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Frugivory and seed dispersal of *Solanum granuloso-leprosum* Dunal (Solanaceae) by birds in deciduous seasonal forest

F. A. F. Jacomassa[a]*

[a]Universidade Regional Integrada do Alto Uruguai e das Missões – URI, Campus de Frederico Westphalen, Av. Sete de Setembro, 1621, Itapajé, CEP 98400-000, Frederico Westphalen, RS, Brazil

*e-mail: fabioafj@gmail.com

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(With 3 figures)

Abstract

The goal of this study was to identify which bird species consume *Solanum granuloso-leprosum* fruits and disperse its seeds. 60 hours of focal observations were carried out between April and May 2006 on the edge of a deciduous forest fragment in the Uruguay River region, Rio Grande do Sul state, Brazil. Ten species were observed in total removing 443 fruits. *Saltator similis* removed 61.8% of the fruits, followed by *Tangara sayaca* (17.1%), *Pipraeidea bonariensis* (11.7%), and *T. preciosa* (6.8%), while the remaining six species accounted for only 2.5% of the fruits removed. Most fruit removal occurred early in the day or mid-afternoon. The most common feeding behaviors were *picking* (60.7%), followed by *stalling* (23%) and *hovering* (16%). Birds flew more than 10 m from the fruit plant in 62% of the removal events. All bird species observed here may be considered potential dispersers of *S. granuloso-leprosum*, as they moved the seeds away from the mother plant where strong competition and predation are likely to occur. Results also suggest that *S. granuloso-leprosum* may be useful in ecological restoration programs.

Keywords: mother plant, ornitochory, pioneer plant, secondary fragment forest.

Frugivoria e dispersão de sementes em *Solanum granuloso-leprosum* Dunal (Solanaceae) por aves em Floresta Estacional Decidual

Resumo

O objetivo deste estudo foi identificar quais as espécies de aves consomem frutos de *Solanum granuloso-leposum* e dispersam suas sementes. Para tanto, 60 horas de observações focais foram realizadas entre abril e maio de 2006 na borda de um fragmento de floresta decídua na região do rio Uruguai, Rio Grande do Sul, Brasil. Dez espécies foram observadas removendo 443 frutos. *Saltator similis* removeu 61,8% dos frutos, seguido de *Tangara sayaca* (17,1%), *Pipraeidea bonariensis* (11,7%), e *T. preciosa* (6,8%), enquanto as restantes seis espécies representaram apenas 2,5% dos frutos removidos. A maioria das remoções dos frutos ocorreram no início do dia ou meio da tarde. Os comportamentos alimentares mais comuns foram *picking* (60,7%), seguido por *stalling* (23%) e *hovering* (16%). As aves voaram mais de 10 m da planta de onde removeram frutos em 62% dos eventos de remoção. Todas as espécies de aves observadas aqui podem ser consideradas potenciais dispersores de *S. granuloso-leprosum*, moveram sementes para longe da planta-mãe, onde a concorrência e a predação são mais susceptíveis de ocorrer. Os resultados também sugerem que *S. granuloso-leprosum* pode ser útil em programas de restauração ecológica.

Palavras-chave: planta mãe, ornitocoria, planta pioneira, fragmento de floresta secundária.

1. Introduction

Seed dispersal by vertebrates is fundamental for the reproductive success of many tropical plant species, particularly in the Neotropical region where vertebrates vector up to 90% of plants (Howe and Smallwood, 1982; Fleming et al., 1987). This process represents the connection between the last plant reproductive stage and the first stage of population recruitment. Studies of plant-frugivore interactions are needed in order to better understand the dynamics of colonization by pioneer plants and other species; of particular importance are studies evaluating frugivore behavior and location of seed deposit (Janzen, 1970; Connell, 1971; Herrera et al., 1994; Vasconcellos-Neto et al., 2009).

Studies of bird frugivory in areas with suppressed vegetation are valuable because they generate subsidies for future management plans for urban environments, and for recovery of degraded areas (Guimarães, 2003). Frugivores are play an important role in the recuperation

of degraded environments because they carry seeds that, when dispersed to suitable locations, can initiate succession processes; for this reason studies of bird frugivores may be applicable to forest management plans (Wunderle Junior, 1997; Galetti et al., 2004). To understand the influence of frugivores in seedling establishment and vegetation succession, it is necessary to understand how they act in seed dispersal. Seeds are carried to suitable places for germination and establishment (i.e., far from the mother plant and seed predators), or seed germination is increased (Janzen, 1970; Connell, 1971; Traveset, 1998). Studies with plant species in early secondary succession may elucidate seed dispersal strategy, and may help to identify plant species for inclusion in ecological restoration programs (Allenspach and Dias, 2012; Allenspach et al., 2012; Gonçalves et al., 2015).

Solanum granuloso-leprosum Dunal (Solanaceae) occurs in mixed and dense ombrophilous forests as well as deciduous and semi-deciduous seasonal forests. It is a pioneer small tree thriving on the edges of both natural and disturbed habitats (Cáceres and Moura, 2003; Mentz and Oliveira, 2004). Infructescences contain on average 12.0 ± 7.1 fruits (n = 100), with a diameter of 14.7 ± 11.3 mm (n = 100). Each fruit contains 140.0 ± 31.5 (n = 100) small seeds (2 mm length × 1.7 mm wide). Unripe fruits are green, acquiring a green-yellowish color when ripe. Maturation is asynchronous, and the fruits produce a faint odor when ripe (Jacomassa and Pizo, 2010). The fruits have zoochoric dispersal syndrome (Van der Pijl, 1972), and the vertebrates typically responsible for removing fruits are common to disturbed environments, including the frugivores that disperse Solanaceae seeds in these areas (e.g. birds, bats, rodents, opossums, and crab-eating foxes) (Marcondes-Machado and Argel-de-Oliveira, 1988; Müller and Reis, 1992; Reis et al., 1993; Rocha et al., 2008; Galetti and Morellato, 1994; Poulin et al., 1994; Sazima et al., 1994; Cáceres, 2002; Cáceres and Moura, 2003; Jacomassa and Pizo, 2010).

The goal of this study was to determine which avian species use *S. granuloso-leprosum* fruits as a food source, as well as to determine the timing of and behaviors associated with fruit removal, the distance that the fruits were carried for feeding (seed dispersal), and to evaluate agonistic behaviours.

2. Material and Methods

This study was conducted in the municipality of Frederico Westphalen, located in the Upper Uruguay River region, northwestern Rio Grande do Sul state, southern Brazil. The focal area was the edge of a 47 ha fragment (27°12'29"S and 53°24'33"W) of secondary deciduous seasonal forest (Atlantic forest *sensulato*), located at the Universidade Regional Integrada do Alto Uruguai e das Missões. I observed a group of seven *S. granuloso-leprosum* plants located at distances of ~2 m from each other,and within an area of ~300 m^2.

I used the animal focal method sampling, which included positioning near plants with ripe fruits (about of 5-10 m), and recording the species feeding on fruits, as well as all feeding behaviors (Altmann, 1974). Birds observed eating fruit were continuously watched and behaviors recorded until the animal was no longer visible. Observations were performed during the season with the highest number of ripe fruits (autumn). In order to assess peak availability of ripe fruit, the phenophases of 33 *S. granuloso-leprosum* plants were monitored every 2 weeks between August 2005 and August 2006.

A total of 60 h of focal observations were carried out between April and May 2006, for five non-consecutive days. The observations started every day at dawn (6h 30min), and ended at dusk (12 h of observation, considering the photoperiod according to List, 1949), and were divided into 1 h intervals between sunrise and sunset. Birds were identified visually, using 10 × 25 mm binoculars when necessary. Birds were classified into trophic categories using Machado and Lamas (1996), Sick (2001) and Manhães et al. (2003), while taxonomic classifications followed the List of Brazilian Birds (CBRO, 2014). The fruit collecting behaviours by frugivorous birds were classified according to Moermond and Denslow (1985), and included: *picking* (taking fruits close to their perch without extending their bodies or assuming any specific positions), *reaching* (bird extends its body out or down from the perch), *hanging* (the bird's entire body and legs are under the perch with the ventral side up), *hovering* (bird pauses in front of the fruit while flapping its wings to take it), and *stalling* (bird in flight pauses briefly in front of the fruit to take it). The distance between the bird and mother plant and the location of fruit consumption were visually estimated, and measurements were made after observations to improve estimates. Any agonistic behaviors were also recorded.

I used a nonparametric Kruskal-Wallis test reporting chi-square values to compare the removal of fruits in different time intervals (95% confidence). This test was done in Past program (Hammer et al., 2001).

3. Results

Three families and ten species of birds were observed removing 443 *S. granuloso-leprosum* fruits (all fruits were effectively removed). *Saltator similis* removed 61.85% of the fruits, followed by *Tangara sayaca* (17.16%), *Pipraeidea bonariensis* (11.7%), and *Tangara preciosa* (6.77%). These four species all belong to the Thraupidae family, and together accounted for 97.48% of ripe fruit removals (Table 1). The remaining six species only accounted for 2.52% of fruit removal (Table 1). Twenty-three hours of observation was sufficient to sample all species of birds that consumed *S. granuloso-leprosum* in this area over the entire study period (i.e., after 23 hours of observation no new species were recorded) (Figure 1).

The main behaviors used to take fruits were *picking* (60.7%, used by eight species), *stalling* (23%, used by seven species) and *hovering* (16%, used by four species).

Table 1. Bird families and species recorded eating the fruits of *Solanum granuloso-leprosum*.

Taxa	N removal	%	FB					DBMP		FDCM	H	TC
			pi	re	ha	ho	st	0	>10m			
Tyrannidae												
Elaenia flavogaster (Thunberg, 1822)	1	0.23	1	-	-	-	-	-	1	-	9th	o
Pitangus sulphuratus (Linnaeus, 1766)	4	0.9	2	-	-	-	2	-	4	-	6th	o
Turdidae												
Turdus rufiventris Vieillot, 1818	2	0.46	-	-	-	-	2	-	2	-	9th	o
Turdus amaurochalinus Cabanis, 1851	1	0.23	-	-	-	-	1	-	1	-	5th	o
Thraupidae												
Saltator similis d'Orbigny & Lafresnaye, 1837	274	61.85	149	-	1	57	67	65	138	71	1st and 9th	o
Tangara sayaca (Linnaeus, 1766)	76	17.16	51	-	-	9	16	5	61	10	9th	o
Tangara preciosa (Cabanis, 1850)	30	6.77	22	-	-	3	5	2	28	-	8th and 9th	f
Pipraeidea melanonota (Vieillot, 1819)	2	0.46	2	-	-	-	-	-	2	-	9th and 11th	o
Pipraeidea bonariensis (Gmelin, 1824)	52	11.7	41	-	-	2	9	14	38	-	8th and 9th	f
Hemithraupis guira (Linnaeus, 1766)	1	0.23	1	-	-	-	-	-	1	-	10th	f
Total	443	100	269	0	1	71	102	86	276	81		

Number (N) of removed fruits, relative frequency (%), feeding behavior (FB), distance of the bird in relation to the mother plant after capturing the fruit (DBMP), fruits dropped under the crown of the mother plant (FDCM), interval (s) of time in which the species removed most of the fruits it ate (H) and trophic category (TC). pi = picking, re = reaching, ha = hanging, ho = hovering, and st = staling; 0 = on the plant, >10m = 10m far from the mother plant, f = frugivorous, o = omnivorous.

In some cases fruit was eaten piecemeal, and mandibulated to such an extent that it was partially flattened or crushed (*mashing*, Moermond, 1983), observed in *S. similis* (n = 52), *T. sayaca* (n = 13), *T. preciosa* (n = 2), and *P. bonariensis* (n = 14). Only *P. sulphuratus* swallowed fruits whole (n = 2). In 62% of the cases, the birds flew more than 10 m from the mother plant after removal of fruits, while the remaining either ate at the mother plant or dropped the fruits under the crown (Table 1). Fruits were eaten throughout the day, though most removals occurred within the 9th time interval (18%), followed by the 1st (14%) and 8th (14%), indicating two peaks of feeding activity, one at dawn and another at mid-afternoon ($_{X}^{2} = 23.2$; df = 11; $p < 0.05$) (Figure 2).

Saltator similis was the only aggressive species, and appeared to defend its food source. There was a single intraspecific interaction involving *S. similis*, as well as interspecific interactions where *S. similis* attacked *Tangara sayaca* (n = 8), *T. preciosa* (n = 5), and *Pipraeidea bonariensis* (n = 6), effectively repelling them from the tree. These behaviors occurred during the first interval of the day, which may explain why the species targeted for aggression had greater feeding peaks mid-afternoon (Figure 3).

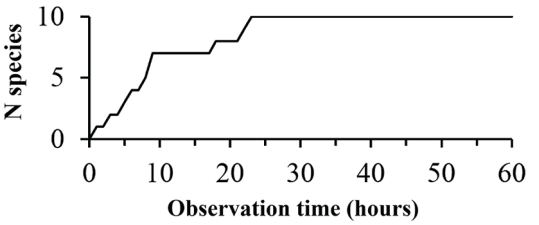

Figure 1. Curve of cumulative number of bird species observed consuming fruit of *Solanum granuloso-leprosum* compared to the observation time.

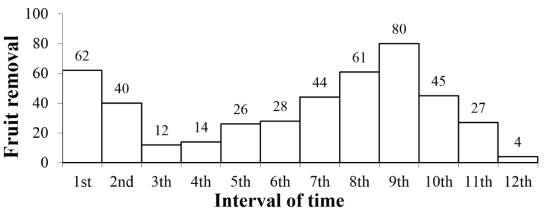

Figure 2. Removals per interval of time. The observations started at dawn (0630) and ended at dusk (1830). The numbers on the bars represent the numbers of fruit removals.

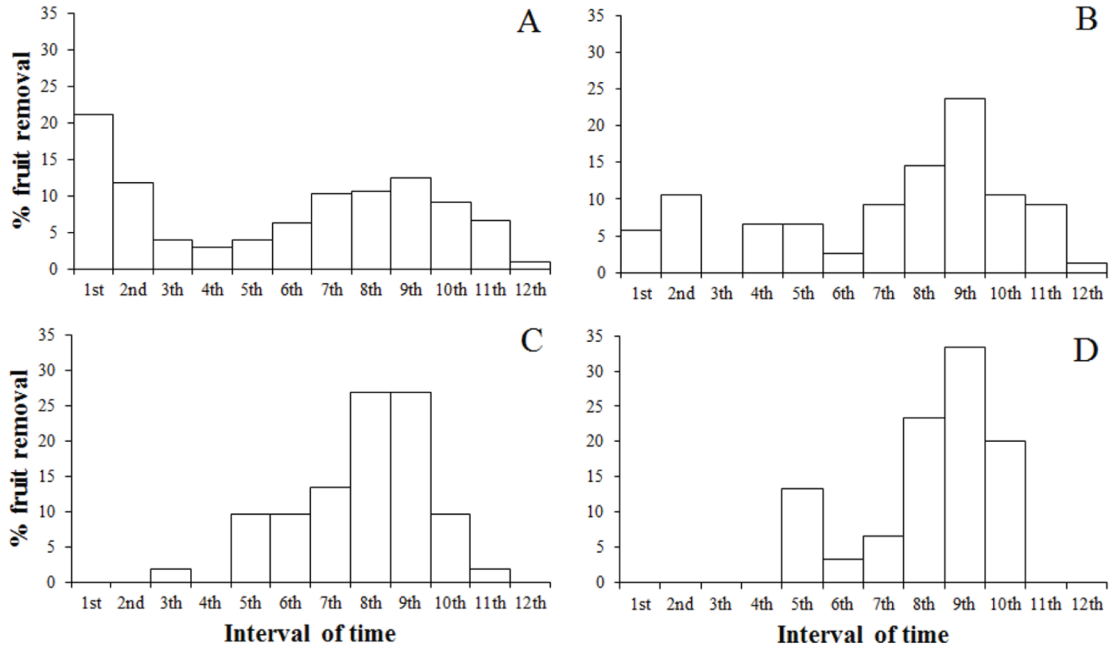

Figure 3. Percentual of removals per interval of time in *S. similis* (A); *Tangara sayaca* (B); *P. bonariensis* (C); and *T. preciosa* (D). The observations started at dawn (0630) and ended at dusk (1830).

4. Discussion

The species reported in this study account for 18% of frugivorous birds species recorded in Frederico Westphalen (Teixeira et al., 2009), suggesting that *S. granuloso-leprosum* is consumed by a large number of bird species despite having a chiropterochoric dispersal system (Van der Pijl, 1972). Fruits from this plant are also consumed by 40% of frugivorous bat species in Frederico Westphalen (Bernardi et al., 2009), indicating a mixed seed dispersal system. Ripe fruits are yellowish in color and produce a faint odor that attracts bats, while unripe fruits are green to attract birds; these taxonomic groups are both important for seed dispersal in this plant (Jacomassa and Pizo, 2010).

Thraupidae are among the most frequent seed dispersers of ornithochoric plants in Brazil (Galetti and Pizo, 1996; Gondim, 2001; Sick, 2001; Francisco et al., 2007; Figueiredo et al., 2008). Although Thraupidae did not efficiently disperse large seeds (Levey, 1987) and sometimes dropped the fruits under the mother plant (Sick, 2001), the small seeds of *S. granuloso-leprosum* were more easily consumed. Additionally, many birds in this family flew more than 10 m from the mother plant after removal of fruits, which suggests dispersal of the seeds. It is also known that seed germination of *S. granuloso-leprosum* is improved by passage through the bird gut (especially Thraupidae) (see Jacomassa and Pizo, 2010).

Feeding behavior could be a limiting factor for the consumption of particular fruits by birds (Moermond and Denslow, 1985), and how fruits are collected may be related to accessibility and location on the tree (Van der Pijl, 1972; Cáceres and Moura, 2003). The exposed outside crown of *S. granuloso-leprosum* facilitates fruit collection during flight by *picking, stalling* and *hovering* (which together accounted for 99.7% of feeding behaviors).

Some birds ate fruits piecemeal, or mandibulated the fruits, crushing them and squeezing out and swallowing much of the pulp and juice. Moermond (1983) suggested that the suction-drinking capability of tanagers developed for efficient swallowing of juice crushed out of watery fruits. Seeds are frequently separated from the pulp and dropped during the mashing process. According Moermond and Denslow (1985), this reduces the bulk of indigestible material to be processed, resulting in limited seed dispersal, especially for moderately large seeds. The authors also suggest that the ability of birds to eat fruits piecemeal increases the size range of exploitable fruits beyond those that are swallowed whole.

Activity period was an important factor for understanding species behavior (Weller and Bennett, 2001). I found some patterns and factors affecting activity period in the studied taxa, some of which maybe considered adaptations to environmental influences (Beltran and Delibes, 1994). For example, *Tangara sayaca*, *T. preciosa* and *P. bonariensis* removed more fruits during similar time intervals (mid-afternoon), which may have been due to the increased morning activity of *Saltator similis*, the more dominant and aggressive species. This overlap in resource use results in intra and interspecific competition and division of resources, which may affect the realized niches of coexisting species (Forsman et al., 2014).

Some birds rested on the mother plant for long periods of time after the fruit was removed (*S. similis* in one case

spent more than 5 min, and *P. bonariensis* in one case spent more than 3 min resting). These birds defecated in the immediate area (intact seeds were found in the feces on site), dropped the fruits, or dropped the seeds while eating under the mother plant, all of which reduce the chances of successful seed dispersal (Janzen, 1970; Connell, 1971).

All of the birds species recorded could be considered potential dispersers of *S. granuloso-leprosum* because the seeds were in many cases taken from the immediate area of the mother plant, where competition and predation are expected to occur (Janzen, 1970; Connell, 1971). The bird species that consumed fruits and dispersed the seeds were all generalists, common to disturbed environments (Cáceres and Moura, 2003; Sick, 2001). The mixed (or generalist) system of seed dispersal of this pioneer plant is vital for the recuperation of degraded environments, because the vertebrates responsible for fruit removal and seed dispersal in this case (i.e., birds and bats) are common indisturbed urban environments. Results also suggest that *S. granuloso-leprosum* may be useful in ecological restoration programs.

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