PERCEPTION OF SCALE AND RESOURCE PARTITIONING BY PECCARIES: BEHAVIORAL CAUSES AND ECOLOGICAL IMPLICATIONS

José Manuel Vieira Fragoso

Departmento de Zoologia, Museu Paraense Emílio Goeldi, Belém, Para, Brasil
Present address: Deptartment of Zoology, University of Florida, Gainesville, FL 32611

Two herds of white-lipped (*Tayassu pecari*) and two herds of collared (*T. tajacu*) peccaries were monitored by aerial and ground radiotelemetry in rainforest and rainforest-savanna-wetland edge vegetation from January 1992 to January 1993 (total locations = 194) in the northern Brazilian Amazon. Small- and large-scale patterns of vegetation in their ranges were quantified and described, and dietary items were noted. One herd of white-lipped peccaries was radiotracked in the dry and wet-flood seasons and the other herd was followed only for the wet-flood season. Considering the total area of ranges of the four herds as available habitat, white-lipped peccaries used palm (*Mauritia flexuosa*) wetlands and savanna wetlands more than expected, whereas collared peccaries used terra-firme forest more often than expected. White-lipped peccaries did not show seasonal differences in habitat use. One herd of white-lipped peccaries spent more time in riverine vegetation and savanna-wetlands than the other, which preferred palm-wetlands and terra-firme forest. Collared peccaries occurred almost exclusively in terra-firme forest; they did not enter savanna-wetlands and rarely used riverine vegetation. Each species may be responding to different levels of organization of the vegetation. Collared peccaries partitioned their habitats at finer scales of resolution than white-lipped peccaries, and the two species may have different habitat requirements due to differences in body size, morphology, and behavior. Apparent requirements of white-lipped peccaries for a large-scale landscape-level mosaic of vegetation types and collared peccaries for a single large-scale vegetation type may explain the higher susceptibility of white-lipped peccaries to extirpation by anthropogenic disturbance.

Key words: *Tayassu pecari, Tayassu tajacu,* peccary, tropical vegetation mosaics, species coexistence, local extinction, resource partitioning, spatial scale

White-lipped (*Tayassu pecari*) and collared (*T. tajacu*) peccaries occur sympatrically over most of their historical range. Previous research has suggested potential mechanisms for resource partitioning. Kiltie (1981, 1982) proposed that in rainforest habitats, differences in bite force may lead to differences in food choice. Bodmer (1990) reported that white-lipped peccaries used wetter habitats than collared peccaries in forests subject to flooding and consequently have somewhat different diets. However, the two species of peccary subsist on different types of food in the wide range of ecosystems and bioregions where they co-occur (Bodmer, 1989; Eisenberg, 1989; Fragoso, 1994; Kiltie and Terborgh, 1983; Leopold, 1959; Redford and Eisenberg, 1992; Sowls, 1984). Here I present a generalized model of resource partitioning based on differences in perception of scale. This model could apply in a variety of ecosystems and explain the greater resilience of collared peccaries compared with white-lipped peccaries to anthropogenic disturbance.

White-lipped peccaries are about twice the size of collared peccaries in areas where they co-occur (16–25 kg versus 28–35 kg in Peru—Bodmer, 1989; 18 kg versus 35 kg at Maracá, Brazil—Fragoso, 1994, 1998*a*).

Behavioral differences also exist between species. Collared peccaries exhibit intraspecific territoriality among herds and patrol range boundaries (Fragoso, 1994; Sowls, 1984), but herds of white-lipped peccaries have overlapping home ranges and show no territorial behavior (Fragoso, 1994, 1998*a*). Herds of collared peccaries normally contain only 3–20 individuals, but herds of white-lipped peccaries can number in the hundreds (Fragoso 1998*a*; Mayer and Brandt, 1982; Mayer and Wetzel, 1987; Sowls, 1984). Herd cohesion is often weak among collared peccaries, whose herds splinter seasonally and daily into subgroups (Barreto and Hernandez, 1988; Castellanos, 1983; Green and Grant, 1984), but herds of white-lipped peccaries show no evidence of similar splitting (Fragoso, 1994, 1998*a*; Kiltie and Terborgh, 1983).

These differences in social behavior and body size between the two species should impose different needs for range and resource patch size, resulting in differences in perception of resource availability and scale of resource use (Holling, 1992; Senft et al., 1987). Thus, an environment that is fine-grained and presents no physical barriers to the white-lipped peccary may be coarse-grained to the collared peccary (cf. Kotliar and Wiens, 1990; Wiens, 1990). Coexistence of the two species may be facilitated by the different perception and use of habitat mosaics. I evaluated this hypothesis by examining habitat use and partitioning of a 114 km^2 area of humid closed-canopy rainforest in the northern Amazon by two herds of white-lipped peccaries and two herds of collared peccaries.

MATERIALS AND METHODS

Study area.—Maracá Island Ecological Reserve (3°25'N, 61°40'W) lies at the northern edge of the Amazon River basin in Roraima State, Brazil. It was formed by the branching of the Uraricoera River, a tributary of the Rio Branco (Amazon drainage). All 1,100 km^2 of tropical rainforest, wetlands, and isolated savanna-wetlands forming the ecological reserve are protected by IBAMA (the Brazilian Agency for the Environment, within the Ministry of the Environment) as a site for research and forest protection. The dominant vegetation of the region was old-growth, tropical evergreen, lowland rainforest, contiguous with the Amazon rainforest (Milliken and Ratter, 1989, 1998; Moskovits, 1985). In addition to peccaries, Maracá supported populations of pumas (*Pume concolor*), jaguars (*Panthera onca*), tapirs (*Tapirus terrestris*), and other animals typical of a Neotropical rainforest undisturbed by Europeans and their descendants (Fragoso, 1994, 1997*a*, 1998*a*; Milliken and Ratter, 1998). There have been no human settlements on the island within historical time, and it was never logged. Approximately eight isolated indigenous and non-indignous families lived at different times along the river banks of the eastern tip until 1977. Minor levels of illegal hunting occurred on the outskirts of the reserve along navigable areas of the river, although hunters avoided the area around the research station. The study site was described by Fragoso (1994) and Milliken and Ratter (1998). My research (December 1990–January 1993) occurred on the eastern one-third of the island, a 114 km^2 area equivalent to the home range of the largest herd of white-lipped peccaries. This area also included the home ranges of the other three herds.

Mapping and habitat description.—Large-scale vegetational types and smaller-scale plant communities were described based on qualitative assessments of vegetation and flooding regimes from December 1990 to December 1992, as seen from the ground and an ultralight airplane. To produce a detailed description of plant communities, my classifications were combined with those of Milliken and Ratter (1989) from the same area.

Vegetation categories used in this study were terra-firme forest, riverine vegetation, palm (*Mauritia flexuosa*) wetland, shrub-thicket, and savanna-wetland (Table 1). Their extent was measured on an aerial photograph and confirmed from the airplane. Coverage for each type was determined by overlaying a grid of squares, each equivalent to 0.1 km^2, over a map of the vegetation and summing number of squares in each type of vegetation. For a square to be counted in a vegetation category that vegetation had to cover >50% of the square. Embedded within this vegetation matrix were smaller-scale plant communities. I did not measure the areal cov-

TABLE 1.—*Large-scale types of vegetation, their extent, and description of embedded plant communities of eastern Maracá Island, Brazil.*

Vegetation type	Km^2	%	Plant communities within habitat	Dominant species	Canopy height (m) and structure	Flooding potential
Riverine	13.6	12.8	Low *Maximiliana* palm forest	*Maximiliana maripa* (almost monodominant)	<5 No overstory	>25 years
			Low-shrub	Shrubs, lianas, grasses	2–3 Closed canopy	2–5 years?
			Low-forest	*Ceiba pendantra, Spondias mombin, Maximiliana, Triplaris gardneriana, Cecropia*	15–25 Broken canopy	2–5 years?
			Mid-to high (tall) forest	Similar to low forest but including *Pradosia surinamensis*	25–35 Closed canopy	>25 years?
Palm-wetland	10.0	9.4	*Mauritia* wetland	*Mauritia flexuosa* (almost monodominant), *Virola surinamensis, Bactris maraja, Euterpe precatoria, Renealmia alpina*	30 Closed canopy	Standing water most of year
			Mauritia wetland high forest edge	Species common to *Mauritia* wetland and terra firme high forest	30–40 Closed canopy	?
Terra-firme forest	71.4	67.2	High forest	*Pradosia, Pouteria venosa, Tetragastris panamensis, Tabebuia uleana, Couratari multiflora*	30–50 Closed canopy	Unflooded
			High forest-*Maximiliana*	As with high forest but dominated by 20–30 m high *Maximiliana* palms	30–50 Closed canopy	Unflooded
			High and low forest	Like high forest but thicker understory often dominated by Bromiliaceae	20–30 Broken canopy	Unflooded
			Low forest	Broken canopy, many lianas and shrubs	10–30 Broken canopy	Unflooded
Savanna-wetland	8.0	7.5	Savanna ponds and seasonal wetlands	Poaceae, Cyperaceae	<2	Seasonal
			Forest patch in savanna	*Curatella americana, Genipap americana, Maximiliana, Humiria balsamifera*	15–20 Closed canopy	>25 years?
Shrub-thicket	3.2	3.1	Wet	*Thalia gardneriana, Mimosa pigra, Senna alata, Canna glauca, Eriochloa punctata*	<3	Seasonal
			Bactris palm	*Bactris maraja*	3–6	Seasonal
Total	106.2	100.0				

erage of plant communities, but their qualitative occurrence within vegetation types was described to evaluate responses of peccaries to patterns of vegetation at different scales (Table 1). Total area for all vegetation types derived from the aerial photograph map was 106.2 km^2. Terra-firme forest covered 71.4 km^2 and was the most extensive vegetation type in the study region. It was followed in order by riverine, palm-wetland, savanna-wetland and shrub-thicket types (Table 1). Plant communities, their vegetative category affiliations, and identifying characteristics were summarized (Table 1).

Seasonal change in flooding conditions influences peccary movements more than does the seasonal change in rainfall (Bodmer, 1989; Fragoso, 1994). On Maracá, the flood season started in June and continued partly into the dry season (December). Most palm-wetlands, shrub-thickets, and savanna-wetlands were inundated. Some low-lying regions of riverine vegetation also may flood every year, and all of it floods every 5–25 years (J. Alves, pers. comm.; G. de Oliviera, pers. comm.). Terra-firme forests remain dry during the wet-flood season, although pools may form on the soil surface.

Capture and handling of animals.—To determine presence of white-lipped peccaries or their sign (e.g., tracks, rooting, scent) in the study area, 60 km of trail were searched usually every 2 days from January 1991 to December 1992 by two teams operating separately. More intensive searches were conducted for sign along areas preferred by peccaries such as palm-wetlands and creek beds. If a herd or fresh sign were encountered, the herd was stalked, and adult individuals darted. Individuals were tranquilized with 250 mg of ketamine hydrochloride and 5 mg of azaperone delivered by means of a Telinject gun (Telinject USA, Inc., Saugus, CA). A Macuxi Amerindian hunter assisted in the tracking and capturing. Captured white-lipped peccaries were marked with an individually numbered ear tag of a color unique to each herd, and radiocollars (Telonics, Inc., Mesa, AZ) were placed around their necks. Animals were monitored until they recovered sufficiently from tranquilization to walk beyond sight (1–3 h). Individuals were visually located a few days after their capture. At least two individuals per herd were outfitted with radiocollars with activity monitors.

Collared peccaries were driven by Macuxi hunters with peccary hunting dogs into giant armadillo (*Priodontes giganteus*) burrows or hollow logs. The dogs kept the animal(s) within the burrows until the entrance was blocked with stakes. A hole was then dug through the roof ca. 50 cm behind the entrance, and a 2–4 m long palm leaf was used to move the animal near the roof hole. Through the roof hole, the peccary was injected in the rump with a mix of 150 mg of ketamine hydrochloride and 5 mg of azaperone delivered by a Telinject pistol. The post-capture treatment was as described for white-lipped peccaries.

Radiocollared individuals (adults only) were monitored closely to avoid capturing animals from herds in which two or more individuals were already radiocollared. To ensure capture of individuals from all collared peccary herds in the eastern end of the island, we avoided hunting within home ranges of herds that were already marked. Herd size for both species was derived from total and partial counts as animals crossed trails.

Tracking.—Radiocollared peccaries usually were located twice per week from the air using an ultralight airplane. Two Telonics H-antennas, one on each wing of the plane, were used to locate signals from radiocollared animals. Searches began by circling over the last location for an animal and flying parallel lines separated by 2 km from that point until the signal was located. Locations were immediately plotted on a map. Due to hazardous climatic and flying conditions and the type of airplane used, flying was limited to 0600–0930 h and 1500–1800 h. Whenever possible, ground telemetry was conducted during the day using a three-element Yagi antenna. In some instances, animals were located only from the ground. The convex polygon method (100% polygon level) of the computer program HOME RANGE (Ackerman et al., 1990) was used to compute home-range size. A detailed description of methods used to calculate home ranges and their size are presented elsewhere (Fragoso, 1994, 1998*a*).

Diet and habitat use.—Vegetation type and plant community were recorded for each peccary location. This information was used to compare: 1) habitat use between seasons for species and herds using χ^2 tests of independence, 2) habitat use within species using χ^2 tests of independence, and 3) habitat preference for species and herds using a χ^2 goodness-of-fit test (distribution of habitats used compared with distribution of available habitats). No statistical analyses were conducted on use of plant communites because of limited samples. All herds of both species had potential access to all habitat types, with parts of ranges of each herd bordering or encompassing the large-scale vegetation categories (Fragoso, 1994, 1998*a*). Due to the limited tracking period for white-lipped peccary herd B, I limited comparison of habitat use by herds of white-lipped peccaries to the months when both were tracked (wet-flood season) and evaluated seasonal use for herd A only. Due to limited samples, a seasonal comparison could not be made for collared peccaries. Interspecific comparisons were not restricted seasonally because data on locations during wet-flood and dry seasons were available for both species. I described diets of white-lipped and collared peccaries from opportunistic observation of individuals feeding in the wild.

RESULTS

Five white-lipped peccaries were captured from herd A, which contained 39 individuals, and two were captured from herd B, which contained 124–134 individuals. Four individuals from herd A and both animals captured from herd B were radiocollared. Locations for a herd consisted of the radiotelemetry data for the longest surviving herd member. I obtained locations from herd A for 13 months (26 January 1992–8 January 1993; 67 locations) and herd B for 5 months (16 July 1992–16 November 1992; 46 locations). The range of herd B (109.6 km ^{2}) subsumed the range of herd A (21.8 km ^{2}; Fragoso, 1998*a*).

Seven collared peccaries were captured from herd C, which contained 34 individuals, and five were captured from herd D, which contained at ≥12 individuals. Five of the individuals captured from herd C and all from herd D were radiocollared. Variation in tracking time and number of locations among individuals occurred because of loss of collars or death of some animals. Herd locations were derived by pooling radiotelemetry data for individuals from each herd whose tracking periods had little overlap (three individuals for herd C and four for herd D). Thus, I obtained location data for herd C for 7 months (16 April 1992–31 October 1992; 38 locations) and herd D for 6 months (12 April 1992–18 September 1992; 43 locations). Herd C ranged over 10.1 km^2 and herd D over 11.7 km ^{2} (Fragoso, 1994, in press). These two herds shared a home range border but did not overlap in their use of the study area. Ranges of both herds of collared peccaries were subsumed within those of the herds of white-lipped peccaries (Fragoso, in press). The two herds of collared peccaries often splintered into four subgroups (Fragoso, 1994). Those were the only two herds regularly using the part of the study area containing the system of trails.

Use of vegetation types and plant communities by peccaries.—White-lipped peccaries did not use vegetation types in proportion to their availability, using palm-wetlands and savanna-wetlands more frequently than expected, riverine vegetation as expected, and terra-firme forest and shrub-thickets less than expected ($\chi^2 = 85.12$, *d.f.* = 4, $P < 0.005$; Table 2). Habitat use varied ($\chi^2 = 63.76$, *d.f.* = 3, $P < 0.001$) between herds of white-lipped peccaries during the wet-flood season. Herd B spent more time in palm-wetlands and terra-firme forest than herd A, but herd A spent more time in riverine vegetation and savanna-wetlands. The area used exclusively by herd A consisted of a 9 km^2 savanna-wetland separating the terra-firme forest from riverine vegetation. Herd B remained almost exclusively within the terra-firme forest, using palm-wetlands embedded within the forest rather than those within the savanna-wetlands, although their range bordered the 9 km^2 savanna-wetland used by herd A (Table 2).

Herd A nearly doubled the size of its home range from 12.5 to 21.7 km^2 during the wet-flood season. That increase was an expansion outward along the entire boundary of the range during the dry season (Fragoso, 1998*a*) and did not reflect a change in use of habitats between seasons ($\chi^2 = 5.38$, *d.f.* = 3, $P > 0.4$).

TABLE 2.—*Number of locations of white-lipped and collared peccary herds by vegetation type, plant community, and season on eastern Maracá Island Ecological Reserve, Brazil.*

Vegetation type	Plant communities within vegetation type	Number of telemetry locations				
		White-lipped peccaries			Collared peccaries	
		Dry season	Wet-flood season		Seasons combined	
		Herd A	Herd A	Herd B	Herd C	Herd D
Riverine	Low *Maximiliana* palm forest	0	1	1	1	7
	Low shrub	0	4	2	0	3
	Low forest	0	6	0	0	0
	Mid to high forest	4	0	0	1	0
Palm-wetland	*Mauritia* wetland	5	9	15	1	2
	Mauritia wetland–High forest edge	0	1	3	4	3
Terra-firme forest	High forest	6	7	16	21	17
	High forest with *Maximiliana* palms	1	1	3	3	2
	High and low forest	0	1	1	4	4
	Low forest	0	1	2	3	4
Savanna-wetland	Savanna-ponds and seasonal wetlands	12	7	1	0	0
	Forest patch in savanna-wetlands	0	0	1	0	0
Shrub-thicket	Wet	0	0	1	0	1
	Bactris palm	0	1	0	0	0
Total locations		28	39	46	38	43

Collared peccaries were found almost exclusively within plant communities in the terra-firme high forest (Table 2). Statistically, they used terra-firme forest, palm-wetlands, and riverine vegetation as expected based on availability ($\chi^2 = 8.23$, *d.f.* = 4, $P > 0.05$; Table 2). They did not use the savanna-wetlands and rarely entered the shrub-thicket habitats. Thus, comparison of use of habitats between the two herds was restricted to terra-firme forest, palm-wetlands, and riverine vegetation, which were used in similar proportions by the two herds ($\chi^2 = 5.41$, *d.f.* = 2, $P > 0.05$).

The two species varied in their use of the palm-wetlands, terra-firme forest, riverine vegetation, and savanna-wetlands ($\chi^2 = 63.76$, *d.f.* = 3, $P < 0.001$). Seventy-seven percent ($n = 33$) of all observations of peccaries within palm-wetlands were of white-lipped peccaries (Table 2). Similarly, white-lipped peccaries accounted for 100% ($n = 21$) and 62% ($n = 18$) of the observations in savanna-wetlands and riverine vegetation, respectively. In contrast, collared peccaries occurred more frequently in terra-firme forests (60% of observations; $n = 58$).

Diets.—Diets of white-lipped peccaries varied with habitat and season (Table 3). From January to March, herd A foraged almost exclusively at a pond within a savanna-wetland, where they ate eels and other fish exposed as the pond dried. They also occasionally foraged in palm-wetlands, where they ate the endocarp contents of palm seeds of *Maximiliana maripa* defecated by tapirs and uprooted and ate the endosperm attached to seedlings of *M. flexuosa*. They only ate ripe fruit pulp of *M. flexuosa* and full-sized immature seeds of *M. flexuosa*, both of which are soft. In terra-firme forests, they rooted around adult *M.*

TABLE 3.—*Plants and animals eaten by white-lipped and collared peccaries by habitat and season.*

Item	Part eaten	Vegetation type and or plant community	Season	Eaten by white-lipped peccaries	Eaten by collared peccaries
Plants					
Maximiliana maripa	Ripe fruit pulp	Terra-firme forest, *Maximiliana* clumps	Wet-flood	Yes	Yes
Maximiliana maripa	Seeds in seed bank	Terra-firme, palm-wetlands	Dry	Yes	No
Maximiliana maripa	Seeds attached to seedlings	Terra-firme forest	Dry and flood-wet	Yes	Yes
Mauritia flexuosa	Very ripe pulp	Palm-wetlands	Dry	Yes	Yes
Mauritia flexuosa	Soft, almost-mature seeds	Palm-wetlands	Dry	Yes	No
Mauritia flexuosa	Seeds attached to seedlings	Palm-wetlands	Dry	Yes	Yes
Pouteria venosa	Ripe pulp	Terra-firme forest	Wet	Yes	Yes
Pouteria venosa	Seeds (mature and green)	Terra-firme forest	Wet	Yes	Yes
Ilex jenmani	Ripe fruit	Terra-firme forest	Wet	Yes	?
Swartzia	Mature & green seeds, seeds joined to seedlings	Terra-firme forest	Wet	?	Yes
Enterolobium cyclocarpum	Seeds	Terra-firme forest	Dry	?	Yes
Psidium	Entire fruit	Riverine low	Dry	No	Yes
Bactris maraja	Seed	Bactris thicket	Dry	?	Yes
Pradosia surinamensis	Seeds	Terra-firme forest	Dry and Wet	Yes	Yes
Poaceae	Root bases	Shrub-thicket	Dry and Wet	Yes	No
Animals					
Snake	Entire body	Terra-firme forest	Wet	Yes	?
Eels	Entire body	Savanna ponds	Dry	Yes	No
Other fish	Entire body	Savanna ponds	Dry	Yes	No

TABLE 4.—*A model of scale perception of landscape units by white-lipped and collared peccaries. The model incorporates movement of both species and the vegetation pattern evident at those spatial scales. Because herds of the two species moved at different spatial scales (i.e., had different home-range sizes), the overall area considered in the model remains constant but vegetation categories were categorized according to how they were used by each species.*

Spatial scale (km^2)	Landscape-level category	Characteristic vegetation	Species-specific landscape category (spatial units)	
			White-lipped peccary	Collared peccary
1,100.00	Landscape	Transitional forest	Tract	—[a]
109.00	Mosaic	Mosaic of vegetation types	Home range	Tract
10.00	Vegetation type	Terra-firme forest	Habitat patch	Home range
1.00	Plant community	Terra-firme forest with *Maximiliana*	Food patch	Habitat patch
0.01	Individual tree or item	*Maximiliana* tree	—[a]	Food patch

[a] No equivalent category.

maripa ≥ 2 months after fruit-fall in search of seeds. They also ate the base of germinated seedlings of *M. maripa* and seeds buried in and around patches of *M. maripa*. Seeds of *M. maripa* remain in the seed bank for >1 year before germinating (J. Fragoso, in litt.) and were thus used year round. In June, white-lipped peccaries were in terra-firme forest, where they fed extensively on seeds of *Pouteria venosa*, ripe fruit pulp of *M. maripa* (they did not eat the new seeds), and fruits of *Ilex jenmani*.

Collared peccaries ate most of the foods consumed by white-lipped peccaries, except fish and seeds of *M. maripa* and *M. flexuosa* (Table 3). Like white-lipped peccaries, collared peccaries uprooted seedlings of both species of palm and ate the attached root and attached endosperm of *M. flexuosa*. They also consumed the pulp of ripe fruit of both species. Collared peccaries also ate seeds of *P. venosa, Pradosia surinamensis*, and *Enterolobium cyclocarpum*.

DISCUSSION

Collared peccaries and white-lipped peccaries on Maracá shared most plant items in their diet (Table 3). As first described by Kiltie (1982), there was some separation of plant diet based on the hardness of at least one species of palm seeds. White lipped peccaries, but not collared peccaries, could crack open endocarps of *M. maripa*. The primary distinction between the diets of the two species, however, was the more intensive use of wetland-associated foods by white-lipped peccaries than collared peccaries: fish, seeds in latrines of tapirs, and soft, full-sized, immature seeds of *M. flexuosa*. This suggests that separation by habitat or vegetation type may play a significant role in resource partitioning by the two species.

Differences in habitat use between collared peccaries and white-lipped peccaries appear to be independent of herd size (i.e., even a large herd of 34 collared peccaries did not establish a territory in savanna-wetland) and suggest that the two species perceive their habitats at different scales. To explore this hypothesis, I created a model to compare relative sizes of spatial units used by the two species on Maracá (Table 4). This model incorporates the movement of both species and the vegetation pattern evident at those spatial scales. The hierarchically ordered landscape-level categories, from largest to smallest, are: "landscape" (all of Maracá Island and the transition forest that covers it, here arbitrarily defined as an area that could support 10 white-lipped peccary herds), "mosaic" (an aggregation of different vegetation types), "vegetation type" (a vegetation grouping dominated by one or a few key physical characters or plant species, and easily identified from the air), "plant community" (dominated by one or few plant species, and easily identified from the air), and "individual tree or item" (area where a herd stopped to feed, its extent estimated from the area rooted during a single feeding bout). Because herds of the two species moved at different spatial scales (i.e. had different home range sizes), the overall area considered in the model remained constant, but categories describing areas used for certain behavioral or ecological functions were scaled to use by each species. In other words, the size of equivalent spatial units varies with species.

At the largest spatial unit (tract, or area that could support 10 home ranges of the focal species) for white-lipped peccaries (Table 4), dominant vegetation is categorized as transition forest (Milliken and Ratter, 1998). Vegetation at the home-range level for a herd of white-lipped peccaries can be categorized as a mosaic of vegetation types. The area occupied by the home range of a herd of white-lipped peccaries potentially could support 10 herds of collared peccaries and thus can be considered a tract for collared peccaries. Similarly, a habitat patch for a herd of white-lipped peccaries, such as a savanna-wetland or terra-firme forest, equals the area of the home range of a herd of collared peccaries. A food patch for a herd of white-lipped peccaries consists of an entire plant community, such as high (tall trees)-terra-firme forest dominated by *M. maripa* palms and is equivalent in size to a habitat patch for a herd of collared peccaries, within which they identify several food patches. The areal extent of a food patch for a herd of collared peccaries lies below the scale potentially recognized by a herd of white lipped peccaries (Table 4).

An implication of the divergent spatial scales for collared and white-lipped peccaries is that collared peccaries perceive their habitats at a finer grain size than what I used to describe the vegetational types. White-lipped and collared peccaries coexisting in the same area thus appear to perceive and react to habitats or resources at different spatial scales (cf. Wiens, 1990). Movements and home ranges of herds of white-lipped peccaries appear to be based at the mosaic scale (109 km^2), whereas herds of collared peccaries may be responding to smaller-scale plant communities (~ 1 km^2). Evidence for a smaller-scale mosaic of plant communities comes from studies that show that individual plant species are distributed in an aggregate fashion within terra-firme forest, both at Maracá (Fragoso, 1997*a*: Milliken and Ratter, 1989; Nunes, 1995) and other tropical sites (Tuomisto et al., 1995).

The two herds of white-lipped peccaries differed in their use of the habitat mosaic although both had access to the same area. White-lipped peccaries from different herds may differ in what they accept as suitable or necessary habitat, or perhaps many vegetation types are suitable for white-lipped peccaries but not all are necessary. In contrast, the two herds of collared peccaries did not differ in their use of the mosaic. However, detecting their "habitat-patch" scale probably would require an analysis at the level of the plant community.

On Maracá, white-lipped peccaries used palm-wetlands, riverine vegetation, and savanna-wetlands more often than collared peccaries; collared peccaries used terra-firme forest more often. Two obvious differences between terra-firme forest and all the other vegetation types are that terra-firme forest never floods and it has a more constant availability of seeds and fruits due to its high diversity of tree species. Other vegetation types are characterized by high densities of only a few tree species: *M. maripa* palms and *Spondias mombin* in the riverine vegetation and *M. flexuosa* palms in the palm-wetlands. Fruits, seeds, seedlings, and seeds in tapir feces are seasonally, but not constantly, available at high densities in these vegetation types. It may be impossible for collared peccaries, with their small home ranges, to defend seasonal habitats where they cannot remain year-round because of flooding or lack of food.

A suite of interrelated characteristics, opposite in their expression in white-lipped and collared peccaries, appear to have diverged in the two species over evolutionary time. Collared peccaries have a smaller body size, escape predators by hiding in logs and holes, have a small home range, and defend their home range, which is probably too small to provide food for additional herds of collared peccaries (Fragoso, 1994). During times of food scarcity, they split into subgroups to use smaller food patches (Green and Grant, 1984; Oldenburg et al., 1985; Robinson and Eisenberg, 1985). White-lipped peccaries, whose large body and herd size allows them to deter predators (Fragoso, 1994; Sowls, 1984) or move out of the predator's home range (Fragoso, 1994), require large food patches to support large herds but are able to move long distances to seasonal habitats that provide temporarily abundant resources (Fragoso, 1994). They cannot defend such a large area, and splintering into subgroups would render them vulnerable to predation (Fragoso, 1994; Kiltie and Terborgh, 1983).

Greater mobility of white-lipped peccaries at first suggests flexibility, but it becomes a limitation if one considers that they require a mosaic of habitats with seasonally abundant food. Because modern humans and white-lipped peccaries perceive the landscape and act upon it at about the same scale, such mosaics are altered easily by anthropogenic factors: savannas converted to cattle pasture, forests to pasture or agriculture, wetlands to rice plantations, and palm-wetlands to fish ponds. More than having large spatial needs, white-lipped peccaries may require large undisturbed areas because the seasonal mosaic covers a large area. Large expanses of homogeneous landscape may not provide the year-round availability of foods required for population persistence. This becomes an important consideration in the design of protected areas. Neotropical forests are a mosaic of vegetation patches (Tuomisto et al., 1995). This characteristic may have allowed evolution of large herd size in the white-lipped peccary, an unusual trait for a large mammal in forested habitats.

Conversely, collared peccaries may better tolerate habitat disturbance by having a small herd size, a fine-grained view of habitats, small area requirements, and subgrouping behavior (Bellantoni and Krausman, 1993; McCoy et al., 1990; Suarez, 1993; Taber et al., 1994). Although a variety of factors are involved in susceptibility of white-lipped peccaries to extinction, including introduced diseases and overhunting (Fragoso, 1997*b*, 1998*a*, 1998*b*), loss of a large-scale habitat mosaic could be one contributing factor.

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LITERATURE CITED

ACKERMAN, B., F. LEBAN, M. SAMUEL, AND E. GARTON. 1990. User's manual for program home range. Second Ed. Idaho Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow.

BARRETO, G. R., AND O. E. HERNANDEZ. 1988. Aspectos bioecológicos de los Báquiros (*Tayassu tajacu* y *T. pecari*) en el Estado Cojedes: Estudio comparativo. B.S. thesis, Universidad Central de Venezuela, Caracas, Venezuela.

BELLANTONI, E. S., AND P. R. KRAUSMAN. 1993. Habitat use by collared peccaries in an urban environment. The Southwestern Naturalist, 38:345–351.

BODMER, R. E. 1989. Frugivory in Amazonian ungulates. Ph.D. dissertation, University of Cambridge, Cambridge, United Kingdom.

———. 1990. Responses of ungulates to seasonal inundations in the Amazon floodplain. Journal of Tropical Ecology, 6:191–201.

Castellanos, H. G. 1983. Aspectos de la organización social del báquiro de collar, *Tayassu tajacu* L., en el Estado Guarico-Venezuela. Acta Biologica Venezolana, 11:127–143.

Eisenberg, J. F. 1989. Mammals of the Neotropics: the northern Neotropics. The University of Chicago Press, Chicago, Illinois.

Fragoso, J. M. V. 1994. Large mammals and the community dynamics of an Amazonian rain forest. Ph.D. dissertation, University of Florida, Gainesville.

———. 1997*a*. Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. The Journal of Ecology, 85:519–529.

———. 1997*b*. Desapariciones locales del baquiro labiado (*Tayassu pecari*) en la Amazonia: migracion, sobre-cosecha, o epidemia? Pp. 309–312, *in* Manejo de Fauna Silvestre en la Amazonía (T.G. Fang, R.E. Bodmer, R. Aquino, and M.H. Valqui, eds.). United Nations Development Program/Global Environment Facility, Washington D.C. and University of Florida, Gainesville.

———. 1998*a*. Home range and movement patterns of white-lipped peccary (*Tayassu pecari*) herds in the northern Brazilian Amazon. Biotropica, 30:458–469.

———. 1998*b*. White-lipped peccaries and palms on the Ilha de Maracá. Pp. 151–163, *in* Maracá: the biodiversity and environment of an Amazonian rainforest (W. Milliken and J. Ratter, eds.). John Wiley & Sons Ltd., Chichester, United Kingdom.

———. In press. Why are collared peccary home ranges larger and population densities lower in the Amazon rain forest than elsewhere? Journal of Zoology (London).

Green, W. E., and W. E. Grant. 1984. Variability of observed group sizes within collared peccary herds. The Journal of Wildlife Management, 48:244–248.

Holling, C. S. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. Ecological Monographs, 62:447–502.

Kiltie, R. A. 1981. The significance of interlocking canines in rain forest peccaries (Tayassuidae). Journal of Mammalogy, 62:459–469.

———. 1982. Bite force as a basis for niche differentiation between rainforest peccaries (*Tayassu tajacu* and *T. pecari*). Biotropica, 14:188–195.

Kiltie, R. A., and J. Terborgh. 1983. Observations on the behavior of rain forest peccaries in Peru: why do white-lipped peccaries form herds? Zeitschrift für Tierpsychologie, 62:241–255.

Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos, 59:253–260.

Leopold, A. S. 1959. Wildlife of Mexico: the game birds and mammals. University of California Press, Los Angeles.

Mayer, J. J., and P. N. Brandt. 1982. Identity, distribution and natural history of the peccaries, Tayassuidae. Pp. 433–455, *in* Mammalian biology in South America (M.A. Mares and H.H. Genoways, eds.). Special publication series, Pymatuning Laboratory of Ecology, University of Pittsburgh, Pennsylvania, 6:1–539.

Mayer, J. J., and R. M. Wetzel. 1987. Tayassu pecari. Mammalian Species, 293:1–7.

McCoy, M. B., C. S. Vaughn, M. A. Rodriguez, and D. Kitchen. 1990. Seasonal movement, home range, activity and diet of collared peccaries (*Tayassu tajacu*) in Costa Rican dry forest. Vida Silvestre Neotropical, 2:6–20.

Milliken, W. M, and J. A. Ratter. 1989. The vegetation of the Ilha de Maraca: first report of the vegetation survey of the Maraca Rainforest Project. Royal Botanical Garden, Edinburgh, United Kingdom.

———. 1998. Maracá: the Biodiversity and environment of an Amazonian rainforest. John Wiley & Sons Ltd, Chichester, United Kingdom.

Moskovits, D. K. 1985. The behavior and ecology of the two Amazonian tortoises, *Geochelone carbonaria* and *Geochelone denticulata* in northwestern Brazil. Ph.D. dissertation, The University of Chicago, Chicago, Illinois.

Nunes, A. 1995. Foraging and ranging patterns in white-bellied spider monkeys. Folia Primatologia, 65:85–99.

Oldenburg, P. W., P. J. Ettestad, W. E. Grant, and E. Davis. 1985. Structure of collared peccary herds in south Texas: spatial and temporal dispersion of herd members. Journal of Mammalogy, 66:764–770.

Redford, K. H., and J. F. Eisenberg. 1992. Mammals of the Neotropics: the southern cone. The Chicago University Press, Chicago, Illinois, 2:1–430.

Robinson, J. G., and J. Eisenberg. 1985. Group size and foraging habits of the collared peccary (*Tayassu tajacu*). Journal of Mammalogy, 66:153–155.

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies: landscape ecology can enhance traditional foraging theory. Bioscience, 37:789–799.

Sowls, L. K. 1984. The peccaries. University of Arizona Press, Tucson.

Suarez, I. M. T. 1993. Ecologia de los grupos de sainos (*Tayassu tajacu*) y daños que ocasionan en los cultivos vecinos a la Estación Biológica La Selva. M.S. thesis, Universidad Nacional de Costa Rica, San Jose, Costa Rica.

Taber, A. B., C. P. Doncaster, N. N. Neris, and F. Colman. 1994. Ranging behavior and activity patterns of two sympatric peccaries, *Catagonus wagneri* and *Tayassu tajacu*, in the Paraguayan Chaco. Mammalia, 58:61–71.

Tuomisto, H., K. Ruololainen, R. Kalliola, A. Linna, W. Danjoy, and Z. Rodriguez. 1995. Dissecting Amazonian Biodiversity. Science, 269:63–66.

Wiens, J. A. 1990. On the use of "grain size" in ecology. Functional Ecology, 4:720–737.

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