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Seasonal diet variation, preferences and availability of resources consumed by *Sturnira lilium* (É. Geoffroy St.-Hilaire, 1810) (Chiroptera: Phyllostomidae) in Brazilian seasonal deciduous forest

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Abstract: *Sturnira lilium* is a frugivorous bat that is known for its high consumption of Solanaceae fruits. We captured *S. lilium*, using mistnets, to study its diet and diet seasonal variation in a seasonal deciduous forest in southern Brazil. We also investigated the predominance of Solanaceae and of *Solanum granulosoleprosum*, the main food source, correlated with the availability of ripe fruits. A total of 11 plant species were identified from 126 fecal samples. Seeds of Solanaceae species were present in 81% of the samples, with *S. granulosoleprosum* seeds being the most common (68.3 %). There was no seasonal variation in the diet; however ANOVA revealed that the consumption of Solanaceae and *S. granulosoleprosum* showed monthly differences. There was no monthly correlation and there was a weak seasonal correlation between ripe fruit availability and the consumption of *S. granulosoleprosum* by *S. lilium*, indicating that this bat species occupies broad home ranges and is capable of locating plants with mature fruits in adjacent areas during most of the year. The mobility of *S. lilium* and high abundance of *S. granulosoleprosum* in the diet suggests that this species as good disperser of plants that are characteristic of early successional stages and areas undergoing regeneration.

Key words: Atlantic Forest, bat-plant interactions, frugivory, phenophases, seed dispersal, *Solanum granulosoleprosum*.

INTRODUCTION

The high vagility of frugivorous bats, in addition to their high consumption of pioneer plant species place these mammals among the most important seed dispersers in Neotropics, especially for plants with small seeds (Fleming & Heithaus 1981, Fleming & Sosa 1994, Lobova et al. 2009, Bredt et al. 2012). Therefore, these bats have potential to promote the recuperation of degraded areas and fragmented environments (Galindo-González 1998, Medellín & Gaona 1999, Bredt et al. 2012).

Among the frugivorous bats, *Sturnira lilium* occurs in the Brazilian Shield portions of Brazil, Bolivia, Paraguay, and Argentina, including areas of Atlantic Forest, Cerrado, and Chaco (Velazco & Patterson 2013, 2014). It is among the most widespread and locally abundant bats of the New World tropics (Velazco & Patterson 2013), and has a highly diverse diet composed predominantly of pioneer plants from the family Solanaceae (Fabián et al. 2008, Bredt et al. 2012, Parolin et al. 2016). Solanaceae contains primarily small-seeded species, many of which are pioneer plants that thrive on the edges of natural and disturbed areas (Mentz & Oliveira 2004). According to Fabián et al. (2008) and Bredt et al. (2012), plants in this family are the most commonly exploited food resources by bats in Latin America.

Beyond predominantly of Solanaceae the diet of *S. lilium* is composed of fruits from Piperaceae, Moraceae, and Urticaceae (Fabián et al. 2008, Lobova et al. 2009, Bredt et al. 2012). *Sturnira lilium* feed mainly on fruits of Solanaceae and Piperaceae, and, to a lesser extent, Moraceae and Urticaceae in both dense ombrophilous and seasonal semi-deciduous forest (Marinho-Filho 1991, Muller & Reis 1992, Passos et al. 2003, Mello et al. 2008).

Some studies have addressed aspects of the interactions between plants and frugivorous bats in seasonal semideciduous forests (Muller & Reis 1992, Mikich 2002), dense ombrophilous forest (Sipinski & Reis 1995, Passos & Graciolli 2004), and mixed ombrophilous forest (Cáceres & Moura 2003), in southern Brazil, however, there is a lack of studies in seasonal deciduous forest.

In the present study, we aimed to assess: (i) the dietary composition of *S. lilium* in seasonal deciduous forest fragments by analyzing fecal samples; (ii) whether seasonal variation exists in the diet of *S. lilium*; (iii) whether the diet of this species is mainly composed of plants from the family Solanaceae, as in other regions; and (iv) whether the consumption of *Solanum granulosoleprosum*, the most common food resource of *S. lilium*, is correlated with the availability of their ripe fruits.

MATERIALS AND METHODS

Study area

We conducted the study in the municipality of Frederico Westphalen (27º21'S and 53º23'W), which is located in the Upper Uruguay River region in northern Rio Grande do Sul State, southern Brazil. The climate in the region according to the Köppen classification is humid subtropical with warm summers (*Cfa*), with average annual temperature of 18 ºC, reaching a maximum of 41 ºC in the summer and a minimum below 0 ºC in the winter (Alvares et al. 2013). Average annual precipitation is between 1,800 and 2,100 mm and rainfall is evenly distributed throughout the year, with the region lacking a well-defined dry season. The region is 522 m above sea level and within the seasonal deciduous forest domain (Atlantic Forest *sensu lato*).

The field work was carried out at three sites. Site 1 consisted of a forest fragment 35 ha in a rural region known as Vila Faguense dominated by late secondary riparian forest of the Tunas stream. Site 2 (45 ha) is a late secondary forest near an urban area on the campus of the Universidade Regional Integrada do Alto Uruguai e das Missões (URI). Finally, Site 3 (4 ha) is an urban woodland located on the property of the Sociedade Aquática Barrilense, composed of grassland with sparse native and exotic vegetation. In these areas, the understory is sparse and chiropterochorous species (Piperaceae and Solanaceae) are rare or absent, but on the forest fragments edges and in disturbed habitats Solanaceae was present (especially on site 2). Site 1 is located approximately two kilometers from the other sites, which are about 600 m apart.

Assessing diet composition for fecal samples

The bats were captured using mist nets (7 × 2.5 m) for one entire night (open at dusk and closed at dawn, period varied throughout the year) per month between October 2005 and September 2006, for a total of 36 nights of sampling (12 nights/site). The mist nets were positioned 0.5 m from the ground and placed along trails, clearings, inside the forest and along the forest edges, and perpendicularly to water bodies. The sampling effort was calculated following Straube & Bianconi (2002) as the product of the mist nets sampling (105 m^2), the number of sampling hours per night (12), and the total number of netting nights (36). For seasonal comparisons, we considered October, November, and December as spring; January, February, and March as summer; April, May, and June as autumn, and July, August, and September as winter. The bats were identified using identification keys (Vizotto & Taddei 1973, Barquez et al. 1999), marked with numerical metal bands (4 or 5 mm) in omega format (Ω) and released.

The captured bats were placed individually into clean, numbered cotton bags where they remained for approximately one hour to obtain fecal samples. To optimize fecal sample collection, transparent plastic strips (7 × 1 m) were placed under the mist nets to collect feces excreted due to the capture stress (Passos & Silva 2003). The fecal samples were individually placed into plastic microtubes with 70% ethanol with their respective ID numbers. Seeds from fecal samples were identified by comparison with our own seed database for seasonal deciduous forest and others domain. The plant species identified in fecal samples were classified into categories (pioneer and secondary) and growth form (tree, shrub, epiphyte and vine).

Assessing the availability of ripe fruits of *Solanum granulosoleprosum*

To assess the seasonal availability of ripe *S. granulosoleprosum* fruits, 33 adult plant with a stem DBH ≥ 5 cm located in Site 2 were monitored fortnightly between October 2005 and September 2006. During this monitoring, we counted the number of plants with ripe fruits. We decided not to estimate abundance of fully ripe fruits because we observed strong daily variation in its availability, and determination of fully ripe fruits was not feasible due to difficulties to access all infructescence and to avoid potential damages caused by evaluating fruit consistency (e.g., fall and/or injury). For data analysis we used the mean monthly number of plants with fully ripe fruits. We chose this particular site due to its high density of plants and ripe fruits and relatively easy sampling access compared to other sites. We also observed plants with ripe fruits in other sites, but this information was not counted. We chose *S. granulosoleprosum* based on previous observation studies of the predominance of its seeds and Solanaceae in bat feces, and also due to high density in the study region at the forest edges, in clearing, and disturbed habitats (Cáceres & Moura 2003, Passos et al. 2003, Mentz & Oliveira 2004).

Data analysis

The diet was assessed qualitatively and quantitatively from identified food items using the frequency of occurrence of seeds of the different plant species in fecal samples and reported as percentages and total numbers of seeds. We evaluated monthly differences in consumption of fruits of Solanaceae with that of other families and with *S. granulosoleprosum*, the main item, with other items. This was done using one-way ANOVA. We used this same test for seasons using mean frequency values over three months occurrence. Correlations between the monthly and seasonal number of *S. granulosoleprosum* with ripe fruits and the number of fecal samples with *S. granulosoleprosum* seeds were evaluated using simple linear regression. For seasons we used mean values of the monthly numbers. The data were log-transformed [log10 (x + 1)] to decrease the effect of the most abundant species (Sokal & Rohlf 1995). All statistical analyses were done in the Past statistical program (Hammer et al. 2001). The plant species whose fruit were found being carried by *S. lilium* but which did not occur in the feces were not considered in the analyses.

RESULTS

We obtained 268 captures of *Sturnira lilium* including 13 recaptures (almost 5% of recapture rate) of 255 individuals with a total sampling effort of 45.360 h.m^2 (monthly average of 22.6 ± 6.3, with a maximum of 84 in June and a minimum of three captures in September). Six recaptures (2.2% of recapture rate) were obtained in sites different from the site of initial capture. A total of 126 fecal samples with identifiable material were collected (monthly average of 9.4 ± 11.2, with a maximum of 33 in June and a minimum of zero fecal samples in March). All the 126 fecal samples contained seeds of only one plant species. Of all fecal samples with seeds, 99.1% were obtained on the transparent plastic strips and less than 10% while the bats were in cotton bags (the same individual from the same catch can produce two samples, one of the plastic strip and other of the cotton bag, these were put together in a single sample). Those fecal samples contained a total of 2952 seeds from 11 plant species as well as insect fragments. We identified seeds of Solanaceae in 81% of the fecal samples (68.3% were *S. granulosoleprosum*), and almost 90% of the identified plant species in the fecal samples were classified as pioneer species (Table I).

The monthly analysis of fecal samples indicated that fruit of Solanaceae species were equally or more frequently consumed than fruit of other plants families (F = 4.019, d.f. =11, p = 0.014), but there were no differences among seasons (F = 0.331, d.f. = 3, p = 0.805) (Figure 1). *Solanum granulosoleprosum* apparently was also more frequently consumed than were other food items in the monthly analysis (except September and December, F = 6.382, d.f. = 11, p = 0.002), but there were no differences among seasons (F = 3.559, d.f. = 3, p = 0.162) (Figure 2). Although there were 14 captures in March no fecal samples containing seeds were obtained (Figures 1, 2 and 3).

In addition to the plant species with small seeds (≤ 3 mm) found in the fecal samples, *S. lilium* were captured transporting large-seeded fruits (≥ 10 mm) such as *Chrysophyllum gonocarpum* (n = 4), *Holocalyx balansae* (n = 6) and *Eriobotrya japonica* (n = 4) on 14 occasions. Thus, in total, we recorded 14 plant species consumed by *S. lilium* in this study.

Correlation between availability of *S. granulosoleprosum* ripe fruits and consumption

At Site 2, the highest number of plants with ripe fruits were observed during autumn and winter (April-September), with a peak at the end of autumn and low proportion of trees with ripe fruits in spring and through most of the summer (with absence in January) (Figure 3).

The simple linear regression showed no monthly correlation between ripe fruit availability and the number of fecal samples containing *S. granulosoleprosum* seeds (R = -0.035, R^2 = 0.001, p = 0.913) (Figure 4a), however it showed a weak seasonally correlation (R = 0.476, R^2 = 0.226, p = 0.523) (Figure 4b).

DISCUSSION

Sturnira lilium ate mainly fruits from Solanaceae, but occasionally consumed fruits of 10 other plants, and the diet of this species did not vary seasonally in the seasonal deciduous forest. Our results also showed that although *S. granulosoleprosum* was s the most commonly consumed species and monthly dominant in the

Table I. Plant species of seeds and other food item recorded in fecal samples of *Sturnira lilium* in Frederico Westphalen municipality, Rio Grande do Sul, Brazil. C = plant category (pi = pioneer, sc = secondary), GF = growth form (t = tree, s = shrub, e = epiphyte, v = vine), N = number of fecal samples with a given taxon, FO = frequency of occurrence in fecal samples (%), NS = total number of seeds obtained.

Taxa	C	GF	N	FO	NS
Solanaceae					
Solanum granulosoleprosum Dunal	pi	s/t	86	68.3	1319
Solanum sanctaecatharinae Dunal	pi	s/t	5	4	44
Vassobia breviflora (Sendtn.) Hunz.	pi	s	10	7.9	267
Not determinate	pi	-	1	0.8	12
Moraceae					
Ficus cestrifolia Schott	sc	t	7	5.6	73
Passifloraceae					
Passiflora sp.	pi	v	3	2.4	15
Vitaceae					
Vitis vinifera L.	pi	v	1	0.8	34
Cactaceae					
Rhipsalis floccosa Salm-Dyck ex Pfeiff.	pi	e	6	4.8	752
Lepismium cruciforme (Vell.) Miq.	pi	e	2	1.6	422
Seed 1 not determinate	-	-	2	1.6	13
Seed 2 not determinate	-	-	1	0.8	1
Insects	-	-	2	1.6	-
Total			126	100	2952

diet of *S. lilium*, it was weakly correlated with seasonal ripe fruit availability.

Our findings support previous studies of the diet of *S. lilium*. The predominance of Solanaceae fruits in the diet was reported by Marinho-Filho (1991) and Muller & Reis (1992) in seasonal semi-deciduous forest, and by Passos et al. (2003) and Mello et al. (2008) in dense ombrophilous forest. *Sturnira lilium* seems to prefer fruit of Solanaceae, although Giannini (1999) showed that this preference depends on other factors like altitude and the temporal and spatial availability of resources. It is also likely that bats are opportunistically selecting fruits based on nutritional value and availability.

In addition to fruits, we identified some other food items in the diet of *S. lilium*. Bredt et al. (2012) reported pollen, nectar, and insects consumed by this species. While our results showed the consumption of insects, we did not identify pollen or nectar, which may be due to our methodological limitations for identifying these items. Although in this study we found that the diet was composed of fruits with small and numerous seeds, we occasionally captured bats consuming large fruits with large seeds. This corroborates findings by Passos et al. (2003), who observed that although the diet of *S. lilium* is based on Solanaceae (78.5%), especially the genus *Solanum*, the diet is likely more diverse.

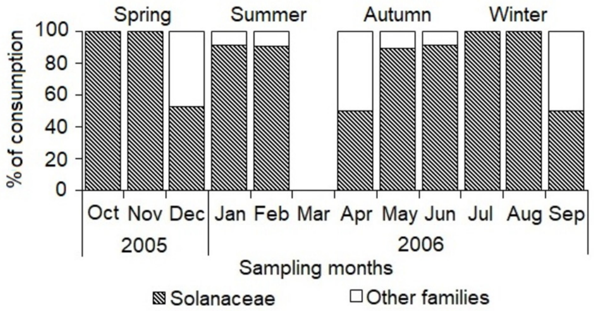

Figure 1. Seasonal percentage of consumption (number of fecal samples with seeds) of Solanaceae and other families in the diet of *S. lilium*.

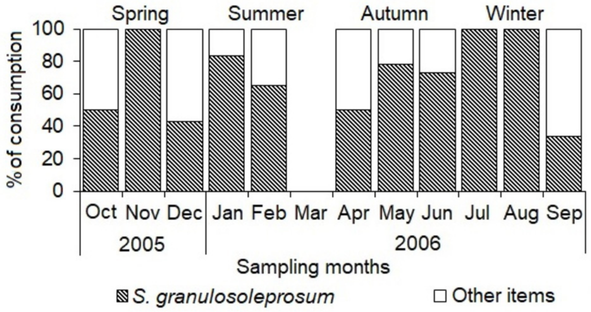

Figure 2. Seasonal percentage of consumption (number of fecal samples with seeds) of *S. granulosoleprosum* and other items in the diet of *S. lilium*.

Jacomassa & Pizo (2010) found no effects (i.e., neutral) on *S. granulosoleprosum* germination of seeds that had passed through *S. lilium* digestive tracts. They disperse most of the seeds ingested within 40 minutes and can cover great distances in a single night and defecate during flight (Bernard & Fenton 2003, Bianconi et al. 2006, Maccarini et al. 2018), suggesting that *S. lilium* is likely a good seed disperser for this plant. Even at short distances, seed dispersal is important for reducing competition and predation underneath the mother plant (Janzen 1970) and promotes gene flow among populations (Heithaus 1982).

Pioneers comprised nearly 90% of the plant species recorded in the fecal samples. Throughout the range of *S. lilium* distribution, there is a prevalence of pioneer species in their diet (Passos et al. 2003, Olea-Wagner et al. 2007, Mello et al. 2008, Bredt et al. 2012). Pioneer species play an important role in forest succession because they facilitate the recovery of degraded areas in fragmented landscapes. Our bat recapture data evidenced that *S. lilium* can commute among fragments. Considering that the Atlantic forest is currently restricted mostly to small fragments embedded in anthropic matrices (Ribeiro et al. 2009), the studied bats can play an important role in improving forest connectivity. Given the pioneer nature of *S. granulosoleprosum*, the high degree of forest fragmentation in the Upper Uruguay River region, and the abundance of *S. lilium* (Bernardi & Passos 2012), this bat likely performs valuable ecological services for environmental regeneration.

The few *S. lilium* captures and absence of fecal samples in March 2006 may be related to population migration or displacement as a function of food availability, as observed by Giannini (1999) in Argentina, and Pedro & Taddei (2002), Passos et al. (2003) and Esbérard et al. (2017) in southeastern Brazil. According to these authors, frugivores tend to respond temporally and spatially to resource availability. On the local scale, changes in food availability may lead to changes in diet or the extensive search for new feeding areas (Dumont 2003). On a larger scale, changes in food availability may result in displacements or migratory behavior (Fleming & Eby 2003), for either short (our recaptures from 600 to 2,000 m) or long distances (Esbérard et al. 2017, mention a recapture of *S. lilium* 78.6 km after 366 days).

In January 2006 there were no ripe fruits of *S. granulosoleprosum* in Site 2, but there were seeds identified in the fecal samples of *S. lilium*. Only in March 2006 seeds of this plant were absent in the fecal samples of *S. lilium*, although ripe fruits were availability at Site

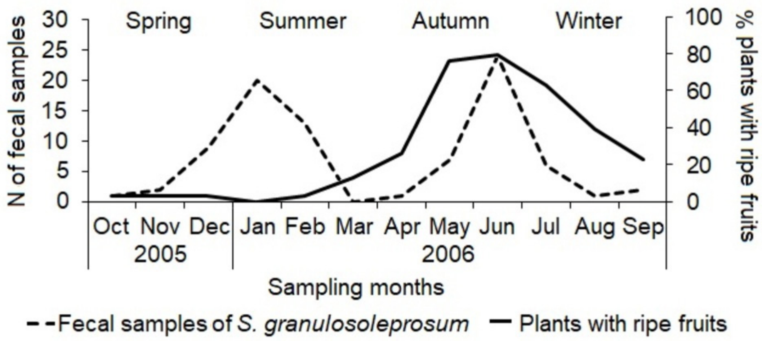

Figure 3. Seasonal number of fecal samples with *S. granulosoleprosum* seeds and percentage of plants of *S. granulosoleprosum* with ripe fruits available.

2. This suggest that *S. lilium* does not always have the same food preferences (Muylaert et al. 2014), or can search for food in other locations, since plant reproductive phenology in tropical forests is highly variable among individuals and populations (Williams-Linera & Meave 2002). Bats may also utilize their sense of smell to search for food in other areas, since *S. granulosoleprosum* ripe fruits produce a stronger odor during the night than during the day, may use memory to return to profitable locations and can be guided by the odor to select the preferred ripe fruits (Thiele & Winter 2005, Jacomassa & Pizo 2010, Parolin et al. 2015). Our results (i.e., from phenophase monitoring and the seasonal dietary analysis, Figure 3) also indicate that ripe fruits of *S. granulosoleprosum* are available throughout the year, indicating this plant as a potentially important food resource for *S. lilium* and other frugivores (Jacomassa & Pizo 2010, Jacomassa 2016).

Our study showed that the relationship between *S. lilium* and Solanaceae, especially *S. granulosoleprosum*, seems to be a relationship of specialization (at least in our study region). Some degree of diet specialization occurs in several bat species; for example, *Carollia* genus is specialized in consumption of several species of Piperaceae (Thies & Kalko 2004, Fabián et al. 2008).

The species *Chrysophyllum gonocarpum*, *Holocalyx balansae*, *Eriobotrya japonica*, *Vitis vinifera*, *Rhipsalis floccosa* and *Lepismium cruciforme* have not previously been identified as part of the *S. lilium* diet and the later two (Cactaceae) are recorded here for the first time in the diet of bats. These results emphasize the importance of dietary studies, even though similar studies have already been done.

We would also like to highlight, as pointed out by other authors (e.g., Passos & Silva 2003, Galindo-González et al. 2009), the utility of transparent plastic strips placed underneath mist nets to receive feces excreted due to capture stress. This method is rarely used when sampling frugivores or in seed dispersal studies; however, it is valuable in such studies due to enabling the collection of virtually all seeds defecated by bats captured in mist nets,

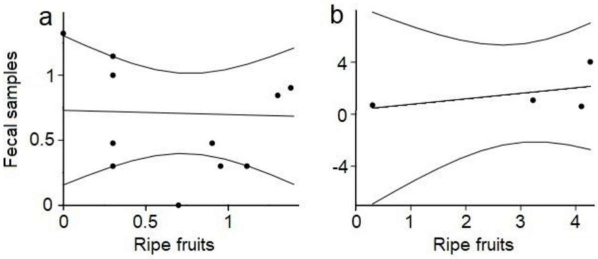

Figure 4. Correlations between the seasonal availability of ripe fruits on the monitored plants and the presence of *S. granulosopeprosum* seeds in fecal samples of *S. lilium*. Monthly in left (a) (R = -0.035, R^2 = 0.001, p = 0.913) and per season in right (b) (R = 0.476, R^2 = 0.226, p = 0.523), with 95% of confidence.

as well as whole fruits in transport to be eaten elsewhere. As mentioned by Jacomassa (2016), this study also reinforces the usefulness of *S. granulosoleprosum* in restoration projects.

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