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Importance of rare habitats and riparian zones in a tropical forest fragment: preferential use by *Tayassu pecari*, a wide-ranging frugivore

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Abstract

In forest fragments, rare habitats contribute to heterogeneity and may provide unique resources for frugivorous species like peccaries with spatially and temporally complex patterns of range use. This study examined seasonal habitat use by two sympatric peccary species (*Tayassu pecari* and *Tayassu tajacu*) in an Atlantic forest fragment on the plateau region of São Paulo state, Brazil. Previous studies showed that range use by *T. pecari* was highly nonrandom, and that both species persisted at population densities typical of larger forest fragments. To explain this, we quantified the use and availability of habitats and riparian zones with compositional analysis. Use by *T. pecari* was nonrandom with respect to availability. Habitat preferences were different during dry and wet seasons and corresponded closely with seasonal movements, core range and fruit use. Although aquatic habitats made up a small proportion of the herd home range, they were most preferred by *T. pecari* during both seasons. Headwater palmito *Euterpe edulis* swamps were most favored in the dry season, whereas swamps and marshes near larger streams were preferred in the wet season. *Tayassu pecari* preferred riparian zones <50 m from streams over drier zones. These habitats were important sources of fruits, travel routes and corridors between forest patches in the agricultural matrix. The least-preferred habitat of *T. pecari* during both seasons was disturbed forest edge dominated by bamboo. Habitat and riparian zone use were herd-specific for *T. tajacu* and related to habitat quality and composition where stable home ranges had been established. The persistence of viable peccary populations after 75 years of fragmentation-associated pressures is related to preservation of rare habitats and overall habitat diversity. Thus, *T. pecari* is an indicator of high habitat diversity in forest fragments and will function as an umbrella species when targeted for conservation.

Introduction

In forest fragments, rare habitats contribute to heterogeneity and species richness. They are also important for habitat specialists with restricted ranges and resource requirements (Laurance, 1990; Newall, 1999; Passos & Keuroghlian, 1999). This study investigates the importance of rare habitats in forest fragments to highly mobile species with spatially and temporally complex patterns of range and resource use.

White-lipped and collared peccaries *Tayassu pecari* and *Tayassu tajacu* are frugivorous/omnivorous, herd-forming ungulates that are sympatric in a variety of neotropical forest biomes from northern Argentina to southern Mexico (Sowls, 1997). They inhabit rain forests, several types of seasonal or transitional, tropical forests, xerophytic thorn forests and the wooded and open vegetation formations of tropical flood plains and savannas.

Large regions within the neotropical ranges of white-lipped and collared peccaries have been severely altered by deforestation, agricultural development and urbanization (March, 1993; Sowls, 1997). One example is the seasonal *Planalto* region of the Atlantic Forest in south-eastern Brazil that historically covered the inland plateau west of the coastal mountains (Fonseca, 1985; Viana, Tabanez & Batista, 1997; Cullen, Bodmer & Valladares-Padua, 2000; Ditt, 2002). Only 2% (*c.* 2800 km^2) of the *Planalto* forest survives in an agriculturally dominated landscape. Forest remnants are mostly small (<10 km^2), isolated and vary in age from 20 to 100 years (Viana *et al.*, 1997; Ditt, 2002).

Populations of collared peccaries exist in about half of the *Planalto* forest fragments that are larger than 400 ha (Cullen *et al.*, 2000; Ditt, 2002). However, only about one-fifth of the fragments contain white-lipped peccary populations (Cullen *et al.*, 2000; Ditt, 2002). Home ranges and herd sizes usually vary from 1900 to 3800 ha and 40 to >200 individuals, respectively (Sowls, 1997; Fragoso, 1998, 1999; Carrillo, Saenz & Fuller, 2002; Keuroghlian, Eaton & Longland, 2004). The large area requirements and herd sizes of the white-lipped peccaries may explain why most of the *Planalto* forest remnants do not sustain viable populations. In contrast, collared peccary populations may be less vulnerable to fragmentation-related declines, because home ranges and herd sizes are smaller, typically from 60 to 600 ha and 5–30 individuals, respectively (McCoy, Vaughan & Rodrigues, 1990; Taber *et al.*, 1994; Judas & Henry, 1999; Keuroghlian *et al.*, 2004). Hunting pressure by landless squatters and poachers has also contributed to local extinctions of the more conspicuous white-lipped peccary herds in *Planalto* forest fragments (Cullen, Bodmer & Valladares-Padua, 2001).

Losses of habitat quality and diversity in forest fragments are important proximal causes of extinctions (MacArthur & Wilson, 1967; Gilpin & Soulé, 1986; Wilcove, McLellan & Dobson, 1986; Terborgh, 1992). Hence, in addition to area restrictions and direct threats (like hunting), factors related to habitat quality and diversity may also affect the persistence of peccary populations in forest fragments. These factors include topography, edaphic characteristics, moisture gradients and the presence of rare habitats (Saunders, Hobbs & Margules, 1991; Wright & Duber, 2001; Tabarelli, Silva & Gascon, 2004; Keuroghlian & Eaton, 2008).

Almost nothing has been reported about habitat use by white-lipped and collared peccaries in tropical forest fragments. Studies from a range of forest types, including continuous tracts and a range of disturbed environments, show that both species prefer forest cover (Taber *et al.*, 1994; Sowls, 1997; Fragoso, 1999; Carrillo *et al.*, 2002). However, collared peccaries use open habitats more than white-lipped peccaries, and they use agricultural and other human-altered areas close to natural habitat remnants (McCoy *et al.*, 1990; Judas & Henry, 1999). White-lipped peccaries have seasonal affinities for specific humid habitats, such as palm-dominated swamps and gallery forests, while collared peccaries use habitats with a wide range of moisture conditions (Bodmer, 1990; Peres, 1994; Fragoso, 1999; Altrichter & Boaglio, 2004; Reyna-Hurtado & Tanner, 2005).

We quantified peccary use versus availability of habitats and riparian zones in a 2178 ha Atlantic forest fragment of the *Planalto* region where populations of both white-lipped and collared peccaries have persisted after 75 years of isolation. Previous population estimates at the study site showed that the densities of both species were similar to those of a much larger (36,003 ha) *Planalto* forest fragment, suggesting that historical densities typical of the region had been maintained (Cullen *et al.*, 2000; Keuroghlian *et al.*, 2004). A 5-year investigation of peccary movements in the fragment and the surrounding region showed that range use was highly variable, both spatially and temporally, despite apparent forest area limitations for the typically wide-ranging white-lipped peccaries, that is white-lipped home-range areas were nearly equal to the area of the principal forest fragment (Keuroghlian *et al.*, 2004). The objectives of documenting habitat and riparian zone use were to provide more detailed information about how peccaries use their ranges in a forest fragment, offer hypotheses concerning the persistence of white-lipped peccaries in a relatively small forest area, develop conservation strategies for other isolated peccary populations in tropical forest fragments and evaluate the importance of rare habitats and habitat diversity for peccaries and other medium- to large-bodied frugivores in tropical forest fragments.

Methods

Study site

Caetetus Ecological Station (EEC), 22°30′S and 49°45′W, is a 2178 ha fragment of seasonal tropical forest in the *Planalto* region of the Atlantic Forest (Keuroghlian *et al.*, 2004) (Fig. 1). Until 1977, when the EEC was acquired by the state Forestry Institute of São Paulo, the forest was a privately owned wildlife reserve established by the coffee farmer, Olavio A. Ferraz. The agricultural matrix surrounding the station, which consists mainly of coffee plantations and pasture, was deforested in the 1920s. Small (50–200 ha) satellite forest fragments and areas of secondary forest are also present in the landscape surrounding the station (Fig. 2).

The vegetation at the EEC is tropical, semideciduous, mesophytic and broadleaf forest (Serra-Filho *et al.*, 1975). A 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).

Radiotelemetry

Methods for capturing, radio collaring and tracking the two peccary species from 1993 to 1998 were described in Keuroghlian *et al.* (2004). Telemetry location errors averaged 74 ± 14 m (SD) as determined by field trials in different habitats ($n = 20$) (Keuroghlian *et al.*, 2004). The results of tests for autocorrelation among radio locations (Swihart & Slade, 1985) showed that fixes collected <80 min apart for white-lipped peccaries and <100 min apart for collared peccaries were not independent (Keuroghlian *et al.*, 2004). Only independent locations were used for the analyses.

Habitat and riparian zone use versus availability

We used compositional analysis to test whether habitat and riparian zone use were random with respect to availability for the peccaries within their home ranges (Aebischer, Robertson & Kenward, 1993). For this method, sample size is equal to the number of radio-collared animals. Data used

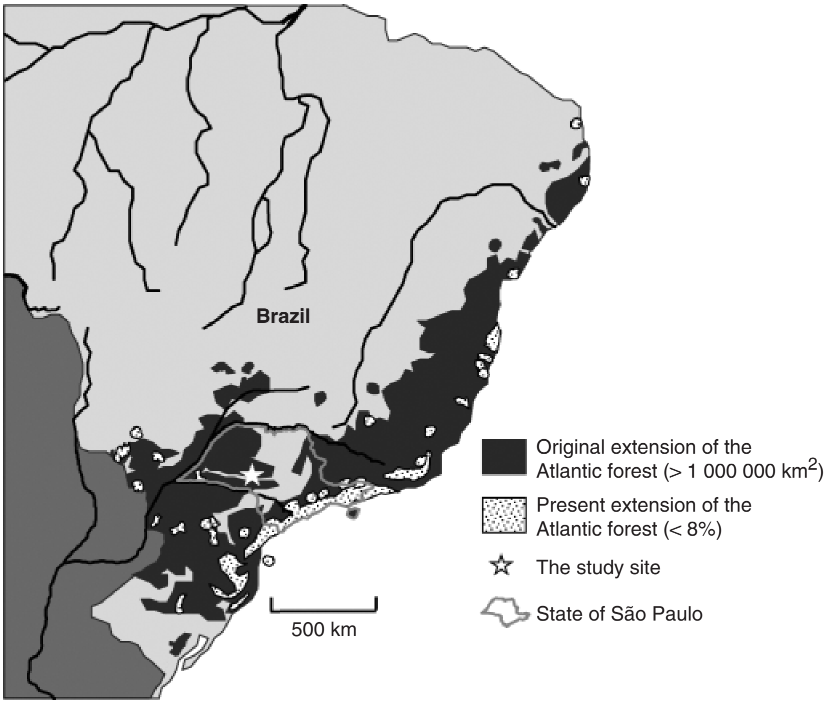

Figure 1 Original and present extension of the Atlantic forest in Brazil, and study site location.

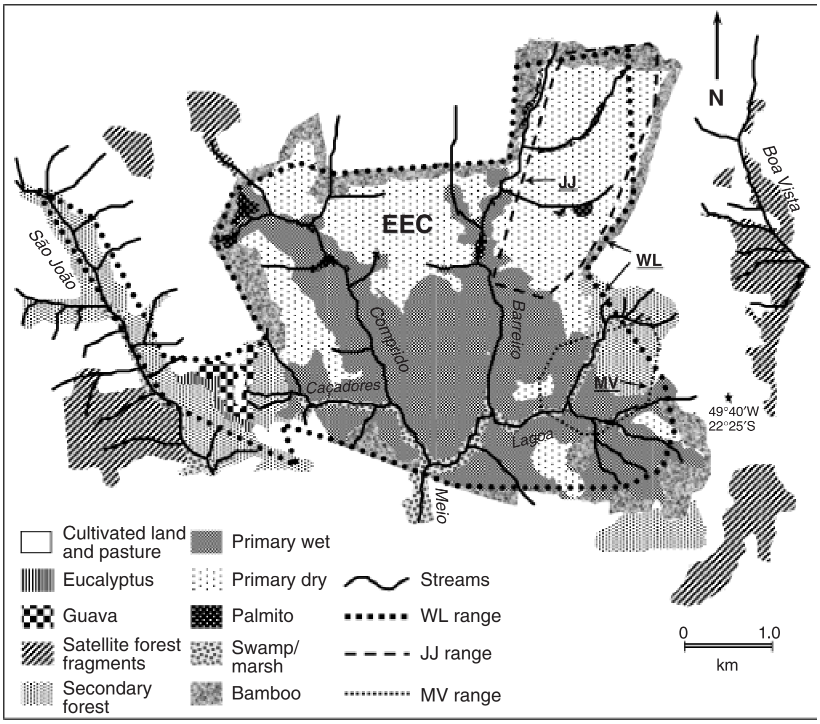

Figure 2 Major habitat types at Caetetus Ecological Station and in the surrounding landscape. Range boundaries for habitat and riparian zone analyses are shown for the white-lipped herd (WL), the Jasper and Junior collared peccary herd (JJ) and the May and Vera collared peccary herd (MV).

in compositional analyses, which consist of proportions indicating use and availability, are log-ratio transformed, so that the problem of nonindependence among proportions is resolved (Aebischer *et al.*, 1993).

Compositional analysis has two steps. The first is a multivariate test to show whether use, over all the categories investigated (e.g. habitat types), is nonrandom with respect to availability. The second, which is carried out only if the first step shows that use is nonrandom, consists of posttests to rank categories with respect to relative preference, that is in order from most to least used relative to availability. Our use of the term, 'preference', does not assume an attraction by the peccaries to a particular habitat. It refers only to nonrandom use of a habitat relative to availability.

Habitat availability

Habitat availability for the peccaries was determined by measuring the area of each habitat type with a Computer Aided Map Reference System (CAMRIS GIS Ecological Consulting Inc., Portland, OR, USA), and then calculating the proportional representation of each habitat within the area studied. We used 100% minimum convex polygons (MCP) of peccary herds as boundaries for the analyses. We used the MCP of herds, rather than of individuals, because herd members could potentially use all of the area within herd home ranges. In addition, we used annual MCP, rather than seasonal polygons, because annual ranges were potentially available during both seasons (Fig. 2). The following habitat categories were used:

(1) Primary forest: mature forest of humid valleys or drier ridges and plateaus that showed no evidence of past cutting or burning and had an emergent canopy height of about 35 m.

(2) Swamp: seasonally inundated areas next to larger streams that included naturally occurring ox-bows bordered by primary forest, and relatively open cattail marshes that had replaced forests along aggraded channels at the downstream edge of the forest fragment.

(3) Bamboo: dry areas with few mature trees and dominated by bamboo *Merostachys riedelianum* that occurred along the edges of the forest fragment next to cultivated lands and extended up to 500 m toward the forest fragment core.

(4) Palmito: permanent swamps near springs and along headwater stream channels that were dominated by palmito palms *Euterpe edulis* and had canopies that were lower and more open in comparison with primary forest.

(5) Secondary forest: a combination of altered forest types outside the EEC boundaries including satellite forest fragments that had never been logged but were highly disturbed due to edge encroachment, secondary forests that had regenerated on previously cultivated farmland and small pure stands of *Eucalyptus* and wild guava *Psidium guajava*.

Riparian zone availability

We used CAMRIS GIS to map and calculate the areas and proportions of four zones corresponding to a moisture gradient from humid stream banks to dry upland ridges: (1) <50 m, (2) 50–100 m, (3) 100–200 m and (4) >200 m distance from watercourses. We will refer to these as ‘riparian zones’, even though the riparian influence is progressively less as the distance from open water increases. Boundaries for the analyses were the same as for habitat availability.

Habitat and riparian zone use

Proportional use of habitats or riparian zones was obtained for each radio-collared peccary by counting the number of fixes in each category and dividing by the total number of fixes collected over all categories. We calculated proportions for the wet and dry seasons separately, so that seasonal use versus availability could be compared. If data were available from more than 1 year for an animal, they were pooled for the seasonal estimates of use.

Analyses

Most of the analyses described below were performed using Systat, version 7.0 (1997, SPSS Inc., Chicago, IL, USA). Before conducting the analyses, proportions equal to zero were replaced with a value 0.1 times the smallest proportion in the dataset (V. Meretski, pers. comm.). For the multivariate analysis, the proportions for use and availability were log-ratio transformed using one of the habitat or riparian zone categories as the denominator of the ratios (Aebischer *et al.*, 1993). For example, we chose the primary habitat proportions as the denominators for habitat analyses. With five habitat types, four log-ratio categories for use and availability resulted from the transformations. For each category, the log ratios of availability were subtracted from the log ratios of use to obtain four log-ratio differences. We used these differences as the dependent variables in the preliminary repeated measures ANOVAs and the multivariate analyses.

Repeated measures ANOVAs were used to decide whether a compositional analysis should be conducted for each season, or whether the seasonal data should be pooled for an annual analysis. The log-ratio differences from the wet and dry seasons were the repeated measures, and they were blocked by log-ratio categories to partition the variability. Repeated measures analysis was necessary, because the same radio-collared individuals (subjects) were monitored during both seasons. If the repeated measure (season) or the interaction of season and log-ratio category were significant, we conducted separate compositional analyses for each season. If not, a single compositional analysis was performed using annual proportions of habitat or riparian zone use. For the collared peccaries, herd was included as an additional factor in the repeated measures ANOVAs. If herd was a significant factor, then we analyzed each herd separately. If not, we pooled individuals from the different herds for compositional analysis.

We used MANOVA to test whether overall habitat or riparian zone use was nonrandom with respect to availability (Aebischer *et al.*, 1993). The log-ratio differences were the dependent variables in a MANOVA model with a constant and no independent variables. We examined the residuals of the log-ratio differences to evaluate whether the assumptions of the test were violated. If violated, we used randomization techniques to determine the significance of the test (Aebischer *et al.*, 1993). This was accomplished by performing MANOVAs on 999 permutations of the log-ratio differences with randomly assigned positive or negative values. The test statistic, Wilks’ lambda, obtained from the observed log-ratio differences was compared with the distribution of Wilks’ lambdas from the randomized datasets to determine the probability of obtaining the observed results (a significance level of $\alpha = 0.05$ was used for the test). If the results from the MANOVA were significant (i.e. that use was nonrandom with respect to availability), we conducted posttests to rank habitat or riparian zone categories with respect to preference.

For the posttests, we calculated log ratios using the proportions of use and availability for all possible pairs of habitat or riparian zone categories. For example, five habitat types generate 10 possible pairwise categories of log ratios for use and availability. As with the multivariate analyses, log-ratio differences were calculated for each category by subtracting the log ratios for availability from the log ratios for use. We conducted multiple *t*-tests to determine whether the log-ratio differences in each category were different from zero, that is whether use was nonrandom with respect to availability. We maintained an experiment-wise significance level of $\alpha = 0.05$ using the sequential Bonferroni technique to determine the significance level appropriate for individual *t*-tests (Rice, 1989). Finally, we used the results of the *t*-tests to rank the habitat or riparian zone categories with respect to relative preference and to determine which rankings were significantly different (Aebischer *et al.*, 1993).

Results

Number of herds, herd sizes and home-range estimates

Herd counts and radiotelemetry data showed that one herd of white-lipped peccaries with 150 (± 52 SD) individuals used a home range of 2302 ha in the study region (Table 1). The herd was consistently divided into four subherds that used very similar ranges during distinct time periods separated by days or weeks (Keuroghlian *et al.*, 2004). We combined data from the four subherds within seasons for estimates of habitat and riparian zone use.

We monitored two collared peccary herds at the EEC (Keuroghlian *et al.*, 2004). The mean herd size was 9 (± 2 SD) individuals, and home-range areas were 415 ha for the Jasper and Junior herd and 164 ha for the May and Vera herd (Table 1). Based on mean herd size and home-range areas, we estimated that seven to 22 herds with a total of 130 (± 66 SD) collared peccaries occupied the study region (Keuroghlian *et al.*, 2004).

Habitat availability and use

Within home-range boundaries of both white-lipped and collared peccary herds, primary forest was the most abundant habitat, disturbed forests (i.e. bamboo and secondary forest habitats) were second in abundance and aquatic environments (i.e. swamp and palmito habitats) were the least abundant (Table 1). The level of habitat disturbance for the two collared peccary herds differed substantially. Approximately 95% of the range available to the Jasper and Junior herd consisted of undisturbed primary forest and palmito habitats, while 50% of the area available to the May and Vera herd consisted of disturbed secondary forest and cattail marsh.

The proportions of habitat use (Table 1) for the white-lipped peccaries were calculated from a total of 926 radio fixes and sightings obtained from six radio-collared individuals in four different subherds. The repeated measures ANOVA indicated that compositional analyses should be conducted separately for dry and wet seasons. Season was not a significant repeated measure ($F = 0.63$, d.f. = 1, 16, $P = 0.437$), but the interaction of season and log-ratio difference category was highly significant ($F = 6.44$, d.f. = 3, 16, $P = 0.005$). We concluded, therefore, that the log-ratio differences should be analyzed within seasons. Examination of the residuals of log-ratio differences showed that variances were not homogeneous, and so randomization techniques were used to determine the significance of the MANOVAs carried out during compositional analyses.

Overall habitat use was nonrandom with respect to availability during both the dry and the wet season (dry season: Wilks' lambda, $\Lambda = 0.00222$, Rao's

Table 1 Habitat availability and use (mean proportion ± SD) for white-lipped peccary *Tayassu pecari* and collared peccary *Tayassu tajacu* herds at Caetetus Ecological Station, São Paulo, Brazil, using 100% minimum convex polygons (MCP) as boundaries for analyses

	White-lipped peccary herd				Collared peccary herds					
			Habitat use		Jasper and Junior			May and Vera		
Habitat categories	Area (ha)	Proportion	Wet	Dry	Area (ha)	Proportion	Habitat use (annual)	Area (ha)	Proportion	Habitat use (annual)
Primary	1741	0.76	0.63 ± 0.09	0.64 ± 0.07	386	0.93	0.89 ± 0.12	81	0.49	0.74 ± 0.05
Swamp	50	0.02	0.14 ± 0.06	0.04 ± 0.05	–	–		17	0.10	0.14 ± 0.02
Palmito	19	0.01	0.07 ± 0.06	0.29 ± 0.11	6	0.02	0.07 ± 0.07	–	–	
Bamboo	161	0.07	0.00 ± 0.00	0.00 ± 0.01	23	0.05	0.04 ± 0.05	–	–	
Secondary	331	0.14	0.16 ± 0.11	0.04 ± 0.06	–	–		66	0.40	0.11 ± 0.03
Herd 100% MCP	2302[a]				415			164		

[a] The 100% MCP was adjusted for the white-lipped peccaries, so that areas that were never visited, that is pasture, coffee fields and roads, were not included.

Table 2 Ranking matrixes for dry and wet season habitat preferences of white-lipped peccaries *Tayassu pecari*, Caetetus Ecological Station, São Paulo, Brazil

	Habitats					
Habitats	Palmito	Primary	Swamp	Secondary	Bamboo	Rank[a]
Dry season						
Palmito		+ + +[b]	+[c]	+ + +	+ + +	4
Primary	− − −[d]		+	+	+ + +	3
Swamp	−[e]	−		+	+	2
Secondary	− − −	−	−		+	1
Bamboo	− − −	− − −	−	−		0
Wet season						
Swamp	+	+ + +		+	+ + +	4
Palmito		+	−	+	+ + +	3
Primary	−		− − −	+	+ + +	2
Secondary	−	−	−		+	1
Bamboo	− − −	− − −	− − −	−		0

[a] Relative preference ranks were determined by counting the number of columns in a row that showed greater use with respect to availability of the row habitat over the column habitat, that is the number of columns with positive signs, + + + or +. A higher preference rank indicated greater use with respect to availability of the habitat (Aebischer *et al.*, 1993).

[b] + + +, row habitat significantly preferred over column habitat.

[c] +, row habitat preferred over column habitat (preference not significant).

[d] − − −, row habitat significantly less preferred than column habitat.

[e] −, row habitat less preferred than column habitat (preference not significant).

approximate F statistic = 224.31, d.f. = 4, 2, $P = 0.012$; wet season: Wilks' lambda, $\Lambda = 0.00003$, Rao's approximate F statistic = 7938.86, d.f. = 4, 1, $P = 0.031$). Therefore, we conducted posttests to identify the habitats that were used nonrandomly and to rank them according to preference. Using an adjusted significance level of $\alpha' = 0.007$, as determined by the sequential Bonferroni technique, four of 10 t-tests from each season showed that the means of the log-ratio differences were significantly different from zero. Habitat preferences are summarized in Table 2 using t-test results to produce ranking matrices (Aebischer *et al.*, 1993).

The relative preferences for habitats by the white-lipped peccaries in the dry season showed the following ranking from most (4) to least (0) preferred: (4) palmito, (3) primary, (2) swamp, (1) secondary and (0) bamboo (Table 2). The preference for the palmito habitat was significantly greater than for all of the other habitats, except swamp. However, the preference for palmito over swamp habitat was nearly significant ($P = 0.012$). The lowest-ranked habitat, bamboo, was significantly less preferred than primary forest, as well as the palmito habitat.

Habitat rankings from most (4) to least (0) preferred for white-lipped peccaries in the wet season were: (4) swamp, (3) palmito, (2) primary, (1) secondary and (0) bamboo (Table 2). The swamp habitat was significantly preferred over the primary habitat, but its ranking was interchangeable with the palmito and secondary forest habitats. As in the dry season, the bamboo habitat was ranked the lowest. Bamboo was significantly less preferred than primary, swamp and palmito habitats, but its ranking was interchangeable with secondary forest. The latter result was borderline, that is the preference for secondary forest over bamboo habitat was nearly significant ($P = 0.027$).

The analyses of collared peccary habitat use were based on 621 radio fixes and sightings from four radio-collared individuals in two herds. The preliminary repeated measures ANOVA showed that separate seasonal analyses were not justified, and that the factor, collared peccary herd, had a nearly significant effect ($F = 4.29$, d.f. = 1, 5, $P = 0.093$). Therefore, separate compositional analyses for each herd using pooled data from both seasons were indicated. However, because only two animals from each herd were radio-tracked, we could not use compositional analyses. The Jasper and Junior herd appeared to use habitats randomly within their home range, that is, the patterns of use closely matched availability (Table 1). In contrast, the May and Vera herd showed evidence of nonrandom use of habitats (Table 1). The annual trends suggested a preference for primary forest habitat and an avoidance of secondary forest habitat. The use and availability of the swamp habitat appeared to be equal for the May and Vera herd.

Riparian zone availability and use

Although the areas of the four riparian zones differed among the herds, the proportions were similar (Table 3). Fixes and sightings from the habitat analyses were also used for riparian zone analyses. The results of the preliminary repeated measures ANOVA indicated that annual proportions of riparian zone use should be used for compositional analysis. Neither season nor the interaction of season and log-ratio difference category showed significant model effects (season: $F = 0.01$, d.f. = 1, 12, $P = 0.926$; season × log-ratio difference categories: $F = 1.53$, d.f. = 2, 12, $P = 0.255$). Randomization techniques were used to determine the significance of the MANOVA stage of

Table 3 Riparian zone availability and annual use for white-lipped peccary *Tayassu pecari* and collared peccary *Tayassu tajacu* herds at Caetetus Ecological Station, São Paulo, Brazil, using 100% minimum convex polygons (MCP) as boundaries for analyses

	White-lipped peccary herd			Collared Peccary					
				Jasper and Junior			May and Vera		
Zones	Area (ha)	Proportion	Habitat use	Area (ha)	Proportion	Habitat use	Area (ha)	Proportion	Habitat use
<50 m	412	0.18	0.44 ± 0.06	47	0.11	0.15 ± 0.01	32	0.19	0.35 ± 0.02
50–100 m	391	0.17	0.19 ± 0.03	49	0.12	0.14 ± 0.04	25	0.15	0.23 ± 0.04
100–200 m	640	0.28	0.20 ± 0.03	87	0.21	0.20 ± 0.05	46	0.28	0.25 ± 0.04
>200 m	859	0.37	0.17 ± 0.07	232	0.56	0.52 ± 0.01	61	0.37	0.16 ± 0.02
Herd 100% MCP	2302[a]			415			164		

[a] The 100% MCP was adjusted for the white-lipped peccaries, so that areas that were never visited, that is pasture, coffee fields and roads, were not included.

Table 4 Results of *t*-tests for annual compositional analysis of riparian zone use by white-lipped peccaries *Tayassu pecari*, Caetetus Ecological Station, São Paulo, Brazil

Log-ratio difference category (numerator/ denominator)	Means of log-ratio differences	t (d.f. = 4)	P	Significance ($\alpha' = 0.017$)[a]
<50 m/50–100 m	0.788	14.7912	0.000122	*
<50 m/100–200 m	1.249	10.3156	0.000498	*
<50 m/>200 m	1.818	6.1577	0.003530	*
50–100 m/100–200 m	0.471	4.6958	0.009338	*
50–100 m/>200 m	1.040	3.2407	0.031654	NS
100–200 m/>200 m	0.569	2.0872	0.105158	NS

[a] A significant difference between the mean of the log-ratio differences and zero is indicated by an asterisk.

*No significant difference is indicated by 'NS',and $\alpha' = 0.017$ is the adjusted significance level for individual *t*-tests as determined by the sequential Bonferroni technique (Rice, 1989).

compositional analysis, because the assumption of variance homogeneity was violated.

On an annual basis, overall riparian zone use by the white-lipped peccaries was nonrandom with respect to availability (Wilks' lambda, $\Lambda = 0.00556$, Rao's approximate F statistic = 119.14, d.f. = 3, 2, $P = 0.036$). Four of the six *t*-tests were significant (Table 4, $\alpha' = 0.017$ for individual *t*-tests as determined by the sequential Bonferroni technique). The following rankings from most (3) to least (0) preferred showed a clear preference for zones closer to water: (3) <50 m, (2) 50–100 m, (1) 100–200 m and (0) >200 m (Table 5). In addition, the differences between the zones increased in significance with increasing proximity to watercourses (Table 4).

For riparian zone use by collared peccaries, the preliminary repeated measures ANOVA indicated that seasonal data should be pooled and that herds should be analyzed separately. Again, we could not use compositional analyses, because only two animals from each herd were radio-tracked. The use of riparian zones by the Jasper and Junior herd appeared to be random with respect to availability (Table 3). However, the May and Vera herd showed a gradual decline in use versus availability with greater distance from watercourses (Table 3).

Discussion

Forest fragment use by wide-ranging white-lipped peccaries: importance of rare habitats, habitat quality and habitat diversity

Considering the sizeable range requirements of white-lipped peccaries, their nearly exclusive use of forested areas and the presence of a large, normal-density herd in the fragmented landscape of the study region, documenting home-range areas that were nearly as large as the largest forest remnant, that is the EEC (Keuroghlian *et al*., 2004), was not surprising. No other large fragments occurred in the region, and areas outside the EEC are dominated by agricultural development (Fig. 2). Despite the limited forest cover, area use by white-lipped peccaries was highly nonrandom. Specific regions within the EEC were avoided by white-lipped peccaries in favor of connected corridors and satellite remnants in the agricultural matrix (Fig. 2). In addition, white-lipped peccaries had distinct seasonal ranges and widely dispersed centers of activity within home-range boundaries (Keuroghlian *et al*., 2004).

This nonrandom use of home range and available forest area within the EEC reflected patterns of habitat and riparian zone use by the white-lipped peccaries, and demonstrated the importance of rare habitats, habitat quality and habitat diversity. The combined area of the aquatic habitats, palmito areas plus stream margin swamps and marshes, made up only 3% of the white-lipped herd home range. However, these areas were used heavily during both seasons (29% use of palmito areas during the dry season and 14% use of swamp habitats during the wet season). The preference of white-lipped peccaries for palmito areas during the dry season was related to the appearance of palmito fruits and a concurrent scarcity of alternative fruits in other habitats (Keuroghlian & Eaton, 2008). The preferential use of this rare habitat provided a partial explanation for the northward movement of the herd during the dry season to

Table 5 Ranking matrix for annual riparian zone preferences of white-lipped peccaries *Tayassu pecari*, Caetetus Ecological Station, São Paulo, Brazil

Riparian zones	<50 m	50–100 m	100–200 m	>200 m	Rank[a]
<50 m		+ + +[b]	+ + +	+ + +	3
50–100 m	− − −[c]		+ + +	+[d]	2
100–200 m	− − −	− − −		+	1
>200 m	− − −	−[e]	−		0

[a] Relative preference ranks were determined by counting the number of columns in a row that showed greater use with respect to availability of the row zone over the column zone, that is the number of columns with positive signs, + + + or +. A higher preference rank indicated greater use with respect to availability of the riparian zone (Aebischer *et al.*, 1993).

[b] + + +, row zone significantly preferred over column zone.

[c] − − −, row zone significantly less preferred than column zone.

[d] +, row zone preferred over column zone (preference not significant).

[e] −, row zone less preferred than column zone (preference not significant).

headwater springs where palmitos were abundant (Keuroghlian *et al.*, 2004; Keuroghlian & Eaton, 2008). Likewise, the southward movement of the herd and the preference for swamp habitats during the wet season appeared to be related to abundant fruit sources that were not available in other habitats or during other seasons (Keuroghlian & Eaton, 2008). These movements and preferences associated with rare habitats demonstrated the importance of habitat quality in terms of fruit type and abundance, and habitat diversity in terms of a temporal succession of fruit sources distributed among different aquatic and forest environments.

Related, in part, to their use of palmito and swamp habitats, white-lipped peccaries showed a highly significant preference for riparian zones <50 m from watercourses. Other types of habitats, however, made up the <50 m riparian zone along much of the stream network within the white-lipped herd home range (Fig. 2). Between the headwater palmito areas and downstream swamps of the EEC, this zone consisted largely of humid primary forest. Outside the EEC boundary, secondary-growth gallery forests lined many of the streams. Both primary and secondary forest habitats within the <50 m riparian zone were used intensively by white-lipped peccaries. In addition to foraging for fruits in these streamside forests, the peccaries used them and the streams as travel routes. Outside the EEC, secondary-growth riparian forests provided cover for episodic forays to satellite forest fragments and fruit sources. Although short-lived, these movements, for example to forage for guava fruits *P. guajava*, increased overall habitat availability and diversity for the white-lipped herd. Likewise, Laurance (1990) showed that extinction proneness was less for mammal species with the ability to use secondary-growth forest in a fragmented landscape.

The use of primary forest habitat by white-lipped peccaries was substantial (63–64%), but random with respect to availability in our analysis (Tables 1 and 2). Primary forest was more heterogeneous than other habitats and included all riparian zone categories, and so fruits and other resources were patchy and temporally variable. A finer-grained habitat classification and larger sample sizes of marked animals may be necessary to discern area-use preferences within the primary forest habitat. Use of secondary forest was also largely random with respect to availability, but it was ranked next to last in terms of preference during both seasons. This is probably related to the episodic nature of secondary forest use in contrast to our analyses that spanned the full dry and wet seasons. Analyses conducted over shorter time periods may be more accurate for portraying the importance of secondary forest to white-lipped peccaries. For both dry and wet seasons, bamboo habitat, which is found almost exclusively within the boundaries of the EEC, was least preferred by the white-lipped peccaries. Extensive bamboo areas were typical of dry forest edges without transitional or buffer vegetation in the agricultural matrix. Very few fruits were available in bamboo habitats (Keuroghlian & Eaton, 2008) and, consequently, use by white-lipped peccaries was rare.

The results of the habitat and riparian zone analyses have clear conservation implications that extend beyond the often-mentioned large area requirements of the white-lipped peccaries. Their intensive, seasonal use of rare, high-quality habitats, like palmito areas, which have been extirpated in most of the agricultural matrix, illustrates the importance of habitat diversity and quality for the persistence of white-lipped peccaries in forest fragments. As a species that requires different habitats during different fruiting periods (Kiltie & Terborgh, 1983; Fragoso, 1999; Altrichter *et al.*, 2001; Carrillo *et al.*, 2002; Keuroghlian & Eaton, 2008), they are highly vulnerable to fragmentation processes that lead to habitat loss (Karr, 1982; Terborgh, 1986; Wilcove *et al.*, 1986; Laurance, 1991; Altrichter & Boaglio, 2004; Reyna-Hurtado & Tanner, 2005). Riparian zones also played a key role for white-lipped peccaries as sources of fruits, travel routes and as corridors for movement in the agricultural matrix, for example among forest fragments or to fruit sources that help sustain isolated herds during specific periods (Keuroghlian & Eaton, 2008). The preference of white-lipped peccaries for secondary forest habitats in the agricultural matrix over disturbed edge habitats within the EEC emphasizes the importance of protecting regenerating habitats on private lands adjacent to forest fragments and restoring degraded, edge-affected habitats within forest fragment conservation units.

Habitat and riparian zone use by collared peccaries

In contrast to white-lipped peccaries, home-range use by collared peccaries at the EEC showed fewer and more diffuse centers of activity and less pronounced seasonal shifts (Keuroghlian *et al*., 2004). The trends of habitat and riparian zone use we observed appeared to be herd specific (Tables 1 and 3). Whereas proportional use was very similar to availability for the Jasper and Junior herd, the May and Vera herd seemed to show correlated trends favoring primary forest habitat and wetter riparian zones over secondary forest and drier zones, respectively. These differences between the herds could have been related to the locations where home ranges were established and the range-specific composition of habitats and other resources. For example, the less frequent use of the most disturbed habitat in the May and Vera home range, secondary forest, may have reflected periods of fruit scarcity that were not as evident in the primary forest and swamp habitats. Because secondary forest comprised 40% of their home range, erratic resource availability could have produced nonrandom habitat use. In contrast, marked differences in use and availability were not observed for the Jasper and Junior herd, because 95% of their home range consisted of relatively undisturbed and, perhaps, equally preferred habitats. Habitat preferences probably existed for this herd as well, but were only detectable at a scale that distinguished microhabitats or individual fruiting trees within our broad habitat categories. Similarly, Fragoso (1999) hypothesized that habitat use by collared peccaries occurred on a finer spatial scale in comparison with white-lipped peccaries.

From a landscape perspective, range and habitat use by collared peccaries were undoubtedly affected by the territorial behavior and minimal overlap of adjoining herds (Keuroghlian *et al*., 2004). Territoriality among herds has been observed by a number of authors (reviewed by Sowls, 1997). At the EEC, the relatively small range shifts between months and seasons and the near absence of dispersal between herds suggested that the local collared peccaries were also territorial (Keuroghlian *et al*., 2004). Unlike the white-lipped peccaries, which continually altered their range to exploit newly available resources, the collared peccaries rarely ventured beyond well-established range boundaries. Therefore, collared peccary herds, such as May and Vera's group, may be restricted to suboptimal edge regions of the forest fragment, and experience episodes when resources (especially fruits) are limited. This and the territoriality of the collared peccary herds would explain their inclusion of abundantly available cultivated crops and fruits outside the EEC (Keuroghlian, 2003). Protection of regenerating wildlife habitat in the agricultural matrix and establishment of buffer zones adjacent to the disturbed edge should improve habitat quality and diversity for herds inhabiting altered forest fragment edges.

Importance of habitat quality and diversity for conservation of peccaries and other species in Atlantic forest fragments

Our results suggest that preservation of habitat quality and diversity at the EEC has been important for long-term persistence of peccary populations. Survival of the initial fragmentation event was possible, because the extent of forest cover remaining met minimum area requirements for both peccary species, and hunting was strictly controlled by neighboring landowners (Cullen *et al*., 2001; Keuroghlian *et al*., 2004). Long-term persistence, however, also required (and will require in the future) the preservation of key resources, like fruits, that are tied to habitat quality and diversity (Keuroghlian & Eaton, 2008). Key features of the EEC and the surrounding landscape that may have contributed to habitat preservation include a varied topography of plateaus and steep valleys and a dense network of streams and springs. These features undoubtedly slowed the pace of wind-induced moisture losses and associated edge encroachment, which are processes that may be more extensive in flatter, drier forest fragments (Saunders, Hobbs & Margules, 1991; Viana *et al*., 1997; Keuroghlian, 2003). However, without active management, for example protection and restoration of riparian zones in the agricultural matrix and establishment of buffer zones along fragment edges, habitat quality and diversity will decline, threatening the long-term viability of peccaries and other frugivores. Because of the spatial and temporal complexity of their habitat requirements as shown by this study, the presence of white-lipped peccary populations in forest fragments should be a strong indication of high levels of habitat heterogeneity. Therefore, conservation efforts targeting white-lipped peccaries will have an umbrella effect for the large number of species with overlapping habitat requirements.

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