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Fruit manipulation of the palm *Syagrus romanzoffiana* by vertebrates in southern Brazil

Manipulação de frutos da palmeira *Syagrus romanzoffiana* por vertebrados no sul do Brasil

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Abstract

A year-long study was carried out in a deciduous forest to examine the vertebrate manipulation on fruits of *Syagrus romanzoffiana* in southern Brazil. Eleven 50x50 cm-track traps (each one baited with ten ripe fruits) were placed monthly around 11 adult palm trees, totalling a sampling effort of 935 traps. The fruits removed (absent) or chewed (left *in situ*) by a given vertebrate species were counted for each trap. Three species of mammals and one bird were monitored. The coati (*Nasua nasua*) removed more fruits (N = 250; 50 %) than chewed (N = 130; 26 %), leaving intact 120 fruits (24 %). The dusky-legged guan (*Penelope obscura*) also removed more fruits (N = 107; 43 %) than chewed (N = 44; 18 %), leaving intact 96 (39 %). On the other hand, the opossum (*Didelphis albiventris*) removed 127 (13 %), but chewed 622 (63 %), leaving intact 236 (24 %). Similarly, the agouti (*Dasyprocta azarae*) removed 16 (12 %), and chewed 64 (49 %), leaving intact 51 fruits (39 %). Results are discussed in light of the roles of these vertebrate species in seed dispersal of *S. romanzoffiana*.

Key words: Atlantic forest, *Dasyprocta azarae*, *Didelphis albiventris, Nasua nasua*, palm tree, *Penelope obscura*, seed dispersal, fruit removal.

Resumo

Este estudo teve a duração de um ano e avaliou a manipulação por vertebrados (três espécies de mamíferos e uma de ave) nos frutos da palmeira *Syagrus romanzoffiana* no sul do Brasil. Onze armadilhas de pegada de 50x50 cm (cada uma iscada com 10 frutos maduros) foram colocadas próximas a onze palmeiras adultas, totalizando um esforço amostral de 935 armadilhas. Os frutos removidos (ausentes) ou mastigados (deixados *in situ*) pelas espécies de vertebrados foram contabilizadas para cada armadilha. Três espécies de mamíferos e uma de ave foram monitoradas. O coati (*Nasua nasua*) removeu 250 frutos (50%), mastigou 130 (26%) e deixou intactos 120 frutos (24%). O jacu (*Penelope obscura*) também removeu mais frutos (N = 107; 43%) do que mastigou (N = 44; 18%), deixando intactos 96 frutos (39%). O gambá (*Didelphis albiventris*) removeu 127 (13%), e mastigou 622 (63%), deixando intactos 236 (24%). Similarmente, a cutia (*Dasyprota azarae*) removeu 16 (12%), mastigou 64 (49%), deixando intactos 51 frutos (39%). Os resultados são discutidos relacionando o papel das espécies de vertebrados na dispersão de sementes de *S. romanzoffiana*.

Palavras-chave: Floresta Atlântica, *Dasyprocta azarae, Didelphis albiventris, Nasua nasua*, palmeira, *Penelope obscura*, dispersão de sementes, remoção de frutos.

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Introduction

Palms are considered keystone species (Fleury, 2003). In many neotropical forests, palms are important by their abundance and species richness, as in the understory as well as in the canopy. This indicates they are elements of great importance in the structure and functioning of the ecosystems (Duran and Franco, 1992).

Syagrus romanzoffiana (Cham.) Glassman (Arecaceae) is a palm tree with broad geographic distribution, occurring from the south to the center-west of Brazil, where it is very common, even in open or edge areas (Lorenzi *et al.*, 1996). Relating to this, it functions as perch to seed dispersers, in woodland areas as well as in forest-grassland edges, favoring the regeneration of other plants (Santos and Souza, 2007).

The removal of fruits by animals is vital for an efficient dispersal of species with fleshy fruits, because the mortality of seeds and seedlings is frequently higher near the parent plants, due to greater predation, pathogens and seedlings competition (Janzen, 1970). The fruits of *S. romanzoffiana* are eaten by many species of mammals and birds (Galetti *et al*., 1992, 2001; Beck-King *et al*., 1999; Guix *et al*., 2001; Cáceres, 2002; Fleury, 2003; Castro and Galetti, 2004). Because of the asynchronous fruiting pattern exhibited by *S. romanzoffiana*, these animals depend upon its fruits during of food shortage (Galetti *et al.*, 2001; Fleury, 2003).

Despite of the diversity of palms and their importance to the fauna, studies on the interactions among palms and vertebrates of the Atlantic Forest remain scarce (Fleury, 2003), in particular for *S. romanzoffiana*, which is widespread in this forest formation (Lorenzi, 2002). This study aimed to analyse manipulation of the fruit by four species of vertebrates that are potential dispersers of fruits of *S. romanzoffiana.* The species were the white-eared opossum *Didelphis albiventris* Lund, 1840, the Coati *Nasua nasua* (Linnaeus, 1766), the Agouti *Dasyprocta azarae* Lichtenstein, 1823 (Mammalia) and the Dusky-legged guan *Penelope obscura* Temmick, 1815 (Aves). For *D. albiventris*, as a generalist small mammal, it was expected that the animal chews as many fruits as it can get, letting seeds mainly *in situ* because of its small body size (Cáceres, 2006). Because of the larger body size of *N. nasua*, and its feeding manipulation as previously reported (Costa, 2003), it was expected that it ingests more fruits than it chews *in situ*. For *D. azarae*, as a medium-sized rodent, and also because of its known "scatter hoarding" behaviour (Hallwachs, 1986; Silva and Tabarelli, 2001), it was expected that it removes more fruits than actually chew them *in situ*. For the large frugivorous bird *P. obscura*, the expected manipulation was ingestion of fruits in large amounts, without leaving them *in situ* (Galetti and Aleixo, 1998).

Material and methods

The study was carried out on the Morro do Elefante, in Santa Maria county, state of Rio Grande do Sul, Brazil (29° 40' S and 53° 44' W, 138 m above the sea level). The climate is sub-tropical with rains distributed evenly throughout the year (Moreno, 1961). The mean temperature during the summer exceeds 22° C. Winter temperatures vary between –3°C and 18°C (Lorenzi, 2002). The foothill of the Morro do Elefante is about 119 m, and its top is 461 m above see level. The vegetation is a disturbed primary forest formation, on the southern scarp of the Serra Geral, classified as a deciduous seasonal forest of the atlantic slope (Quadros and Pillar, 2002). The study area is located within a continuum of forests along this southern forested scarp.

Syagrus romanzoffiana grows from 10 to 15 m tall. It blooms almost the entire year, but usually more intensively from September to March. Its globosely fruits with a fleshy, fibrous yellow pulp, ripen from February to August. For data collection on *S. romanzoffiana* 17 field surveys were done, each with a five-day duration, and with a 15 to 18-day time interval between each of them, for a 12-month total observation period (from June 2005 to June 2006).

Eleven sand plots (namely here as "track traps") were prepared around 11 adult palm trees (one sand plot per plant) in a 3 m radius from the base of the trunk, totalling a sampling effort of 935 traps (11 palm traps x 5 days' field phases x 17 field surveys). Each track trap averaged 80 m apart from each other, being distributed in an area of 100 ha. Several adult palm trees were discarded from the experimental design due to the proximity of a given elected palm. Thus, elected adult palm trees were not displaced in transect lines, but near from a uniform distribution in the study area. Ten ripe palm fruits were placed in the center of each track trap during the daylight of the beginning of a field phase, being replaced by new ripe fruits when there was manipulation by the fauna in the next days. The traps consisted of a wooden square measuring 50 x 50 cm covered with moist sand. Tracks were identified in the field, following the field guide of Becker and Dalponte (1999). When this was not possible, the tracks were photographed and/or plaster casted for further identification in the laboratory.

Aiming to analyse the manipulation of fruits of *S. romanzoffiana* by a given animal, the fruits removed (absent from the trap and adjacencies) or chewed *in situ* (i.e., removed the pulp without ingesting or damaging the seed) were counted for each trap. When tracks of different species were observed at a given trap, this event was not considered in the analysis.

We used the t test to determine the magnitude of differences between the numbers of fruits removed and chewed *in situ* for each vertebrate

species. ANOVA was used to test the differences between removal and chewing of fruits *in situ* among all vertebrate species. Bioestat 5.0 (Ayres *et al.*, 2007) was used for statistical analyses.

Results

From a total of 9,390 mature fruits placed in the traps, 1,334 were removed, 1,532 were chewed *in situ*, and 6,524 were left intact, without manipulation by the entire vertebrate community. Other vertebrate species other than the four actual studied species (but including non identified species) were responsible for 2,693 fruits left in track traps, being 56 % manipulated by them. *Nasua nasua* had access to 500 fruits and from these removed 250 (50 %) and chewed 130 (26 %). *Didelphis albiventris* had access to 980 fruits and from these removed 127 (13 %) and chewed 622 (63 %). *Dasyprocta azarae* had access to 130 fruits and from these removed 16 (12 %) and chewed 64 (49 %). *Penelope obscura* had access to 250 fruits and from these removed 107 (43 %) and chewed 44 (18 %) (Figure 1).

Comparing the removal rate between *N. nasua* and the other species, it was observed that *N. nasua* removed more fruits than *D. albiventris* ($t = 2.07$, $p = 0.04$), *D. azarae* ($t = 4.21$, $p < 0.001$) and *P. obscura* ($t = 2.58$, $p = 0.012$). For the chewing behaviour, *D. albiventris* chewed more fruits than *N. nasua* ($t = 3.61$, $p < 0.001$), *D. azarae* ($t = 4.10$, $p < 0.001$) and *P. obscura* ($t = 4.24$, $p < 0.001$).

Comparing the removal among the four vertebrate species along the 17 field phases, it was observed that *N. nasua* removed on average more fruits than the other species ($F = 6.04$, $p < 0.05$). On the chewing behaviour, it was observed *D. albiventris* chewing and letting *in situ* on average more fruits than the other species ($F = 8.08$, $p < 0.001$).

Discussion

We have identified two types of behaviour on the fruits of *S. romanzoffiana*, those that remove fruits away (*N. nasua* and *P. obscura*), and those that consume by chewing the fruits (*D. albiventris* and *D. azarae*), letting them *in situ*.

Results show that *N. nasua* and *D. albiventris* play a different role in seed dispersal of *S. romanzoffiana.* The former removes more fruits than all the other species, and the second chews more fruits than the other ones, letting them *in situ* or near the mother plant. Thus *N. nasua* seems to be more involved in increasing the variability of the *S. romanzoffiana* population, dispersing seeds to longer distances (through ingestion and the consequent endozoochory), even so only few individuals of the plant will survive (Godoy and Jordano, 2001). In the view of long distance dispersers, specific sites of seed deposition are even more important than the dispersal distances themselves (Schupp, 1993). On the other hand, most recruitments will occur in the proximity (but not so close to) of the parent plant, which can be provided by *D. albiventris* and also *D. azarae*, based on our data. Then two types of dispersal quality would be estimated for seeds here: one given by longer distance dispersers (such as by *N. nasua* and *P. obscura* by endozoochory) and other given by shorter distance dispersers (*D. albiventris* and *D.*

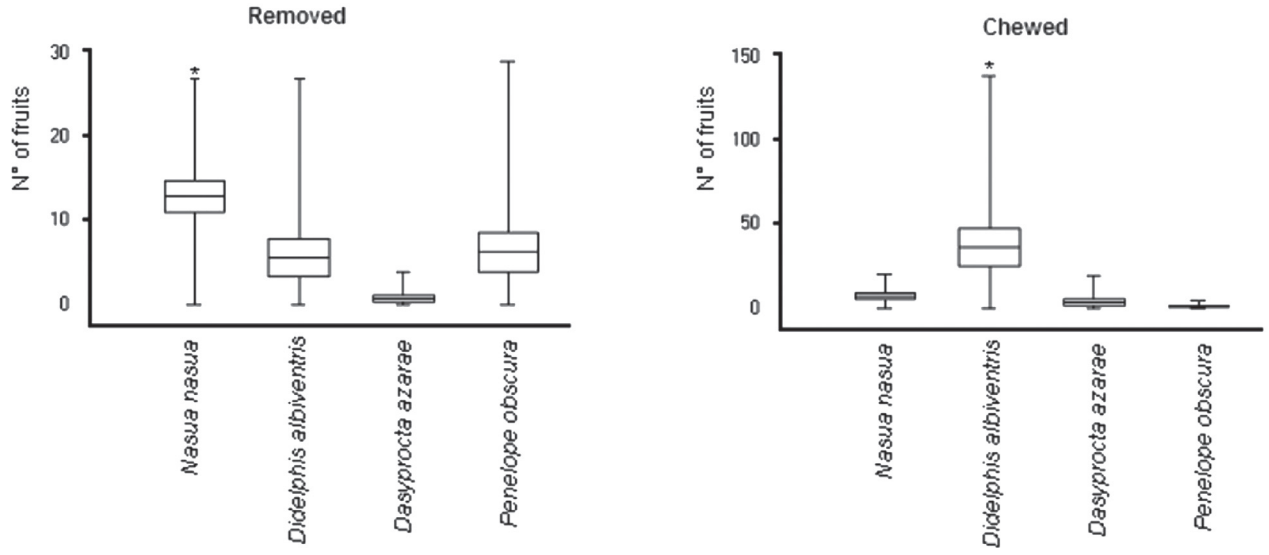

Figure 1. Comparison between the number of removed and chewed fruits of the palm *Syagrus romanzoffiana* by the more frequent vertebrate species in a seasonal deciduous Atlantic forest in southern Brazil. Asterisk shows a significant, high value among species using ANOVA ($p < 0.001$).

azarae by manipulation followed by discarding in the surroundings or by scatterhoarding). In fact, when fruits were found *in situ*, they were not always on the sand plots but outside and around them.

The minimum distances of dispersal would be related to the complete success of seedling establishment and their development after the dispersal event. For species of palms, the success of the dispersed plants appears to happen even a few meters apart from the parent plant but the optimum will happen at a minimum distance of 4 m apart from the parent plants (Silva and Tabarelli, 2001; Pimentel and Tabarelli, 2004; personal observation). In this sense, *D. albiventris* would be perhaps the less successful seed disperser of *S. romanzoffiana* because of the shortest distances of dispersal estimated for it (Pimentel and Tabarelli, 2004; see later) when comparing with the local assemblage of dispersers.

Therefore, each species plays an estimated, unique role in the seed dispersal of *S. romanzoffiana,* through the differential manipulation of seeds, resulting in estimated differential fates. *Didelphis albiventris* does not carry seeds away from the parent plant, and *N. nasua* carries seeds to longer distances than *D. albiventris* (Pizo and Simão, 2001; Costa, 2003; Pimentel and Tabarelli, 2004). *Nasua nasua* shows a differential pattern of seed deposition, based on its physiological characteristics (Jordano, 2000), i.e., the time of gut passage. The same is predicted to the dusky-legged guan *P. obscura* since it presents larger body size and adaptations to swallow fruits (Kruger *et al*., 2006; see latter). In the actual assemblage, the largest body size of *N. nasua* (5 kg) explains why these animals remove more fruits of *S. romanzoffiana* than they chew *in situ*. Our field observations in the study area revealed the presence of *S. romanzoffiana* seeds in scats of *N. nasua* and their absence in scats of *D. albiventris*, corroborating our results of fruit manipulation. Because seeds are not dispersed to long distances when fruits fall from the parent plant, dispersal agents that manipulate them *in situ* (pulp consumers) tend to spread them somewhat further as are the cases of *D. albiventris* and *D. azarae* here, although not so far when compared to vertebrates that ingest seeds (*N. nasua* and *P. obscura* here). These distances of dispersal for shorter distance disperser vary from two to six meters for Atlantic Forest palm trees (Silva and Tabarelli, 2001; Pimentel and Tabarelli, 2004).

Didelphis albiventris is an outstanding example of an animal that manipulates large numbers of fruits near the parent plant, showing that at least quantitatively the species contributes to dispersal of *S. romanzoffiana*, by increasing the chances of some seeds reach some meters away from the parent tree. The fact that *D. albiventris in situ* chews more *S. romanzoffiana* fruits (without damaging the endosperm) than removes may be related to the large size of the seed (2.2 mm in length) in relation to its relative small body size (1 kg on average). This implies that *D. albiventris* does not swallow fruits of this size, which is indicated by the observation of only fibres in *S. romanzoffiana* scats (Cáceres, 2002). We suggest, however, that the disappearance of 13 % of the seeds manipulated by *D. albiventris* is related to some longer dispersal than expected for this species.

Although the number of manipulated fruits by *D. azarae* has been small (80 fruits), it contradicted our expectations. *Dasyprocta azarae* was mainly an *in situ* consumer of *S. romanzoffiana* fruit pulp and not a great remover in the study area, similarly to *D. albiventris*. This behaviour differs from studies on *Dasyprocta,* which have reported the species as a scatter-hoarder. This non-expected behaviour differs from reports on other plant species, in which it scatter-hoards more effectively (e.g. Hallwachs, 1986; Pimentel and Tabarelli, 2004). However, this differential behaviour does not necessarily imply in absence of *S. romanzoffiana* dispersal, as discussed for *D. albiventris*, and because a percentage (12 %) of the manipulated fruits could have been in fact dispersed by scatter hoarding. A possible explanation is that the fruiting peak of these palm species in the study area occurred in the coldest season (personal observation) when there are often fewer resources available in the environment (e.g. Smithe, 1970; Morellato *et al*., 2000). Thus, this can have induced *D. azarae* to exploit the fruits of *S. romanzoffiana* more at that moment (due to starvation) rather than storing them (by scatter-hoarding) for later consumption.

Penelope obscura removed more fruits than that consumed *in situ*, being an expected result because of its large body size (more than 2 kg) combined to a broad beak and other digestive adaptations of birds (Krügel *et al*., 2006; Sick, 1984), allowing swallowing the entire fruit. Similarly to *N. nasua*, this allows it transports the seeds away from the parent plant. This was confirmed by observations of feces of this large bird containing *S. romanzoffiana* seeds in several sites in the study area. Guix and Ruiz (1997) also observed this same species feeding on *S. romanzoffiana* in southeastern Brazil.

Because of these different patterns of fruit manipulation, we can conclude that *P. obscura* and *N. nasua* contribute in a significant way for seed dispersal of *S. romanzoffiana* than do *D. albiventris* and *D. azarae*, but these last two species also have their merit.

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