica*	1.19
Leg.-Faboideae	Morcegeiro	*Andira*	*sp.*	1.15
Myrtaceae	Araca	*Psidium*	*Guineense*	1.14
Opiliaceae	Quina brava	*Agonandra*	*Brasiliensis*	1.10

DISCUSSION

Fruit availability and diet analysis

Examining seasonal fruit availability trends, we found that species diversity and quantity were greater in the wet season. The greater diversity of fruits in the wet season corresponded to a greater diversity of fruits consumed by WLP. This increase in the variety of fruits consumed suggested a nutritive improvement in their diet during the wet season (Keuroghlian and Eaton, 2008a). *A. phalerata* was consumed less during the wet season when diversity of fruit availability was highest.

The dry season in the Pantanal of Rio Negro region is a period of fruit scarcity in terms diversity and in terms of fruit quantity. Fecal contents examined by Desbiez et al. (2009) in central Pantanal, reported a dramatic change in the percentage of WLP wet and dry season fruit diet, 65.4 and 21.2%, respectively. Consequently, area requirements of peccaries will be affected by total fruit availability, seasonal availability and distribution of fruit sources, and a suite of other resource-related factors specific to different vegetation/habitat types. At the same study site, use of gallery forests by WLP was significantly grea-

Table 4. Richness, diversity, and evenness indices for fruit availability (numbers and dry weights) and fruit use (based on white-lipped peccary foraging trails) during the wet and dry seasons at Fazenda Rio Negro, Mato Grosso do Sul, Brazil. Fruit censuses and foraging trails were conducted from 2000 - 2004.

Indices	Fruit availability				Fruit use by *Tayassu pecari*	
	Numbers		Dry Weight			
	Wet	Dry	Wet	Dry	Wet	Dry
Hill's numbers						
N0 (richness)	65	33	65	33	65	32
N1	23.09	13.79	18.75	6.68	9.83	6.97
N2	15.74	9.57	10.72	4.65	7.29	4.47
Evenness						
E5	0.67	0.67	0.47	0.64	0.71	0.58
Diversity						
Simpson	0.064	0.104	0.093	0.215	0.137	0.223
Shannon	3.14	2.62	2. 93	1.90	2.285	1.942

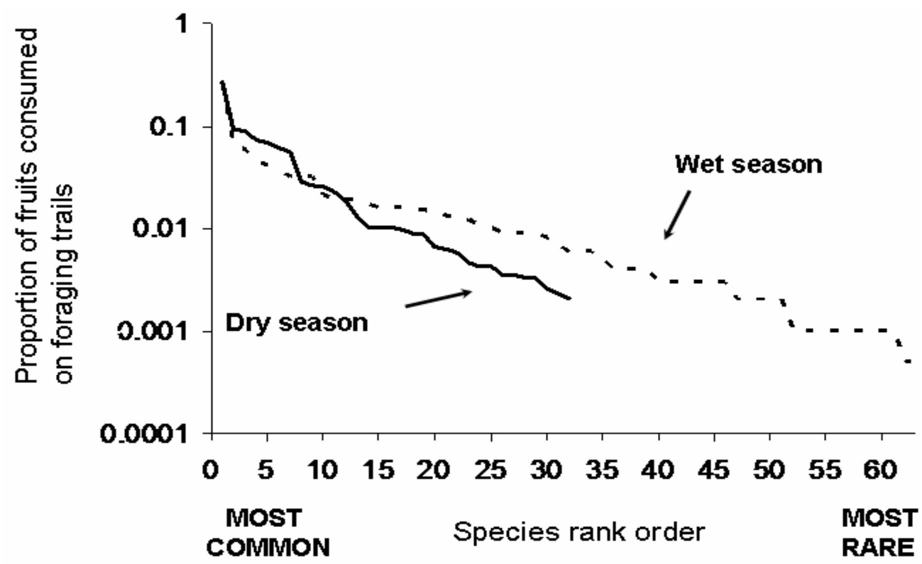

Figure 3. Relative abundance distributions of fruit species consumed by white-lipped peccaries during the dry and wet seasons at Fazenda Rio Negro, Aquidauana, Mato Grosso do Sul, Brazil. Proportions of consumed fruits were obtained from surveys of white-lipped peccary foraging trails (2000 - 2004).

ter than use of all other habitat categories, and *cordilheira* forests and *baias* were used significantly more than grasslands and *salinas* (Keuroghlian et al., 2009). This coincides with the greater number of fruits found in the gallery forest compared to other habitats. Habitat use trends indicated that there is a strong association between WLP and forested areas (Desbiez et al., 2009b), especially gallery forest (Keuroghlian et al., 2009). Other studies have also shown that WLP, prefer forest cover (Taber et al., 1994; Fragoso, 1999; Reyna-Hurtado and Tanner, 2005; Keuroghlian and Eaton, 2008b; Desbiez et al., 2009b). Similar to our results from the Pantanal, WLP from other regions have affinities for specific humid habitats, such as palm-dominated swamps and gallery forests (Bodmer, 1990; Fragoso, 1999; Keuroghlian and Eaton, 2008b). In another study area in central Pantanal, white lipped peccary densities where also highest in forested landscapes, compared to the floodplain landscape where they were rarely sighted (Desbiez et al., 2009a). Even though the floodplain landscape has over 10% forest cover (Desbiez et al., 2009b), the forest is distributed in small island pockets, while in the forested landscape, dominated with 63% forest cover, there are large stretches of continuous forest (cordilhera).

Conservation implications

Our results on fruit and habitat use and availability, have clear conservation implications. The non random use of habitats observed for WLP (Keuroghlian et al., 2009) illustrates the importance of habitat diversity, especially diversity of forest types and their associated fruiting species.

Working in a pristine region of continuous forest, Bodmer (1990) found that WLP migrated in and out of flooded forests as the seasons changed but did not alter their diet in terms of major food categories (i.e. fruit, leaf, fiber, or grass). In the seasonal tropical forest of 47,000 ha Corcovado National Park, Costa Rica, Altrichter et al. (2001) found that periods of fruit scarcity in the park were associated with above-average long-distance movements by the WLP. During a period when fruit availability was low, Altrichter et al. (2001) documented a three month absence of three radio-tracked herds from the park. Presumably, the herds had expanded their ranges in search of fruits outside the park. Due to fluctuations in the accessibility and quantity of fruit resources at the Amazonian and Costa Rican study sites, the WLP required more area at certain times of the year to maintain a predominantly frugivorous diet.

A unique characteristic of the Pantanal, related to the dynamic nature of its seasonal rainfall and flooding cycles, is its high level of productivity, that is, the amount of organic matter produced by plants and other photosynthetic organisms per area per year. Tropical freshwater wetlands, along with tropical rain forests, marine algal beds, and coral reefs, are the most productive ecosystems, per unit area, on earth (Whittaker 1975). As flood waters expand and recede over vast areas in the Pantanal, there is a rapid growth and senescence of aquatic plants and low-lying grasslands. This rapid production and turnover of organic matter forms the basis of many important food webs and explains the incredible abundance of wildlife that is observed in the Pantanal (Eaton and Keuroghlian, 2003) Consequently, in central Pantanal, using fecal analysis, periods of reduced fruit production coincided with a greater consumption of plant vegetation (leaves, roots, and fiber) 72.4 and 31.8 percent, dry and wet season, respectively (Desbiez et al., 2009a). When fruits are reduced, WLP switch to other resources, such as aquatic plants and native grasses (Desbiez et al., 2009a).). However, their alternate food sources are also being threatened by recent development trends such as intensive agriculture and erosion on the highlands surrounding the Pantanal, channelization of the Rio Paraguay, “modernized” ranches that are deforested and implanted with exotic pastures, pollution from agricultural runoff, mining, and urban centers, and introductions of exotic species (Eaton and Keuroghlian, 2003).

The Pantanal landscape is heterogeneous, and consequently, fruiting patterns and species will vary according to the Pantanal eco-region and habitat diversity (e.g. presence or absence of rivers vs. flooded grasslands). However, dominance of fruits in peccary diets (Keuroghlian and Eaton, 2008a; Desbiez et al., 2009a), and the existence of dramatic fruit scarcity periods during the dry season exists in most eco regions of the Pantanal. Deforested regions will obviously have diminished fruit abundance and/or diversity, and will not support the nutritional needs of the characteristically large white-lipped peccary populations. The eventual consequences for peccaries and other frugivores are starvation or forced emigration. The preservation of habitat quality and diversity was key to WLP preservation in small Atlantic forest fragments (Keuroghlian and Eaton, 2008). Similarly, the preservation of high quality forested areas is key to the maintenance of peccary population in the Pantanal. These facts and the growing environmental threats in the Pantanal, have important management conservation implications. Preventing further deforestation, hydrological and habitat degradation, and further fragmentation of an already naturally patchy habitat are priorities for conservation projects in the Pantanal.

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