

NICHE PARTITIONING AMONG WHITE-LIPPED PECCARIES (*TAYASSU PECARI*), COLLARED PECCARIES (*PECARI TAJACU*), AND FERAL PIGS (*SUS SCROFA*)

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The introduction of a species into an ecosystem with species already occupying a similar trophic level is predicted to lead to a high degree of niche overlap. The feral pig (*Sus scrofa*), one of the world's worst invasive species, was introduced to the Pantanal about 200 years ago and is thought to compete with the native white-lipped peccary (*Tayassu pecari*) and collared peccary (*Pecari tajacu*). Resource partitioning between the 3 species was examined, including analysis of fruit items and plants in fecal samples as well as encounter rates in different habitats, to help generate hypotheses about competitive interactions among the species. Overlaps in food resources and habitat use between feral pigs and peccaries were found to be lower than expected. In fact, niche overlap was highest between the native species. Results indicate that currently, feral pigs are not a direct threat to the native peccaries in the study area. Differences in morphology and behavior indicate possible mechanisms of niche partitioning between the species. Feral pigs may, nevertheless, impact the wildlife community in other ways as predators of eggs, by destruction of vegetation through rooting, or by functioning as disease reservoirs. Cattle-ranching activities may favor feral pigs and the current anthropogenic changes in the landscape could lead to changes in competitive dynamics between feral pigs and native species.

Key words: competition, frugivore, introduced species, niche overlap, Pantanal, *Pecari tajacu*, peccary, resource partitioning, *Sus scrofa*, *Tayassu pecari*

Community ecologists traditionally assume that species differ in some aspects of their traits or responses to the environment that allow them to coexist in the same habitat (Chase 2005; MacArthur and Levins 1967). Resource partitioning, defined as the differential use by organisms of resources such as food and space (Schoener 1974), may help to explain how species with extensive overlap in ecological requirements can coexist (MacArthur and Wilson 1967; Morin 1999). Over evolutionary time, ecological separation or extinction occurs between species. For this reason, the introduction of an exotic species within a community of native

species will often have a disastrous impact (Shea and Chesson 2002; Simberloff 2003). There are many examples of invasive species altering the evolutionary pathway of native species through competition, niche displacement, hybridization, predation, and modification to ecosystems (Lowe et al. 2000; Mooney and Cleland 2001). Exotic species introductions are now 2nd only to habitat loss as a cause of species endangerment and extinction (Lowe et al. 2000; Rodriguez 2001; Shea and Chesson 2002; Simberloff 2003).

The feral pig (*Sus scrofa*) is considered to be one of the world's worst invasive species (Lowe et al. 2000). Worldwide, the loss of biodiversity and extinction of native species due to the introduction of feral pigs has been widely documented (Wolf and Conover 2003). Feral pigs were introduced to the Pantanal about 200 years ago and can now be found throughout the floodplain (Mourão et al. 2002). White-lipped peccaries (*Tayassu pecari*) and collared peccaries (*Pecari tajacu*) are

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native to the region and occur sympatrically over most of their geographic range (Sowls 1997). Although pigs and peccaries superficially resemble each other, they have been separated at least since the Oligocene (Herring 1985). Because of the apparent gross similarities between feral pigs and peccaries in allopatry as well as observations in the field, a high level of competition among these 3 species in the Pantanal has been speculated (Alho et al. 1988; Mourão et al. 2002; Sicuro and Oliveira 2002).

Competition is considered to be the major selective force causing the differential use of resources (Keddy 2001; Schoener 1986). Competitive exclusion argues that species that compete, and occupy precisely the same niche, cannot coexist (Morin 1999). Given that peccaries have not disappeared from the Pantanal since the introduction of feral pigs, competitive exclusion can be ruled out. To prove the existence of competition between species, an effect on fitness must be demonstrated (Keddy 2001). Overlap in resource use is not sufficient evidence of competition (Keddy 2001; Schoener 1983). High overlap may indicate that resources are shared in the absence of competition (Gotelli and Graves 1996), that resources are superabundant (Gordon and Illius 1989), or that strong competition has not yet led to divergence in resource use. Furthermore, other processes, such as predation or different responses of species to environmental gradients, also may lead to resource partitioning (Schoener 1986). Experimental field manipulations provide the most convincing evidence for the presence of competition. However, because feral pigs have now spread throughout the Pantanal floodplain, a shift in use of resources by peccaries resulting from sympatry with feral pigs is difficult to evaluate.

Although it does not provide direct proof of competition, examining resource partitioning can help generate hypotheses about competitive interactions among species (Colwell and Futuyama 1971; Tilman 1987; Wiens 1993). Niche theory holds that coexisting species should move toward a tolerable level of overlap determined by the abundance and diversity of resources available (MacArthur and Levins 1967). The introduction of a species into an ecosystem with species already occupying a similar trophic level is predicted to lead to a high degree of overlap. Native species that have coevolved will likely exhibit less niche overlap than ecologically similar species that evolved allopatrically and are confronted with each other through introduction (Goodyear 1992). We tested this prediction. Niche overlap between feral pigs and the peccaries was expected to be higher than niche overlap between the native peccaries. We used extent in overlap of food and habitat use between the 3 species to generate hypotheses about possible competitive interactions. The greater the overlap between feral pigs and the peccaries, the greater the likelihood of competitive interactions, and the greater the potential impact of this introduced species on the native peccaries.

MATERIALS AND METHODS

Animal care and use.—This study did not involve the capture and handling of animals. Guidelines of the American

Society of Mammalogists (Gannon et al. 2007) for handling and for transport of fecal samples were followed.

Study area.—Research took place on traditionally managed ranches in the Nhecolândia subregion of the Brazilian Pantanal at the Embrapa Pantanal Nhumirim ranch and 6 neighboring ranches covering an area of $>200 \text{ km}^2$ ($18^{\circ}59'S$, $56^{\circ}39'W$). Traditionally managed ranches are mostly composed of native vegetation, cattle range freely within large grazing areas, and human densities and impact are very low (Mittermeier et al. 2002). The Nhecolândia subregion and the study area present a complex mosaic of habitats that includes permanent and temporary ponds, seasonally flooded and scrub grasslands, forest patches, and scrub forests (Soriano et al. 1997). Feral pigs, white-lipped peccaries, and collared peccaries are sympatric throughout the region. Desbiez (2007) found that feral pigs are currently the main hunting target of people living in the Nhecolândia region of the Pantanal, whereas the native peccaries are seldom hunted. Further details of the study area are provided in Desbiez (2007) and Soriano et al. (1997).

Differences in use of food resources.—We relied on the collection of fecal samples from all 3 species to identify food items consumed. Fecal samples were collected opportunistically at any time in the field between August 2002 and November 2003. Following fresh trails or groups of animals, fecal samples were collected soon after they had been deposited and before they were scattered by dung beetles. Fecal samples that were not associated with recognizable tracks or direct animal observations were excluded from the analyses. At every possible opportunity feeding behavior of the animals was recorded. A total of 114 fecal samples of white-lipped peccaries, 56 fecal samples of collared peccaries, and 94 fecal samples of feral pigs were collected. Fecal samples were collected and stored in 70% alcohol. They were washed with water over 1-mm and 0.57-mm sieves for analysis.

Macroscopic analysis of fecal samples was conducted using a 10-point sampling frame following a method described by McCoy et al. (1990) and Keuroghlian and Eaton (2008). Fecal contents were spread from the 1-mm sieve onto an aluminum sheet. A 10-point sampling frame was then placed parallel over the sheet. Each pin was lowered toward a fecal particle that was then identified. Items were grouped into 6 categories: invertebrates; leaves including plant leaves, stems, and grasses; fibers; roots; fruits including seeds as well as fruit skins or fruit pulp; and unidentified, which included items that did not fit in other categories. Frequency of occurrence of each item was recorded from the 10 points of each frame. The frame was placed on different areas over the sheet, and the analysis was repeated 10–20 times until cumulative means, based on sets of 10 points, of the most common food items stabilized within 1% between frames. A total of 100–200 points was collected for each fecal sample analyzed. Seeds and pieces of seeds were separated and identified. Seeds from 36 different fruits were found in the fecal samples of the 3 species. To measure months of fruit availability, at least 10 trees or shrubs from 28 different species in the study area were checked monthly for signs of mature fruit between July 2002 and December 2003. Presence of leaves, flowers, fruit, and maturity were noted.

Microhistological analysis was used to determine the botanical composition of plant materials found in the fecal samples (Alipayo et al. 1992; Holeček et al. 1982; McInnis et al. 1983). Once large materials such as seeds were removed, contents from both sieves were ground in a blender and 3 microscope slides were prepared using Hoyer's solution. Slides were then air-dried for 2 weeks before being analyzed. Each slide was scanned repeatedly to identify plant species present in each fecal sample. An interactive key based on the DELTA software (Dallwitz et al. 2007) containing detailed descriptions of the epidermal cells of more than 180 common forage plants from the study area was created to facilitate this work and is described in Desbiez (2007). Microhistological analysis also was used to identify presence of fruit fibers of the palm *Attalea phalerata*. The fruit is large and protected by a fibrous pericarp that the animals chew off. The pulp surrounding the large seed is masticated and spit out by both species of peccaries, but swallowed by adult feral pigs and may go undetected during macroscopic analysis.

Differences in use of habitat.—Twenty-one transects ranging between 3.5 and 5 km and marked at 50-m intervals were randomly placed within the study area with no previous knowledge of animal distribution. Habitat was categorized every 50 m, based on vegetation and composed of open grasslands, scrub grasslands, scrub forest, forest, and forest edge. Availability of habitat in the study area was calculated from the sum of 50-m transect sections of each habitat from all transects. Transects were slowly walked at sunrise by the same observer. On each transect, the frequency of sightings for each species in each 50-m section was determined. Peccaries and pigs are social animals and for detections to remain independent events, sightings of groups were recorded as a single sighting. Landscapes in the Pantanal are composed of a mosaic of exceptionally different habitats, therefore on the same line transect, the observer may walk through a forested environment with a maximum visibility of 25 m and later find him(her)self in open grasslands, where the maximum visibility is well over 400 m. To make sure that animals all had the same probability of being counted regardless of habitat and visibility, encounter rates were calculated using only sightings made at <15 m from the transect. Habitat use for each species was determined by grouping the frequency of sightings of each species in each habitat category. A total of 2,174 km of transects were walked between October 2002 and November 2004 and a total of 38 white-lipped peccaries, 69 collared peccaries, and 53 feral pigs were sighted at <15 m from the trail.

The botanical composition of plants from the fecal samples was used to reflect habitat use patterns because plants are excellent indicators of habitat. Plants were classified according to the habitat type where they grow, which included water, edge of water, grasslands prone to flooding, grasslands that do not flood, edge between the forest and grassland, semi-deciduous forest, and scrub forest. Classification into different habitat types was based on the literature (Pott and Pott 1994, 2000) and field experience. Frequency of plants encountered in the fecal samples was used to confirm habitat overlap trends.

Statistical analysis.—Overlap in resource use (e.g., habitat, fruits, or plants) was determined by Pianka's index of niche overlap. Pianka's index yields a symmetric measure of overlap that ranges from 0 with no resources in common, to 1 complete overlap (Gotelli and Entsminger 2004; Krebs 1998; Pianka 1975). Pianka's index is calculated as:

$$O_{jk} = \frac{\sum^n p_{ij}p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}},$$

where O_{jk} is Pianka's measure of niche overlap between species j and species k , p_{ij} is proportion of resource i of the total resources used by species j , p_{ik} is proportion of resource i of the total resources used by species k , and n is total number of resource types.

To determine the probability that overlap of the observed magnitude is greater or less than would be expected randomly, we did 5,000 Monte Carlo randomizations of different frequencies of resources use to simulate possible overlaps among the 3 species using the program EcoSim 7.72 (Gotelli and Entsminger 2004). The diversity and niche breadth for fruit and plant consumption was also compared using Levin's measure of niche breadth (Krebs 1998):

$$B = \frac{1}{\sum p_j^2},$$

where B is Levin's measure of niche breadth and p_j is proportion of individuals found using resource j .

Levin's B is minimal when all the individuals occur in only 1 resource state, indicating minimum niche breadth or maximum specialization (Krebs 1998). The Bray–Curtis similarity coefficient (Clarke and Gorley 2006) was used to examine resemblance between frequency of occurrence of items between the 3 species. The Bray–Curtis similarity coefficient between species 1 and 2 is defined as:

$$S = 100\{1 - [(\sum_i |y_{i1} - y_{i2}|) / (\sum_i y_{i1} + \sum_i y_{i2})]\},$$

where y_{i1} is the count of the i th plant species from species 1. Square root transformation was used for Bray–Curtis, to prevent overdominance. Species with exactly the same frequency of items identified in their fecal samples have a Bray–Curtis similarity coefficient of 1. Cluster analysis and nonmetric multidimensional scaling was used to visualize similarities using the program PRIMER version 6.1.6 (Clarke and Gorley 2006). The frequencies of items encountered in the fecal samples were grouped into 3-month periods (July–September, October–December, January–March, or April–June), or wet season (October–March) and dry season (April–September). Differences in frequency of items, as well as temporal changes, were analyzed using 1-way analysis of variance with pairwise multiple comparisons or t -tests. Variations of frequency of occurrence of food items between species and fruit availability were compared using Pearson product moment correlation.

RESULTS

Diet overlap.—The Bray–Curtis similarity coefficients between the frequency of occurrence of food items in the

TABLE 1.—Taxonomic identification of the most common items consumed by white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Pecari tajacu*), and feral pigs (*Sus scrofa*).

White-lipped peccary		Collared peccary		Feral pig	
Species	%	Species	%	Species	%
Fruit species present in >5% of the samples					
<i>Attalea phalerata</i>	38	<i>Ximenia americana</i>	29	<i>Attalea phalerata</i>	56
<i>Ximenia americana</i>	25	<i>Solanum viarum</i>	25	<i>Vitex cymosa</i>	14
<i>Solanum viarum</i>	21	<i>Attalea phalerata</i>	21	<i>Annona dioica</i>	6
<i>Byrsonima orbignyana</i>	19	<i>Vitex cymosa</i>	18	<i>Byrsonima orbignyana</i>	6
<i>Vitex cymosa</i>	14	Seed 2	14		
Seed 1	11	<i>Byrsonima orbignyana</i>	7		
<i>Hancornia speciosa</i>	11	<i>Hancornia speciosa</i>	7		
Seed 2	7	Seed 3	5		
<i>Enterolobium contortisiliquum</i>	5				
<i>Acrocomia aculeata</i>	5				
Plant species present in >15% of the samples					
<i>Sida</i>	62	<i>Sida</i>	93	Unidentified sp. 1	53
<i>Bromelia balansae</i>	42	<i>Bromelia balansae</i>	43	<i>Hymenachne amplexicaulis</i>	49
Unidentified sp. 1	35	Unidentified sp. 2	41	<i>Pontederia cordata</i>	27
<i>Mimosa obtusifolia</i>	15	<i>Cereus</i> sp. roots	39	<i>Panicum laxum</i>	20
<i>Commelina nudiflora</i>	15	<i>Waltheria albicans</i>	34	<i>Hydrocleys nymphoides</i>	18
		Unidentified sp. 3	30	<i>Panicum repens</i>	16
		<i>Cereus</i>	23	<i>Setaria geniculata</i>	15
		<i>Longsdorpha hypogaea</i>	21		
		<i>Mimosa</i>	20		
		<i>Solanum viarum</i>	20		
		<i>Desmodium barbatum</i>	18		
		Unidentified sp. 1	18		

fecal samples of white-lipped peccaries, collared peccaries, and feral pigs were very high (similarity > 80) during both the wet and dry season. However, even though the diets of these species appear similar, taxonomic identification of food items such as fruit and plant species (Table 1) shows there are differences and that overlap in food resources is higher between the native peccaries than between the peccaries and the introduced feral pig.

Almost all of the items encountered in the fecal samples of the 3 species varied throughout the seasons (Table 2). However, only the variation in frequency of fruit items was correlated between pairs of the 3 species: collared and white-lipped peccary ($C = 0.953, n = 6, P = 0.003$), collared peccary

and feral pig ($C = 0.918, n = 6, P = 0.009$), and white-lipped peccary and feral pig ($C = 0.905, n = 6, P = 0.013$). The monthly distribution of trees producing fruit indicated a period of higher fruit availability during the wet season and a period of lower fruit availability during the dry season ($t = 3.94, d.f. = 10, P = 0.003$). During the wet season, fruit was encountered more frequently in the fecal samples of the 3 species, but the number and diversity of fruit species encountered in the fecal samples was highest for the peccaries. In addition, niche breadth of the peccaries was found to be broader than that of feral pigs (Table 3). In fact, the diversity of fruits consumed by feral pigs is low and fruits from the palm *A. phalerata* were found in more than one-half of the fecal samples. Pianka's index of niche overlap was calculated using frequency of fruit encountered in the fecal samples of the 3 species both including and excluding the fruit of *A. phalerata* from the analysis (Table 4). The highest overlap occurred between the white-lipped peccary and the collared peccary and overlap was lowest between the peccaries and feral pigs, particularly when *A. phalerata* fruit was excluded from the analysis.

Attalea phalerata was 1 of the most important fruits for all 3 species. Although immature and green fruits of *A. phalerata* were found throughout the year, mature fruits were found to be available mostly between June and December. Using microhistology, the frequency of occurrence of fruit fibers of *A. phalerata* in the fecal samples of white-lipped peccaries was found to be different between seasons ($t = 7.096, d.f. = 4, P = 0.002$) and was very high during periods of high fruit availability (80%) and low during periods of low fruit

TABLE 2.—Frequency of occurrence of items encountered in fecal samples of white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Pecari tajacu*), and feral pigs (*Sus scrofa*) from August 2002 to November 2003, during the dry season (July–September 2002, April–June 2003, and July–September 2003) and during the wet season (October–December 2002, January–March 2003, and October–December 2003).

Items	White-lipped peccary			Collared peccary			Feral pig		
	Total	Dry	Wet	Total	Dry	Wet	Total	Dry	Wet
Invertebrates	0.1	0.0	0.1	0.4	0.2	0.9	1.7	3.2	0.9
Leaves	13.0	21.1	12.2	9.5	21.0	1.1	21.1	21.4	23.8
Fibers	14.0	20.5	9.9	35.3	37.6	28.0	10.1	9.3	11.3
Roots	20.2	30.8	9.7	19.1	17.6	16.7	27.7	40.4	5.1
Fruit	48.4	21.2	65.4	28.3	14.1	49.3	30.4	13.7	55.1
Unidentified	4.5	6.4	2.8	7.4	9.6	4.0	9.0	12.1	3.7

TABLE 3.—Fruit and plant diversity and niche breadth for white-lipped peccaries (*Tayassu pecari*; WL), collared peccaries (*Pecari tajacu*; CP), and feral pigs (*Sus scrofa*; FP) based on analysis of fecal samples.

Species	Diversity of fruit species	Niche breadth based on fruit	Diversity of plant species	Niche breadth based on plants
WL	23	9.465	56	13.67
CP	25	10.731	64	21.64
FP	13	2.804	59	16.1

availability (15–20%). There were no seasonal differences for collared peccaries ($t = 0.0928$, $d.f. = 3$, $P = 0.932$); the occurrence of fruit fibers of *A. phalerata* was low (20%) and relatively stable. For feral pigs, changes appear random rather than seasonal ($t = 0.387$, $d.f. = 3$, $P = 0.725$). Fruit fibers were found in approximately 60% of the feral pig fecal samples.

Plant materials include roots, stems, or leaves. They enable peccaries to survive periods of fruit scarcity, especially in the dry season (Table 2). Plant species similarity indices were higher between the 2 species of peccaries than between the peccaries and feral pigs (Fig. 1). When frequency of plants in the fecal samples was used to calculate Pianka's index in the wet and dry season, overlap was always highest between the peccaries and lowest between feral pigs and collared peccaries (Table 5). Pianka's index for plant overlap was higher during the wet season than the dry season. Fecal samples of both species of peccaries had a higher frequency of herbs (dicotyledon plants without lignin) than other plant types, whereas feral pigs had higher frequencies of grasses (Table 1). The number of species identified was highest in the diet of collared peccaries, which also had the broadest niche breadth (Table 3).

Habitat overlap.—Proportions of habitat available, estimated from the transects, and habitat used, estimated by the frequency of sighting of each species in the different habitats, were used to calculate Pianka's index of overlap in habitat use among the 3 species (Table 6). The highest niche overlap occurred between collared peccaries and white-lipped peccaries, and the lowest between white-lipped peccaries and feral pigs (Table 7). These results were confirmed by the micro-histological analysis using plants as indicators of habitat (Table 7). Once again the highest habitat overlap value was between the peccaries, whereas the lowest value was between collared peccaries and feral pigs. The microhistological analysis also showed that feral pigs tended to use "floodable habitats," whereas the peccaries used "nonfloodable habitats" (Fig. 2). The frequency of plants from nonfloodable habitats was higher than plants growing in floodable habitats for white-lipped peccaries in both the wet ($T = 3,857.0$, $n = 70$, $P < 0.001$) and dry ($t = 10.711$, $d.f. = 86$, $P < 0.001$) season as well as for collared peccaries in both the wet ($T = 345.0$, $n = 24$, $P < 0.001$) and dry ($t = -21.527$, $d.f. = 62$, $P < 0.001$) season. The opposite was true for feral pigs. The frequency of plants from floodable habitats was higher than plants growing in nonfloodable habitats in both the wet ($T = 1,217.5$, $n = 31$, $P < 0.001$) and dry ($T = 5,074.5$, $n = 63$, $P < 0.001$) season.

TABLE 4.—Niche overlap for fruit use both including *Attalea phalerata* (above the diagonal) and excluding *A. phalerata* (below the diagonal) among white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Pecari tajacu*), and feral pigs (*Sus scrofa*) determined by Pianka's index. Observed mean fruit consumption including *A. phalerata* overlap was 0.716 after 5,000 Monte Carlo simulations, whereas expected mean fruit consumption overlap was 0.192. Observed mean fruit consumption excluding *A. phalerata* overlap was 0.638, whereas expected mean fruit consumption overlap was 0.230.

Species	White-lipped peccary	Collared Peccary	Feral pig
White-lipped peccary	1	0.886	0.734
Collared peccary	0.888	1	0.526
Feral pig	0.483	0.543	1

DISCUSSION

We found overlap in food resources and habitat use between feral pigs and the 2 species of native peccaries to be lower than expected, and instead niche overlap in every dimension examined was highest between the native species throughout the year. Overlap between ecologically similar native species has been used as a measure of the tolerable range of overlap native species confronted with an introduced species may withstand (Goodyear 1992). Although results cannot be used to draw conclusions for all the different landscapes of the Pantanal, or may differ in years of extreme flood, our study does suggest that potential impacts of feral pigs on peccary populations may be less than previously suspected. In Texas, feral pigs are sympatric with collared peccaries, and Ilse and Hellgren (1995a) found that although overlap in diet and habitat use varied throughout the seasons it also was moderate overall.

During periods of highest availability, fruits were the most frequently encountered item in the fecal samples from the 3 species and can be considered a key resource. In the

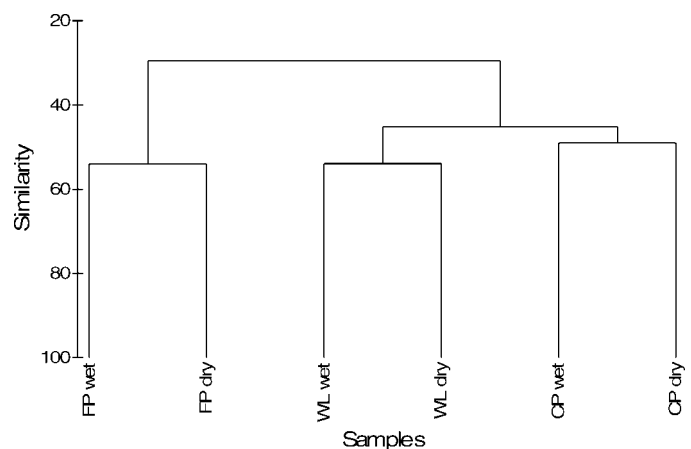


FIG. 1.—Cluster analysis of Bray-Curtis similarity indices of plant species identified in fecal samples of white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Pecari tajacu*), and feral pigs (*Sus scrofa*) in the wet season and dry season. WL = white-lipped peccary; CP = collared peccary; FP = feral pig.

TABLE 5.—Pianka’s index of niche overlap for plant species between white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Pecari tajacu*), and feral pigs (*Sus scrofa*) during both the wet (W) and dry (D) season. In the wet season observed mean niche overlap was 0.489 after 5,000 Monte Carlo simulations, whereas expected mean fruit consumption overlap was 0.103. In the dry season observed mean niche overlap was 0.467 after 5,000 Monte Carlo simulations, whereas expected mean fruit consumption overlap was 0.151.

	White-lipped peccary	Collared peccary	Feral pig
White-lipped peccary	1	(W) 0.787	(W) 0.223
Collared peccary	(D) 0.664	1	(W) 0.458
Feral pig	(D) 0.183	(D) 0.219	1

Neotropics, peccaries are generally considered frugivores (Beck 2005). Feral pigs, on the other hand, are opportunistic and the type of food items consumed varies greatly depending on the geographic location and resources available. Herbaceous vegetation generally dominates their diet (Baber and Coblentz 1986; Choquenot and Ruscoe 2003; Dexter 1998), but if fruit is available it can predominate in their diet during periods of availability (Loggins et al. 2002; Sierra 2001). Niche breadth based on fruits was lowest for feral pigs and many species of fruit present in the fecal samples of the peccaries were not present in the fecal samples of feral pigs. Feral pigs did not exploit the diverse fruit resources available as efficiently as the peccaries. White-lipped peccaries apparently overlap more with feral pigs than collared peccaries, but this was due to fruit of *A. phalerata*. *A. phalerata* is the most abundant fruit available in the study area and agoutis (*Dasyprocta azarae*) are its main consumer (Desbiez 2007). These results confirm the frugivorous nature of the peccaries and suggest that consumption of fruit resources by feral pigs probably does not impact fitness of peccaries.

Proportions of plant materials in fecal samples of the 3 species increased during periods of fruit scarcity. Increase in plant material during periods of fruit scarcity has been reported in white-lipped peccaries (Altrichter et al. 2001; Beck 2005; Mayer and Wetzell 1987), collared peccaries (Bodmer 1990; McCoy et al. 1990; Wilber et al. 1991), and feral pigs (Baber and Coblentz 1986; Chimera et al. 1995; Loggins et al. 2002; Sierra 2001; Thomas and Challies 1988). It is possible that fruit items consumed in the dry season by the peccaries are underestimated in our study. During the dry season, palm

TABLE 6.—Proportions of habitat available and frequency of sightings (sighting/100 km) of white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Pecari tajacu*), and feral pigs (*Sus scrofa*) in the study area.

Habitats in the study area	Proportion of habitat available	White-lipped peccary	Collared peccary	Feral pig
Open grassland	0.290	1.09	1.09	2.85
Scrub grassland	0.172	0.35	3.14	2.10
Scrub forest	0.228	0.84	7.56	3.08
Forest	0.215	7.04	5.22	2.61
Forest edge	0.094	4.41	5.04	0.00

TABLE 7.—Niche overlap for habitat use by white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Pecari tajacu*), and feral pigs (*Sus scrofa*) based on encounter rates (ER; above the diagonal) and microhistological analysis (MH; below the diagonal), determined by Pianka’s index. Observed mean niche overlap (based on encounter rates) was 0.610 after 5,000 Monte Carlo simulations, whereas expected mean niche overlap was 0.655. Observed mean niche overlap (based on microhistology) was 0.787 after 5,000 Monte Carlo simulations, whereas expected mean niche overlap was 0.559.

Species	White-lipped peccary	Collared peccary	Feral pigs
White-lipped peccary	1	(ER) 0.864	(ER) 0.369
Collared peccary	(MH) 0.960	1	(ER) 0.596
Feral pigs	(MH) 0.797	(MH) 0.607	1

fruits from *Copernicia alba*, *Acrocomia aculeate*, and *A. phalerata* are consumed, but the peccaries frequently expectorate the seeds, whereas feral pigs swallow them. For white-lipped peccaries, the proportion of plant material, particularly of roots and fibers, was found to increase when the proportion of fruit decreased. In the arid caatinga of northeastern Brazil where resources such as fruits are dependent on unpredictable rainfall, white-lipped peccaries adopted a similar feeding strategy, and roots supplied almost 80% of their diet (Olmos 1993). Collared peccaries responded to fruit scarcity by a major shift in their diet and the frequency of occurrence of leaves became almost equal to that of fruit during the dry season. Observations confirmed by microhistological analysis also showed that collared peccaries frequently consumed both the roots and flesh from cactus plants during the dry season. In the most arid areas of their range, the diet of collared peccaries is characterized by the seasonal occurrence of numerous plant

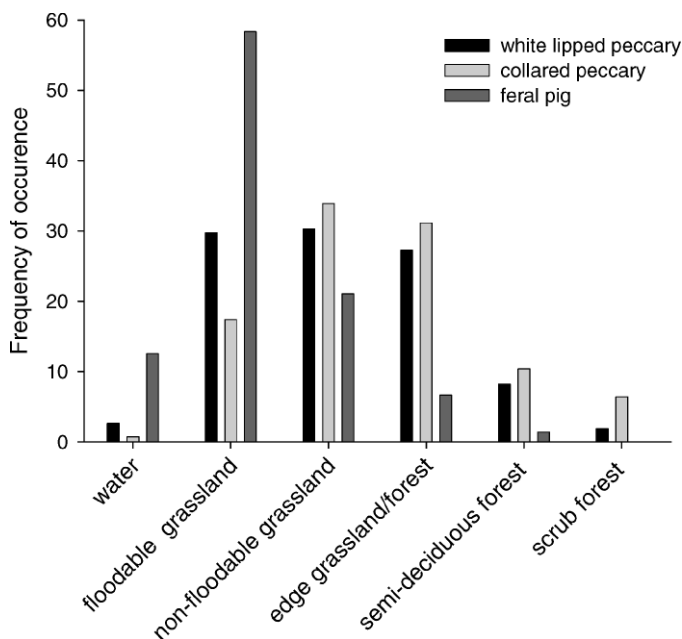


FIG. 2.—Proportion of plants from different habitats identified in the fecal samples of white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Pecari tajacu*), and feral pigs (*Sus scrofa*).

species (Corn and Warren 1985) and during droughts collared peccaries are reported to consume succulent plants, primarily prickly pear cactus (*Opuntia lindheimeri*), to satisfy water and energy needs (Corn and Warren 1985; Gallagher et al. 1984). During periods of fruit scarcity, presence of both leaves and roots increased in feral pig fecal samples. In California, herbaceous plants and forbs were the primary constituents of the diet of feral pigs, except when acorns became available and then became predominant (Loggins et al. 2002). The amount of animal protein consumed by feral pigs is underestimated in this study because it is based on fecal sample analysis. Direct observations showed that consumption of animal protein, especially earthworms and cow carcasses, is a very important part of the diet of feral pigs, particularly during the dry season.

Overlap in resources during periods of scarcity can change the competitive interactions between native and exotic species and lead to competition for resources (Ives et al. 1999; Keddy 2001; Shea and Chesson 2002; Wiens 1993). Similarity indices and Pianka's index of niche overlap for plant species consumed were always higher between the peccaries during both seasons than between the peccaries and feral pigs. Most importantly, overlap in use of plant resources decreases between the 3 species during the period of fruit scarcity, ruling out a possible increase in competition for plant resources during this period.

Using 2 different methodologies, overlap in habitat use was found to be higher between the native peccaries and lower between feral pigs and the peccaries. This may indicate habitat partitioning due to interspecific competition or to differences in resource use and needs. For example, differences in habitat use may reflect a difference in dependency on water. The microhistological analysis showed that feral pigs tended to use floodable habitats, whereas the peccaries used nonfloodable habitats. Feral pigs have a physiological need to drink water daily and they are not as efficient as collared peccaries at conserving water by concentrating urine (Gabor et al. 1997; Zervanos and Naveh 1988). Feral pigs were often observed in water at the edge of ponds where they create characteristic deep wallows. Feral pigs lack sweat glands and rely on behavioral thermoregulation to maintain favorable heat balance in hot environments (Baber and Coblenz 1986; Barrett 1978; Choquenot and Ruscoe 2003; Dexter 1998; Ilse and Hellgren 1995b). Differences in morphology, social behavior, home range, body size, and foraging behavior indicated other possible differences in resource utilization.

Differences in morphology and bite force have been suggested as a potential mechanism for niche partitioning between the 2 peccary species (Kiltie 1982), as well as between feral pigs and peccaries (Sicuro and Oliveira 2002). However, comparison of bite force between pigs and peccaries is extremely misleading, because the biomechanics of mastication are very different between them (Herring 1985). Peccaries are limited to orthal movements of their jaws, whereas pigs are not (Herring 1985; Kiltie 1982). The skull morphology of the 3 species is associated with efficient soil-digging performance. Because of the larger size of their skulls, feral pigs may be able to dig deeper and more efficiently. Feral pigs were observed to

excavate young palm trees (*A. phalerata*) within minutes, leaving behind holes that could be more than 50 cm deep. Feral pigs also characteristically root at the edges of water to search for invertebrates. Collared peccaries were observed to dig deep holes to consume roots and tubers. They were observed to return several days in a row to dig and consume the excavated roots. White-lipped peccaries generally rooted through vast areas, but mostly only in the top layer of soil and leaf litter. Differences in rooting between the 3 species may be due to behavioral differences rather than morphological traits.

Digestive systems of peccaries and feral pigs differ in form and function (Stevens 1988). Peccaries are foregut fermenters (Bodmer 1989) with a complex stomach containing large concentrations of protozoa (Langer 1978). The peccary fore-stomach has a large storage capacity and many folds that slow the passage of food (Langer 1979) and allow more time for microbial fermentation to occur (Carl and Brown 1986; Gallagher et al. 1984). The feral pig, a hindgut fermenter, has a simple stomach, and microbial fermentation occurs primarily in the large intestine (Reece 1990; Stevens 1988). In spite of these differences, Elston et al. (2005) found that neither collared peccaries nor feral pigs have a competitive advantage in dry matter digestion of plant material.

Differences in body size, home range, and social behavior may result in differences in feeding strategies between the 3 species. In the Pantanal, collared peccaries have an average weight of 18 kg, have a home range of approximately 2.3 km² (A. Keuroghlian, pers. obs.), and in the study area typically occur in groups of 5–10 individuals. White-lipped peccaries have an average weight of 30 kg, have home ranges of approximately 30 km² (A. Keuroghlian, pers. obs.), and in the study area occur in groups of 25–75 individuals. Feral pigs weigh between 25 and 40 kg, have variable home-range sizes, and have been observed in the study area in groups of 2–50 pigs. Direct observations in the field show that both collared peccaries and feral pigs return to an abundant resource several days in a row, whereas white-lipped peccaries were generally not observed in the same place on consecutive days.

It has been suggested that home ranges and movements of white-lipped peccaries are based on changes at large scales composed of aggregations of different vegetation types, whereas collared peccary herds respond to smaller-scale changes in plant communities (Bodmer 1990; Fragoso 1999; Keuroghlian and Eaton 2008; Keuroghlian et al. 2004). *A. phalerata* occurs in high-density aggregations scattered around the landscape, and its fruit was 1 of the most frequently encountered fruit species in the fecal samples of the 3 species. White-lipped peccaries responded to availability of fruit of *A. phalerata* at the landscape scale and consumed fruits when they were most available. Collared peccaries responded to the changes in availability from aggregations of palms. They consume mature fallen fruits, green fruits, or fruits scatter-hoarded by rodents within the aggregation of palm trees throughout the seasons. This explains why the frequency of occurrence of fruit fibers was low and relatively stable in collared peccaries and variable in white-lipped peccaries. Feral pigs appear to concentrate their fruit consumption on fruit of *A. phalerata*. Frequency of

encounter of fruit fibers from *A. phalerata* in the fecal samples was high throughout the sampling period and niche breadth of feral pigs regarding fruit consumption was low. Thus, feral pigs may use both foraging strategies shown by peccaries.

Are feral pigs a threat to the native peccaries?—Our study shows that resource partitioning appears to be occurring between the peccaries and feral pigs. In addition, differences in morphology and behavior have indicated possible mechanisms of niche partitioning between the species. Whether this is the result of interspecific competition, facilitation, coexistence, or due to different resource needs and behaviors is difficult to demonstrate without experimental manipulation. Regardless of the reasons for resource partitioning, the low niche overlap suggests that feral pigs are not currently a direct threat to the native peccaries in the study area.

Feral pigs may, nevertheless, impact the wildlife community in other ways. Although few generalizations are possible, invasive predators generally have dramatic effects on the community into which they are introduced. Feral pigs have been shown to depredate eggs of *Caiman yacare* (Campos 1993), and in our study egg shells from ground-nesting birds were regularly found in feral pig fecal samples. Through their rooting activities, feral pigs can disturb large areas (Hone 1988). Some studies have found that rooting activity of feral pigs could affect and change plant communities in pastures (Cushman et al. 2004; Hone 1980) as well as forested areas through the destruction of seedlings and saplings (Drake 2001; Loggins et al. 2002; Singer et al. 1984; Thomas and Challies 1988). In the Pantanal, when present at high densities, herds of feral pigs are reported by local people to cause damage to pastures. Also, the uprooting of *A. phalerata* observed in this study could affect the recruitment of the palm. Most importantly, the potential of feral pigs as reservoirs of disease (Corner 2006; Doran and Laffan 2005; Herrera et al. 2005; Ruiz-Fons et al. 2007) needs to be considered.

The theory of community ecology predicts that spatial and temporal environmental variations have a crucial role in species coexistence. Consequences from environmental fluctuations can change the dynamics between invaders and residents (Shea and Chesson 2002). The Pantanal is subject to natural environmental fluctuations that will affect both habitat and resource use of the mammal community. These environmental fluctuations may favor the locally adapted native species. However, in addition to these environmental fluctuations, new anthropogenic changes in the landscape are occurring. Recent intensification of ranching practices that includes deforestation to plant exotic invasive grasses is changing the habitats and niche opportunities available to wildlife. Encounter rates of peccaries were highest in forested habitats and for this reason they may be the most impacted by these changes. Cattle ranching also may favor feral pig populations by creating a buffer against environmental fluctuations. Ranches build artificial water holes, which can become the only source of water available during the dry season. Feral pigs further benefit from an added source of protein from the carcasses of dead cows. Anthropogenic alterations of the natural landscape, in particular increased deforestation and habitat fragmentation,

therefore could lead to changes in competitive dynamics between feral pigs and native species.

RESUMO

A introdução de espécies em ecossistemas onde ocorram espécies que ocupam níveis tróficos similares pode resultar em altos níveis de sobreposição de nicho, o que pode levar à extinção. O porco monteiro (*Sus scrofa*), uma das espécies invasoras mais destrutivas do mundo, foi introduzido ao Pantanal Brasileiro cerca de 200 anos atrás e acredita-se que este animal esteja em competição com os porcos nativos queixada (*Tayassu pecari*) e cateto (*Pecari tajacu*). A divisão de recursos entre as 3 espécies foi examinada através do uso de diferentes metodologias, incluindo análises de frutos e partes vegetais encontradas em amostras fecais, bem como taxas de encontro em diferentes tipos de habitat, gerando hipóteses sobre as possíveis interações competitivas entre as espécies. A sobreposição em termos de consumo de recursos alimentares e uso de habitat entre o porco monteiro, queixadas e catetos foi mais baixa do que esperada. Em fato, a sobreposição de nicho foi maior entre catetos e queixadas. Os resultados indicam que, na situação atual, os porcos monteiros não se constituem em uma ameaça direta às espécies nativas de porcos na área de estudo. Adicionalmente, as diferenças em termos de morfologia e comportamento indicam a presença de possíveis mecanismos de divisão de recursos entre as três espécies. Apesar disso, o porco monteiro pode causar impactos às espécies nativas de outras maneiras, como predadores de ovos, através da destruição de vegetação quando revirando o solo em busca de invertebrados, ou como reservatórios de doenças. Além disso, especula-se que atividades de pecuária favoreçam o porco monteiro e que as mudanças antropogênicas que vêm ocorrendo atualmente na paisagem do Pantanal possam levar a alterações na dinâmica de competição entre o porco monteiro e as espécies nativas.

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