

SHORT COMMUNICATION

Fleshy pulp enhances the location of *Syagrus romanzoffiana* (Arecaceae) fruits by seed-dispersing rodents in an Atlantic forest in south-eastern Brazil

Paulo R. Guimarães Jr.*¹, Priscila F. M. Lopes*, Mariana L. Lyra† and Ana Paula Muriel‡

* Programa de Pós-Graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas (UNICAMP), Caixa Postal 6109, 13083-970, Campinas, SP, Brazil

† Programa de Pós-Graduação em Genética e Biologia Molecular, Instituto de Biologia, Universidade Estadual de Campinas (UNICAMP), Caixa Postal 6010, 13083-970, Campinas, SP, Brazil

‡ Instituto de Biologia, Universidade Estadual de Campinas (UNICAMP), Campinas, SP, Brazil

(Accepted 2 May 2004)

Key Words: Caviomorpha, food hoarding, palm, seed dispersal, seed predation

Rodents are the most diverse group of terrestrial mammals in neotropical forests (Emmons & Feer 1997). The interaction of rodents with plants is often pivotal for seed survival (Peres & Baidier 1997, Vander Wall 1990). Many rodent species are seed predators (Brewer 2001, Galetti *et al.* 1992, Hoch & Adler 1997). However, some neotropical rodents, especially dasyproctids (such as *Dasyprocta* and *Myoprocta*) and echimyids (*Proechimys*), are important secondary seed dispersers for large-seeded plants (Forget 1993, 1994; Hoch & Adler 1997, Wenny 1999).

The seeds of some plants, such as the Brazil-nut tree *Bertholletia excelsa* and other Lecythidaceae species (including *Lecythis* spp.) have traits convergent with temperate rodent-dispersed nuts, e.g. large seeds with no fleshy tissue. However, several large-seeded genera dispersed by rodents have fleshy pulp, and include palms such as *Acrocomia* (Guimarães, pers. obs.) and *Astrocaryum* (Brewer 2001, Brewer & Rejmánek 1999, Hoch & Adler 1997), and legume trees such as *Hymenaea* (Asquith *et al.* 1999) and *Dipteryx* (Forget 1993). The presence of pulp in these large-seeded fruits may be an adaptation to promote predator satiation (Smith 1975, Smythe 1970), an anachronism (Janzen & Martin 1982), a defence against insect predation (Silvius & Fragoso 2002), or simply a trait related to seed dispersal by mammals (van der Pijl 1982).

Whatever the origin of fleshy pulp, its presence can have an impact on rodent behaviour and, consequently, plant recruitment. Although several studies have indicated that neotropical rodents such as agoutis and pacas consume fleshy pulp (Beck-King *et al.* 1999, Henry 1999, Nowak

1991), few studies have investigated how the presence of pulp affects the interaction between a plant species and the rodent community in the neotropics (Silvius & Fragoso 2002). In this study, we examined how rodent species in an Atlantic forest in Brazil interact with fruits and seeds of the jerivá palm *Syagrus romanzoffiana*. We focused on the role of fleshy pulp on diaspore location, manipulation, removal and fate.

In April 2001, fieldwork was conducted in a secondary-growth rain forest in the Parque Estadual Intervales (PEI) (24°16'S, 48°25'W), located in São Paulo State, Brazil (Mantovani 2001). The altitude of the park varies between 40 and 1000 m and the climate is relatively cold and wet (Campos 2001). The annual rainfall is 1558 mm (mean for 1990–1993), with a relatively cold, dry season from April to August and a warm, wet season from September to March. The PEI, together with other three ecological reserves, form a large continuum of nearly 120 000 ha of Atlantic forest (Campos 2001). The PEI has 84 mammalian species, 28 of which are rodents, including scatterhoarding rodents such as species of *Dasyprocta* and *Proechymis* (De Vivo & Gregorin 2001).

Syagrus romanzoffiana (Chamisso) Glassman is 10–20-m tall palm that is widespread in semi-deciduous forests and rain forests of south-eastern Brazil, produces ripe fruit throughout year, especially from February to August (Lorenzi 1992). *Syagrus romanzoffiana* fruits are 3-cm long, elliptical, fibrous, orange drupes with a hard endocarp nearly 3 mm thick. The seed is deeply grooved and has only one embryo. The heavy consumption of palm fruit by rodents, and the evidence of scatterhoarding by squirrels (Galetti *et al.* 1992) and agoutis (P. R. Guimarães, unpubl. data), made this palm an interesting system

¹Corresponding author. Email: paulomiudo@uol.com.br

for studying the influence of fruit pulp on the foraging behaviour of rodents.

Seed dispersal by rodents is often difficult to investigate directly (but see Galetti 2002, Guimarães *et al.* 2003), so that rodent interaction can only be assumed. We estimated rodent activity by considering all manipulated fruits in a station to be the result of rodent–fruit interactions. Although deer, peccaries, and tapirs occur in the PEI and may also consume fruits of *Syagrus romanzoffiana*, these large animals occur at low densities and were not recorded during this fieldwork. In most cases, there was strong evidence of rodent interaction such as rodent teeth marks and the burial of fruits. Exclosures were not used because important, highly frugivorous large rodents, such as pacas and agoutis, would probably also be excluded.

Fleshy fruits (control) and fruits from which we removed the pulp (treatment – seeds plus endocarp, hereafter referred as cleaned fruits) were used to investigate the influence of pulp on rodent interactions with *S. romanzoffiana*. All fruits were collected from the same palm and were randomly assigned to the control or treatment group. Fruits with clear evidence of insect infestation were excluded from the experiment. Ten units of only one of the two groups were placed at each station, with a fixed distance of 100 m between the stations ($N = 30$ for each group). The control and treatment stations were located alternately along and always close to (within ~ 1 – 2 m) the sand trails. A 30-cm nylon line with a numbered orange plastic flag was attached to each fruit or seed (adapted from Forget 1990). All of the stations were established simultaneously and checked after 3 d.

The number of visited stations of cleaned fruits and fleshy fruits was compared. We also compared the probabilities of (1) manipulated units per visited station, (2) removed units per manipulated unit and (3) removed units per unit. A two-sample randomization test (TSR) was used to test the significance (Manly 1997). Randomization tests were used because our data did not fit a normal distribution. Since units at the same station are not independent (Jansen *et al.* 2002), we calculated the three probabilities for each station and recorded the mean probability for each group (fleshy fruits and cleaned fruits).

All of the fruits that were removed were sought and classified into three classes of seed fate: (1) predated: the seed was at least partially consumed, (2) abandoned: the fruit or seed was removed and found intact and lying on the leaf litter and (3) cached: the fruit or seed was buried in the ground or under the leaf litter. Diaspores that were not found were excluded from the probability estimates. The number of cleaned fruits and fleshy fruits in each seed fate category were compared using TSR (Manly 1997).

An interaction between fruits and animals was recorded for 127 fleshy fruits (42.3% of fruits) at 25 stations (83.3% of stations) but for only 27 cleaned fruits (9% of fruits) at 13 stations (43% of stations). There

were significantly more visits to stations with fleshy fruits than with cleaned fruits (TSR, $P = 0.001$; 10 000 permutations). Strong evidence for rodent interactions, such as teeth marks and the burial of fruits, was recorded for 71 fleshy fruits (55.9% of manipulated fruits), including 88% of the stations with fleshy fruits visited. Of the 27 cleaned fruits that were handled, only one had identifiable rodent teeth marks. However, peccaries are the only other vertebrate seed predator that can remove *S. romanzoffiana* cleaned fruits, but they normally consume all seeds as soon as they find them (M. Galetti, pers. comm.). In addition, the maximum number of removed cleaned fruits at a given station was only three. These observations indicated that rodents were responsible for most, if not all, interactions recorded in the study.

The probability of manipulation at the stations visited was higher for fleshy fruits (0.58 ± 0.33 ; mean \pm SD) than for cleaned fruits (0.21 ± 0.11 ; TSR; $P < 0.0001$; 10 000 permutations). However, the probability of manipulated fleshy fruits being removed (0.68 ± 0.32) was lower than for cleaned fruits (0.88 ± 0.30 ; TSR; $P = 0.032$; 10 000 permutations). Although fleshy pulp reduced the probability of visited fruits being removed, the overall probability of a fruit being removed was higher for fleshy fruits (0.35 ± 0.30) than for cleaned fruits (0.08 ± 0.13 ; TSR; $P < 0.0001$; 10 000 permutations).

The presence of pulp also influenced the fate of manipulated fruits. Thus, 20 caching events were recorded for fleshy fruits (15.7% of all manipulated fleshy fruits) but none for cleaned fruits. The presence of pulp enhanced the probability of removed fruits being cached (0.34 ± 0.45 for fleshy fruits, zero for cleaned fruits, TSR; $P = 0.057$; 10 000 permutations). These caches were attributed to small rodents such as *Proechimys* (the fruit or seed was placed under the leaf litter) and not to large rodents such as agoutis (that usually bury individual diaspores in 4-cm-deep caches) (for a detailed review of scatterhoarding behaviour see Smythe 1978, Vander Wall 1990). Caches were always found close to a station (< 1 m away, for all cache events). The probability that a fleshy fruit that had been removed would be abandoned intact on the leaf litter was lower for fleshy fruits (0.46 ± 0.46) than for cleaned fruits (1.00 ± 0.00 , TSR; $P = 0.007$; 10 000 permutations). No seed predation was observed, but 49 fleshy fruits (16.3% of all fleshy fruits from 18 stations) and 14 cleaned fruits (4.7% of all cleaned fruits, in 9 stations) could not be found.

The presence of pulp strongly influenced rodent behaviour by increasing the frequency of visitation and the rate of manipulation at stations with fleshy fruits of *S. romanzoffiana*. The higher visitation rates could be related to the chemical attraction (odour) of pulp while the greater manipulation perhaps reflected the fact that some neotropical rodents use pulp as a key food resource (Henry 1999). Whereas the visitation and manipulation rates were higher for fleshy fruits, the removal rate for

manipulated fruits was lower in the presence of pulp. Although pulp reduced the probability of manipulated fruits being removed, it enhanced the overall proportion of *S. romanzoffiana* fruits that were removed.

Fleshy pulp also enhanced the probability of caching. Smith (1975) suggested that fleshy pulp enhanced caching by temporarily satiating the scatterhoarder and, consequently, reducing predation. In this study, the satiation hypothesis is probably not applicable since no predation was observed, i.e. increased caching was not associated with decreased predation. The lack of seed predation is surprising because rodents are important seed predators elsewhere (Bond & Breytenbach 1985, Brewer & Rejmánek 1999, Edwards & Crawley 1999, Forget 1992, Forget *et al.* 1994, Hoffmann *et al.* 1995, Hulme & Hunt 1999), and palm seeds are a common food item in their diets (Brewer 2001, Brewer & Rejmánek 1999, Forget *et al.* 1994, Galetti *et al.* 1992, Hoch & Adler 1997). However, some neotropical rodents are primarily pulp consumers (Henry 1999), and the hard nuts of palm fruits may offer a defence against small neotropical rodents (M. Galetti, pers. comm.). It is possible that some rodents cache fruits for later consumption of the pulp, although this kind of resource is very perishable.

In conclusion, fleshy fruits showed an initial advantage in attracting rodents and, although the fleshy pulp reduced the removal rates of manipulated fruits, it enhanced the overall probability of fruit removal. In addition, fleshy fruits were cached more than cleaned fruits. If rodent has learnt to locate the fruits, seed removal will continue after the pulp has rotted, even after the chemical cues have ceased to be effective. We suggest that the presence of pulp acts as a signal to rodents, thereby increasing visitation and, hence, seed dispersal by scatterhoarding rodents.

ACKNOWLEDGEMENTS

The authors thank the students of the Curso de Ecologia de Campo, Instituto de Biologia, UNICAMP, for their help during the fieldwork, and also H. P. Dutra, J. José, M. S. Araujo, R. Cogni, S. B. Vander Wall, S. F. dos Reis, V. Bonato and three anonymous reviewers for critical reading of the manuscript and discussions. S. Hyslop revised the English language. The authors are in debt to J. R. Trigo and UNICAMP for providing logistical support. PRG was supported by grants from FAPESP and CAPES. This work is one contribution by Curso de Ecologia de Campo, Instituto de Biologia, UNICAMP.

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