Brazilian Journal of Biology
ISSN 1519-6984 (Print)
ISSN 1678-4375 (Online)

http://dx.doi.org/10.1590/1519-6984.166617
Original Article

The effect of size and density on nut removal in *Syagrus loefgrenii* Glassman (Arecaceae) in the Brazilian Cerrado

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Received: July 13, 2016 – Accepted: September 15, 2016 – Distributed: February 28, 2018
(With 2 figures)

Abstract

In this study I tested the effect of *Syagrus loefgrenii* nut size and number on the intensity of removal by rodents across seasons. Trials were performed in which piles of either small or large endocarps (1, 3, 6, 12, and 25) were subjected to removal by rodents in the Cerrado (Brazilian savanna). Despite of variations in the intensity of removal, always this process decrease conform endocarp number. Also, mean proportion of endocarp removal was unrelated to year period, initial number, and size of endocarps. Hence, endocarp removal was consistently negative density-dependent. As, in principle, the observed patterns of nut removal point out similar survival chances for both nut sizes, the pervasive negative density-dependent response emerges as a strategy in *S. loefgrenii* to swamp rodents all year round irrespective of seed size.

Keywords: seed predation, density-dependence, plant-animal interaction, palm fruits, Brazil, Cerrado palm.

Efeito do tamanho e densidade sobre a remoção de sementes em *Syagrus loefgrenii* Glassman (Arecaceae) no Cerrado brasileiro

Resumo

Avaliei o efeito do tamanho e densidade de endocarpos de *Syagrus loefgrenii* sobre a intensidade de remoção por roedores conforme a estação do ano. Para tanto, desenvolvi experimentos no Cerrado em que pilhas de endocarpos pequenos ou grandes (1, 3, 6, 12 e 25), foram sujeitos à remoção por roedores. Apesar da intensidade de remoção variar ao longo do ano, sempre esse processo teve relação inversa com o número de endocarpos. Além disso, em qualquer estação do ano, as proporções médias de endocarpos removidos sempre foram menores nas pilhas maiores, independentemente do tamanho dos endocarpos. Portanto, o processo de remoção de endocarpos foi negativamente dependente da densidade. Como, em princípio, os padrões de remoção em *S. loefgrenii* sugerem chances similares de sobrevivência tanto para endocarpos grandes, quanto pequenos, a preponderância de resposta negativamente dependente da densidade emerge como uma estratégia de *S. loefgrenii* voltada a saciar roedores em qualquer período do ano independentemente do tamanho de suas sementes.

Palavras-chave: predação de sementes, densidade-dependente, interação planta-animal, frutos de palmeira, Brasil, palmeira do Cerrado.

1. Introduction

Palms (Arecaceae), are often abundant in tropical and subtropical regions across the world (Dransfield et al., 2008). Given their wide distribution, species richness, and variation in life forms, palms are an adequate model system for studying plant-animal interactions (Henderson, 2002). These diverse monocots exhibit an extraordinary variety of reproductive patterns (Zona and Henderson, 1989). In this respect, their flowers and fruits are important for much of animal communities (Zona and Henderson, 1989; Henderson, 2002). Indeed, palm fruits are among the most consumed resources by a diversity of invertebrates and vertebrates from arid zones to rainforests around the world (Zona and Henderson, 1989). Palm diaspores may represent a keystone food resource for frugivores during the periods of fruit shortage (Peres, 2000), and often are severely depredated by both bruchid beetles (Coleoptera: Bruchidae), and rodents, which are among the few animal groups capable of penetrating the endocarp (Henderson, 2002). Conversely, many palm species rely on scatter-hoarding of endocarps by rodents for seed dispersal (Jansen et al., 2014). A result of the rapid sequestering and burial of seeds by scatter-hoarding rodents is the prevention of insect access to seeds, which favors the further consumption of adequate seeds (Vander Wall, 2010). Scatter-hoarding rodents are well known by the use of the nutritious endosperm of palm seeds (Zona and Henderson, 1989). Thus, interactions with rodents may be risky for palm seeds, since they are much more likely to be eaten than dispersed (Henderson, 2002; Vander Wall, 2010; Jansen et al., 2014).

Frugivory, seed dispersal and seed predation may affect the ecological dynamics of plant populations (Wright, 2002). In this respect, seed predation by vertebrates and invertebrates is among the principal process underlying plant recruitment patterns both in Neotropical forests (Harms et al., 2000; Terborgh, 2012), and savannas (Vaz Ferreira et al., 2011). Rodents are the most abundant terrestrial mammals in many natural communities (Robinson and Redford 1986), where they play a significant role on seed mortality (Brewer and Rejmánek, 1999). According to local seed offer and relative abundance of rodents, seed predation may be either positively or negatively density-dependent (Terborgh, 2012). When food resources are scarce for a particular seed predator population, predation is likely to be positively density-dependent, but when the resources are abundant, seed predators become satiated and a negatively density-dependent response is expected to occur (Jansen et al., 2014). Lack of response may arise if factors other than the relative abundance of seeds determine the behavior of seed predators.

In addition to variation in seed production, plant species often present substantial range in seed size, a factor with important consequences for the reproductive success of individual plants (Silvertown, 1989). Seed predators are important selection agents acting on seed size because they are likely to select the most profitable seeds (Moegenburg, 1996; Brewer, 2001). Seed mass can have substantial effects on seed survival according to the different threats to which they are exposed in the course of their development, dispersal, and establishment as seedlings (Baraloto et al., 2005). Larger seeds may experience shorter dispersal distances (Howe et al., 1985), their production per individual is often comparatively reduced (Jakobsson and Eriksson, 2000), and they result in competitive seedlings (Turnbull et al., 1999). Even then, few studies have focused on the effect of intraspecific seed size variation on seed predation and dispersal (but see: Moegenburg, 1996; Brewer, 2001; Pizo et al., 2006).

Syagrus loefgrenii Glassman is a small palm inhabiting the Cerrado of Southwestern Brazil, which often has multiple subterranean stem (Lorenzi et al., 2010). A previous study documented non seasonal fruit production in *S. loefgrenii* (1 to 30 nuts/infrutescence), as well as aggregated distribution (Ragusa-Netto, 2016). Hence, at a given place and time of the year, palm nut availability may be high variable according to the number of fruiting stems. In every season, local availability of 40 nuts may swamp rodents, while smaller fruit crop sizes were likely to be completely removed by these mammals (Ragusa-Netto, 2016). Besides the variation in fruit crop size, this palm exhibit variation in nut size, as other palm species studied elsewhere (Brewer, 2001; Pizo et al., 2006). In extremes of size spectrum, nuts may present at least two-fold difference in size. Multiple factors may favor large seeds (Baraloto et al., 2005), and, among them, might be an enhanced potential to swamp seed predators as yet tested for seed cotyledons (Harms and Dalling, 1997; Mack, 1998). Then, palms producing moderate number of larger nuts might swamp rodents, as those ones with increased production of small fruits. In this study, I tested for the combined effect of seed size and number on the intensity of removal by rodents across seasons. Specifically, I evaluated whether endocarp removal intensity conformed to density-dependence across seasons in two extremes of seed size. Therefore, this was an analysis of the potential survival of seeds in the tails of a relatively broad mean-size distribution of seeds produced by individuals of *Syagrus loefgrenii*, which is year round important in the diet of Cerrado rodents (Bueno et al., 2004; Ragusa-Netto, 2016).

2. Material and Methods

2.1. Study site

This study was developed from January to December 2015 in the Cerrado (Brazilian savanna) of Estação Ecológica de Itirapina (EEI), in the municipalities of Itirapina and Brotas (State of São Paulo, Brazil: 22° 15’ S and 47° 49’ W; altitude varies between 700 and 750 m) including an area of 2,720 ha. Mean annual temperature is 19.7 °C. Higher mean temperature is recorded in January and February (±22.5 °C). In June and July mean temperature is 16.3 °C. During this period, the day-break temperature often drops to 2 °C or less and frost may occur. Mean annual rainfall is around 1400 mm, with 1000 mm between October and March. Hence, there is a wet-hot season extending from October to March and a dry-cold season from April to September, when large number of trees and bushes shed their leaves (Motta-Junior et al., 2008). There are cattle ranching, housing (a condominium), *Pinus* spp. and *Eucalyptus* spp. plantations as land uses surrounding the reserve. The main threats to the EEI are the expansion of African grasses, *Urochloa decumbens* (Stapf) R.D.Webster and *Melinis minutiflora* P.Beauv., and exotic trees, including *Pinus* and *Eucalyptus* spp. Other disturbance factors are hunters and exotic animals such as cattle, pigs and goats (Motta-Junior et al., 2008). The deciduous Cerrado vegetation consists mainly of a continuous ground layer dominated by grasses, and a woody layer varying in ground cover from 10 to 20% of trees of 2-6 m high. Common tree species are *Pouteria torta* (Mart.) Radlk., *Hancornia speciosa* Gomes, *Stryphnodendron obovatum* Benth., *Anadenanthera falcata* (Benth.) Speg., and *Couepia grandiflora* (Mart. & Zucc.) Benth. (pers. obs.). The richest plant families are Asteraceae, Fabaceae, and Poaceae (Tannus and Assis, 2004).

2.2. Study species

Syagrus loefgrenii is a monoecious palm which often has multiple inclined subterranean stems, rarely more than 0.7 m tall; has 4-8 erect leaves with 26-66 leaflets at each leaf side, irregularly arranged across the raquis. This palm is considered confined to Cerrado remnants of the Brazilian

State of São Paulo (Lorenzi et al., 2010). *Syagrus loefgrenii* exhibit clumped distribution and bore fruits all year round (Ragusa-Netto, 2016). These diaspores are an important food resource for the rodent *Clyomys bishopi* (Avila-Pires and Wutke, 1981), which can be found in great numbers where this palm is abundant (Bueno et al., 2004).

2.3. Experimental design

The experiment was designed to compare endocarp removal in relation to both endocarp size and number across seasons. *Syagrus loefgrenii* endocarps have an ovoid shape with 17.8 ± 2.7 mm in length (Ragusa-Netto, 2016). To compare removal rates of endocarps of contrasting size, experimental endocarps were divided into two size classes: "large" ≥ 2.0 mm long (≅ 1.40 g), and "small" ≤ 15.0 mm long (≅ 0.80 g). Nut length was used in determining the categories, since it is the least ambiguous dimension, is the most easily measured character, and because it is significantly correlated with endocarp mass ($r = 0.52$, $p = 0.0001$, $n = 100$; Ragusa-Netto, 2016). I used 50 experimental endocarp piles in which 25 had small, while the rest large endocarps. Round shallow black plastic trays (15 cm diameter × 1 cm deep) were used to prevent endocarps being washed away or lost during rain events. Small drainage holes were drilled in the tray bases. Trays were embedded in the soil and stabilized using wood pegs. In each trial endocarps were placed inside trays, hereafter referred to as depots, which included 1, 3, 6, 12, and 25 endocarps (in each case $n = 5$). I delineated these numbers of endocarps because were often present in *S. loefgrenii* infrutescences, and 40 endocarps always swamp rodents (Ragusa-Netto, 2016). Then, in principle, 25 large nuts might correspond to an amount enough to swamp rodents, while 25 small nuts might suffer complete removal as was the case of 15 average-sized nuts (Ragusa-Netto, 2016). I established a 1.7-km-long transect in which I positioned 50 points (30 m apart from each other), and the disposition of depots conform both endocarp size and number was rotated. The definition of this system of points was made irrespective of the number of palms close to the points, as this factor was unrelated to *S. loefgrenii* nut removal (Ragusa-Netto, 2016). Each depot was assumed as a replicate for analyses as 30 m assure independence between samples (Chauvet and Forget, 2005). An area of approximately 50 cm^2 was cleared of grass or leaf litter for the placement of each depot. Taking into account the asynchronous fruiting pattern in *S. loefgrenii* (Ragusa-Netto, 2016), besides the fact that intra-seasonal changes in general food resources availability, might have implications on seed consumption (Van Schaik et al., 1993; Ragusa-Netto and Silva, 2007), I tested *S. loefgrenii* endocarp removal in four periods of the year. Depots with endocarps were set out 3 January, 7 April, 1 July, and 4 November 2015 in order to run trials during the middle of each of the four periods of the year (the late wet season [January-March], the early dry season [April-June], the late dry season [July-September], and the early wet season [October-December]). Endocarps were counted and removed from depots after 30 days, between 10:30 and 14:30. Any endocarp that was preyed upon *in situ* (confirmed by the presence of a hole with rodent teeth marks), or removed was considered to have been subject to predation, while those remaining in the depots were considered to have survived. However, because I do not know the fate of each endocarp after they were removed from depots, rates of endocarp removal will be used instead of endocarp predation when discussing the results. For each trial I collected > 600 *S. loefgrenii* fruits from over 30 palms located in the understory of a *Pinus ellioti* plantation which is part of the EEI. In this site *S. loefgrenii* was highly abundant and infrutescences easily of harvest. I peeled away the pulp to expose the hard endocarp, and discarded all seeds with insect holes or other damage, such as fungus infection. I tested for endocarp viability by placing them in water, and excluding the floating unsound ones, which were also likely to be parasitized or aborted.

2.4. Analyzes

As in principle predators should concentrate their activities in sites where foraging success is likely to be maximum (Schupp, 1988), foraging rodents, for example, might be differently attracted to depots conform endocarp number. In this respect, firstly I analyzed the relationship between initial number of endocarps (both sizes), and the chance of removal (at least one of them) across seasons, through Chi-square contingency analysis. Moreover, I compared proportions of endocarps removed under the effect of number, size and season at the end of each experiment (day 30), with a three-way analysis of variance (ANOVA). The first fixed factor had two levels: small and large endocarps, the second fixed factor had five levels: the number of endocarps per depot (1, 3, 6, 12, and 25), and the third fixed factor had four levels: the periods of the year (see above), including all possible interactions. The proportions of endocarps removed were arc-sine square-root transformed before analysis in order to approach normality and reduce heteroscedasticity.

To assess endocarp removal intensity caused by the initial number of endocarps per depot, I assessed the relationship ($I = aR^b$) between the initial number (I) and the number of removed endocarps (R). Then, I analyzed the initial-removed relationship by linear regression of log transformed values of $I + 1$ and $R + 1$ (power law equation), to normalize residuals. Indeed, with: $\log(y+1) = a + b\log(x + 1)$, I assessed density-dependent effect, where x is the initial number of endocarps at a given depot and y is the respective number of endocarps removed at the end of the experiment; b is the slope representing the rate in which the number of endocarps removed increases in relation to the initial number of endocarps. The constant b may be equal, minor or higher than 1. Higher values imply in positive density-dependence, while $b = 1$, independence. Values of less than 1 imply in negative density-dependence because per endocarp probability of removal is inversely related to endocarp density (Harms et al., 2000). To improve the evaluation on the occurrence of density-dependence, the number of endocarps removed according to observed *b* values were confronted (paired t-test) with the predicted number if $b = 1$. Finally, due to the potential temporal variations in the intensity of endocarp removal, I compared the relationship between the initial and total number of endocarps removed (*b* values) during the four periods of the year by ANCOVA. All analyses were performed with SYSTAT 12.0 for Windows (SYSTAT, 2007).

3. Results

Across seasons no significant association emerged between initial number of endocarps in each size class and the chance of removal of at least one endocarp (Chi-square contingency analysis, $\chi^2 = 3.04$, df = 28, p = 0.997). Indeed, in each season depots were similarly detected by removers ($\chi^2 = 0.78$, df = 4, p = 0.964, Jan-March; $\chi^2 = 0.14$, df = 4, p = 0.983, Apr-Jun; $\chi^2 = 0.35$, df = 4, p = 0.980, Jul-Sept; $\chi^2 = 0.42$, df = 4, p = 0.960, Oct-Dec). On the other hand, total proportions of endocarps removed high vary across seasons: 45.5% for large, and 39.2% for small nuts in Jan-March; 93.2%, and 71.1% (respectively, Apr-Jun); 72.8%, and 80.0% (Jul-Sept); finally 69.8%, and 75.0% (Oct-Dec), ($\chi^2 = 241.51$, df = 7, p = 0.0001; n = 235 large or small endocarps). However, despite of seasonal variations in total proportions of endocarp removal, there was a permanent trend for moderate removal rates in depots with higher densities of either large or small endocarps (Table 1). Indeed, removal rates were inversely related to the initial number of endocarps in depots (Three-way ANOVA, F = 2.61, p = 0.020; Figure 1, Table 1). On the other hand, the endocarp size, and seasons had no effect on nut removal (F = 1.30, p = 0.247; F = 1.53, p = 0.162, respectively). Also, there was no significant interaction between the main factors (initial number, and size of endocarps, besides year periods), on mean proportion of endocarp removal (number x size: F = 1.17, p = 0.228; number x season: F = 1.04, p = 0. 413; size x season: F = 1.68, p = 0.174; number x size x season: F = 0.96, p = 0. 540).

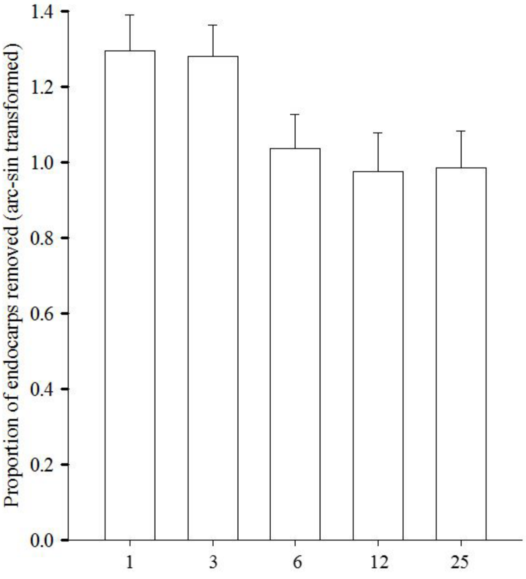

Figure 1. Proportions (mean ± se) of *Syagrus loefgrenii* endocarps removed in relation to the initial number inside depots (data grouped for the four periods of the year [2015], and size of endocarps: n = 40 depots for each initial number of endocarps in the Cerrado of Estação Ecológica de Itirapina [EEI, State of São Paulo, Brazil]).

The intensity of endocarp removal varied across seasons. In Jan-March, slopes for the initial-removed regressions were $b = 0.54$ for large, and $b = 0.28$ for small endocarps. These slope values had no significant difference (ANCOVA, F = 0.97, p = 0.329). In Apr-Jun were $b = 1.00$ for large, and $b = 0.86$ for small endocarps (ANCOVA, F = 0.74, p = 0.393). In Jul-Sept were $b = 0.72$ for large, and $b = 0.94$ for small endocarps (ANCOVA, F = 0.92, p = 0.342). Finally, in Oct-Dec were $b = 0.72$ for large, and $b = 0.78$ for small endocarps (ANCOVA, F = 0.92, p = 0.342). However, across the year variations in slope values were significant (ANCOVA, F = 2.20, p = 0.037, Figure 2). With two exceptions, the intensity of observed endocarp removal was significantly smaller than expect if $b = 1$, in Jan-March: t = 4.95, p = 0.0003, and t = 6.72, p = 0.00006, for large and small endocarps, respectively; in Apr-Jun: t = 0.16, p = 0.876, and t = 2.21, p = 0.037; in Jul-Sept: t = 3.11, p = 0.005, and t = 1.12, p = 0.273; and in Oct-Dec: t = 3.38, p = 0.002, and t = 3.89, p = 0.0007). Hence, irrespective of year period and nut size, the intensity of endocarp removal often followed *b* values ≤ 1.

4. Discussion

Small rodents can prey on a variety of seed species (Adler and Kestell, 1998), and often damage high proportions of seed crops (Hoch and Adler, 1997). In spite of that, as habitat use by Cerrado rodents is likely to change temporally, mostly due to changes in their densities (Vieira, 1997), it would not be surprising to find high variations in the propensity of seed source detection by them. Besides that, it is important to take into account the potential positive relationships between local seed density and the probability of seed detection by rodents (Willson and Whelan, 1990). However, in this study, endocarp depots were detected by rodents irrespective of both endocarp number and size. In every season either depots with few or 25 endocarps were equally likely to be discovered. *Syagrus loefgrenii* is abundant in the study area (Ragusa-Netto, 2016), as well as, at least, one rodent species highly associated to this palm, *Clyomys bishopi* (Bueno et al., 2004). Although, temporal changes in food resources availability may be pronounced, mainly at community level (Schupp, 1988; Van Schaik et al., 1993), the absence of any detectable effect of either size, or number of endocarps on depot detection, suggests that rodents intensely foraged for

Table 1. Removal of *Syagrus loefgrenii* nuts from depots including gradient of densities, as well as, two contrasting sizes of endocarps (n = 5 depots for each size [S: small; L: large], and density [1, 3, 6, 12, and 25] of endocarps).

	Year Period							
Nº and size of endocarps	**Jan-Mar**		**Apr-June**		**July-Sept**		**Oct-Dec**	
	proportions	**numbers**	**proportions**	**numbers**	**proportions**	**numbers**	**proportions**	**numbers**
1S	0.80 ± 0.20	0.80 ± 0.20	0.80 ± 0.20	0.80 ± 0.20	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00
1L	0.40 ± 0.25	0.40 ± 0.25	1.00 ± 0.00	1.00 ± 0.00	0.60 ± 0.24	0.60 ± 0.24	1.00 ± 0.00	1.00 ± 0.00
3S	0.80 ± 0.11	2.40 ± 0.40	0.80 ± 0.20	2.40 ± 0.60	0.80 ± 0.20	2.40 ± 0.60	0.80 ± 0.13	2.40 ± 0.40
3L	0.87 ± 0.08	2.60 ± 0.24	0.80 ± 0.20	2.40 ± 0.60	0.80 ± 0.20	2.40 ± 0.60	0.87 ± 0.13	2.60 ± 0.40
6S	0.60 ± 0.21	2.80 ± 1.02	0.53 ± 0.13	3.20 ± 0.80	0.75 ± 0.20	3.60 ± 0.13	0.60 ± 0.21	3.60 ± 0.13
6L	0.47 ± 0.17	4.13 ± 0.48	0.90 ± 0.10	5.40 ± 0.60	1.00 ± 0.00	6.00 ± 0.00	0.53 ± 0.16	3.20 ± 0.97
12S	0.42 ± 0.19	5.00 ± 2.28	0.47 ± 0.17	5.60 ± 2.04	0.95 ± 0.05	11.40 ± 0.60	0.42 ± 0.19	5.00 ± 2.28
12L	0.45 ± 0.21	5.40 ± 2.54	0.85 ± 0.15	10.20 ± 1.80	0.80 ± 0.20	9.60 ± 2.40	0.60 ± 0.25	7.20 ± 2.93
25S	0.26 ± 0.19	6.60 ± 4.67	0.83 ± 0.14	20.80 ± 3.50	0.76 ± 0.10	19.00 ± 2.59	0.26 ± 0.19	6.60 ± 4.68
25L	0.41 ± 0.18	10.20 ± 2.50	0.99 ± 0.01	24.80 ± 0.20	0.62 ± 0.23	15.60 ± 5.80	0.75 ± 0.17	18.80 ± 4.32

Values refer to either the proportions or numbers of removed endocarps/depot (mean ± se). This experiment was performed in the Brazilian Cerrado (Brotas, State of São Paulo), during each of the four periods of the year.

S. loefgrenii seeds all year round (Terborgh et al., 1993; Ragusa-Netto, 2016).

In marked seasonal areas, one can expect that large nuts might offer enhanced energetic return and should be preferred by foraging rodents, mainly when food availability is relatively high (Brewer, 2001). This might be the case during the wet season when fruiting is plentiful (Batalha and Martins, 2004; Munhoz and Felfili, 2007; Ragusa-Netto and Silva, 2007). On the other hand, in periods of low fruit availability, nut size may become unimportant in the selection of seeds by foraging rodents under food shortage. However, in each of the four periods of the year, the similar removal rates experienced by nuts of either sizes suggest that seeds of a substantial size spectrum might provide enough nutritional and energetic reward for rodents all year round. As documented in some studies, rodents prey on seeds irrespective of their size (Osunkoya, 1994; Pizo et al., 2006). The absence of selection based on seed size suggests that rodents were not sensitive to the range of nut size produced by the population of *S. loefgrenii* studied. It is important to consider that nut size range in *S. loefgrenii*, however, might be too narrow to provide any significant difference in seed exploitation by rodents. Indeed, Brewer (2001) found more than 120% of variation in the size of palm seeds studied, while I reported here 75% and Pizo et al. (2006) 70%. Moreover, all rodent species in the area (Vieira, 1997), had access to depots, so that variables as rodent species, abundance, and activity pattern, besides sex, maturity, and foraging experience, were uncontrolled. These factors might interact with seed size on nut removal. Important, as small rodent populations fluctuate, for example, so might the proportion of individuals experienced enough to distinguish between seeds of low and high food value. Then, despite of the potential weight of one, or the synergism among these variables, the observed patterns of nut removal in *S. loefgrenii* point out similar survival chances for either large or small seeds.

In spite of rodents' ability to detect endocarp depots, they often removed moderate amounts of endocarps from larger depots (Figure 1). Indeed, predators can respond functionally or numerically to traits of a seed patch. Functional response relates to the proportion of prey consumed by individual predators, while numerical response relates to the changes in the density of predators. In principle, nut removal patterns in *S. loefgrenii* sounds as functional response, as rodents did not persisted foraging in larger depots, as might be expected for specialized seed predators (Abramsky, 1983). By the simulation of *S. loefgrenii* fruit crop sizes observed in their natural states (Ragusa-Netto, 2016), the present study was done in a large area and across seasons in an effort to document nut removal patterns under potential variations of general food resource availability and rodent community dynamics (Clark and Clark, 1984). Indeed, in the study site rodent species exhibit seasonal variation of abundance and, particularly *Clyomys bishopi*, the most common species and an important consumer of *S. loefgrenii* (Bueno et al., 2004), is often abundant during the dry season (Vieira,

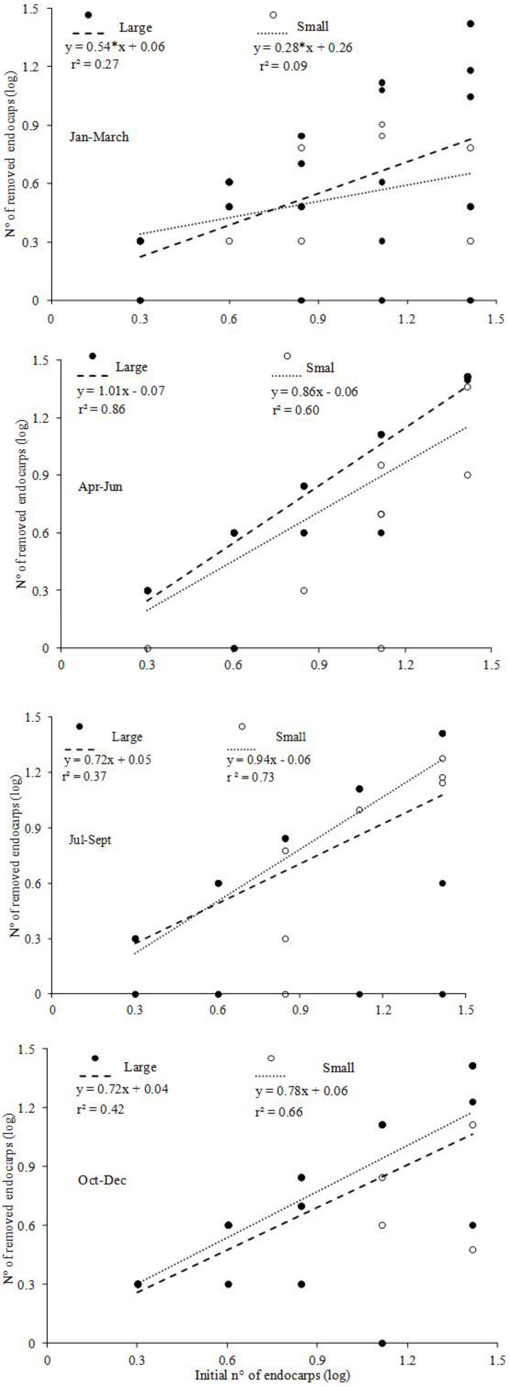

Figure 2. The relationship between initial number of endocarps and number of *Syagrus loefgrenii* endocarps removed across seasons in the Cerrado of Estação Ecológica de Itirapina (EEI, State of São Paulo Brazil, from January 2015 to December 2015; Summer: January-March, Autumn: April-June, Winter: July-September, Spring: October-December; n = 5 depots for each size [Small; Large], and density [1, 3, 6, 12, and 25] of endocarps]). Symbols and linear regressions of log transformed values are also provided. Asterisks in the regressions indicate significantly smaller *b* values (ANCOVA, F = 2.20, p = 0.037).

1997). Even then, while foraging in dense nut patches rodents always removed moderate number of endocarps. Therefore, the permanent negative density-dependent response emerges as strategy present in *S. loefgrenii* to swamp rodents all year round irrespective of nut size.

The impact of generalist seed predators on a given seed population is under the influence of factors such as general fruit abundance (Willson and Whelan, 1990). In this respect, the rich flora of IEE includes a large number of plant species which produces fruits all year round (Tannus and Assis, 2004; Tannus et al., 2006). The availability of other food resources might have consequences for *S. loefgrenii* seed fate, because foraging efforts of rodents are influenced by the total amount of resources available, rather than by only specific fruit density (Forget et al., 1999). It is worth of note that in Jan-March nut removal intensity was the lowest, when, simultaneously, the abundant *Pouteria torta* (Lilienfein et al., 2001), fruited massively, and consequently too many seeds were scattered in the Cerrado floor (J. Ragusa-Netto, pers. obs.). Perhaps, this substantial seed offer influenced the minor removal of *S. loefgrenii* nuts. This is consistent with the hypothesis of satiation at the community level, since consumer satiation seems to occur during the whole fruit-peak (Schupp, 1992).

The present results provide support to the satiation hypotheses at the population scale. However, it is important to consider the possibility that predator satiation might be acting at the community level. Cerrado rodents, in addition to foraging on *S. loefgrenii* nuts, presumably, exploited other seed species, besides insects. This emphasizes the importance of conducting ecological studies at different spatial and temporal scales, and at different levels of organization (individual, population and community) as already noted by Schupp (1992). Indeed, the influence of resource abundance on the intensity of seed predation by rodents has implications for Cerrado community dynamics. When fruits are plentiful, *Syagrus loefgrenii* might suffer reduced seed predation by rodents, which favor seed survival and consequent regeneration success.

Acknowledgements

The author is grateful to an anonymous reviewer for the constructive comments on an earlier version of this study. Financial support was provided by CNPq.

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