# PALM HARVESTING AFFECTS SEED PREDATION OF *Euterpe edulis*, A THREATENED PALM OF THE BRAZILIAN ATLANTIC FOREST

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(With 1 figure)

## ABSTRACT

The palm tree *Euterpe edulis* is endemic to the Atlantic Forest, where it constitutes an economically important forest product. The often unplanned and illegal harvesting of palm hearts has led to drastic reductions in the populations of *E. edulis* in many areas where this palm used to be the dominant understorey tree species. We investigated the effects of harvesting on seed and seedling predation of *E. edulis*. We tested the predictions of the dominance-predation hypothesis according to which predator satiation leads to an inverse relationship between the amount of predation and the dominance of a tree species. During two consecutive years, seeds were set experimentally on an unharvested (> 250 adult palms/ha) and a neighboring harvested site (few, if any, adult palms) located in the Atlantic Forest of SE Brazil. Seedling mortality was studied at both sites for a six-month period in each of two consecutive years. Seed predation caused by rodents was higher at the harvested site, while insects caused more damage to seeds placed at the unharvested site. The proportion of seeds preyed upon by rodents varied annually, while insect predation did not. Seedling mortality did not differ between harvested and unharvested sites. The dominance-predation hypothesis was confirmed for generalist rodent seed predators, but not for specialist insect predators. This result shows that density-dependent mortality, not only at the individual level but also at the population-level scale, is a function of the class of predators and their types of foraging behavior.

*Key words*: Atlantic Forest, *Euterpe edulis*, harvesting, seed predation.

## RESUMO

**Extração de palmito afeta a predação de sementes de *Euterpe edulis*, uma palmeira ameaçada da Mata Atlântica**

O palmito-jussara, *Euterpe edulis*, é uma árvore endêmica da Mata Atlântica e constitui-se em produto extrativista economicamente importante. A exploração ilegal e descuidada do palmito tem levado a drásticas reduções em suas populações ao longo de toda sua distribuição, que outrora fora abundante. Neste estudo investigamos o efeito da extração do palmito sobre a predação de suas sementes e plântulas por roedores e insetos. Especificamente, testamos a hipótese segundo a qual, em razão da saciação dos predadores, deve haver relação inversa entre a magnitude da predação sobre as sementes e a abundância da planta em determinada área. Durante dois anos consecutivos, sementes de *E. edulis* foram colocadas em uma área preservada (> 250 indivíduos adultos de *E. edulis*/ha) e em uma área vizinha explorada com baixíssima densidade de plantas adultas, ambas localizadas na Mata Atlântica do Estado de São Paulo. A mortalidade das plântulas foi estudada e comparada entre ambas as áreas por um período de seis meses. A predação das sementes por roedores foi maior na área explorada que na área preservada e variou entre os anos. A predação por insetos foi maior na área preservada e não variou entre os anos. A mortalidade das plântulas foi similar em ambas as áreas. A relação inversa

entre a abundância da planta e a predação de suas sementes foi confirmada para predadores generalistas (roedores), mas não para predadores especializados (insetos). Os resultados mostram que a mortalidade de sementes dependente de densidade, não apenas em nível individual, como já demonstrado, mas também em escala populacional, depende do tipo de predador considerado.

*Palavras-chave*: conservação, *Euterpe edulis*, Mata Atlântica, predação de sementes.

## INTRODUCTION

The palm *Euterpe edulis* Martius is endemic to the Atlantic Forest (Henderson *et al.,* 1995) and constitutes an economically important forest product (Galetti & Fernandez, 1998). Unlike the multi-stemmed *E. oleracea* from the Amazon basin, which permits the extraction of selected stems year after year, the harvesting of the palm heart (i.e., the edible apical meristem) from the single-stemmed *E. edulis* results in the death of the plant. This is because, once cut, it is unable to sprout. Thus, sustainable exploitation of *E. edulis* depends upon regeneration from seeds.

Despite being one of the dominant understorey plant species in many Atlantic Forest sites (Siqueira, 1994), the overexploitation of *E. edulis*, mainly by illegally-established factories, has led to its virtual disappearance from many areas. Nowadays, over a great part of its range, *E. edulis* is found only in protected reserves which are, however, frequently invaded by illegal poachers (Galetti & Chivers, 1995). All of these put the once abundant *E. edulis* in a vulnerable position (Dransfield *et al.,* 1988).

When conducted in an unmanaged way, harvesting of forest plant species may drastically reduce their populations, with important consequences for species interactions (Bawa & Seidler, 1998), among them the interaction between the harvested plant and its seed predators. Several studies have tested and confirmed the predictions of the dominance-predation hypothesis, according to which there is an inverse relationship between the amount of seed predation and the dominance of a tree species (Boucher, 1981; Smith, 1987; Smith *et al.,* 1989; Forget, 1992; Schupp, 1992; Cintra, 1997; but see McKee, 1995). In areas where the plant species in question occurs in high density, seed predators are satiated by the great amount of seeds produced, thus increasing the mean probability of seed survival. But if harvesting greatly reduces the population of that species, the relationship may be altered, leading to unusual levels of seed predation as well as changes in the pattern of plant recruitment (Smith, 1987).

In this paper we tested the dominance-predation model for *E. edulis* seeds and seedlings experimentally set in one harvested and one unharvested site differing greatly in *E. edulis* density. We predicted that, due to predator satiation at the unharvested site, seed predation would be more intense at the harvested site. Because rodents and insects usually differ in their response to the characteristics and overall availability of seeds (Hammond & Brown, 1998; Notman & Gorchov, 2001), we tested this prediction separately for each of these two categories of seed predators.

### Natural history background

*Euterpe edulis* is widespread in the Atlantic Forest, inhabiting the coastal forest from 15°S to 29°S, penetrating into the interior through gallery forests, and ultimately reaching Paraguay and Argentina (Henderson *et al.,* 1995). Siqueira (1994) detected the presence of *E. edulis* in 49% of the 63 Atlantic Forest community studies she surveyed. Each individual of *E. edulis* produces 1-5 infructescences annually and bears an average of over three thousand fruits each (Mantovani & Morellato, 2000). Fruits are globose drupes containing a single seed (mean ± SD = $13.5 \pm 1.3$ mm length, $14.2 \pm 1.2$ mm width, n = 10) covered by a thin black pulp. Fruit maturation period in the study areas extends from April to September, peaking in June-July (Galetti *et al.,* 1999). Under shade house conditions, seeds started germination in 20-25 days (M. A. Pizo, unpubl. data), but in the field seeds may take longer to germinate (e.g., on average 118 days according to Matos & Watkinson, 1998). During the 1996 fruiting season, *E. edulis* was responsible for 17% (September) to 98% (May) of monthly fleshy fruitfall (in terms of fresh weight) at the unharvested site (Galetti, 1996; M. A. Pizo, unpubl. data).

The fruits of *E. edulis* serve as food for a variety of fruit-eating vertebrates, including large mammals (e.g., tapirs; Rodrigues *et al.,* 1993), bats

(Faria, 1996), rodents (E. M. Vieira, unpubl. data), lizards (e.g., *Tupinambis merianae*; Reis, 1995), and birds. Twenty-five bird species were recorded eating the fruits of *E. edulis* at Parque Intervales, including the highly endangered Black-fronted Piping-guam or Jacutinga *Pipile jacutinga,* the Blue-bellied Parrot *Triclaria malachitacea*, and the Cinnamon-vented Piha *Lipaugus lanioides* (Laps, 1996; Galetti & Aleixo, 1998; Galetti *et al.,* 1999). According to Collar *et al.* (1992), the elimination of *E. edulis* from extensive areas represents a sizable threat to the survival of these three bird species, which rely heavily upon its fruits, an assertion recently questioned by more detailed studies (Galetti *et al.,* 1997; Galetti & Aleixo, 1998).

Post-dispersal predation of *E. edulis* seeds is caused by a scolytid beetle (*Coccotrypes palmarum* Eggers 1933, Scolytidae) and rodents (Pizo & Simão, 2001). Adults of *C. palmarum* were present in 96.6% of the 268 insect-attacked *E. edulis* seeds collected at both sites, the remainder being infested by an unidentified insect larva. Seeds of *E. edulis* offered to non-starved rodents in captivity were completely eaten by *Nectomys squamipes* and *Oryzomys intermedius*, the two most abundant rodents at the study sites (Vieira, 1999). Both these species are diet generalists, being able to eat fruits and seeds of several species and invertebrates as well (Emmons & Feer, 1997; E. M. Vieira, unpubl. data). According to Reis (1995), several agents may cause mortality in *E. edulis* seedlings, including fungus, mollusks, insect larvae (e.g., the butterfly *Antirrhaea archaea*, Morphinae), and peccaries (*Tayassu tajacu*).

## STUDY SITES

The harvested and unharvested sites chosen were located in the lowland Atlantic Forest of the municipality of Sete Barras, São Paulo State, southeast Brazil. The *Parque Estadual Intervales* (Saibadela Research Station; 24º14'S, 48º04'W), a 49,000 ha reserve, constituted the unharvested site. Saibadela Station presents a dense populaton of *E. edulis* (255.6 plants [dbh > 5 cm] ha⁻¹; Almeida-Scabbia, 1996), relatively undisturbed by illegal harvesting (but see Galetti & Chivers, 1995). The harvested site was established on privately owned land 1 km distant from the unharvested site and separated from it by the Saibadela River, a small stream, and a 100-300 m wide strip of pastures and banana plantation. The total area covered by the harvested forest is difficult to estimate, but certainly comprises several hundred hectares (for more details about the two sites see Galetti & Aleixo, 1998; Aleixo, 1999). At the harvested site illegal palm harvesting is frequent, resulting in a very low density of adult *E. edulis* palms. As a consequence of the contrasting adult *E. edulis* density, harvested and unharvested sites differ greatly in seedfall (0 *vs.* 10.5 seeds m⁻², data for the 1995 fruiting season; M. A. Pizo, unpubl. data), and seedling density (0 *vs.* 2.3 seedlings [< 30 cm height] m⁻², respectively; M. A. Pizo and E. M. Vieira, unpubl. data).

The region received a mean annual rainfall ± SD of 4216.2 ± 245.5 mm between 1994-96. Rains are well distributed throughout the year with no month receiving less than 100 mm, but a period of less intense and less frequent rains happens between April and August. During this period, low temperatures may occur but rarely dropping below 10ºC (mean ± SD = 20.8º ± 2.5ºC for the study period), in contrast with the wetter period when maximum temperature may reach 42ºC (25.7º ± 2.8ºC). Old-growth forest (*sensu* Clark, 1996) predominates in both sites. The understorey is open and the canopy is 25 m in height with a few emergent trees reaching 30 m (Almeida-Scabbia, 1996).

## METHODS

### Seed predation

The effects of palm harvesting on post-dispersal seed predation of *E. edulis* were investigated in June-July of 1996 and 1997 by setting seeds on two parallel, 300 m long transects established at the harvested and unharvested sites, and then recording the number of seeds that had been preyed upon by rodents and insects one month later. The parallel transects with 30 experimental stations each were set 2-3 m off-trail on opposite sides of the trails crossing the two sites. Stations were 10 m distant from the next station on the same transect, and at least 5 m from the nearest station on the opposite parallel transect. Each station received five seeds, totaling 300 seeds (60 stations x 5 seeds per station) at each site each year. The seeds used on the transects had been regurgitated by birds and collected in the field. To be sure that the disappearance of seeds from the stations was in fact due to removal by rodents and not washed away by heavy rains, we cemented individual seeds with epoxy resin to 20 cm pieces of 4.7 kg fishing lines. The opposite ends of the lines were then tied to saplings

at each station. This method has been used by other authors (e.g., Schupp, 1988) with no apparent effect on seed exploitation by rodents. We considered to have been removed (and possibly preyed upon) by rodents every seed not found attached to the fishing line. Insect predation was verified by looking for the typical entrance hole left by beetles entering the seeds. It is important to note that, unless rodents avoid insect-infested seeds, a possible but presently unavailable information (see Sallabanks & Courtney, 1992), we may have underestimated insect predation, because insect-infested seeds might have been removed by rodents prior to our censuses.

Data obtained with the aid of spool-and-line devices (as described by Boonstra & Craine, 1986; Key & Woods, 1996) in the same study area indicated that the probability of a food item being found by rodents does not increase with the presence of another food source placed 5-10 m (E. M. Vieira, unpubl. data). Thus, seed stations were considered independent of each other. The seed predation data were not normally distributed, thus we used the Friedman two-way block test (Sokal & Rohlf, 1981) to explore the main effects of the independent variables (harvesting regime [i.e., harvested *vs.* unharvested] and year) on the dependent ones (proportion of seeds preyed upon by rodents and insects). We first asked if the harvesting regime had an effect upon seed predation when data were blocked by year, and then asked if year had an effect when data were blocked by harvesting regime. Mann-Whitney tests were used to identify site differences in the combined proportions of seeds preyed upon by insects and rodents. Values presented refer to medians and first-third quartile ranges.

### Seedling mortality

To investigate the possible effect of palm harvesting on seedling mortality, in August 1996 we planted seeds in plastic trays filled with sand and kept in a sheltered green house (25% full sun-light) constructed at Saibadela station especially to nurse *E. edulis* seedlings. In November 1996, the newly-germinated seedlings (approximately 6 cm in height, with the still-closed leaves pointing upright) were transplanted to the parallel transects established for the seed-predation study at both harvested and unharvested sites.

Each station received one seedling whose position was marked with a colored flag. We monitored seedling survival at 1, 2, 4, and 6 months after transplanting. Since we were unable to assign a mortality agent to all seedling deaths, analyses were performed by pooling the data irrespective of mortality agent, except for one seedling killed by branch fall at the unharvested site. The hypothesis that seedling survival differed between harvested and unharvested sites was tested with a 2 x 2 contingency table constructed with the total number of seedling deaths recorded at the end of the study (i. e., six months after transplanting).

### RESULTS

The harvesting regime significantly affected rodent and insect predation, but in opposite directions (Table 1, Fig. 1). Overall, predation caused by rodents presented slightly higher values at the harvested site than at the unharvested one (median of the proportion of preyed upon seeds/station plus first-third quartile range, both years pooled: 0.0, 0.0-0.2 *vs.* 0.0, 0.0-0.0 for the harvested and unharvested sites, respectively), while insects caused more damage to the seeds placed at the unharvested site (0.2, 0.0-0.2 *vs.* 0.0, 0.0-0.2, respectively). In addition, the proportion of seeds preyed upon by rodents was affected by year; a slightly higher proportion of seeds were preyed upon in 1996 (0.0, 0.0-0.2; both sites pooled) when compared to 1997 (0.0, 0.0-0.0). Insect predation, in contrast, was not affected by year (0.1, 0.0-0.2 and 0.0, 0.0-0.2 for 1996 and 1997, respectively; Table 1).

The combined proportion of seeds damaged, either by rodents or insects, between harvested and unharvested sites, did not differ either in 1996 (0.27 *vs.* 0.20, respectively; U = 1.74, p = 0.08), or in 1997 (0.20 *vs.* 0.22; U = 1.54, p = 0.12).

Six months after transplanting, 20.0% and 33.8% of the seedlings planted at the harvested and unharvested sites, respectively, were dead, a non-significant difference ($\chi^2$ = 2.26, df = 1, p = 0.13).

### DISCUSSION

Combined rodent and insect predation yielded a range of 20%-27% of seeds preyed upon during the two years of study. A similar percentage (23.4%) was found by Reis (1995) who made 800 seeds available to predators during 150 days in a forested area south of our study sites. It is important to note,

however, that these figures may not represent the final predation pressure over a cohort of seeds since seeds continue to be preyed upon by rodents well beyond the fruiting season, even after germination (Reis, 1995; see also Notman & Gorchov, 2001).

Although large frugivorous birds cross the intervening space separating the harvested and unharvested sites and deposit seeds in the former site (Galetti & Aleixo, 1998), the influx of seeds there is minimal when compared to the unharvested site (M. A. Pizo, unpubl. data; see Study Site above). Given equal predator densities at both sites, this would represent a higher individual probability of a seed being preyed upon at the harvested site due to predator satiation occurring at the unharvested site. The combined predation caused by rodents and insects, however, did not differ between harvested and unharvested sites, thereby apparently contra-dicting our initial prediction. Only by looking separately at each class of predators could this issue be clarified. Rodent and insect seed predators responded differently to contrasting seed availability resulting from different harvesting regimes.

Although between-site differences in the amount of seed predation were not great, results showed that predation by rodents was more intense at the harvested site while insect attack predo-minated at the unharvested one. The lower rodent-caused predation observed at the unharvested site was probably a result of predator satiation rather than low densities of rodent populations. As ge-neralist seed predators, rodents are unlikely to respond numerically to temporally abundant sup-plies of *E. edulis* seeds through either rapid popu-lation increase or long-distance seasonal movements (see Schupp, 1992). In fact, overall annual fruit production, which might limit the rodent population, does not differ between harvested and unharvested sites outside the fruiting period of *E. edulis* (Galetti, 1996), and population sizes of rodent species were not correlated with biomass of *E. edulis* seeds at the unharvested site (Vieira, 1999). Thus, po-pulation densities of small, terrestrial rodents are likely to be similar at both sites. As a consequence of the higher density of *E. edulis* seeds at the un-harvested site, rodents became satiated, resulting in a proportional lower predation pressure there than at the harvested site. The significantly greater seed removal at the unharvested site in 1996 than in 1997 was probably determined by temporal

fluctuations in rodent populations. The overall biomass of small rodents ($< 300$ g) estimated in June 1996 was more than twice as great as in June 1997 (1.8 kg ha$^{-1}$ *vs.* 0.8 kg ha$^{-1}$; Vieira, 1999).

In contrast to the pattern observed for rodents, attack by insects predominated at the unharvested site. Specialist seed-eating insects tend to concentrate their activities in places where the density of their preferred seeds is higher (Hammond & Brown, 1998). *Coccotrypes* scolytids are specialized in exploiting palm seeds (Janzen, 1972; Wood, 1982), thus the abundance of *C. palmarum* is possibly higher at the unharvested site, resulting in the higher predation levels observed there.

Early seedling survival appeared not to be related to seedling density, at least during the 1996 experimental period. Matos & Watkinson (1998) found that the probability of *E. edulis* seedling survival decreased with increasing seedling density in a fragment of semideciduous forest in southeast Brazil, but these authors worked on a scale (1 x 1 m plots) much smaller than ours. In such small plots com-petition may be a crucial factor in determining seedling survival (Pizo & Simão, 2001). It should be noted, however, that seedling survival may vary from year to year (Schupp, 1990), and that mortality factors may act upon seedlings for longer than the six-month period in which we investigated. All of these claim for caution in generalizing our results to other areas bearing *E. edulis* populations. In any case, there is no obligatory linkage between seed and seedling predation (Houle, 1992; Schupp, 1995). Indeed, the differences observed in patterns of seed predation between harvested and unharvested sites may not hold for seedlings.

In conclusion, this study confirmed the dominance-predation hypothesis for the *E. edulis* population but only when we consider small, generalist rodent seed predators, and not specialized insect predators. This result shows that density-dependent mortality, not only at the individual level (Hammond & Brown, 1998), but also at the population-level scale, is a function of the class of predators and their types of foraging behavior (see Cintra, 1997).

### Conservation implications

Although the combined impact of the two classes of predators is similar between harvested and unharvested sites, we suspect that the predation verified in the former site has more drastic effects

on the recruitment of the *E. edulis* population. Judging from the great input of seeds and the great amount of seedlings that annually cover the floor at the unharvested site, an oversupply of seeds appears to occur in relation to the availability of safe sites for development. In such situations, seed predators kill only excess seeds, with no serious consequence for the recruitment of the population (Andersen, 1989). At the harvested site, in contrast, population recruitment depends heavily upon the few seeds delivered via avian seed dispersal and likely coming from the neighboring unharvested site. However, because predators do not kill all the seeds that arrive and seedling survival during the critical period of the early months of development is comparable to that observed at the unharvested site, natural recovery and maintenance of the *E. edulis* population at the harvested site would be possible if the unharvested site were protected, and some harvesting control measures were applied.
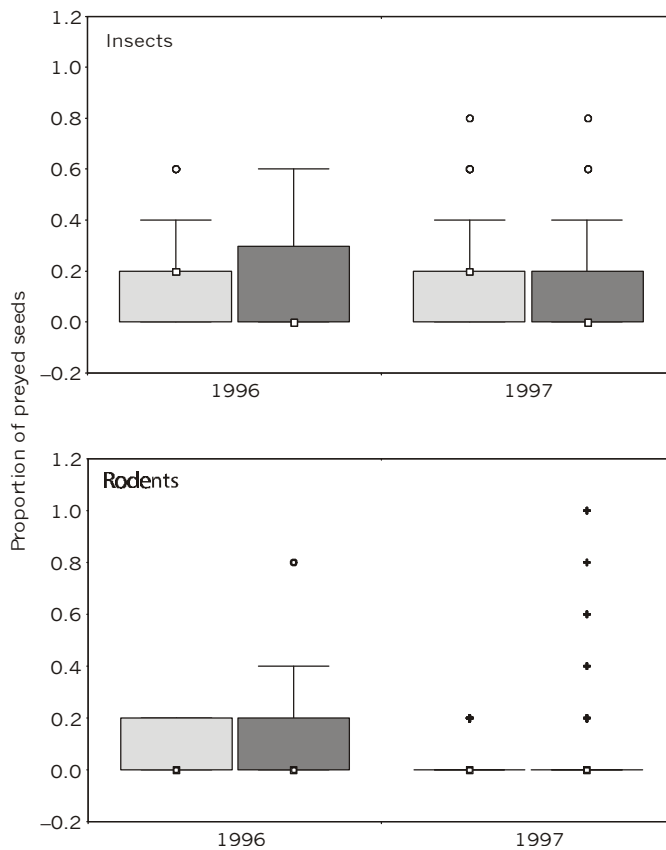


**Fig. 1** — Box and whisker plots showing the proportions of *Euterpe edulis* seeds preyed upon by insects and rodents at the harvested (filled boxes) and unharvested (white boxes) sites in 1996 and 1997. Represented are medians (small squares), first-third quartile ranges (boxes), non-outlier ranges (set at $\pm$ 1.5 * the height of the box; vertical lines), outliers (circles), and extreme values (crosses).

**TABLE 1**

**Friedman block tests for the effects of harvesting and year on the proportion of *Euterpe edulis* seeds preyed upon by rodents and insects. Significant results (i.e., p ≤ 0.05) are underlined.**

| Test | Effects | Rodent predation | | | | Insect predation | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | df | Mean square | F | p | df | Mean square | F | p |
| Harvesting when blocked by year | Harvesting | 1 | 2891.20 | 4.19 | <u>0.04</u> | 1 | 5236.00 | 5.30 | <u>0.02</u> |
| | Error | 238 | 689.56 | | | 238 | 987.90 | | |
| Year when blocked by harvesting | Year | 1 | 5170.50 | 7.37 | <u>0.007</u> | 1 | 133.50 | 0.14 | 0.71 |
| | Error | 238 | 701.17 | | | 238 | 978.11 | | |

Sowing *E. edulis* seeds in areas where natural stands have been depleted has been done by local farmers to recover natural populations of *E. edulis*. Such seeds, sown in areas of low *E. edulis* density, may suffer severe predation by rodents (and, to a lesser extent, by insects) in the long run. Thus, albeit more expensive and time-consuming, planting of seedlings should be considered, in conjunction with protection from illegal extraction, for a more efficient recovery strategy (see also Nodari *et al.,* 2000).

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