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ORIGINAL PAPER

Removal of palm fruits and ecosystem engineering in palm stands by white-lipped peccaries (*Tayassu pecari*) and other frugivores in an isolated Atlantic Forest fragment

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Abstract Long-term studies in a 2,178 ha fragment of semideciduous Atlantic Forest demonstrated important interactions between white-lipped peccaries (*Tayassu pecari*) and the common palms, *Syagrus romanzoffiana* and *Euterpe edulis*. We conducted fruit removal and medium-to-large-sized mammalian exclusion experiments to: (1) quantify seasonal fruit consumption from high-density patches beneath parent trees by *T. pecari* and other consumers, and (2) measure impacts of *T. pecari* rooting and foraging activities on seedling dynamics in *E. edulis* stands. A diverse array of fauna consumed *S. romanzoffiana* fruits. During the dry season, when *S. romanzoffiana* palms provided 68% of fruit dry weight in the fragment, *T. pecari* consumed significantly greater amounts than other consumers, and along with *Pecari tajacu* and *Tapirus terrestris*, were potential seed dispersers. The rodents, *Sciurus ingrami* and *Agouti paca*, consumed most *S. romanzoffiana* fruits in the wet season, acting as both seed dispersers and predators. More than 95% of *E. edulis* fruit removal was due to seed predation by *T. pecari*. Intense removal during the dry season was closely linked with previously documented range shifts and habitat preferences by *T. pecari*. Exclusion plot experiments in *E. edulis* (palmito) stands showed that the number and proportion of nonpalmito (not *E. edulis*) seedlings increased dramatically in the absence of *T. pecari* rooting and foraging activities that disturbed soil and thinned seedlings. We discuss the importance of these ecosystem engineering activities and palm-peccary trophic interactions for long-term maintenance of *E. edulis* stands and *T. pecari* populations, as well as water balance, in the forest fragment.

Keywords Collared peccary · *Euterpe edulis* · Ecosystem engineer · Exclusion experiment · Frugivory · Fruit removal · *Syagrus romanzoffiana* · Tropical forest fragment · White-lipped peccary

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Introduction

White-lipped peccaries (*Tayassu pecari*) are wide-ranging frugivorous/omnivorous ungulates that form large herds (40 to >200 individuals) and comprise up to 34% of non-flying mammalian biomass in Neotropical forest formations (Kiltie and Terborgh 1983; Sowls 1997; Fragoso 1998a; Cullen et al. 2001). They are important seed predators and dispersers and have secondary impacts on forest vegetation via soil disturbance and seedling damage during rooting and foraging activities (Kiltie and Terborgh 1983; Fragoso 1998b; Painter 1998; Silman et al. 2003; Keuroghlian and Eaton 2008a). These activities may be especially concentrated in relatively pure stands of fruiting trees, like palm-dominated swamps (Fragoso 1998b; Keuroghlian and Eaton 2008a), where in addition to trophic effects, their impacts on soil, litter, and subsequent seedling dynamics could be considered ecosystem engineering (Jones et al. 1994; Beck 2005).

Studies from a diverse range of tropical locations have shown that both white-lipped peccaries and the smaller collared peccaries (*Pecari tajacu*) have a variety of important interactions with palms (Terborgh 1986; Bodmer 1989a, b; Kiltie 1981; Fragoso 1998b; Painter 1998; Silman et al. 2003; Keuroghlian and Eaton 2008a). In Peru, Kiltie and Terborgh (1983) observed extensive foraging episodes by white-lipped peccaries in areas of high palm density and fruit abundance. Kiltie (1980) noted that white-lipped peccaries consumed large quantities of *Iriartea* sp. palm seeds in a predatory manner and showed movement patterns that appeared to link concentrated patches of the *Iriartea* sp. seeds. Bodmer (1989a, b) found that the fruits of *Iriartea* sp. were available most of the year, and that they were the most common food items in 75% of white-lipped peccary stomach samples. He also noted that the hard seeds of the palm *Jessenia* sp. were potentially dispersed by white-lipped and collared peccaries (Bodmer 1989a). In Bolivia, Painter (1998) noted that white-lipped peccaries predated a large proportion of the fruits produced by the palm, *Socratea exorrhiza* and played an important role in limiting *S. exorrhiza* palm aggregations. Fragoso (1998b) noted that both white-lipped and collared peccaries ate and potentially dispersed seeds of the palm *Mauritia flexuosa*, and that white-lipped peccaries spent a large portion of their time foraging in wetlands dominated by this palm. Silman et al. (2003) demonstrated the cascading effects of altered *Astrocaryum murumuru* seed predation by white-lipped peccaries in a Peruvian tropical forest.

Palms are often considered keystone plant resources, because they are abundant during periods of general fruit scarcity, and they are consumed by a wide variety of frugivorous species (Leighton and Leighton 1983; Terborgh 1986; Bodmer 1990a; Peres 1994; Galetti et al. 1999; Keuroghlian and Eaton 2008a). In the absence of these palm species, local extinctions of frugivore species would be expected (Mills et al. 1993; Galetti and Aleixo 1998). Similarly, alterations of the frugivore fauna have important consequences for palm species, e.g., when seed predation or seed dispersal are affected (Silman et al. 2003; Galetti et al. 2006).

In southeastern Brazil, the seasonal inland-plateau region (*Planalto*) of the Atlantic Forest is highly fragmented (Viana et al. 1997). In the state of São Paulo, it covers only 2% of its original extent (Viana et al. 1997; Ditt 2002). Mammal surveys in the *Planalto* region of São Paulo showed that collared peccaries remained in about half and white-lipped peccaries in only about one-fifth of the surviving forest fragments (Cullen et al. 2000; Ditt 2002). Hypotheses explaining population declines and local extinctions of peccary populations encompass a combination of fragmentation-related pressures, including range reduction, hunting, edge encroachment, loss of habitat diversity, and loss of key resources, like fruits, which may be tied to rare or threatened habitats (Cullen et al. 2000; Keuroghlian et al. 2004; Keuroghlian and Eaton 2008a, b).

In forest fragments, reductions in the production of fleshy fruits have been documented (Wright and Duber 2001; Tabarelli et al. 2004). A decline in fruit production, as well as a host of other possible fragmentation-related changes in the abundance and distribution of fruit resources (Galetti and Aleixo 1998; Fleury and Galetti 2006), would be expected to impact fruit consumers, including the highly frugivorous peccaries (Bodmer 1990a; Keuroghlian and Eaton 2008a). One of the larger Atlantic Forest fragments in the *Planalto* region, i.e., 2,178 ha Caetetus Ecological Station (EEC), has white-lipped and collared peccary populations that persist at densities similar to a much larger (16 times) *Planalto* fragment (Cullen et al. 2000; Keuroghlian et al. 2004), suggesting that historical densities have been maintained. Long-term studies at the EEC have provided several lines of evidence demonstrating interactions between peccaries and the palm species, *Syagrus romanzoffiana* and *Euterpe edulis* (Keuroghlian et al. 2004; Keuroghlian and Eaton 2008a, b). *S. romanzoffiana* and *E. edulis*, locally called “jerivá” and “palmito”, respectively, are two of the most widespread palms in the semideciduous *Planalto* region of the Atlantic Forest (Fleury and Galetti 2004). Both palms play an important role in sustaining a wide variety of wildlife, especially during periods of low fruit diversity and availability (Paschoal and Galetti 1995; Galetti and Aleixo 1998; Matos and Watkinson 1998; Galetti et al. 1999, 2001; Cullen et al. 2001; Fleury and Galetti 2004; Keuroghlian and Eaton 2008a), though their importance varies according to the abundance and diversity of alternative fruits at specific locations. Altrichter et al. (2001) reported similar variability in the importance of *Ficus* sp. fruits to white-lipped peccaries in Costa Rica.

A 5-year survey of forest-floor fruit availability among all habitats at the EEC showed that the diversity of fruit species was greater in the wet season (Keuroghlian and Eaton 2008a). However, the quantity (dry weight and numbers) of available fruits was higher in the dry season. Dry season abundance was due primarily to the fruits of *S. romanzoffiana*, which made up 68% of total fruit dry weight (vs. 38% of total fruit dry weight in the wet season). Due to its contribution to overall fruit abundance and because of the diverse array of mammals, birds, reptiles, and insects that consumed the fruits (Keuroghlian 1990; Galetti et al. 2001; Guimarães et al. 2005; Keuroghlian and Eaton 2008a), *S. romanzoffiana* could be considered a keystone species at the EEC (Keuroghlian and Eaton 2008a). Keuroghlian and Eaton (2008a) found a significant correlation between the availability of *S. romanzoffiana* fruits (based on dry weight) and consumption of the fruits by white-lipped peccaries (based on surveys of foraging trails), indicating that white-lipped peccaries were tracking the abundance of *S. romanzoffiana* fruits at the EEC. An analysis of 20 white-lipped and thirteen collared peccary scats showed that the pulp (exocarp) fibers of *S. romanzoffiana* fruits were dominant components of fecal samples for both peccary species during both seasons (white-lipped peccaries: 35% of plant particles in the dry season and 26% in the wet season; collared peccaries: 34% of plant particles in the dry season, and 16% in the wet season) (Keuroghlian and Eaton 2008a). Whole fruits and seeds of *S. romanzoffiana* also dominated tapir (*Tapirus terrestris*) scats collected at the EEC (Galetti et al. 2001).

Even though the abundance of *E. edulis* fruits (dry weight and numbers) was relatively low, ranking 14th out of 34 fruit species collected during the dry season, it was the second most consumed fruit by white-lipped peccaries (based on surveys of foraging trails) (Keuroghlian and Eaton 2008a). *E. edulis* fruit abundance (dry weight) was significantly correlated with consumption of the fruits by white-lipped peccaries, and *E. edulis* fruit fibers and seed parts made up a significant percent of white-lipped peccary fecal samples in the dry season (15% of plant particles in the dry season, and 2% in the wet season). In addition, the seasonal movements and ranges of the white-lipped peccaries (based on a 5-year radio telemetry study), as well as their most significant habitat preferences, were linked to *E. edulis* stands and fruiting periods (Keuroghlian et al. 2004; Keuroghlian and Eaton 2008b). The stands were aggregated near headwater streams and springs, and the fruiting periods peaked several times during the dry season (Keuroghlian et al. 2004; Keuroghlian and Eaton 2008b). During concentrated foraging bouts in *E. edulis* stands, white-lipped peccaries characteristically rooted the humid soil and litter in search of fruits, leaving many tracks and signs of vegetation disturbance. In comparison to white-lipped peccaries, collared peccaries and tapirs at the EEC consumed negligible quantities of *E. edulis* fruits, i.e., seed fibers made up 0.1% of plant parts in fecal samples from 13 collared peccary scats, and out of 46 tapir scats examined, only one *E. edulis* seed was found (Galetti et al. 2001; Keuroghlian and Eaton 2008a).

For the current study, we used two experiments to: (1) improve our understanding of the interactions between peccaries and palm species in an Atlantic Forest fragment and (2) complement long-term forest fragment studies of peccary frugivory, habitat preference, and range use. Focusing on the two palm species, *S. romanzoffiana* and *E. edulis*, that are widespread in the seasonal *Planalto* region of the Atlantic Forest, we simulated high-density fruit patches characteristic of areas beneath parent trees and documented removal to measure the quantity of fruits consumed by peccaries and other fruit consumers during the dry and wet seasons. These experiments allowed us to evaluate the relative importance of different fruit consumers in terms of palm seed predation or potential seed dispersal. In stands of *E. edulis* palms, where the wet soil was extensively rooted and trampled by white-lipped peccaries during fruiting periods, we investigated seedling dynamics using plots that excluded medium to large-sized mammals. Our objective was to measure changes in seedling numbers and composition (i.e., *E. edulis* vs. all other plant species) over 1 year in the presence and absence of white-lipped peccary activity. This experiment allowed us to evaluate the importance of white-lipped peccaries in modifying or maintaining the plant community of *E. edulis* stands. We hypothesized that *E. edulis* seedling densities and percent composition would increase in the absence of white-lipped peccary activity (i.e., in exclusion plots). Finally, we integrated results from both experiments and previous long-term studies to evaluate the role of white-lipped peccaries as ecosystem engineers in *E. edulis* habitats.

Methods

Study site

Caetetus Ecological Station (EEC), 22°30′S and 49°45′W, is a 2,178 ha fragment of seasonal tropical forest in the *Planalto* region of the Atlantic Forest (Keuroghlian et al. 2004). 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 a local 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 (Keuroghlian et al. 2004; Nunes and Galetti 2007).

The vegetation at the EEC is classified as tropical, semideciduous, mesophytic, broadleaf forest, which places it in the general category of seasonal tropical forests (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 1,200–1,600 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).

Three palm species occur at the EEC: *S. romanzoffiana*, *S. oleracea*, and *E. edulis* (Keuroghlian and Eaton 2008a). *S. romanzoffiana* occurs in primary forest formations of both humid stream valleys and drier plateau regions of the EEC. The trees may occur singly or in low-density, open aggregations. *E. edulis* at the EEC occurs in dense aggregations (hereafter called *E. edulis* or palmito habitats) that are closely associated with springs, seeps, and headwater streams. *E. edulis* dominates these forest formations making up about 31% of the trees >1 m in height (A. Keuroghlian, unpublished data). Throughout much of its range in the Atlantic Forest, *E. edulis* is threatened by illegal harvesting for “hearts of palm”, i.e., the apical meristem of the palm that is a popular food item (Galetti and Fernandez 1998). Except for the absence of jaguar (*Panthera onca*), the non-flying mammalian fauna of the EEC is well represented in comparison to other *Planalto* forest fragments of similar or larger area (Cullen et al. 2000).

Short-term fruit removal experiments

During 1998 and 1999, we conducted 2-week fruit removal experiments (Vander Wall 1994) during the dry and wet seasons to measure short-term quantitative impact of peccaries and other ground-dwelling frugivores on the two most common palm species at the EEC, i.e., *E. edulis* and *S. romanzoffiana* (Keuroghlian and Eaton 2008a). Both palm species produced fruits asynchronously, so the duration and intensity of fruiting peaks within their ranges varied temporally and spatially (Keuroghlian and Eaton 2008a). Typically, fruits that fell to the forest floor were clumped beneath parent trees in patches of 50 to more than 300. At the patches, a wide variety of animal tracks and signs of fruit consumption were readily observed. For the removal experiments, we set up fruit patches that simulated the seasonal timing and distribution of forest-floor palm fruits beneath parent trees.

We conducted three to four removal experiments (hereafter called experimental runs) for each palm species during both dry (May–August) and wet (December–March) season months. For each experimental run, we collected 1,000 ripe fruits from the infructescences of several *E. edulis* or *S. romanzoffiana* trees and set out 10 plots of 100 fruits beneath 10 randomly selected parent trees. Within the EEC, stands of *E. edulis* ranging from 0.05 to 3 ha have a clumped distribution due to their association with headwater streams and springs (total area of *E. edulis* habitat within EEC, 19 ha) (Keuroghlian and Eaton 2008b), so selection of parent trees included two steps, i.e., random selection of stands followed by random selection of individual trees within stands. The trees of *S. romanzoffiana* are more widely and evenly distributed over a large area that includes a range of primary forest formations (total area of primary habitat within EEC, 1,800 ha) (Keuroghlian and Eaton 2008b), so parent trees were selected by locating individuals close to randomly selected trails and trail markers (trails marked every 20 m). The trails, which had been established for fruit and mammal censuses, formed a grid that sampled habitat types in proportion to their availability at the EEC (Keuroghlian 1990; Keuroghlian and Eaton 2008a). To ensure that fruits fallen from parent trees were not mixed with those in the experimental plots, we chose trees that had recently completed or were about to begin fruiting.

After fruits had been placed beneath parent trees, we cleared the area around plots so that tracks of visiting animals could be identified. We returned to the plots daily to document the number of fruits removed and identify fruit consumers from indirect signs, i.e., tracks and method of consumption (described in "Results"). Fruits that were missing from the plots or eaten were considered removed. For analyses of daily and final (end of run) fruit removal, the sample size of an experimental run was equal to the number of fruit plots (usually ten), and for seasonal comparisons, experimental runs were the replicates (3–4 runs per season).

To describe fruit removal trends of white-lipped and collared peccaries during experimental runs and compare them between seasons, we regressed cumulative daily removal of the palm fruits on day and used a dummy variable to indicate season (Neter et al. 1996). This technique, regression with an indicator variable (season), allowed us to fit dry and wet season regression models and test for differences between dry and wet season regression coefficients (intercepts and slopes) (Neter et al. 1996). Both cumulative daily removal and day were natural-log transformed to meet regression assumptions, i.e., homogeneity of variance and normal distribution of residuals.

To compare palm fruit removal by peccaries with other fruit consumers, and compare fruit removal by non-peccary consumers between seasons, we used final (end of run) fruit removal as the dependent variable in two factorial ANOVAs in CRD, one for *E. edulis* fruits and one for *S. romanzoffiana* fruits. The model factors were consumer category (white-lipped peccaries, collared peccaries, tapir, rodents, and other), season (dry and wet), and the interaction of consumer category and season. If we found a significant difference among consumer categories in terms of final fruit removal, we conducted pair-wise post tests (Wilkinson 1990) to identify the species or consumer categories that differed significantly. We maintained an experiment-wise significance level of $\alpha = 0.05$ by using the Dunn-Šidák comparison-wise adjustment (Sokal and Rohlf 1981).

We compared final (end of run) fruit removal totaled over all consumer categories between the two palm species and between seasons with a 2 × 2 factorial ANOVA in CRD. Final removal by all consumers was the dependent variable, and model factors were palm species (*E. edulis* and *S. romanzoffiana*), season (dry and wet), and the interaction of palm species and season. For all of the regressions and ANOVAs described above, we used Breusch-Pagan and Kolmogorov tests to evaluate variance homogeneity and normality of error terms (Neter et al. 1996).

Exclusion experiments

To investigate the impacts of white-lipped peccaries and other ground-dwelling mammals on the seedling dynamics of *E. edulis* stands, we conducted exclusion plot experiments beginning in September 1999. The experimental set up included random selection of ten *E. edulis* stands with areas greater than 1 ha, followed by random selection of one location within each stand for placement of adjacent exclusion and control plots. Stands with areas greater than 1 ha were used to increase the probability of mammal visits. The exclusion plots measured 1.5 × 1.5 m (2.25 m^2) and were enclosed by 1.2 m high fencing to prevent medium to large-sized mammals from entering the plots. Control plots without fencing also measured 1.5 × 1.5 m and were located adjacent to the exclusion plots.

At the beginning of the experiment, we marked and counted all seedlings (plants <50 cm in height) in the control and exclusions plots, and classified them as palmito (*E. edulis*) or nonpalmito (all other plant species). We marked the plants in order to document the appearance of new seedlings during the experiment. Using the counts at the beginning of the experiment, we compared the number of palmito and nonpalmito seedlings between control and exclusion plots using a 2 × 2 factorial ANOVA in CRD ($\alpha = 0.05$). Model factors were plot type (control and exclusion), seedling type (palmito and nonpalmito), and the interaction of plot type and seedling type. To meet the assumptions of the ANOVA, we used a natural-log transformation of the count data.

For 1 year, we repeated the counts and marked new palmito and nonpalmito seedlings every 4 months. To analyze changes in the plots, we compared the number of new palmito and nonpalmito seedlings that appeared in control and exclusion plots during the first year of the experiment, again, applying a 2 × 2 factorial ANOVA in CRD ($\alpha = 0.05$). Similar to the ANOVA at the beginning of the experiment, we used a natural-log transformation of the count data.

Results

For both *E. edulis* and *S. romanzoffiana* fruit removal experiments, we conducted three wet season and four dry season experimental runs. All experimental runs with *E. edulis* included ten plots of 100 fruits each (70 total plots). However, because of the difficulty of finding sufficient ripe fruits of *S. romanzoffiana* during some months, one of the wet season runs had 6 plots of 100 fruits each, and two runs during the dry season had 7 and 9 plots of 100 fruits, respectively (62 total plots). After day 10 of the removal experiments, only minor fruit consumption by small mammals occurred, either because fruit plots had been depleted, or in some cases, because fruits had been significantly altered by fungus and fermentation. Consequently, for regressions and estimates of final (end of run) fruit removal, we designated day 10 as the end of experimental runs.

Short-term removal of *S. romanzoffiana* fruits

Indirect animal signs at fruit plots, including tracks and the manner (or method) of fruit consumption demonstrated that *S. romanzoffiana* fruits were removed by a wide variety of consumers including both peccary species, tapirs (*Tapirus terrestris*), and medium to large-sized rodents (primarily *Sciurus ingrami* and *Agouti paca*) (Fig. 1). An assortment of species that were infrequent consumers of forest-floor *S. romanzoffiana* fruits, or that could not be identified reliably from indirect signs, were placed in an "other" category (Fig. 1). These included primates (*Cebus apella*, *Leontopithecus chrysopygus*), raccoons (*Procyon cancrivorus*), coatis (*Nasua nasua*), opossums (*Didelphis albiventris*), crab-eating foxes (*Cerdocyon thous*), and unidentified small mammals and birds. We differentiated white-lipped and collared peccary tracks by their size and number. White-lipped peccary subherds at the EEC, which foraged independently in groups of 40 or more animals, left many more tracks at plots than collared peccary herds, which had an average of nine individuals (Keuroghlian et al. 2004). Similar to the observations of Fragoso (1998b) on peccary consumption of *M. flexuosa* fruits, both peccary species would characteristically chew or suck off the soft outer exocarp of *S. romanzoffiana* fruits and spit out the fruit remains as they foraged (Keuroghlian and Eaton 2008a). The chewing and spitting of the peccaries caused the exocarp fibers that remained on the fruits to protrude unnaturally, opposite to the natural lie (or grain) of the fibers. Many of the fruits were spit out as the peccaries foraged near the fruit plot, while others were discarded as they walked varying distances from the parent trees. This behavior classifies both peccary species as potential dispersers of *S. romanzoffiana* seeds. Tapir visits to the plots were easily identified with track evidence, and based on observations of scat, we know that tapirs swallowed the fruits whole and were potential dispersers of *S. romanzoffiana* seeds (Galetti et al. 2001). The medium to large-sized rodents, i.e., squirrels (*S. ingrami*) and pacas (*A. paca*), removed the soft exocarp leaving the woody endocarp clean or with indentations.

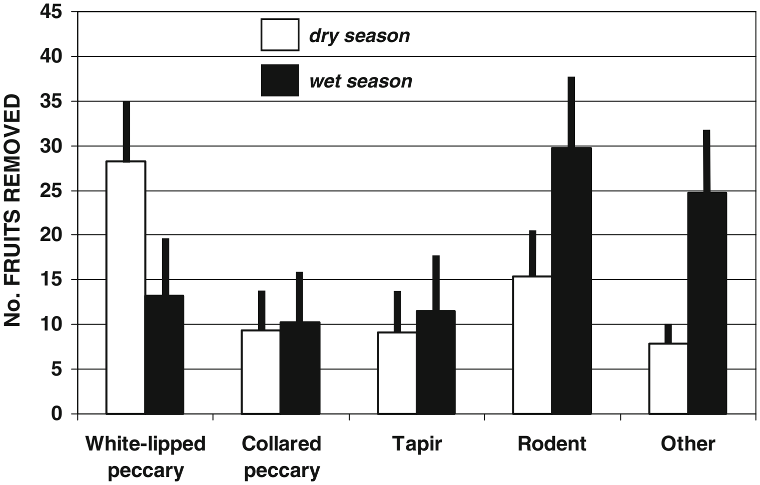

Fig. 1 Seasonal removal of *S. romanzoffiana* fruits by different fruit consumer categories at Caetetus Ecological Station, São Paulo, Brazil. Means plus standard errors of final removal are shown (final removal = the number of fruits removed from plots of 100 fruits after 10 days). The Rodent category included *S. ingrami* and *A. paca*, and the "other" category included species that could not be identified reliably from tracks and other animal signs

Many of the rodent-manipulated seeds were intact indicating that *S. ingrami* and *A. paca* were potential primary dispersers. However, *S. ingrami* is known to be an important predator of post-dispersal *S. romanzoffiana* seeds (Fleury and Galetti 2006). Brown capuchins (*Cebus apella*) would bite and scrape off part of the exocarp with their teeth and then toss the fruits aside. In contrast to the peccaries, they scraped the exocarp with the lie (natural grain) of the fibers.

Regressions of natural-log transformed cumulative daily removal of *S. romanzoffiana* fruits on natural-log transformed days with season as a dummy variable were significant for both peccary species (white-lipped: $F = 20.48$, $df = 3, 678$, $P < 0.0001$; collared: $F = 8.02$, $df = 1, 680$, $P = 0.0047$). For the white-lipped peccaries, the dry season removal rate, i.e., the slope, was significantly greater than the wet season removal rate ($t = 2.97$, $df = 1$, $P = 0.0031$), and, as expected, intercepts did not differ significantly between the seasons ($t = -1.22$, $df = 1$, $P = 0.2203$). Figure 2a shows means of cumulative daily removal of *S. romanzoffiana* fruits by white-lipped peccaries for dry and wet season runs. Dry season removal reached an asymptote of 28% after 7 days, while wet season removal leveled off at 14% after only 2 days. For collared peccaries, neither removal rates nor intercepts differed significantly between the seasons (slope: $t = 0.23$, $df = 1$, $P = 0.8151$; intercept: $t = -0.44$, $df = 1$, $P = 0.6613$). Therefore, we pooled seasonal data to present means of cumulative daily removal (Fig. 2b). For the collared peccaries, a removal asymptote of 9% was reached after 3 days.

The comparison of final (end of run) removal of *S. romanzoffiana* fruits among five consumer categories (white-lipped peccaries, collared peccaries, tapirs, rodents, and other), and two seasons (dry and wet), using a 5 × 2 factorial ANOVA, showed that the interaction of consumer category and season was significant ($F = 2.41$, $df = 4, 300$, $P = 0.0495$). Therefore, we compared consumer categories within seasons employing 20 pair-wise post tests, and we compared seasonal final removal within non-peccary consumer categories using an additional three post tests (Dunn-Šidák comparison-wise significance level for 23 comparisons: $\alpha' = 0.0026$). The results of the post tests are presented in Table 1 and summarized in Fig. 3.

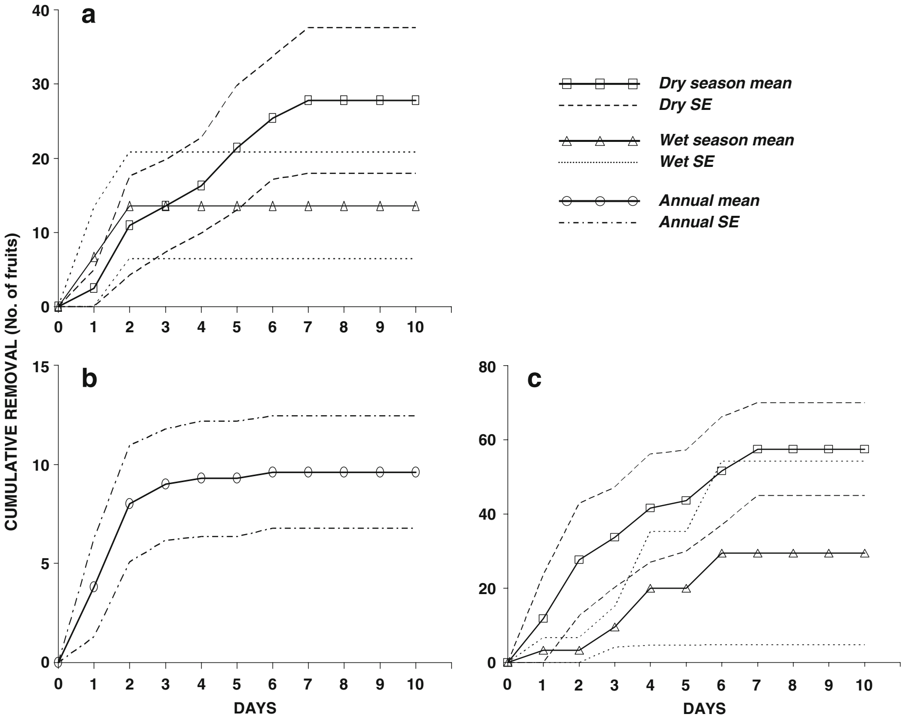

Fig. 2 Mean cumulative fruit removal (±SE) over 10 days from experimental plots of 100 fruits located beneath parent palms: **a** *S. romanzoffiana* fruits removed by white-lipped peccaries during the dry and wet season runs, **b** *S. romanzoffiana* fruits removed by collared peccaries during all runs (i.e., annual means and SE), and **c** *E.edulis* fruits removed by white-lipped peccaries during dry and wet season runs at Caetetus Ecological Station, São Paulo, Brazil

During the dry season, white-lipped peccaries removed significantly more *S. romanzoffiana* fruits (28.3%, SE ±7.00) than all other consumer categories, and large rodents removed significantly more fruits than collared peccaries, tapirs, and the "other" category (Table 1; Figs. 1, 3). Final removal did not differ significantly between collared peccaries, tapirs, and "others" for the dry season (Table 1; Figs. 1, 3). During the wet season, large rodents consumed significantly more *S. romanzoffiana* fruits (29.8%, SE ±8.11) than the remaining consumer categories, and the "other" category consumed significantly more fruits (24.8%, SE ±7.20) than both peccary species and tapirs (Table 1; Figs. 1, 3). There were no significant differences among the peccary and tapir categories during the wet season. Post test comparisons of seasonal removal within non-peccary consumer categories showed that rodents and "others" removed significantly more *S. romanzoffiana* in the wet season (Table 1; Figs. 1, 3), while removal by tapirs did not differ seasonally.

Short-term removal of *E. edulis* fruits

Records of animal tracks and the state of partially eaten fruits at *E. edulis* plots, as well as seasonal patterns of fruit removal, showed that white-lipped peccaries were the predominant consumers of these fruits. The white-lipped peccaries predated *E. edulis* seeds and frequently discarded the outer fibrous husks (Keuroghlian and Eaton 2008a). On average, they

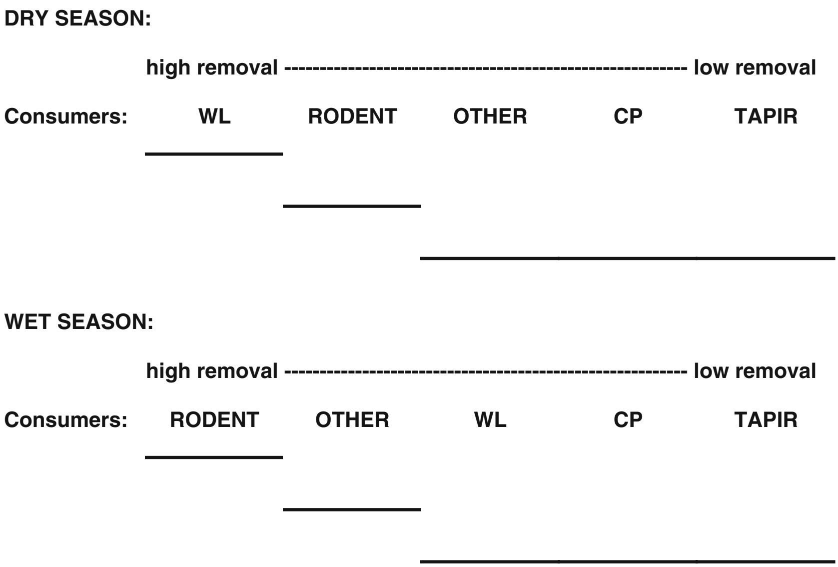

Fig. 3 Summary of post test results comparing final removal (after 10 days) of *S. romanzoffiana* fruits between fruit consumer categories during the dry and wet seasons, Caetetus Ecological Station, São Paulo, Brazil. Consumer categories that do not share a horizontal line were significantly different in terms of the number of fruits removed (WL white-lipped peccaries, CP collared peccaries, rodent = *S. ingrami* and *A. paca*, and "other" = species not identified reliably from tracks and other animal signs)

removed 59.8% (SE ±7.81) of the fruits in the dry season and 29.5% (SE ±8.38) in the wet. These values corresponded to 95 and 97% of total forest-floor *E. edulis* fruits removed by all fruit consumers during dry and wet season experimental runs. Thirty-seven% of the fruits during the dry season and 70% during the wet season remained untouched. Besides white-lipped peccaries, the only other consumers of forest-floor *E. edulis* fruits were unidentified small mammals and birds, which we included in an "other" category. These removed 3.2% (SE ±1.43) and 0.8% (SE ±0.64) of the fruits during the dry and wet seasons, respectively. Collared peccaries, tapirs (*T. terrestris*), pacas (*A. paca*), and squirrels (*S. ingrami*) did not remove *E. edulis* fruits from the experimental plots. Previous scat analyses also showed negligible consumption of *E. edulis* fruits by collared peccaries and tapirs at the EEC (Galetti et al. 2001; Keuroghlian and Eaton 2008a).

For the 2 × 2 factorial ANOVA comparing final (end of run) removal of *E. edulis* fruits between the two consumer categories (white-lipped peccaries and other) and seasons (dry and wet), the interaction between consumer category and season was significant ($F = 5.65$, $df = 1, 136$, $P = 0.0188$). Therefore, we used post tests to compare final removal between consumer categories within seasons, and final removal by the "other" category between seasons. Removal of *E. edulis* fruits by white-lipped peccaries was significantly greater than removal by the "other" category during both seasons (dry: $F = 67.41$, $df = 1, 136$, $P < 0.0001$, wet: $F = 11.76$, $df = 1, 136$, $P = 0.0008$, Dunn-Šidák comparison-wise significance level: $\alpha' = 0.0253$). Final removal by the "other" category did not differ significantly between seasons.

The regression of natural-log transformed cumulative daily removal of *E. edulis* fruits by white-lipped peccaries on natural-log transformed days with season as a dummy variable was highly significant ($F = 61.42$, $df = 3, 876$, $P \ll 0.0001$). The removal rate of

Table 1 Results of post tests comparing final removal (after 10 days) of *S. romanzoffiana* fruits among consumer categories within seasons, and between seasons within non-peccary consumer categories, Caetetus Ecological Station, São Paulo, Brazil (Dunn-Šidák comparison-wise significance level for 23 comparisons, $\alpha' = 0.0026$)

Post test comparison	*F*	*df*	*P* (* = Significant difference)
Consumer category comparisons			
Dry season			
White-lipped versus collared	24.95	1, 300	≪0.0001*
White-lipped versus tapir	24.59	1, 300	≪0.0001*
White-lipped versus rodents	33.54	1, 300	≪0.0001*
White-lipped versus other	22.97	1, 300	≪0.0001*
Collared versus tapir	5.99	1, 300	0.0149
Collared versus rodents	10.77	1, 300	0.0012*
Collared versus other	5.21	1, 300	0.0232
Tapir versus rodents	10.53	1, 300	0.0013*
Tapir versus other	5.04	1, 300	0.0255
Rodents versus other	9.48	1, 300	0.0023*
Wet season			
White-lipped versus collared	6.98	1, 300	0.0,087
White-lipped versus tapir	7.78	1, 300	0.0,056
White-lipped versus rodents	23.48	1, 300	≪0.0001*
White-lipped versus other	18.33	1, 300	<0.0001*
Collared versus tapir	6.03	1, 300	0.0146
Collared versus rodents	20.35	1, 300	≪0.0001*
Collared versus other	15.58	1, 300	0.0001*
Tapir versus rodents	21.71	1, 300	≪0.0001*
Tapir versus other	16.77	1, 300	<0.0001*
Rodents versus other	37.84	1, 300	≪0.0001*
Seasonal comparisons			
Non-peccary categories			
Tapir, dry versus wet	3.39	1, 300	0.0667
Rodents, dry versus wet	22.55	1, 300	≪0.0001*
Other, dry versus wet	15.61	1, 300	0.0001*

E. edulis fruits (i.e., the slope) during the dry season was significantly greater than the removal rate during the wet season ($t = 2.65$, $df = 1$, $P = 0.0081$). Intercepts, as expected, did not differ between seasons ($t = 0.55$, $df = 1$, $P = 0.5850$). Figure 2c shows means of cumulative daily removal of *E. edulis* fruits by white-lipped peccaries for dry and wet season runs. Dry season cumulative removal reached an asymptote of 59% after 7 days, while wet removal reached asymptotes of 20 and 30% after 4 and 6 days, respectively.

S. romanzoffiana versus *E. edulis* removal

The 2 × 2 factorial ANOVA comparing final (end of run) removal of *E. edulis* and *S. romanzoffiana* fruits summed over all consumer categories showed a significant interaction between the two model factors, palm species and season ($F = 13.61$, $df = 1, 128$, $P = 0.0003$). Consequently, we conducted four post tests to compare palm species within seasons and compare seasons within palm species category (Dunn-Šidák comparison-wise significance level for four comparisons: $\alpha' = 0.0127$). Removal summed over all consumer categories was significantly greater for *S. romanzoffiana* fruits than *E. edulis* fruits during both seasons (dry: $F = 208.38$, $df = 1, 128$, $P < 0.0001$; wet: $F = 124.68$, $df = 1, 128$, $P \ll 0.0001$) (Fig. 4). Comparisons between seasons showed that *E. edulis* fruit removal was greatest in the dry

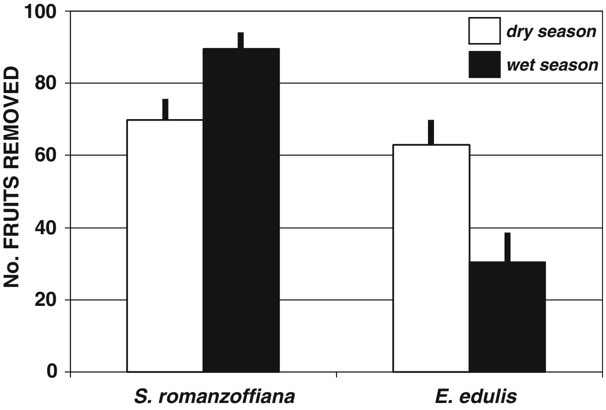

Fig. 4 Total removal of *S. romanzoffiana* and *E. edulis* fruits summed over all fruit consumer categories for the dry and wet seasons at Caetetus Ecological Station, São Paulo, Brazil. Means plus standard errors of final removal are shown (final removal = the number of fruits removed from plots of 100 fruits after 10 days)

season (dry: 62.9%, SE ±7.38; wet 30.3%, SE ±8.39; $F = 93.00$, $df = 1, 128$, $P \ll 0.0001$), while *S. romanzoffiana* fruit removal was greatest in the wet season (dry: 69.9%, SE ±6.05; wet: 89.5%, SE ±4.47; $F = 239.02$, $df = 1, 128$, $P < 0.0001$) (Fig 4).

Exclusion experiment in *E. edulis* stands

At the start of the exclusion plot experiment in *E. edulis* (palmito) stands, a 2 × 2 factorial ANOVA showed no significant difference in seedling counts between control and exclusion plots ($F = 0.53$, $df = 1, 36$, $P = 0.472$), a significant difference between the number of palmito seedlings and nonpalmito seedlings ($F = 26.24$, $df = 1, 36$, $P < 0.001$), and no significant interaction between the model factors, plot type (control and exclusion) and seedling type (palmito and nonpalmito) ($F = 0.39$, $df = 1, 36$, $P = 0.537$). With respect to counts of seedling types at the beginning of the experiment, 20% were palmito and 80% were nonpalmito species (palmito: mean = 1.6 seedlings per plot, SD = 1.63, nonpalmito: mean = 6.6 seedlings per plot, SD = 4.22).

One pair of control and exclusion plots was destroyed by a tree fall several months after the start of the experiment, so we did not include it in the final (after 1 year) analyses. The 2 × 2 factorial ANOVA comparing new seedlings that appeared in the plots during the first year of the experiment, showed a significant interaction of plot type and seedling type ($F = 7.38$, $df = 1, 32$, $P = 0.011$), so we used post tests to compare counts of new seedlings between control and exclusion plots within seedling type categories, and compare counts of new palmito seedlings with counts of new nonpalmito seedlings within plot type categories. Contrary to our prediction, there was no significant difference in the number of new palmito seedlings between control and exclusion plots ($F = 0.003$, $df = 1, 32$, $P = 0.957$) (Fig. 5). However, the number of new nonpalmito seedlings was significantly greater in exclusion plots compared to control plots ($F = 14.339$, $df = 1, 32$, $P < 0.001$) (Fig. 5).

Similar to results at the start of the exclusion experiment, the number of new nonpalmito seedlings was significantly greater than the number of new palmito seedlings in both control and exclusion plots (control: $F = 6.71$, $df = 1, 32$, $P = 0.014$, exclusion: $F = 41.36$, $df = 1, 32$, $P < 0.001$) (Fig. 5). However, the percent composition of nonpalmito seedlings increased to a greater extent in exclusion plots. In control plots, the percentage of nonpalmito

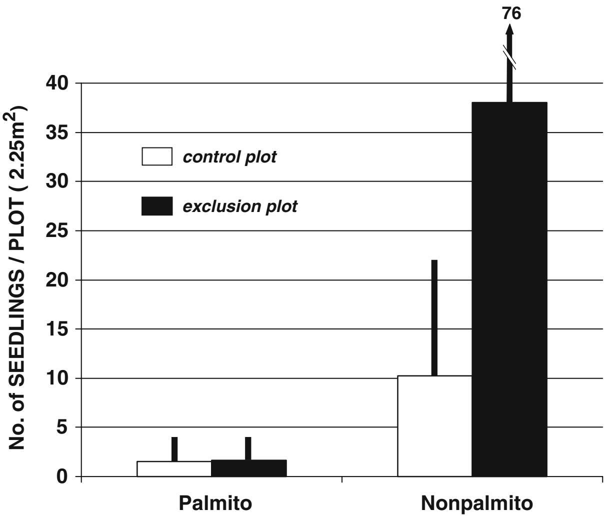

Fig. 5 Means plus standard deviations of the number of new palmito (*E. edulis*) and nonpalmito (all other plant species) seedlings appearing in control and medium-to-large-sized mammalian exclusion plots after 1 year. Paired control and exclusions plots measuring 2.25 m^2 were randomly located in ten different *E. edulis* stands at Caetetus Ecological Station, São Paulo, Brazil

seedlings increased from 80 to 87% during the year, while in exclusion plots, nonpalmito seedlings increased from 80 to 96%.

Discussion

Although removal of *S. romanzoffiana* fruits by all fruit consumers combined was 20% greater in the wet season, this trend was reversed for white-lipped peccaries, i.e., 13 and 28% of total removal in the wet and dry seasons, respectively. White-lipped peccaries not only removed more *S. romanzoffiana* fruits from experimental plots during the dry season, but they prolonged the removal period over more days than they did during the wet season (Fig. 2a). This suggested that they were more actively seeking *S. romanzoffiana* fruits in the dry season and making return visits to fruit plots. In contrast, their wet season removal patterns appeared more random, i.e., *S. romanzoffiana* fruits were encountered and consumed by chance during searches for other types of fruits. In support of this hypothesis, Keuroghlian and Eaton (2008a) found that greater diversity of fruits available in the wet season at the EEC corresponded to greater diversity of fruits consumed by white-lipped peccaries, the latter possibly contributing to a wet season nutritive improvement in their diet. During the dry season, a period of scarcity at the EEC in terms of fruit diversity, there were fewer options, and *S. romanzoffiana* fruits remained very abundant, i.e., they comprised 68% of available forest-floor fruits (as dry weight) (Keuroghlian and Eaton 2008a). This would help explain return visits and increased removal by white-lipped peccaries during the dry season and lowered interest during the wet season when more preferred fruits were available, e.g., those of the families Lauraceae and Annonaceae (Keuroghlian and Eaton 2008a).

In contrast to white-lipped peccaries, removal of *S. romanzoffiana* fruits by collared peccaries and tapirs did not show significant seasonal trends. For collared peccaries, this implied that the smaller herds were less dependent on highly productive fruiting species, and could sustain themselves on less abundant fruits and alternative food sources (e.g., tubers) within their home range (Judas and Henry 1999; Keuroghlian and Eaton 2008a). Alternative food sources for tapirs, e.g., a variety of herbaceous vegetation, would also explain the relatively low removal of *S. romanzoffiana* fruits and lack of seasonality (Demment and Van Soest 1985; Bodmer 1990b; Galetti et al. 2001). The medium to large-sized rodents, i.e., *S. ingrami* and *A. paca*, like white-lipped peccaries, removed substantial proportions of *S. romanzoffiana* fruits during both seasons. Greater removal by the rodents during the wet season suggested return visits and prolonged availability of the fruits. Return visits to *S. romanzoffiana* plots during the dry season may have been reduced or precluded because of fruit depletion by white-lipped peccaries near parent palm trees. In support of this idea, Fleury and Galetti (2006) showed that in smaller Atlantic Forest fragments (200–400 ha), where white-lipped peccaries were absent, *S. ingrami* was responsible for a majority of *S. romanzoffiana* fruit consumption.

In contrast to the diversity of animal species that consumed *S. romanzoffiana* fruits, one species, the white-lipped peccary, was responsible for greater than 95% of *E. edulis* fruit removal from the forest floor during both dry and wet seasons. Fruit removal was highly seasonal and corresponded closely with seasonal range shifts and habitat preferences of white-lipped peccaries (Keuroghlian et al. 2004; Keuroghlian and Eaton 2008b), as well as seasonal availability of *E. edulis* fruits (Keuroghlian and Eaton 2008a). During fruiting peaks of *E. edulis* early in the dry season (April and May), white-lipped peccaries shifted their range to the northern headwaters of the EEC where *E. edulis* habitats are concentrated (Keuroghlian et al. 2004). The white-lipped peccaries continued to use *E. edulis* stands throughout the dry season and demonstrated a significant preference for the habitats (Keuroghlian and Eaton 2008b). As we observed for *S. romanzoffiana* fruit plots, removal periods of *E. edulis* fruits during the dry season were prolonged for an average of 1 week, suggesting repeat visits and active searches for the fruits. Galetti (1996) showed that the caloric value of *E. edulis* fruit was ranked among the top 10 of 50 fruits tested at an Atlantic Forest site. Combining the evidence from the *E. edulis* fruit removal experiments, a long-term fruit availability survey, and studies of white-lipped peccary frugivory, habitat preferences, and ranging habits at the EEC, we concluded that the abrupt range shift and habitat preferences of white-lipped peccaries in the dry season were due to the appearance and prolonged availability of nutritious *E. edulis* fruits coupled with a scarcity of alternative fruit resources (Keuroghlian et al. 2004; Keuroghlian and Eaton 2008a, b).

An intriguing question, which emerged from this and previous studies conducted at the EEC, is why the other large fruit consumers, like collared peccaries, tapir, and pacas did not remove *E. edulis* fruits? In a survey of 46 tapir scats from the EEC, only one *E. edulis* seed from one scat was discovered (Galetti et al. 2001), and in a microscopic analysis of 13 collared peccary scats, *E. edulis* fruit fibers comprised an average of 0.1% of the plant particles in fecal samples (Keuroghlian 2003). In a large reserve of lowland Atlantic Forest, where white-lipped peccaries are extremely rare, Galetti et al. (1999) documented consumption of *E. edulis* fruits (mostly in tree crown infructescences) by 14 bird species and the squirrel, *S. ingrami*. Working in the same reserve, Pizo and Simão (2001) cited bats and small rodents as potential dispersers and predators, respectively, of *E. edulis* seeds, and Rodrigues et al. (1993) found 300 *E. edulis* seeds in one of two tapir scats examined. At the EEC, the unique behavior shown by white-lipped peccaries of removing the outer fibrous husks before consumption of *E. edulis* seeds suggested a level of unpalatability or toxicity that discouraged consumption by other ground-foraging frugivores.

Results from *E. edulis* exclusion plot and removal experiments strongly support the hypothesis that white-lipped peccaries are ecosystem engineers responsible for significant soil, litter, and vegetation alterations, which may have cascading effects in tropical forests (Fragoso 1998b; Painter 1998; Silman et al. 2003; Beck 2005; Keuroghlian and Eaton 2008a, b). In addition to demographic changes related to seed predation in *E. edulis* stands, the plant community was affected by the foraging activities of large white-lipped peccary subherds. These activities included rooting through soil, clearing and redistributing litter, uprooting and trampling seedlings of several plant species, and eating the vegetative parts of some seedlings. At fruit removal plots, both seed predation and rooting reduced *E. edulis* seed densities beneath parent trees, potentially improving survivorship and development of the remaining seeds (Matos and Watkinson 1998; Pizo and Simão 2001). Daily records from removal experiments showed that white-lipped peccaries frequently removed 90–100 fruits during a single visit to an *E. edulis* plot. Furthermore, the stampeding, rooting, and plowing by the white-lipped peccaries buried some of the remaining palmito seeds in the soil and shifted others to new locations. By moving some seeds away from the parent trees, white-lipped peccaries may have improved seedling survival and development. Matos and Watkinson (1998) showed that most of *E. edulis* fruit fall was aggregated 0.6 m from adult plants, and they demonstrated that seedling survival and growth decreased with increased seedling density. They found that survival and growth was optimal for seeds dispersed at least 4 m from adult plants. Pizo and Simão (2001) also showed that *E. edulis* seedling survival and development was improved when bird dispersed (regurgitated or defecated) seeds were less clumped.

Other examples demonstrating the trophic effects and engineering impacts of white-lipped peccaries on tropical forest communities include Fragoso (1998b), Painter (1998), and Silman et al. (2003). Fragoso (1998b) documented seed thinning by white-lipped peccaries around parent palm plants of *Maximiliana maripa* and *M. flexuosa* in an Amazonian forest. Similar to our observations in *E. edulis* stands, he noted extensive rooting, seedling damage, and the burying of seeds by white-lipped peccaries in *M. flexuosa* swamps. Painter (1998) showed that white-lipped peccary predation of *S. exorrhiza* palm fruits in Bolivia limited palm aggregations and increased forest diversity. Silman et al. (2003), working at Cocha Cashu Biological Station in southeastern Peru, documented cascading effects related to the presence and absence of palm seed predation by white-lipped peccaries. They showed that the quantity and distribution of *A. murumuru* palm seedlings were strongly altered during and after a 12-year absence of white-lipped peccaries. Silman et al. (2003) related an increase in palm seedling numbers during the period of white-lipped peccary absence to reduced palm seed predation, and hypothesized that seedling distributional changes were caused by white-lipped peccary mediated alterations of scatter-hoarding rodent behavior and/or spatially-biased rooting of palm seedlings during periods when white-lipped peccaries were present.

At the EEC, a variety of large mammals, like collared peccaries, tapirs, and pacas used *E. edulis* habitats during exclusion experiments, but the effects of rooting, trampling, and seedling consumption were almost exclusively associated with the distinctive tracks and well defined foraging trails characteristic of white-lipped peccaries (Keuroghlian and Eaton 2008a). The dramatic reduction of nonpalmito seedlings in control plots had indirect positive impacts on *E. edulis* seedlings, i.e., reducing crowding and, potentially, reducing interspecific competition for light and other resources. Based on these results, we concluded that regular thinning of nonpalmito seedlings by white-lipped peccaries helped to maintain *E. edulis* populations and the important habitats that they encompass at the EEC. In turn, the persistence of these habitats and their dry season fruit output helped to maintain white-lipped peccary populations. The persistence of *E. edulis* populations, as modulated by the ecosystem engineering of white-lipped peccaries (i.e., rooting and thinning of nonpalmito seedlings), may have had another positive impact at the EEC, i.e., maintenance of the natural water balance in headwater stream basins. *E. edulis* stands are associated with springs that have relatively constant flows and feed numerous headwater streams (D. Eaton, unpublished data). In deforested spring areas adjacent to the EEC, headwater stream flows are intermittent or nonexistent due to increased evapotranspiration by annual plants that have replaced *E. edulis* palms and associated forest vegetation (Tabanez et al. 2005). For the *E. edulis* stands within the EEC, we predict that the absence of regular foraging and soil disturbance by white-lipped peccaries would cause dramatic, long-term vegetation alterations, and have similar, but less severe, impacts on water balance and stream flows.

Both *E. edulis* and white-lipped peccaries are threatened species in the Atlantic Forest due to an array of consequences related to forest fragmentation and habitat loss, including range reduction, isolation, edge effects, and loss of habitat diversity (Cullen et al. 2000; Ditt 2002; Keuroghlian and Eaton 2008b). In addition, *E. edulis* is threatened by illegal harvesting of “hearts of palm” (Galetti and Fernandez 1998), and white-lipped peccary populations have been decimated in some locations by hunting pressure (Cullen et al. 2000). Moreover, the effects of both *E. edulis* harvesting and peccary hunting may be exacerbated in forest fragments (Galetti and Fernandez 1998; Cullen et al. 2000). At the EEC, palm harvesting and hunting are tightly controlled, so the most prominent threats to these species are edge encroachment, loss of habitat diversity, catastrophes, and the consequences (as described in this study) related to alterations of *E. edulis*-white-lipped peccary interactions. Unfortunately, studies from other fragments and regions in the Atlantic Forest documenting interactions between *E. edulis* and white-lipped peccaries do not exist. Therefore, we do not know if the interactions documented are peculiar to the EEC, or if they are present in other forest fragments that still maintain white-lipped peccary populations? We also do not know the history of the interactions, i.e., whether they were of similar importance before fragmentation of the *Planalto* region of the Atlantic Forest? We can conclude, however, that the loss of either species would have dire consequences for the other at the EEC, and that associated species would be threatened by a variety of cascading effects (Galetti and Aleixo 1998).

This study documents a substantial quantitative impact of both white-lipped and collared peccaries on *S. romanzoffiana* fruits in terms of removal and potential dispersal. However, *S. romanzoffiana* is a keystone fruit species in the Atlantic Forest consumed by a wide variety of animals (Galetti et al. 2001; Keuroghlian and Eaton 2008a). So, although declines or extinctions of peccaries at the EEC would undoubtedly lead to alterations of *S. romanzoffiana* populations, the diversity of alternative seed dispersers, like *T. terrestris*, *A. paca*, and *C. apella*, would reduce the chances of local extinction. However, in smaller Atlantic Forest fragments (200–400 ha), where white-lipped peccaries have been extirpated, seed predation (mainly by *S. ingrami*) has increased, threatening long-term viability of *S. romanzoffiana* populations (Fleury and Galetti 2006).

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References

Altrichter M, Carillo E, Saenz J, Fuller T (2001) White lipped peccary (*Tayassu pecari*) diet and fruit availability in a Costa Rican rain forest. Biol Trop 49:1105–1114

Beck H (2005) Seed predation and dispersal by peccaries throughout the Neotropics and its consequences: a review and synthesis. In: Forget PM, Lambert JE, Hulme PE, Vander Wall SB (eds) Seed fate: predation, dispersal and seedling establishment. CABI Publishing, Wallingford, pp 77–115

Bodmer RE (1989a) Ungulate biomass in relation to feeding strategy within Amazonian forests. Oecologia 81:547–550. doi:10.1007/BF00378967

Bodmer RE (1989b) Frugivory in Amazonian Artiodactyla: evidence for the evolution of the ruminant stomach. J Zool (Lond) 219:457–467

Bodmer RE (1990a) Responses of ungulates to seasonal inundations in the Amazon floodplain. J Trop Ecol 6:191–201

Bodmer RE (1990b) Fruit patch size and frugivory in the lowland tapir (*Tapirus terrestris*). J Zool 22:121–128

Cullen L Jr, Bodmer RE, Valladares-Padua C (2000) Effects of hunting in habitat fragments of the Atlantic forests, Brazil. Biol Conserv 95:49–56. doi:10.1016/S0006-3207(00)00011-2

Cullen L Jr, Bodmer RE, Valladares-Padua C (2001) Ecological consequences of hunting in Atlantic forest patches, Sao Paulo, Brazil. Oryx 35(2):137–144. doi:10.1046/j.1365-3008.2001.00163.x

Demment MW, Van Soest PJ (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. Am Nat 125:641–672. doi:10.1086/284369

Ditt EH (2002) Fragmentos florestais no Pontal do Paranapanema. Annablume Editora/IPE^/IIEB, Sao Paulo

Fleury M, Galetti M (2004) Effects of microhabitat on palm seed predation in two forest fragments in southeast Brazil. Acta Oecol 26:179–184. doi:10.1016/j.actao.2004.04.003

Fleury M, Galetti M (2006) Forest fragment size and microhabitat effects on palm seed predation. Biol Conserv 131:1–13. doi:10.1016/j.biocon.2005.10.049

Fragoso JMV (1998a) Home range and movement patterns of white lipped peccary (*Tayassu pecari*) herds in the Northern Brazilian Amazon. Biotropica 30:458–469. doi:10.1111/j.1744-7429.1998.tb00080.x

Fragoso JMV (1998b) White-lipped peccaries and palms on the Ilha de Maraca. In: Milliken J, Ratter J (eds) Maraca: the biodiversity and environment of an Amazonian rainforest. John Wiley, New York, pp 151–163

Galetti M (1996) Fruits and frugivores in a Brazilian Atlantic forest. Ph.D. thesis, University of Cambridge, England

Galetti M, Aleixo A (1998) Effects of the harvesting of a keystone palm on frugivores in the Atlantic forest of Brazil. J Appl Ecol 34:286–293. doi:10.1046/j.1365-2664.1998.00294.x

Galetti M, Fernandez JC (1998) Palm heart harvesting in the Brazilian Atlantic forest: changes in industry structure and the illegal trade. J Appl Ecol 35:294–301. doi:10.1046/j.1365-2664.1998.00295.x

Galetti M, Zipparro VB, Morellato PC (1999) Fruiting phenology and frugivory on the palm *Euterpe edulis* in a lowland Atlantic forest of Brazil. Ecotropica 5:115–122

Galetti M, Keuroghlian A, Hanada L, Morato MI (2001) Frugivory and seed dispersal by the Lowland Tapir (*Tapirus terrestris*) in Southeast Brazil. Biotropica 33(4):723–726

Galetti M, Donatti CI, Pires AS, Guimarães PR Jr, Jordano P (2006) Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation. Bot J Linn Soc 151:141–149

Guimarães PR, Lopes PFM, Lyra ML, Muriel AP (2005) Fleshy pulp enhances the location of *Syagrus romanzoffiana* (Arecaceae) fruits by seed-dispersing rodents in an Atlantic forest in southeastern Brazil. J Trop Ecol 21:109–112

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386. doi:10.2307/3545850

Judas J, Henry O (1999) Seasonal variation of home range of collared peccary in tropical rain forests of French Guiana. J Wildl Manag 63:546–555. doi:10.2307/3802641

Keuroghlian A (1990) Observations on the behavioral ecology of the black lion tamarin (*Leontopithecus chrysopygus*) at Caetetus Reserve, São Paulo, Brasil. M.S. thesis, University of West Virginia, West Virginia

Keuroghlian A (2003) The response of peccaries to seasonal fluctuations in an isolated patch of tropical forest. Ph.D. dissertation, University of Nevada, Reno, Reno, Nevada

Keuroghlian A, Eaton DP (2008a) Fruit availability and peccary frugivory in an isolated Atlantic forest fragment: effects on peccary ranging behavior and habitat use. Biotropica 40:62–70

Keuroghlian A, Eaton DP (2008b) Importance of rare habitats and riparian zones in a tropical forest fragment: preferential use by *Tayassu pecari*, a wide-ranging frugivore. J Zool (Lond) 275:283–293. doi:10.1111/j.1469-7998.2008.00440.x

Keuroghlian A, Eaton DP, Longland WS (2004) Area use by white-lipped and collared peccaries (*Tayassu pecari* and *Tayassu tajacu*) in a tropical forest fragment. Biol Conserv 120:411–425. doi:10.1016/j.biocon.2004.03.016

Kiltie RA (1980) Seed predation and group size in rain forest peccaries. Ph.D. dissertation, Princeton University, Princeton, New Jersey

Kiltie RA (1981) Stomach contents of rain forest peccaries (*Tayassu tajacu* and *T. pecari*). Biotropica 13:234–236

Kiltie RA, Terborgh J (1983) Observations on the behavior of rain forest peccaries in Peru: why do white-lipped peccaries form herds? Z Tierpsychol 62:241–255

Leighton M, Leighton DR (1983) Vertebrate responses to fruiting seasonality within a Bornean rainforest. In: Sutton SL, Whitmore TC, Chadwick AC (eds) Tropical rainforests: ecology and management. Blackwell Scientific, Oxford, pp 181–209

Matos DM, Watkinson AR (1998) The fecundity, seed, and seedling ecology of the edible palm *Euterpe edulis* in southeastern Brazil. Biotropica 30:595–603. doi:10.1111/j.1744-7429.1998.tb00099.x

Mills LS, Soulé ME, Doak DF (1993) The keystone-species concept in ecology and conservation. Bioscience 43:219–224. doi:10.2307/1312122

Neter J, Kutner MH, Nachtsheim CJ, Wasserman W (1996) Applied linear regression models, 3rd edn. Irwin, Chicago

Nunes MFC, Galetti M (2007) Use of forest fragments by blue-winged macaws (Primolius maracana) within a fragmented landscape. Biodivers Conserv 16:953–967. doi:10.1007/s10531-006-9034-9

Painter LRE (1998) Gardeners of the forest: plant-animal interactions in a Neotropical forest ungulate community. Ph.D. dissertation, University of Liverpool, Liverpool

Paschoal M, Galetti M (1995) Seasonal food use by the Neotropical Squirrel *Sciurus ingrami* in Southeastern Brazil. Biotropica 27:268–273. doi:10.2307/2389006

Passos FC (1997) Padrão de atividades, dieta e uso do espaço em um grupo de mico-leão-preto (*Leontopithecus chrysopygus*) na Estacão Ecológica dos Caetetus, SP. Ph.D. dissertation, Universidade de São Carlos, São Carlos, SP

Peres CA (1994) Primate responses to phenological changes in an Amazonian terra-firme forest. Biotropica 26:98–112. doi:10.2307/2389114

Pizo MA, Simão I (2001) Seed deposition patterns and the survival of seeds and seedlings of the palm *Euterpe edulis*. Acta Oecol 22:229–233. doi:10.1016/S1146-609X(01)01108-0

Rodrigues M, Olmos F, Galetti M (1993) Seed dispersal by tapir in southeastern Brazil. Mammalia 57:460–461

Serra-Filho R, Cavalli CA, Guillaumon JR, Chiarini JV, Nogueira FP, Montfort LCM, Barbier JL, Donzeli PLSC, Bittencourt I (1975) Levantamento da cobertura natural e de reflorestamento no Estado de São Paulo. Boletim tecnico do Instituto Florestal 1–53

Silman MR, Terborgh JW, Kiltie RA (2003) Population regulation of a dominant rain forest tree by a major seed predator. Ecology 84(2):431–438. doi:10.1890/0012-9658(2003)084[0431:PROADR]2.0.CO;2

Sokal RR, Rohlf FJ (1981) Biometry: the principles and practice of statistics in biological research, 2nd edn. W. H. Freeman and Co., San Francisco

Sowls LK (1997) Javelinas and other peccaries: their biology, management, and use, 2nd edn. Texas A & M University Press, College Station

Tabanez MF, Durigan G, Keuroghlian A, Barbosa AF, Freitas CA, Silva CEF, Silva DA, Eaton DPE, Brisolla G, Faria HH, Mattos IFA, Lobo MR, Rossi M, Souza MG, Machado RB, Pfeifer RM, Ramos VS, Andrade WJ, Contieri WA (2005) Plano de Manejo da Estação Ecológica dos Caetetus. Inst Florestal Ser Registros Sao Paulo 29:1–103

Tabarelli M, Silva MJC, Gascon C (2004) Forest fragmentation, synergisms and the impoverishment of neotropical forests. Biodivers Conserv 13:1419–1425. doi:10.1023/B:BIOC.0000019398.36045.1b

Terborgh J (1986) Keystone plant resources in the tropical forest. In: Soulé ME (ed) Conservation biology, the science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, pp 330–344

Vander Wall SB (1994) Removal of wind-dispersed seeds by ground foraging vertebrates. Oikos 69:125–132

Viana VM, Tabanez AAJ, Batista JLF (1997) Dynamics and restoration of forest fragments in the Brazilian Atlantic moist forest. In: Laurance WF, Bierregaard RO Jr (eds) Tropical forest remnants: ecology, management, and conservation of fragmented communities. The University of Chicago Press, Chicago, pp 351–365

Wilkinson L (1990) SYSTAT: the system for statistics, Evanson, IL: SYSTAT, Inc.

Wright SJ, Duber HC (2001) Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm Attalea butyraceae, with implications for tropical tree diversity. Biotropica 33:583–595