Fate of native and introduced seeds consumed by captive white-lipped and collared peccaries (*Tayassu pecari,* Link 1795 and *Pecari tajacu,* Linnaeus 1758) in the Atlantic rainforest, Brazil

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(With 2 figures)

Abstract

We studied the role of white-lipped and collared peccaries (*Tayassu pecari* and *Pecari tajacu*) as seed predators and dispersers in the Atlantic rainforest of Brazil. The Atlantic rainforest ecosystem is highly threatened and has experienced dramatic declines in its populations of large mammals. Local extinctions can disrupt essential plant-animal interactions such as seed dispersion and seed predation. We tracked seeds from time of consumption to germination to assess the direct impact peccaries have on seed survival. We offered fruits of 20 species found in the Atlantic rainforest to the peccaries. Seeds were categorised as intact, scarified, ingested or defecated, and germination tests were performed. The overall impact by both peccary species was similar. Seeds were sometime scarified by mastication, always with fatal consequences. Most seeds that were consumed were destroyed during ingestion and digestion. Only small seeds (<10 mm) were found in the feces and germination tests suggest a positive effect from the passage through the guts. Peccaries clearly have a double role as both seed predators and as small seeds dispersers, which is a specialised role within the granivore/frugivore community of the Atlantic rainforest.

Keywords: seed dispersal, seed predation, peccaries, *Tayassuidae*, Atlantic rainforest.

Destino das sementes consumidas por queixadas e catetos (*Tayassu pecari* e *Pecari tajacu*) na Mata Atlântica, Brasil

Resumo

O papel dos porcos-do-mato, cateto (*Pecari tajacu*) e queixada (*Tayassu pecari*), como predadores e dispersores de sementes foram estudados no contexto da Mata Atlântica. Neste ecossistema extremamente ameaçado, as populações de grande mamíferos vêm diminuindo drasticamente. A extinção local de algumas dessas espécies pode modificar as interações plantas-animais como a dispersão e a predação de sementes. Sementes de 20 espécies de plantas lenhosas da Mata Atlântica foram acompanhadas desde a ingestão até a germinação para avaliar o impacto direto que queixadas e catetos têm sobre a sobrevivência destas sementes. As sementes foram categorizadas em: ignoradas, escarificadas (danos mecânicos), engolidas ou defecadas. Também foram realizados testes de germinação. O impacto das duas espécies de foi similar. Às vezes, as sementes foram escarificadas por mastigação, com consequências letais. A maioria das sementes consumidas foi destruída durante a ingestão e digestão. Somente sementes pequenas (<10 mm) foram defecadas. Os testes de germinação sugerem um impacto positivo nas sementes que passaram pelo trato digestivo. Os porcos desempenham claramente um papel duplo: predadores de sementes e dispersores de sementes pequenas, um papel especializado dentro da communidade de frugívoros/granívoros na Mata Atlântica.

Palavras-chave: dispersão de sementes, predação de sementes, porcos-do-mato, *Tayassuidae*, Mata Atlântica.

1. Introduction

Two species of peccaries (family Tayassuidae) can be found in the Atlantic rainforest of Brazil: the white-lipped peccary (*Tayassu pecari*, Link 1795) and the collared peccary (*Pecari tajacu*, Linnaeus 1758). However, the viability of peccary populations in the Atlantic rainforest, especially in the north of the São Francisco river (Northeast states) remains highly precarious. This biome has a history of exploitation that has led to a severe habitat reduction and fragmentation, reducing the abundance of mammalian species, especially those with large spatial requirements (Viana and Tabanez, 1996; Chiarello, 1999; Uchôa Neto and Tabarelli, 2002). Hunting of large mammals exacerbates the effects of fragmentation on these populations (Chiarello, 1999; Laurance et al., 2000; Nasi et al. 2008). *T. pecari* are very rare or even absent from the northeast of Brazil, whereas *P. tajacu* persist in forest fragments throughout the Northeast Atlantic forest (Mendes Pontes et al., 2005; Monteiro da Cruz et al., 2002).

Peccaries inhabiting the rainforest are opportunistic frugivores consuming fruits and seeds from a wide morphological and taxonomical range, and are important biomass consumers (Sowls, 1997; Keuroghlian et al., 2004; Beck, 2005). In the Amazon, Bodmer (1989) found that 60 to 65% of the stomach content was fruits and seeds in both species. More recently, a study by Keuroghlian and Eaton (2008) found that fruits comprise up to 80% of the white-lipped peccary diet in the Atlantic rainforest.

Many Neotropical mammals play a key role in plant communities by their interaction with the seeds of numerous plant species (Lazure and Almeida-Cortez, 2006; Almeida-Neto et al., 2008), and these interactions can significantly affect the forest community dynamics and structure. Animal-mediated seed dispersal can reduce intra-specific competition, assist in colonisation of disturbed area, increase gene flow, and reduce density-dependent predation (Howe and Smallwood, 1982; Willson, 1992; Beck, 2005). Conversely, seed predation can also result in selective survival of seeds due to predator preference, reduction of competition by abundant plant species (therefore a higher survival of rare species), modification of distribution patterns, maintenance of low density of individuals from the same species, and increase diversity within a given area (Janzen, 1970; Fragoso, 1997; Hulme and Benkman, 2002).

Previous studies have often emphasised the predatory role of peccaries (Silman et al., 2003; Wyatt and Silman, 2004; Fleury and Galetti, 2006), although some studies have recognised the peccary dual-role as seed disperser and predator (Beck, 2005; Keuroghlian and Eaton, 2008). Peccaries may disperse seeds through either epizoochory or endozoochory. In the first case, peccaries disperse seeds across short distances by shuffling and trampling seeds while eating, and by expelling seeds after eating the pulp (Fragoso, 1997; Beck, 2006). Little is known of the potential for endozoochory (dispersal of seeds carried inside the animal), and it remains unclear whether seeds remain viable after ingestion and defecation. Motta et al. (2008) studied the role of collared peccaries (*Pecari tajacu*) as seed dispersers and predators of ten fleshy fruited species, including both native and naturalized exotic plants to the Atlantic rainforest remnants of Southern Bahia, Brazil, and the authors observed that most seeds were killed and only guava seeds had improved germination after passage through peccary guts when compared to the control.

The aim of our study is to assess the role of peccaries both as seed dispersers by endozoochory and seed predators for plant species of the Atlantic rainforest of Brazil. Specifically, 1) we evaluated the fate of seeds in fruits consumed by peccaries and 2) the relationship between seed fate and size; 3) we tested the germination rate of the seeds following scarification and digestion; and 4) we determined whether differences exist between the two peccary species.

2. Material and Methods

We worked within an Atlantic rainforest fragment situated in a sugar-cane plantation (26,000 ha), the Usina Serra Grande (USGA), in the state of Alagoas, Brazil (8° 58' 24" S and 36° 3' 55" W). The forest fragment is one of the largest in the region (approximately 3,500 ha). Within the fragment there were two free-ranging populations of peccaries (30 *T. pecari* and 145 *P. tajacu*), kept out of the plantation by fencing. The majority of their diet at the USGA is composed of domestic pig food (wheat, corn and added nutriments) provided by the animal keeper on a daily basis. We conducted our fieldwork between February and July 2006.

Initially, we captured three to six individual peccaries into a smaller pen (approximately 40 m^2) that had been carefully cleaned of all fruits and seeds. The animals are often fed in the pen, so the animal keeper simply had to close the gate when the animals were in. Each species had its own pen, and the animals were kept inside for a week. In total, five experiments were performed for both species. Confinement in the smaller pens is not an unusual procedure for these peccaries, as it is part of an annual veterinary examination to evaluate the state of health of the animals on the USGA premise. No invasive or forced procedures were performed on the animals.

We fed the peccaries 20 tree and shrub species of fruits (Table 1) that were collected or bought from one of three sources: 1) the forest fragments of USGA, 2) *Mata de Dois Irmãos* at the *Dois Irmãos* State Park in Recife, Pernambuco (8° 02' 30" S and 34° 56' 32" W), and 3) from local markets in Recife. Some of the species we used were not native to the Atlantic rainforest, but all are currently found in the north-eastern Atlantic rainforest and are potentially eaten by wild peccaries. We chose fruits with seeds of different sizes, from the small *Psidium cattleianum* (seed size of 2 ± 0 mm;

Table 1. List of all the species offered to the peccaries (*Tayassu pecari* and *Pecari tajacu*), seed sizes, number of seeds tested (N) and scarification and germination rates from both peccary species combined. N for scarification is the number of seeds offered to the peccaries; the N for defecation is the number of seeds ingested by the peccaries. Defecated seeds that also showed scarification are accounted for in both columns in the two species where it occurred: *S. morototonii* (150) and *S. paniculatum* (11).

Family/Species	Seed size (mm ± SE)	Scarification		Defecation	
		N	Rate (%)	N	Rate (%)
ANACARDIACEAE					
Mangifera indica L.	77 ± 9	43	2.3	3	0.0
Spondias spp.	28 ± 3	230	0.4	3	0.0
APOCYNACEAE					
Rauvolfia sp.	22 ± 4	44	2.3	0	-
ARALIACEAE					
Schefflera morototonii (Aubl.) Maguire, Steyermark and Frodin	5 ± 0	402	0.0	352	25.3
ARECACEAE					
Attalea oleifera Barb. Rodr.	61 ± 2	328	3.0	25	0.0
Euterpe oleraceae C. Martius	14 ± 1	484	8.3	158	0.6
Mauritia flexuosa L. f.	30 ± 1	212	0.9	45	0.0
CHRYSOBALANACEAE					
Licania tomentosa Benth.	49 ± 11	22	4.5	20	0.0
EUPHORBIACEAE					
Margaritaria nobilis L. f.	4 ± 1	2,803	0.0	812	9.4
FABACEAE					
Clitoria fairchildiana R. A. Howard	18 ± 2	150	10.7	89	0.0
Inga spp.	15 ± 1	837	5.0	365	0.5
Tamarindus indica L.	13 ± 2	100	1.0	18	0.0
MALPIGHIACEAE					
Byrsonima spicata (Cav.) Kunth	6 ± 0	586	0.0	268	25.7
MORACEAE					
Artocarpus heterophyllus Lam.	31 ± 2	300	6.3	258	0.0
Brosimum guianense (Aublet) Huber	11 ± 1	40	0.0	40	0.0
MYRTACEAE*					
Psidium cattleianum Sabine	2 ± 0	0	-	0	-
Psidium guajava L.	4 ± 0	0	-	0	-
SAPINDACEAE					
Unknown	13 ± 1	138	0.0	138	0.0
SOLANACEAE†					
Solanum paniculatum L.	3 ± 0	1,749	0.0	1,068	11.3
Solanum stramonifolium Jacq.	3 ± 0	29,280	0.0	16,542	1.0

* The two Myrtaceae were only used in germination tests. The seeds were collected from feces outside the pen.

† The number of seeds in Solanaceae was calculated using the average seed count per fruit (*S. paniculatum*: N = 13, mean = 31; *S. stramonifolium*: N = 15, mean = 78).

mean ±SD) to the big-seeded mango, *Mangifera indica* (77 ± 9 mm).

Because the emphasis of the experiment is to look at seed fate, and not fruit choice-preference, we did some manipulation with the food before giving it to the animals. In order to measure and count the seeds of some fruits, it was necessary to extract them carefully from the pulp. Seeds were measured along their longest axis in millimetres using a calliper, and mean and standard deviation were calculated. Then we incorporated those seeds to the pulp of the same fruits that were offered. This methodology allows accurate tracking of the seeds from the moment of ingestion to germination. We offered fruits the day after we captured the peccaries and individuals were fed cereals for the remainder of the week. Seeds not consumed after 24 hours were collected so that we could precisely calculate the number of seeds ingested and the percentage of seeds defecated. All fecal matter within the enclosure was collected each morning for six days following the fruit feeding; based on prior observations, retention time ranges from less than a day to six days. Seeds were extracted from the fecal matter by mixing the feces with water, and subsequently sifting the mixture through a small-meshed sieve (1 × 1 mm), using pliers to collect the seeds. We rinsed the seeds with water, dried them in the open air and stored them in plastic bags. Not all plant species were used in every experiment due to constraints including limited amount of fruits harvested or available at the market, timing of fruit availability, and some species that the fruits were ingested but we did not find a sufficient number of intact seeds in feces to use in the assay.

We first categorised seeds as refused, scarified but not ingested, or ingested. Then the seeds later collected in the feces were further classified as destroyed during consumption and digestion, scarified or intact. In this study, we define scarified seeds as those that had damage to the seed coat or endocarp as a result of mastication; damage was assessed by visual inspection, therefore only relatively important mechanical damage was detected. We calculated scarification rate (number of seeds scarified over the total of seeds found in the pen and in the feces) and defecation rate (number of seeds defecated over the number of seeds ingested).

We used analysis of covariance (ANCOVA) to examine the relationship between scarification or defecation rate (dependent variables) and seed size (covariate), and to account for the difference between peccary species (independent categorical variable). Seed size was transformed ($\log_{10}$) to meet the normality assumption. Statistical analyses were performed with SPSS 16.0 (SPSS Inc., Chicago, USA).

We conducted two different germination tests on scarified but not ingested seeds and on intact defecated seeds. The smaller seeds (≤4 mm) were placed in Petri dishes on filter paper, in a laboratory under diffuse light and room temperature. The rest of the seeds were planted in plastic cups filled with soil in the greenhouse at the Universidade Federal de Pernambuco (UFPE). These seeds were moderately watered every two days. Control and treatment tests for each species were performed under the same conditions. Germination was confirmed at the emergence of the seedling. If there was no germination after one month, we considered the seed "not germinated" (following Motta-Junior and Martins, 2002).

3. Results

Of the 20 seed species we studied, 17 were ingested, 11 were spit with scarification, nine were defecated (only two with some cases of scarification) and three germinated after passage through the digestive system.

Maximal scarification rate was 15.3% (for *Euterpe oleraceae* eaten by *P. tajacu*). Among the eleven species that were damaged, the average scarification rate was 7.1%. In all cases, scarified seed size exceeded 13 mm (Figure 1). Three species of Palmae (*Attalea oleifera, E. oleraceae* and *Mauritia flexuosa*), three Fabaceae (*Clitoria faichildiana*, *Inga* spp. and *Tamarindus indica*) and five other species suffered scarification. Nevertheless, there was no interaction between peccary species and seed size ($F_{1,21} = 0.064$, $p = 0.803$), no difference in scarification rate between the two peccary species ($F_{1,22} = 0.001$, $p = 0.974$) and no significant effect of seed size on scarification rate ($F_{1,21} = 1.029$, $p = 0.322$). We also observed in the feces that the very hard seeds from Palmae species were broken in small parts.

The majority of defecated seeds were smaller than seven millimetres, ranging from 2 to 6 mm (Figure 2). Defecation rates ranged from zero (10 species) to 56.3%

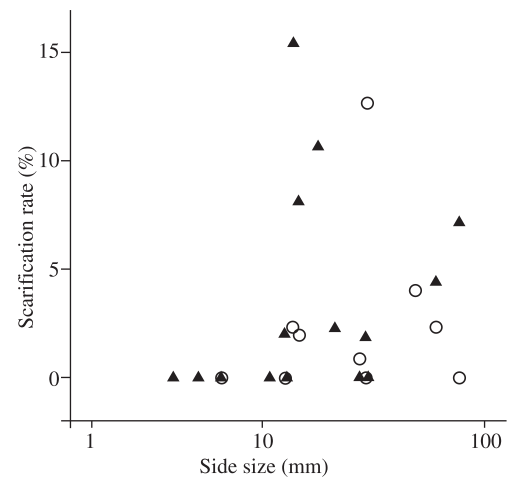

Figure 1. Relation between scarification rate (seeds scarified/seeds offered) and seed size for 16 Atlantic rainforest plant species consumed by white-lipped and collared peccaries (*Tayassu pecari* = ○; *Pecari tajacu* = ▲)

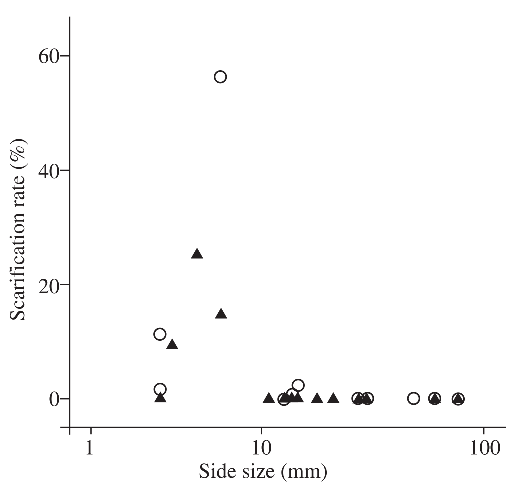

Figure 2. Relation between defecation rate (seeds defecated/seeds ingested) and seed size for 16 Atlantic rainforest plant species consumed by white-lipped and collared peccaries (*Tayassu pecari* = ○; *Pecari tajacu* = ▲)

(*Mauritia flexuosa*). Consequently, a very high proportion of the seeds consumed by the peccaries were likely simply destroyed during mastication and digestion. Of a total 2,230 seeds defecated, only three seeds were larger than six millimetres, representing *Inga* spp. (15 ± 1 mm) and *E. oleraceae* (14 ± 1 mm). Seed size had a significant effect on defecation rate ($F_{1,25}$ = 5.947, p = 0.022), showing increased seed size resulted in lower defecation rate. No interaction between the variables peccary species and seed size was observed ($F_{1,25}$ = 0.220, p = 0.643) and no significant difference in defecation rate between the two peccary species was found ($F_{1,25}$ = 0.841, p = 0.368).

Nine out of the 17 species tested did not germinate during control tests (Table 2). For the successful control tests, the germination rate varied from 3.2 to 86.4%. None of the 84 scarified seeds tested (six species) germinated, although at least three of these species (*E. oleraceae*, *Artocarpus heterophyllus* and *Inga* spp.) had high rates of germination during control tests. Three defecated species germinated (*Solanum paniculatum*, *S. stramonifolium*, and *P. guajava*), following passage through *T. pecari* (0.7, 0.4 and 16.3% respectively), and one species (*S. stramonifolium*) underwent germination after passing through the gut of *P. tajacu* (6.7%). None of these four species germinated in the control experiments.

4. Discussion

4.1. Seed fate

Although size effect is not significant, scarification was observed only in mediums and large seeds (>10 mm).

Table 2. List of the 18 species on which germination tests were performed on scarified, defecated and control seeds, with number of seeds tested and germination percentage (regardless of the peccary species).

Family/Species	Scarification		Defecation		Control	
	N	(%) of seeds germinated	N	(%) of seeds germinated	N	(%) of seeds germinated
ANACARDIACEAE						
Spondias spp.	1	0.0	-	-	76	0.0
APOCYNACEAE						
Rauvolfia sp.	2	0.0	-	-	-	-
ARALIACEAE						
Schefflera morototonii	-	-	522	0.0	100	0.0
ARECACEAE						
Attalea oleifera	-	-	21	0.0	30	0.0
Euterpe oleraceae	29	0.0	2	0.0	101	59.4
Mauritia flexuosa	1	0.0	-	-	31	3.2
CHRYSOBALANACEAE						
Licania tomentosa	-	-	-	-	22	86.4
EUPHORBIACEAE						
Margaritaria nobilis	-	-	97	0.0	90	0.0
FABACEAE						
Clitoria fairchildiana	-	-	-	-	96	17.7
Inga spp.	38	0.0	-	-	155	40.6
Tamarindus indica	-	-	-	-	16	6.3
MALPIGHIACEAE						
Byrsonima spicata	-	-	74	0.0	165	0.0
MORACEAE						
Artocarpus heterophyllus	13	0.0	-	-	55	60.0
MYRTACEAE						
Psidium cattleianum	-	-	70	0.0	200	17.5
Psidium guajava	-	-	205	12.2	183	0.0
SAPINDACEAE						
Unknown	-	-	1	0.0	79	0.0
SOLANACEAE						
Solanum paniculatum	-	-	145	0.7	32	0.0
Solanum stramonifolium Jacq.	-	-	525	4.4	116	0.0

The difference in scarification rates can be explained as smaller seeds can be swallowed without further breaking into smaller parts or can be totally destroyed in a single bite. Given that no scarified seeds germinated, mastication and subsequent spitting does not appear to contribute to increased germination rates in the focal species. Palm (Arecaceae) and legume (Fabaceae) taxa seem particularly susceptible to negative effects by scarification. Furthermore, a large number of seeds consumed, regardless of size, were simply destroyed by the combined action of chewing and digestion and no visible trace was found in the feces. The fact that some seeds were extracted from the pulp for count and measurement could have influenced scarification rate in two ways: an increase in scarification because the pulp offered less protection to the seed, or a decrease due to reduced chewing of the seeds to get the pulp. We believe that, most likely, neither process was predominant and that our measurements are representative.

Small seeds were significantly more defecated than larger seeds. Also, the only seeds that germinated after passage through digestive systems were small ones. The three smallest species (the two *Solanum* and *P. guajava*) had higher germination rates after defecation by at least one of the peccary species, when compared to controls. The increase was relatively small, but suggests a positive impact of the passage through the gut for these species. Combining the germination results with the potential beneficial effect of manure as a fertilizer, these species may achieve even greater seed germination and seedling survival (Traveset et al., 2007). These results are in accordance with previous studies showing that small seeds (≤10 mm) from numerous tree species germinated successfully after being recovered in peccary feces (Beck, 2005).

4.2. Role of peccaries

Our results show the double role of peccaries of both species and that there is a separation in the seed fate based on seed size. The consumption and subsequent defecation of small seeds defines peccaries as seed dispersers. Undoubtedly, peccaries have the potential to disperse small seeded species over long distances, and seem to have a beneficial effect on seed germination for at least some species. Considering that peccaries have large home ranges (up to 8,000 ha for *P. tajacu* and 20,000 ha for *T. pecari*; Sowls, 1997) and have retention times of up to six days, they have the ability to generate a large seed-shadow, aiding the dispersion of small seeded species through landscapes and habitats and promoting gene flow among plant populations (Beck, 2005). On a smaller scale, expectoration of seeds a few metres away from where the fruit is picked up is a short-distance mode of dispersion and, although not measured, we observed this behaviour during consumption.

Seed predation is an important mechanism structuring the plant community (Janzen, 1970; Fragoso, 1997; Hulme and Benkman, 2002). From the large proportion of seeds consumed and destroyed, it is also clear that peccaries are efficient seed predators. Peccaries are highly specialised among granivores due to their ability to break very solid seeds (Kiltie, 1982; Bodmer, 1991). Peccaries have a negative impact on the survival of large seeds, but also impact a large proportion of small ones.

4.3. Conservation in the Northeastern Atlantic rainforest

The only large mammal that is known with certainty to be present in the Northeastern Atlantic rainforest is the collared peccary (*P. tajacu*). The white-lipped peccary (*T. pecari*), the tapir (*Tapirus terrestris* Linnaeus, 1758) and the brocket deer (*Mazama* spp.) are possibly regionally extinct (Mendes Pontes et al., 2005; Monteiro da Cruz et al., 2002). Because peccaries are predators, their disappearance from the ecosystem could lead to decreased biodiversity, changes in species composition and altered community dynamics (Janzen, 1970; Fragoso, 1997; Silman et al., 2003; Wyatt and Silman, 2004). According to the results of our study, long distance dispersal of some small-seeded species would be altered. However, birds and smaller mammals could probably disperse many of these species (Hulme and Benkman, 2002), although neither birds nor other mammals are known to be as generalist as peccaries. Also, the herd size of peccaries has no equivalent in the Atlantic rainforest.

The principal problem facing a fragmented Atlantic rainforest is the limited dispersal or even extinction of tree species with large fruits (Silva and Tabarelli, 2000; Santos et al., 2006). We suggest that peccaries do not act as long distance dispersers for these plant species, but rather as predator. Actually, primates are more likely to act as the legitimate dispersers for species with large seeds (Lapenta et al., 2008). With the disappearance of peccaries, the dispersal problem is more acute. Hard and large seeded species, such as a majority of palms, would have higher recruitment near the mother plants and therefore more clumped or aggregated spatial distributions, leading to localised reduction in tree diversity (Wyatt and Silman, 2004).

Peccary conservation in Atlantic rainforest fragments of the Northeast is mainly promoted for the unique and efficient seed predation of a large diversity of fruits and seeds, and contribution to the dispersal of small seeded species. The double role of peccaries as predators and dispersers is unmatched among animals of the Atlantic rainforest and their disappearance certainly will affect plant community composition and diversity.

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