

Area use by white-lipped and collared peccaries (*Tayassu pecari* and *Tayassu tajacu*) in a tropical forest fragment

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Abstract

We present the first long-term radio telemetry study of area use by white-lipped and collared peccaries in a tropical forest fragment. Population densities of both species in a 2178-ha fragment of semideciduous Atlantic forest in southeastern Brazil were similar to estimates from another regional fragment with 16 times the area. The population of 150 (± 52) white-lipped peccaries was divided among 3–4 subherds. We observed a high frequency of switching of individuals among subherds and documented periodic subherd fusion. Seven to 22 collared peccary herds (mean herd size, 9) persisted in the main forest fragment. Average home range size for the white-lipped peccaries was 1871 ha (90% HM). This was similar to the few reliable estimates available from continuous tropical forests. Despite supposed area restrictions, white-lipped peccaries maintained distinct seasonal ranges with a minimum of overlap. Within seasons, subherds overlapped spatially, but were separated temporally. Average home range sizes of two radio-tracked collared peccary herds were 305 and 123 ha. Home range boundaries and seasonal ranges of collared peccary herds shifted minimally, and herd subgrouping was short-lived. Spatial overlap between the two peccary species varied seasonally with white-lipped herd movements. We discuss future research needs and management actions for conservation of these species in fragmented landscapes.

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1. Introduction

The Atlantic forest of Brazil, which historically covered much of the country's eastern coast and extended inland to the plateau regions of states like Minas Gerais and São Paulo (Por, 1992; Ranta et al., 1998), is considered one of the most endangered tropical forest ecosystems on earth (Mittermeier et al., 1982). Less than 7% of the original 1,000,000 km² remains, and much of that persists as forest fragments within an agriculturally dominated landscape (Ranta et al., 1998). As early as the 16th century, the Atlantic forest region was exploited by European colonists. Current land uses include agriculture, exotic timber production, industry, and urbanization. Only a small percentage of the extant forest is under federal or state jurisdiction leaving much of the

area open to further destruction. This study was conducted on the inland plateau, the *Planalto*, of São Paulo state, which was historically covered by seasonal, semi-deciduous tropical forest (Chiarini and Souza-Coelho, 1969). Less than 2% of the *Planalto* forest survives (approximately 280,000 ha), and only 26% of the remaining area is officially protected (Viana and Tabanez, 1996; Cullen, 1997; Ditt et al., 1999).

Fragmentation of tropical forests has dramatically disturbed the natural dynamics of these systems, resulting in the extinction of an unknown number of species, and altering the ecology of the surviving species (Lovejoy et al., 1986; Schelhas and Greenberg, 1996; Laurance and Bierregaard, 1997). For mammalian frugivores, the consequences of fragmentation can include reduction in range size, loss of habitat diversity and availability of preferred fruits, alteration in size and structure of social groups, and intensification of interactions between species (Terborgh, 1986, 1992). In response to these pressures, some frugivorous mammals emigrate from forest fragments, especially during

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periods of fruit scarcity (Lovejoy et al., 1986; Terborgh, 1986; Rylands and Keuroghlian, 1988). Other less mobile frugivores may be forced to adjust their ranging and foraging patterns, while continuing to inhabit the fragments (Bodmer, 1990, 1991). The loss of habitat diversity in small forest fragments affects fruit diversity as well and may intensify naturally occurring periods of fruit scarcity (Terborgh, 1986).

Several important studies have been conducted on the response of mammals to fragmentation of tropical forest habitats (e.g., Glanz et al., 1982; Janzen, 1986; Lovejoy et al., 1986; Laurance, 1990, 1991, 1994). However, few studies of this sort have taken place in the Atlantic forest (Fonseca and Robinson, 1990; Chiarello, 1999; Cullen et al., 2000). The study by Cullen et al. (2000), investigating mammalian communities of forest fragments on the inland plateau of São Paulo State, suggested that hunting pressure, a factor closely associated with habitat fragmentation, has been the principal cause for local extinctions of white-lipped peccaries (*Tayassu pecari*) in the region. However, populations of collared peccaries (*Tayassu tajacu*) appeared to be less affected by hunting and other fragmentation-related factors. Both species are important frugivores in Neotropical forests and play key roles as seed predators and dispersers (Kiltie, 1981; Bodmer, 1991). In addition, white-lipped peccaries are the only rain forest ungulates in the Neotropics that form large herds, so local extinctions could have dramatic impacts on forest biodiversity (Painter, 1998).

Observations of white-lipped peccaries in continuous tracts of forest have shown that they are wide-ranging and that their movements may be a response to changes in the availability of abundant fruit patches (Kiltie and Terborgh, 1983; Bodmer, 1990; Mendez, 1970; Sowls, 1984). Some investigators have described their movements as migratory (Bodmer, 1990; Mendez, 1970), while others believe they are nomadic within a large home range (Kiltie and Terborgh, 1983; Barreto and Hernández, 1988). In either case, the consensus has been that large areas are required for survival. Kiltie and Terborgh (1983) estimated home range areas of 6000–20,000 ha for white-lipped peccaries in the Peruvian Amazon, based on encounter rates of unmarked herds. Fragoso (1998) reported a maximum home range of 10,960 ha (100% minimum convex polygon) for an individual that was radio tracked for 5 months (46 locations) in the Brazilian Amazon. However, 4 individuals from a second group that he tracked for 3–13 months (33–67 locations), had an average home range area of 1628 ha. Home ranges closer to the latter estimate have also been reported by Sáenz and Carrillo (1999) and Carrillo et al. (2002) during their studies of white-lipped peccary herds in Corcovado, Costa Rica. Sáenz and Carrillo (1999) observed a mean home range size of 2145 ha, and Carrillo et al. (2002) reported annual herd ranges of 3200–3780 ha. These observations cast doubt

on the idea that vast home ranges (i.e., >10,000 ha) are characteristic of white-lipped populations in relatively undisturbed continuous forests.

In comparison to the white-lipped peccaries, collared peccaries use much smaller areas (approximately 50–700 ha) and show relatively minor shifts in range use over time (McCoy et al., 1990; Taber et al., 1994; Judas and Henry, 1999). Studies of collared peccaries in the tropics have shown that home range estimates from different regions are quite variable, and that they inhabit a wide variety of habitat types (Castellanos, 1983; McCoy et al., 1990; Suarez, 1993; Taber et al., 1994; Fragoso, 1994; Judas and Henry, 1999).

Using radio telemetry, we conducted a five-year study of white-lipped and collared peccary populations coexisting in a 2178-ha Atlantic forest fragment on the inland plateau region of São Paulo state. We were interested in discovering how the species survived in a restricted range with minimal potential for emigration or immigration. In addition, collared peccaries appear to tolerate a wider range of human-altered environments (Bellantoni and Krausman, 1993), so we wanted to compare the status of the two species in a forest fragment situation. Here, we present observations on area use and compare our results with data available from continuous forests. Our specific objectives were to;

- (1) document population densities, number of herds, and herd sizes,
- (2) document herd dynamics (i.e., subherd formation, aggregation of herds, and intergroup switching),
- (3) estimate home ranges, seasonal ranges, and core areas of use for individuals and herds,
- (4) measure the spatial overlap of ranges for each species within and between seasons, and
- (5) measure the spatial overlap of white-lipped and collared peccary herds.

We discuss the management implications of our results and suggest research priorities and conservation actions for peccaries in fragmented landscapes.

2. Methods

2.1. Study site

The study site is located on the “Planalto” of São Paulo state in the municípios (counties) of Gália and Alvinlândia (22°30'S and 49°45'W), approximately 400 km west of São Paulo city (Fig. 1). The principal forest fragment at the site is the 2178-ha state reserve, Caetetus Ecological Station. The area surrounding Caetetus was deforested in the 1920s for coffee production and pasture, but small (50–200 ha) satellite forest fragments and areas of secondary forest persist in the landscape surrounding the station. Until 1977, when Caetetus was acquired by the state Forestry Institute of São Paulo, the

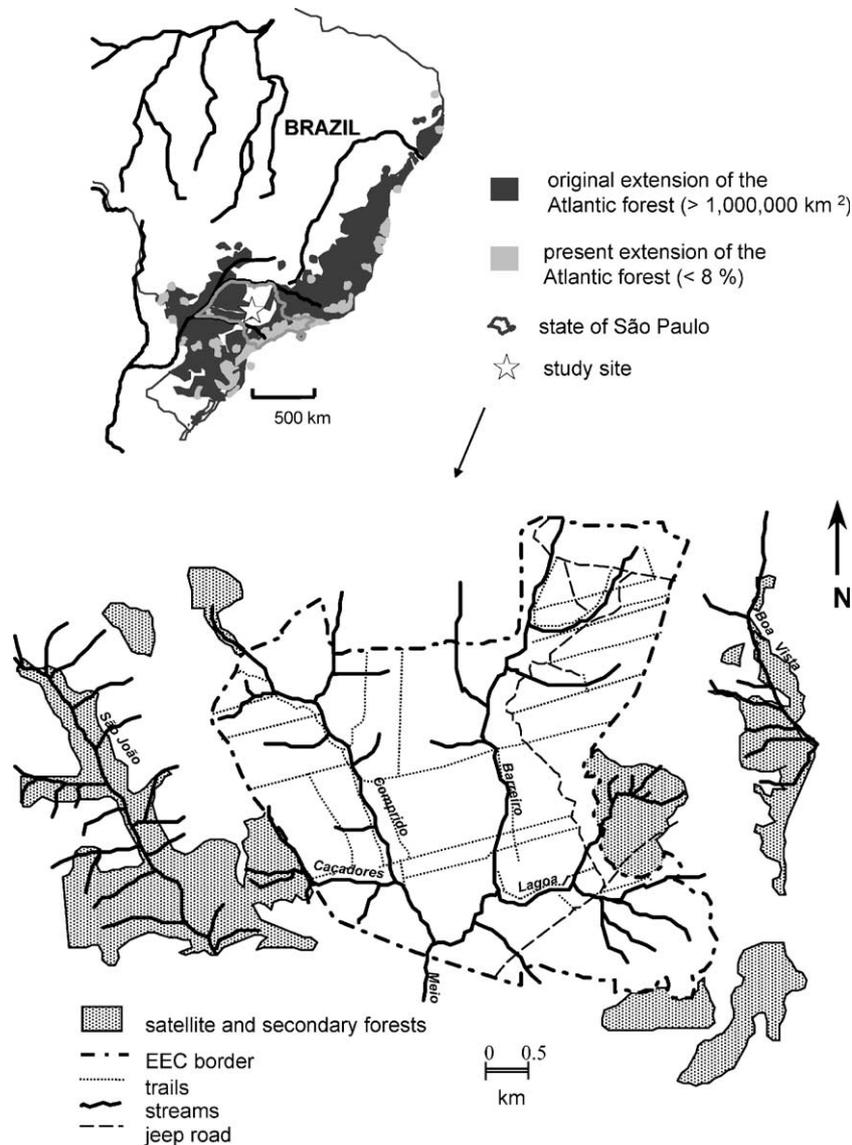


Fig. 1. Study site showing the fragmented landscape surrounding Caetetus Ecological Station (EEC), São Paulo, Brazil, and the original and present extension of the Atlantic forest in Brazil (adapted from Corrêa, 1997). The streams, trails (foot paths), and the station's border are also shown for the study site.

forest was a privately owned wildlife reserve established by a local coffee farmer.

The vegetation at Caetetus is classified as tropical, semideciduous, mesophytic, broadleaf forest, which places it in the general category of tropical transitional, or seasonal, forests (Eiten, 1974; Serra-Filho et al., 1975; Torres, 1983). The distinct dry season lasts 5–6 months, from April or May through September or October. The average rainfall is 1200–1600 mm, most of which falls between October and March, and average monthly temperatures range from 16 °C in the dry season to 25 °C in the wet (Passos, 1997; M.R. Barbosa, unpubl. data).

Illegal hunting of wildlife occurs at Caetetus, but is not prevalent. Despite its isolation (e.g., the nearest

population of white-lipped peccaries is approximately 300 km), the non-volant mammalian fauna of Caetetus is largely intact and typical of “*Planalto*” forests (Cullen, 1997).

2.2. Herd sizes, number of herds, and density estimates

Herd size estimates were obtained from direct counts of animals. Visibility was restricted in the forest (<20 m), so counts were limited to occasions when most of a herd or subherd (as defined for white-lipped peccaries in Results) was visible, e.g., when crossing a road. For collared peccaries, we estimated the number of herds at Caetetus by dividing the station's area by the minimum and maximum home range areas (described below)

obtained from radio-collared individuals. The quotients, i.e., estimates of the minimum and maximum number of herds, were multiplied by the average herd size to obtain estimates of the minimum and maximum number of collared peccaries at Caetetus. For white-lipped peccaries, we determined the number of subherds by simultaneously tracking and observing the movements of radio-collared and unmarked animals (see Results). The minimum and maximum subherd sizes were multiplied by the number of subherds to obtain minimum and maximum estimates of the number of white-lipped peccary species by dividing the number of animals (minima and maxima) by the area of Caetetus Ecological Station. We compared these densities with results from line transect censuses conducted during the study period by Cullen (1997).

2.3. Capture, radio-collaring, and handling of animals

The capture process was facilitated by setting up temporary baiting stations in areas that the peccaries used frequently. Box traps and wire panel traps (120 l × 90 h × 60 w cm) were placed at these stations and baited with salt, corn, “mandioca” (*Manihot* sp.), and squash. When a peccary was captured, we estimated its weight and immobilized it with ketamine (20 mg/kg). White-lipped peccaries were fitted with the MOD 500 model radio collar (Telonics Inc., total weight of battery and collar = 570 g), and collared peccaries with the HLPM-31100 model radio collar (Wildlife Materials, weight = 340 g). We also determined the animal’s sex, placed it in a rough age class based on tooth wear (Sowls, 1984; Bodmer et al., 1996), and attached an ear tag.

2.4. Radio-telemetry and home range dynamics

From 1994 to 1999, we monitored the radio-collared animals using standard radio tracking techniques (Kenward, 1987). Signals were monitored with a Wildlife Materials TRX 1000S receiver and a hand-held directional antenna. For each fix, we took 2–3 bearings over a 3–5 min time span. Receiver locations were at least 100 meters apart. We monitored the positions of radio-collared peccaries for a two-week period each month. Because peccaries are socially cohesive, tracking individuals allowed us to monitor the movements of their respective herds or subherds (Byers and Bekoff, 1981). We evaluated fix accuracy with field trials that allowed us to compare known radio collar positions with those determined by triangulation. The mean (\pm SD) of the difference between true and triangulated positions was 74 ± 14 m. We tested for autocorrelation among fixes using procedures described by Swihart and Slade (1985). Time intervals required for fixes to be in-

dependent were 80 min for white-lipped and 100 min for collared peccaries. Fixes collected over shorter time intervals were excluded from further analyses.

For home range analyses, we only included radio-collared individuals with asymptotic estimates of range area (Odum and Kuenzler, 1955). Using Ranges V software, we determined the number of fixes required to reach a range area asymptote by randomly selecting fixes obtained for a particular individual, and then plotting range area versus the number of fixes (Kenward and Hodder, 1996). This method is recommended for discontinuous radio tracking data (Harris et al., 1990).

We calculated annual home, seasonal (wet and dry), and core area ranges for individuals and herds using Ranges V software (Kenward and Hodder, 1996). The ranges were estimated using the minimum-convex polygon (MCP) (Mohr, 1947), harmonic mean (HM) (Dixon and Chapman, 1980), and kernel methods (KM) (Worton, 1989). The 100% MCP estimates were used to facilitate comparisons between studies and regions. Ninety-five percent “peeled” MCP estimates, which eliminate some of the outliers associated with 100% MCP estimates, were calculated using harmonic mean fixes (rather than arithmetic means) as range centers (Kenward and Hodder, 1996). We preferred the harmonic mean (HM) and kernel (KM) range analyses, because in addition to estimating range size, they revealed range use patterns. Based on our estimate of radio fix accuracy (above), we used 200×200 m (4 ha) grid cells for both methods. For the harmonic mean analysis, we centered fixes between grid intersections (Spencer and Barrett, 1984; Kenward and Hodder, 1996). For comparability with other studies (e.g., Judas and Henry, 1999), we performed fixed kernel analyses using the “optimal” or “reference” smoothing factor (Worton, 1989; Seaman and Powell, 1996).

Based on the recommendations of Seaman and Powell (1996), we also performed fixed kernel analyses using smoothing factors determined by least squares cross validation (LSCV). Because the resulting smoothing factors varied among individual animals, range area comparisons were difficult to interpret. To resolve this, we calculated a median LSCV-determined smoothing factor for each species and reperformed the fixed kernel analyses (Seaman and Powell, 1996; R. E. Kenward, personal communication). With the Ranges V software, the LSCV-determined smoothing factors are expressed as multiples of the optimal smoothing factor. For white-lipped peccaries, the median was $0.2 \times$ the optimal smoothing factor ($n = 5$ individuals), and for collared peccaries, it was $0.4 \times$ the optimal ($n = 4$ individuals).

Because of distinct seasonal differences in range use (see results) and the complexity of range shapes within forest fragments, we calculated home ranges for individuals and herds by summing wet and dry season

ranges and then subtracting the area of overlap. The alternative method, i.e., using fixes from both seasons simultaneously, overestimated home ranges by including large areas that were never used by the peccaries. Fixes from more than one year, if available, were included in the estimates. We compared home ranges between species and between collared peccary herds with independent *t*-tests (Systat, version 7.0, 1997). To compare ranges between seasons and species, we used a single-factor repeated measures ANOVA with season (wet and dry) as the repeated measure and species as the factor. We used a similar repeated measures ANOVA to compare ranges between seasons (repeated measure) and collared peccary herds (factor). For the three analyses above, estimates were natural log transformed to meet the variance homogeneity assumption.

We attempted to determine core areas by locating inflection points on range utilization plots, e.g., home range area vs. harmonic mean isopleth value (Harris et al., 1990; Kenward and Hodder, 1996). However, the plots for both species often showed smooth curves without distinct inflection points. As discussed in the results, the fixed kernel isopleths, based on the median LSCV-determined smoothing factors, were effective for locating and estimating core areas and demonstrating the number of activity centers within ranges.

We used harmonic mean estimates for range overlap analyses, because they showed both the area and intensity of overlap. For each species, we estimated the degree of spatial overlap of individual ranges within and between seasons using Ranges V (Kenward and Hodder, 1996). The area of overlap was expressed in hectares and as a percentage of home range. To test whether seasonal overlap was different for white-lipped and collared peccaries, we compared species-specific regressions of between-season overlap percentages on HM isopleth percentages (Zar, 1996). Because variances were heterogeneous and the data sets included zeros, we natural log transformed the percents after adding one. Finally, we used the harmonic mean estimates of seasonal herd ranges to evaluate the degree of spatial overlap between the two peccary species.

3. Results

A total of 11 white-lipped and 8 collared peccaries were captured. Six of the white-lipped and 5 of the collared peccaries were fitted with radio collars, and the rest were ear-tagged according to sex.

3.1. White-lipped peccary subherds, subherd switching, and density estimates

One large herd of white-lipped peccaries, typically divided into 3–4 subherds, inhabited the study site. We were able to identify the number of different subherds by tracking different radio-collared individuals during the same monitoring period. On more than five occasions, we simultaneously (within a few hours) obtained signals from three different subherds in three well-separated (>500 m) locations and observed a fourth subherd without a radio-collared member. We defined these groups as subherds rather than herds, because we observed a high frequency of intergroup switching by radio-collared and ear-tagged animals. Four of the nine marked white-lipped peccaries (44%) switched subherds at least once during the monitoring period. One individual was a member of three different subherds during a 13-month period. It is likely that subherd switching was more frequent than reported here, because continuous monitoring was not possible.

We also did not use the terms “groups” or “subgroups” for the subherds, because the former usually refer to more transient aggregations that change on a daily or weekly time scale (Robinson and Eisenberg, 1985). Periods of stable subherd membership for monitored white-lipped peccaries ranged from 2 to 21 months. In addition, we documented short periods when subherds appeared to fuse into larger groups. For example, there was a period of three months when four of the radio-collared individuals, previously split between 2 subherds, were together in a single group. There was a mean of 41.7 individuals per subherd ($n = 10$ full subherd counts) (Table 1). In the mid-1970s, Sowls observed a similar number of individuals, i.e., 60, in the

Table 1

Herd sizes, number of herds (or subherds), and density estimates of white-lipped (WL) and collared peccaries (CP), using direct observations (means, minima, and maxima shown) and line-transect censuses (means and 95% confidence limits shown) at Caetetus Ecological Station, São Paulo, Brazil

Species	Direct observations (this study)			Line-transect censuses (Cullen, 1997)			
	Individuals/herd ^a mean (min–max)	Total no. of herds ^a at site (min–max)	Total no. of individuals at site mean (min–max)	Individuals/km ² mean (min–max)	Individuals/herd mean (min–max)	Total no. of individuals at site (\bar{x} mean 95% CL)	Individuals/km ² (\bar{x} mean 95% CL)
WL	41.7 (32.6–50.7)	3–4	150 (98–203)	6.9 (4.5–9.3)	37.5 (30.0–45.0)	127 (78–206)	6.3 (3.9–10.2)
CP	8.8 (7.2–10.5)	7–22	128 (62–194)	5.9 (2.8–8.9)	13.5 (4.0–15.0)	130 (74–226)	6.4 (3.7–11.2)

^a For the white-lipped peccaries, the heading, “herd”, refers to subherds.

Table 2

Home range, core area, and seasonal range estimates for: (a) white-lipped peccaries and (b) collared peccaries (individual animals and herds) at Caetetus Ecological Station, São Paulo, Brazil, using the minimum convex polygon (MCP), harmonic mean (HM), and Kernel (KM) methods

	No. months tracked	No. radio fixes	Home range estimates (ha) ^a				Core area estimates			Seasonal range estimates (ha)					
			100% MCP	95% MCP	90% HM	90% or 95% KM ^b	100% KM, LSCV ^c	% of home range ^d	No. activity centers	95% MCP		90% HM		90% or 95% KM ^b	
										Wet	Dry	Wet	Dry	Wet	Dry
(a) White-lipped peccary															
Catherine	18	298	2164	1945	1924	1837	935	51	5	1452	1047	1163	938	1303	718
Thelma	35	236	1902	1687	1832	1538	661	43	6	1025	1390	1347	914	984	824
Spencer	37	228	2691	2390	2416	2581	1325	51	5	1041	1753	1358	1304	1465	1341
Conde	34	86	1624	1493	1313	1839	626	34	7	953	1064	725	946	434	1206
Julho	28	40	843	781	607	602	117	19	8	622	241	385	243	431	228
Louise	3	38	206	171	89	83	40	48	3	171	81	83			
Mean ($n = 4$) ^e			2095	1879	1871	1949	887	45	6	1118	1314	1148	1025	1046	1022
SD			454	388	452	444	323	8	1	226	333	296	186	455	299
Herd Range ^f		888	2951	2374	2550	2254	1948	86	1	1398	1393	1774	1347	1561	1039
(b) Collared peccary															
Boris	3	17	36	30	37	50	13	26		30		37	50		
Jasper	9	166	348	321	356 ^g	357	330	93	1	202	215	206	389	171	255
Junior	5	132	269	253	255	296	252	85	1	245	208	245	138	282	196
Mean ($n = 2$) ^h			308	287	305	326	291	89	1	224	212	226	263	226	226
SD			56	48	72	43	55	5	0	31	5	27	177	79	42
Herd range	13	315	415	407	443	369	431	117	1	256	367	258	394	245	303
May	9	139	125	98	107	159	94	59	4	83	57	82	65	154	68
Vera	11	167	144	117	139	183	140	77	2	112	52	121	55	171	61
Mean ($n = 2$)			135	107	123	171	117	68	3	97	55	101	60	163	64
SD			13	14	22	16	33	13	1	21	3	29	7	12	5
Herd range		306	164	120	143	180	148	82	3	113	57	128	61	171	68

^a Home range estimates calculated as wet plus dry season ranges minus overlap.

^b Area of 90% isopleth (for white-lipped peccaries) and 95% isopleth (for collared peccaries) for the fixed kernel estimate, calculated with the “optimal” smoothing factor (Worton, 1989).

^c Core area shown as the area of 100% isopleth for the fixed kernel estimate, calculated with the median of the smoothing factors determined by least squares cross validation (LSCV), i.e., $0.2 \times$ “optimal” for white-lipped peccaries and $0.4 \times$ “optimal” for collared peccaries.

^d Core percents were calculated as the 100% KM (LSCV) estimate divided by the 90% KM estimates (for the white-lipped peccaries) times 100, and divided by the 95% km estimates (for the collared peccaries) times 100.

^e Means and standard deviations did not include Julho and Louise.

^f Herd range does not include Louise.

^g The 85% HM estimate was used for Jasper, because the 90% isopleth showed a “ballooning” effect (Harris et al., 1990).

^h Means and standard deviations did not include Boris.

group he was observing at Caetetus (Sowls, 1997). Assuming 3–4 subherds in the study region, minimum and maximum estimates of the number of white-lipped peccaries were 98 and 203 individuals, respectively. Based on numbers per area of the ecological station, our density estimates ranged from 4.5 to 9.3 individuals/km². The estimates presented by Cullen (1997), based on the repeat transect method (Emmons, 1984), were quite similar (Table 1). He reported a total population of 78–206 individuals and densities ranging from 3.9 to 10.2 individuals/km².

3.2. Collared peccary herds and density estimates

During the study, we captured collared peccaries from 2 different herds and observed direct and indirect evidence (i.e., sightings, tracks, diggings, hairs, and scat) of several other groups in the study region. Using the minimum and maximum home range areas calculated for radio-collared individuals (95% MCPs, Table 2b), and assuming no overlap among herds, we estimated that the station could potentially contain from 7 to 22 separate herds (Table 1). The mean herd size was 8.8 individuals ($n = 12$ full herd counts, Table 1). Therefore, the total number of collared peccaries inhabiting the station was estimated to be between 62 and 194 individuals, and the densities from 2.8 to 8.9 individuals/km². Cullen (1997) reported similar estimates, i.e., 74–226 total individuals and 3.7–11.2 individuals/km². We did not observe evidence of subgrouping for extended time periods, but it was common for 1–3 individuals to forage separately for several hours during the day.

3.3. Home range and core area estimates

A total of 926 independent radio fixes and sightings were documented for white-lipped peccaries and 621 for collared peccaries during monthly radio tracking periods. Home range asymptotes were obtained for four of six white-lipped and four of five collared peccaries. Only these individuals were used for statistical comparisons of ranges. We obtained asymptotes for individual white-lipped peccaries after randomly selecting 70–80 of their fixes (Fig. 2(a)). In practice, more fixes were required to reach asymptotes because of seasonal and annual shifts in range areas. For example, using the chronological sequence of fixes, asymptotes were reached only after two years of tracking (equivalent to approximately 150 fixes). This is because new areas were used by the peccaries seasonally and annually. To incorporate these range shifts in the home range estimates, we have reported areas based on fixes from multiple years and seasons. Home range asymptotes for individual collared peccaries were reached after randomly sampling 50–60 fixes (Fig. 2(c)).

An evaluation of range analysis methods showed that the best representations of home range area for the white-lipped peccaries were the 90% isopleths of the harmonic mean (90% HM) and the fixed kernel calculated using the optimal smoothing factor (90% KM). These isopleths accurately represented range shape, connected areas between concentrated patches of fixes, and included a minimum of unused area. Based on the same criteria, we concluded that the best estimates of home range area for the collared peccaries were the 90%

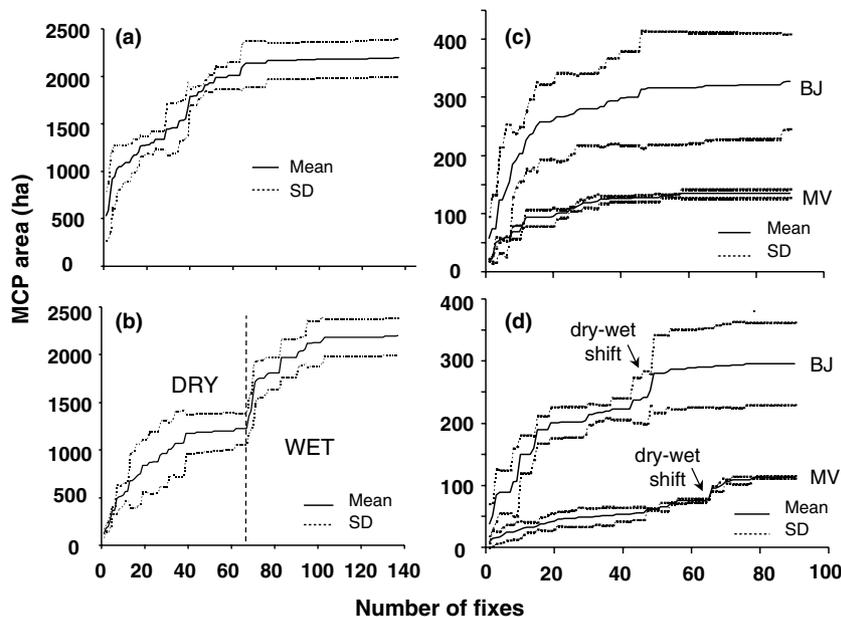


Fig. 2. (a) Home range asymptote for the white-lipped peccaries ($n = 4$ animals). Fixes were chosen randomly. (b) Seasonal range asymptotes for the white-lipped peccaries ($n = 4$ animals). (c) Home range asymptotes for two collared peccary herds ($n = 2$ animals from each herd). BJ is the Boris, Jasper, and Junior herd, and MV is the May and Vera herd. (d) Seasonal range asymptotes for the BJ and MV collared peccary herds ($n = 2$ animals per herd).

harmonic mean isopleths and the 95% kernel isopleths using the optimal smoothing factor (95% KM). We used these “best” range estimates for the analyses. The 100% and 95% minimum convex polygons included large areas which were never visited by the animals, but we present the estimates for comparisons with studies that use them (Table 2a and b).

The tracking time, total number of fixes obtained, and home range estimates for radio-collared white-lipped peccaries are shown in Table 2a. Mean home range areas, as estimated by 90% HM and 90% KM, were 1871 and 1949 ha, respectively. These ranges, which were nearly the area of Caetetus, extended beyond station boundaries into secondary forests and small forest fragments on private lands (Keuroghlian, 2003). Because we considered all of the white-lipped peccaries to be members of one herd, we combined fixes from radio-collared individuals to calculate estimates of herd home range (Table 2a). The 90% HM and KM herd estimates were 2550 ha and 2254 ha, respectively.

Table 2b shows home range estimates for the two herds of collared peccaries. Mean and herd (fixes of individuals combined) estimates are presented. The Boris, Jasper, and Junior herd had 12 individuals, and the May and Vera herd had 8. The mean home range estimate of the former herd was 2.5 times larger than for the latter, based on the 90% HM. This difference was marginally insignificant when comparing the ln-transformed 90% HM estimates ($t = 4.2551$, $df = 2$, $P = 0.0510$), but significant for the ln-transformed 95% KM estimates ($t = 5.5690$, $df = 2$, $P = 0.0308$).

As expected, comparisons of the two species showed that white-lipped home ranges were significantly larger (i.e., 9 times) than those of the collared peccaries. Using the ln-transformed 90% HM estimates, the t -test results were; $t = 7.4721$, $df = 6$, $P = 0.0003$. Using the ln-transformed 95% KM estimates, the results were; $t = 9.6731$, $df = 6$, $P = 0.00007$.

Core areas were not easily determined from inflection points on plots of home range areas versus home range isopleths (Harris et al., 1990; Kenward and Hodder, 1996). Most of the plots had gradually changing slopes, so the choice of an inflection point was quite subjective. This could be interpreted as the absence of distinct core areas for these species, or a result of smoothing caused by the methods we used to estimate home range (Kenward and Hodder, 1996). We noted, however, that fixed kernel isopleths, calculated with the median LSCV-determined smoothing factors, defined core-like configurations within home range areas (as determined by the methods described previously, i.e., 90% HM, 90% KM, and 95% KM). The isopleths formed tight outlines around the fix distributions, and separated areas with high fix densities. For the white-lipped peccaries, the 100% isopleths from this method appeared to be good representations of core areas (Table 2a). These areas, on

average, covered 45% of home range areas, and were spread among five to seven principle centers of activity (Table 2a). For the collared peccaries, the 100% fixed kernel isopleths, calculated with the median LSCV-determined smoothing factor, were closer in size to the previously presented estimates of total home range area (Table 2b), so we were less confident about using them as core area estimates. For the two herds, the core areas estimated from this method covered 67–89% of home range areas, and there were 1–3 centers of activity (Table 2b).

3.4. Seasonal range estimates and range overlap between and within seasons

To determine whether seasonal range estimates reached stable asymptotes, we randomly chose fixes obtained within each season and plotted range area versus number of fixes for the two seasons in sequence. The white-lipped peccaries reached seasonal range asymptotes after 30–40 fixes (Fig. 2(b)). The plot also demonstrates that there was a large shift in area use between the dry and wet seasons. After the dry season asymptote, range area increased 80% as wet season fixes were added to the plot. The range estimates of collared peccaries did not reach definite asymptotes within the first season (dry), but did after 10 to 20 fixes from the second season (wet) were added (Fig. 2(d)). This suggested that distinct seasonal ranges were not used by the collared peccaries during the period studied. In addition, seasonal shifts in area use were much less pronounced than the shift observed for the white-lipped peccaries. The Boris, Jasper, and Junior and the May and Vera herds showed 25% and 45% increases in range area between seasons, respectively.

Table 2a and b present seasonal range estimates for white-lipped and collared peccaries. Again, white-lipped peccary ranges were most accurately represented by the 90% HM and 90% KM estimates and collared peccary ranges by the 90% HM and 95% KM estimates. During a single season, white-lipped peccaries used 52–61% of their total home range area, while collared peccaries used as much as 97%. Repeated measures ANOVAs that compared range area between seasons, peccary species, and collared peccary herds showed that, between seasons, areas did not differ significantly within species or herds. However, white-lipped seasonal ranges were significantly larger than collared peccary seasonal ranges (using ln-transformed 90% HM estimates; effect of species, $F = 37.2176$, $df = 1, 6$, $P = 0.0009$), and seasonal ranges of the Boris, Jasper, and Junior herd were significantly larger than those of the May and Vera herd (effect of herd, $F = 23.4041$, $df = 1, 2$, $P = 0.0402$).

Fig. 3 shows the percent overlap of seasonal ranges for both species at different isopleths estimated by the harmonic mean method. We regressed percent overlap

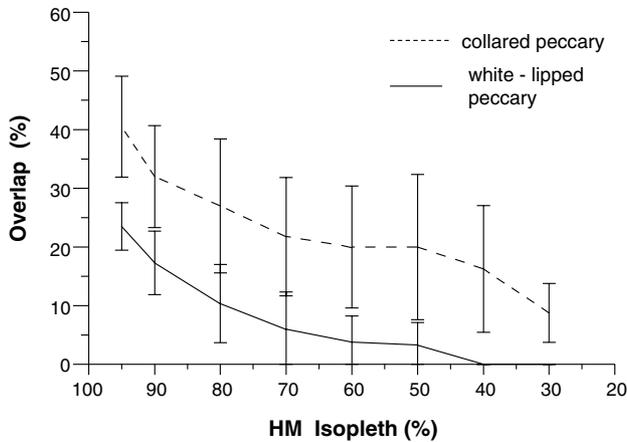


Fig. 3. Percent overlap of seasonal ranges for collared and white-lipped peccaries at isopleths estimated by the harmonic mean method. Means and standard errors are shown ($n = 4$ animals for each species).

(ln-transformed percents plus 1) on isopleth values and compared the regressions obtained for the two species. Both regressions were significant (collared peccary –

regression, $F = 7.370, df = 1, 30, P < 0.025$; white-lipped – regression, $F = 52.600, df = 1, 30, P < 0.0005$). The slopes and elevations of the 2 regressions differed significantly from each other (slope, $t = 2.071, df = 60, P < 0.05$; elevation, $t = 5.089, df = 61, P < 0.001$). Elevation was higher for collared peccaries, indicating that percent overlap of their seasonal ranges was greater overall, and slope was steeper for white-lipped peccaries, showing that overlap of their core isopleths (smaller percent values) was less.

In contrast to the spatially distinct ranges that we observed for white-lipped peccaries between seasons, within season range comparisons showed a high degree of spatial overlap among individuals and their respective subherds. Using 90% HM isopleths, we recorded 70% overlap during the dry and 54% during the wet season. However, we know from radio tracking that individuals from different subherds were almost never in the same place at the same time (except for the few occasions discussed previously when white-lipped subherds fused into larger groups). While one subherd was being

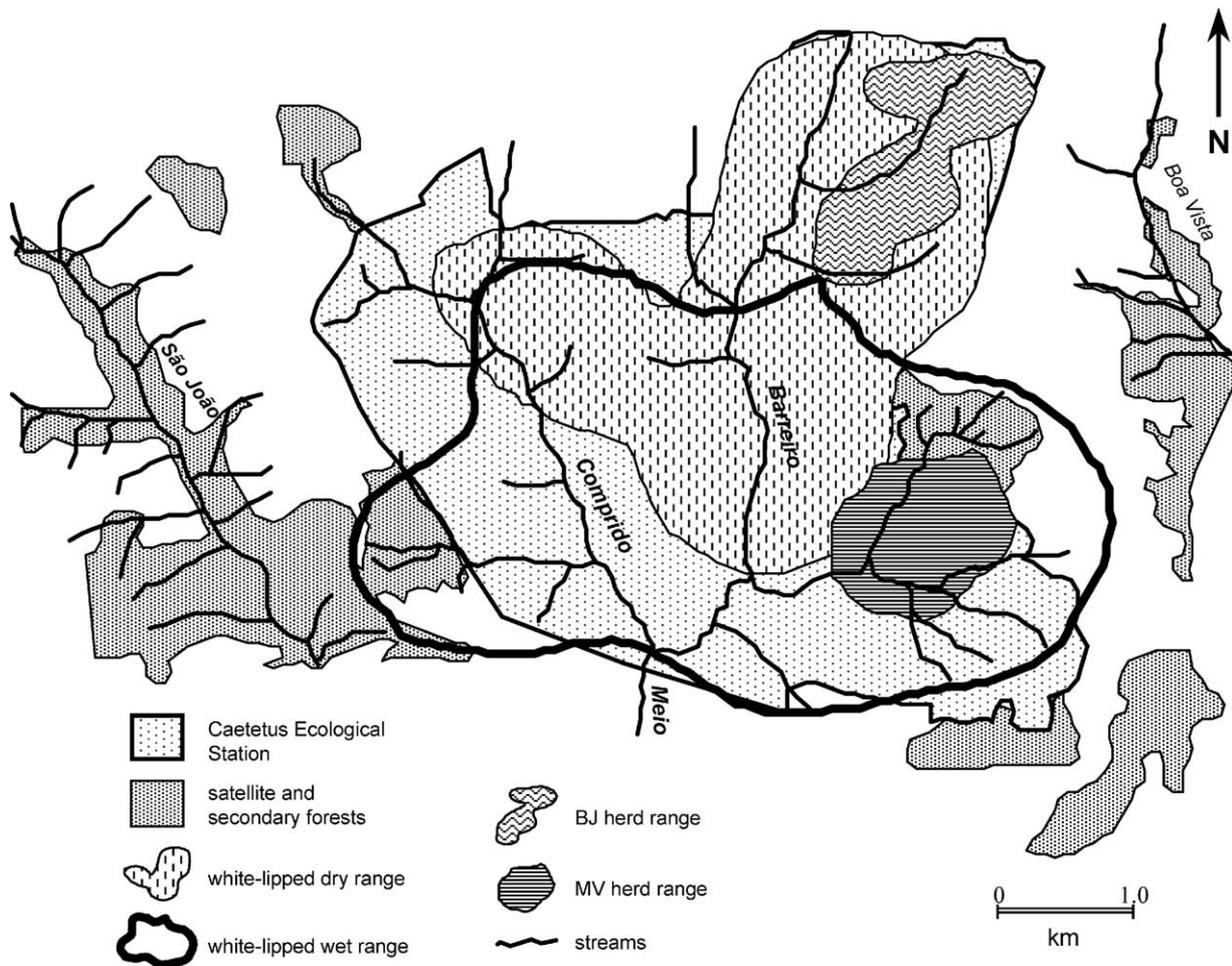


Fig. 4. Seasonal overlap of white-lipped and collared peccary herds. Ranges are 95% fixed kernel estimates (optimal smoothing factor). BJ and MV are separate collared peccary herds.

tracked, the others were typically out of radio range (> 500m in the forest). Therefore, overlap within seasons was spatial, but not temporal.

3.5. *Overlap of white-lipped and collared peccaries*

Spatial overlap between the two species changed seasonally and corresponded with the range shifts and movements of white-lipped peccaries. Fig. 4 shows the home ranges of the two collared peccary herds tracked during this study and the seasonal ranges of the white-lipped herd (95% KM estimates). Collared peccary home ranges remained within relatively restricted areas throughout the year, but white-lipped ranges shifted from the southern portion of the station in the wet season (May and Vera's home range) to the northern portion during the dry season (Boris, Jasper, and Junior's home range). On nine occasions during the study, we were able to document encounters of the two species by simultaneously tracking a collared peccary herd and a white-lipped subherd. Within minutes of the encounters, collared peccaries rapidly vacated the area that white-lipped peccaries were entering.

4. Discussion

4.1. *Peccary densities, herd sizes, and herd dynamics*

White-lipped and collared peccaries have maintained "normal" levels of abundance at Caetetus Ecological Station, based on density estimates from a much larger forest fragment in the plateau region of São Paulo state (Cullen, 1997). The larger fragment, Morro do Diabo State Park, is similar in most respects to Caetetus, e.g., vegetation type and the level of protection from hunting, but it has an area of 35,800 ha, i.e., 16 times the area of Caetetus. Therefore, it was surprising that the densities at Morro do Diabo (6.94 individuals/km² for white-lipped and 5.67 individuals/km² for collared peccaries; Cullen, 1997) were so similar to those at Caetetus (Table 1).

Herds of white-lipped peccaries much larger than the 42 individuals per subherd that we observed have been reported in the literature (Kiltie and Terborgh, 1983; Mayer and Wetzell, 1987; March, 1993; Fragoso, 1994). Sightings of 100 or more individuals in a single herd are common. However, herds (or possibly subherds) with approximately 50 ± 15 individuals have also been observed in a variety of relatively undisturbed locations unaffected by habitat fragmentation (Kiltie and Terborgh, 1983; Barreto and Hernández, 1988; Fragoso, 1994; Taber et al., 1994; Sows, 1997; Cullen, 1997; Painter, 1998; Eisenberg and Redford, 1999; R. Loureiro, pers. comm). These observations and the previous

comparisons with Morro do Diabo State Park suggest that the densities and subherd sizes of white-lipped peccaries at Caetetus were typical and may not have been altered by fragmentation related phenomena. In order to evaluate this hypothesis, however, it will be necessary to collect comparable, long-term data from more continuous tracts of forest. Another hypothesis suggested by these results is that the large herds observed principally in Amazonian forests consist of temporary aggregations of subherds during migratory or mating periods, and that white-lipped peccaries travel more commonly in smaller subherds. Alternatively, the extensive subherding that we have observed may be a consequence of forest fragmentation, range restriction, and alteration of foraging patterns. Again, to investigate these ideas, more complete baseline information is needed from undisturbed forested regions.

The 150 white-lipped peccaries inhabiting the study region used approximately the same 1100 ha area during a single season. However, they were divided into 3–4 subherds with an average of 42 individuals. Although the subherds showed a high level of spatial overlap during a single season, radio telemetry demonstrated that they seldom overlapped temporally. The temporal use of the seasonal ranges by the subherds often followed a train-like pattern. For example, one subherd would remain in a particular area, e.g., a palmetto habitat along one of the headwater streams, for 2–3 days and then move to another habitat. A day or so after the first subherd had left the palmetto area, freshly fallen fruits were available on the forest floor, and a second subherd would come through and stay for 2–3 days, and so on. Eventually, the first subherd which had visited the palmetto habitat would return, usually after 7–10 days depending on the season, habitat, and rate of fruit fall. By dividing habitat and fruit resources temporally among subgroups, white-lipped peccaries at Caetetus could be adjusting their area use patterns for survival in a forest fragment.

Recent data presented by Sáenz and Carrillo (1999) suggest that the spatial overlap of subherds that we have observed may not be a consequence of inhabiting a forest fragment. Sáenz and Carrillo (1999) have been studying the ranging habits of six herds of white-lipped peccaries in Corcovado National Park (54,500 ha), Costa Rica. In the continuous forest of the park, they observed a high level of spatial overlap between herds (Carrillo et al., 2002; see also Fragoso, 1994). The frequent exchange of individuals between subherds that we observed led us to hypothesize that white-lipped peccaries in our study region make up one herd. It was impossible to tell from radio telemetry data which radio-collared individuals switched and which ones remained in their respective subherds, because only a few members of each group had radios. It is possible that a core group does not switch subherds, while others move frequently. Finally, we do

not know whether switching among subherds is related to dispersal and reproduction and/or if it is an event that occurs at random during fusion and fission of the groups.

Data demonstrating the high degree of spatial overlap among temporally separated subherds and the frequent movement of individuals among these subherds are novel insights into white-lipped peccary behavior. These observations also have important implications for conservation and management. Obviously, without information on the number of subherds and the degree of spatial overlap, estimates of population densities could be misleading (Robinson and Eisenberg, 1985). An observer witnessing 3–4 unidentified subherds passing through a particular area at different times could conclude that just one group exists. Thus, population density and habitat carrying capacity could be underestimated. The temporary union of subherds could also be misinterpreted as the appearance of a new larger group of animals. As demonstrated by this and other studies (Sáenz and Carrillo, 1999; Carrillo et al., 2002; Robinson and Eisenberg, 1985), identification of individuals, via radio transmitters or other markers, is essential for accurate population estimates, home range estimates, and the interpretation of herd dynamics.

Observations on herd sizes of collared peccaries in the tropics vary substantially in the literature, but groups identified as herds, as opposed to subgroups or aggregate herds, typically have between 5 and 25 members (Kiltie and Terborgh, 1983; Robinson and Eisenberg, 1985; McCoy et al., 1990; Taber et al., 1994; Judas and Henry, 1999; but see Castellanos, 1983). The herds at Caetetus had group sizes near the lower end of this range (Table 1). They also formed temporary subgroups which were similar to those described by other investigators (Isle and Hellgren, 1995; Judas and Henry, 1999). Subgrouping of herds occurred on a different spatial and temporal scale than the subherding of white-lipped peccaries. Usually, a herd would be united early in the morning and again in late afternoon, but would split into groups of 1–3 individuals during the day. These subgroups appeared to forage separately and were from 30 to 250 m apart. Sightings of lone collared peccaries or groups of 2–3 individuals have frequently been reported from sites in both the Neotropics and the southwestern United States (Kiltie and Terborgh, 1983; Robinson and Eisenberg, 1985; SOWLS, 1997; Castellanos, 1983; Oldenburg et al., 1985; Bissonette, 1976; Green et al., 1984). The similarities we have noted between the collared peccaries at Caetetus and those from less disturbed forested regions suggest that forest fragmentation has not affected their densities, herd sizes, or subgrouping behavior.

4.2. *White-lipped peccary ranging behavior*

This and other recent studies conducted on the seasonal plateau of the Atlantic forest (Cullen, 1997; Ditt

et al., 1999) have shown that white-lipped peccaries are able to survive in forest fragments as small as 2000 ha. These results were surprising considering the large number of descriptive studies that discuss long range movements by white-lipped peccaries (reviewed by SOWLS, 1997) and the large home range estimates reported from the Amazon region (Kiltie and Terborgh, 1983; Fragoso, 1998). A comparison of our results with the only other radio telemetry investigations of white-lipped peccaries (Fragoso, 1998; Sáenz and Carrillo, 1999; Carrillo et al., 2002) showed that our average home range estimate, 1879 ha (90% HM), was within the range of estimates observed in continuous forests. Radio-collared individuals in the smaller herd (39–53 individuals) tracked by Fragoso (1998) had an average home range of 1580 ha based on 95% MCP estimates, and Sáenz and Carrillo (1999) reported an average home range of 2145 ha for 25 radio-collared individuals in six Costa Rican herds. Both of these studies were conducted within large forest tracts indicating that results from Caetetus were not unique to forest fragments.

Based on the assumption that range area was limited for white-lipped peccaries at Caetetus, we had expected a relatively intense and homogeneous use of all available forest throughout the year. However, core area analyses showed that large areas within their home range were used infrequently and probably served as travel corridors between centers of concentrated activity. In addition, seasonal analyses showed that wet and dry season ranges were located in distinct regions with a minimum of overlap and that specific sites within seasonal ranges were used unpredictably from year to year. The ranges shifted north toward the headwaters of the station during the dry season and south toward the valley floors during the wet season. Bodmer (1990) found that in response to seasonal flooding in the Amazon basin, white-lipped peccaries migrated in and out of flooded forests. The causes of the seasonal movements at Caetetus appear to be related to the availability of key fruit sources in specific habitats during periods of fruit scarcity (Keuroghlian, 2003). An interesting question to emerge from this work is whether the seasonal ranges would have been even more distinct and movements even less predictable in a larger tract of forest?

Our study provides new insights about the area requirements and ranging behavior of white-lipped peccaries in the Atlantic forest and, perhaps, similar regions, e.g., the forests of Costa Rica (Sáenz and Carrillo, 1999) and Venezuela (Barreto and Hernández, 1988). A population of apparently typical density has been able to survive in a forest fragment with an area of only 2178 ha and appears to have maintained distinct seasonal ranges. In addition, comparative data from continuous forests suggest that our results are not necessarily related to forest fragmentation. Local extinctions which have been observed in similar sized Atlantic

forest fragments are probably related to factors that are less pronounced at Caetetus, e.g., hunting pressure (Cullen et al., 2000), loss of habitat diversity, or degraded water quality.

4.3. Collared peccary ranging behavior and interactions with white-lipped peccaries

The two collared peccary herds showed a large difference in range size. However, variation of home range size among different herds in the same region is not unusual (Table 3). One hypothesis presented to explain these observations is that larger herd sizes are correlated with larger home range sizes (Castellanos, 1983; Fragoso, 1994), which is a phenomenon observed with primate groups (Clutton-Brock and Harvey, 1977). However, McCoy et al. (1990) observed the opposite trend for collared peccaries. At Caetetus, herd sizes were similar, but locations where separate herds of collared peccaries established home ranges varied substantially in terms of habitat types, fruits, etc. (Keuroghlian, 2003). In a heterogeneous environment, the distribution and abundance of resources would be expected to vary among the small, spatially-stable home ranges of collared peccary herds, because each herd uses a unique subset of the available habitat types (also see Fragoso, 1999). Therefore, we hypothesized that the differences in home range size observed among collared peccary herds at Caetetus were due to differences in habitats and available resources where home ranges had been established.

In comparison to the dramatic movements observed for white-lipped peccaries, small seasonal range shifts were characteristic of the collared peccary herds at Caetetus. However, both collared peccary herds showed a range expansion (although not statistically significant) during periods of overlap with the white-lipped peccaries. These range expansions by the collared peccaries may be related to avoidance of white-lipped peccaries and concomitant shifts in diet during periods of inter-specific overlap.

4.4. Management implications

Because much of the remaining Atlantic forest consists of unmonitored, unprotected forest fragments, local extinctions and population declines of white-lipped and collared peccaries will continue without active management (Viana et al., 1997; Cullen, 1997). Recent surveys on the seasonal plateau of the Atlantic forest (Cullen, 1997; Ditt et al., 1999) have shown that white-lipped peccary populations persist in only a few scattered forest fragments (i.e., 6 of 28 surveyed). Most of the fragments, like Caetetus, are around 2000 ha (or smaller) and have been isolated for 20–80 years. Unfortunately, the viability of some of the surviving populations is in question. Although other factors, e.g., reduced habitat diversity and the degradation of water quality are undoubtedly involved, the intensity of hunting pressure appears to be strongly associated with population declines and extirpations (Cullen, 1997; Ditt et al., 1999; Cullen et al., 2000). At Caetetus, hunting has been controlled since the forest was established as a private wildlife reserve in the 1920s. The level of protection that Caetetus has received is unusual for Atlantic forest fragments and was principally a result of the conservation ethic of the farmer who settled the area, Senhor Olavo Amaral Ferraz (Sowls, 1997). Cullen (1997) described the negative consequences for white-lipped peccaries and other wildlife when areas adjacent to forest fragments, which were neither monitored nor protected, were settled by large numbers of landless squatters who hunted for subsistence. Population declines and extirpations of wildlife occurred in only a few years. White-lipped peccaries have been especially vulnerable to hunting because of their large herds and habit of confronting threats rather than fleeing (Peres, 1996; Cullen et al., 2000). In contrast, collared peccary populations have been less affected by hunting, because herd sizes are small and their first reaction to predators is flight.

Even in forest fragments where hunting pressure is maintained at low levels, there are other factors which potentially threaten the persistence of white-lipped and

Table 3
Mean home range estimates (ha) of radio-tracked collared peccaries adapted from other Neotropical studies

Authority	Locality	Number of herds	Home range estimates (ha)			
			100% MCP ^a	95% MCP	80% MCP	95% KM ^b
McCoy et al. (1990)	Northwestern Costa Rica	3	83–141	64–109		
Suarez (1993)	La Selva, Costa Rica	3			70	
Fragoso (1994)	Maracá Island, Brazil	2	620–910	460–543		
Taber et al. (1994)	Paraguay, Chaco	1	685			
Judas and Henry (1999)	St. Eugene Field station, French Guiana	3				157–243
This study	São Paulo, Brazil	2	135–309	107–287	84–246	171–326

^aMCP, minimum convex polygon method.

^bKM, kernel method, “optimal” smoothing factor used.

collared peccaries. At Caetetus, important deterministic factors include alterations of forest habitats along fragment edges, which reduce range area, habitat diversity, and fruit availability (Keuroghlian, 2003), and the gradual degradation of riparian zones, aquatic habitats, and water quality due, principally, to erosion in deforested headwater valleys. The latter problems affect fruit availability and may potentially be involved in disease transmission between domestic animals and wildlife. Stochastic events, such as extreme droughts, frosts, fires, or epidemics are also potential threats. During the study period, we observed a frost combined with an extreme drought in 1995, a small tornado which toppled numerous large trees along the northern edge of the station, and a late dry season fire which destroyed approximately half of a 300 ha satellite fragment less than 1 km from the station.

Based on existing conservation strategies (Bodmer and SOWLS, 1993; March, 1993) and results from this and related studies, we recommend the following research priorities and management actions to increase basic knowledge about peccaries and to improve population viability in Atlantic forest fragments: 1) studies must identify individual animals through the use of radio collars or other marking techniques, and individuals should be tracked over seasons and years (if possible), so that ranges, population densities, and complex herd dynamics are described accurately, 2) long-term studies from continuous forest regions are needed to determine the ranging habits and herd dynamics of white-lipped peccaries that are not affected by habitat fragmentation, 3) buffer zones, riparian forests, and other vegetation that provide cover for peccaries outside habitat fragments should be protected to increase resource availability and promote exchange of individuals among isolated populations, 4) hunting must be controlled in Atlantic forest fragments on private and government owned lands to prevent rapid loss of white-lipped populations (Cullen et al., 2000), 5) preventative measures (such as fire breaks) should be implemented by forest fragment managers to reduce the chances of catastrophic events, and 6) in cases of local extinction or population collapse, reintroduction programs should be evaluated for well-preserved, protected forest fragments.

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