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Structure of mutualistic networks between bats and plants and other feeding strategies in a semiarid Caatinga forest of Rio Grande do Norte, Brazil

Eugenia Cordero Schmidt

Natal, RN, 2016

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Dissertação apresentada ao Programa de Pós
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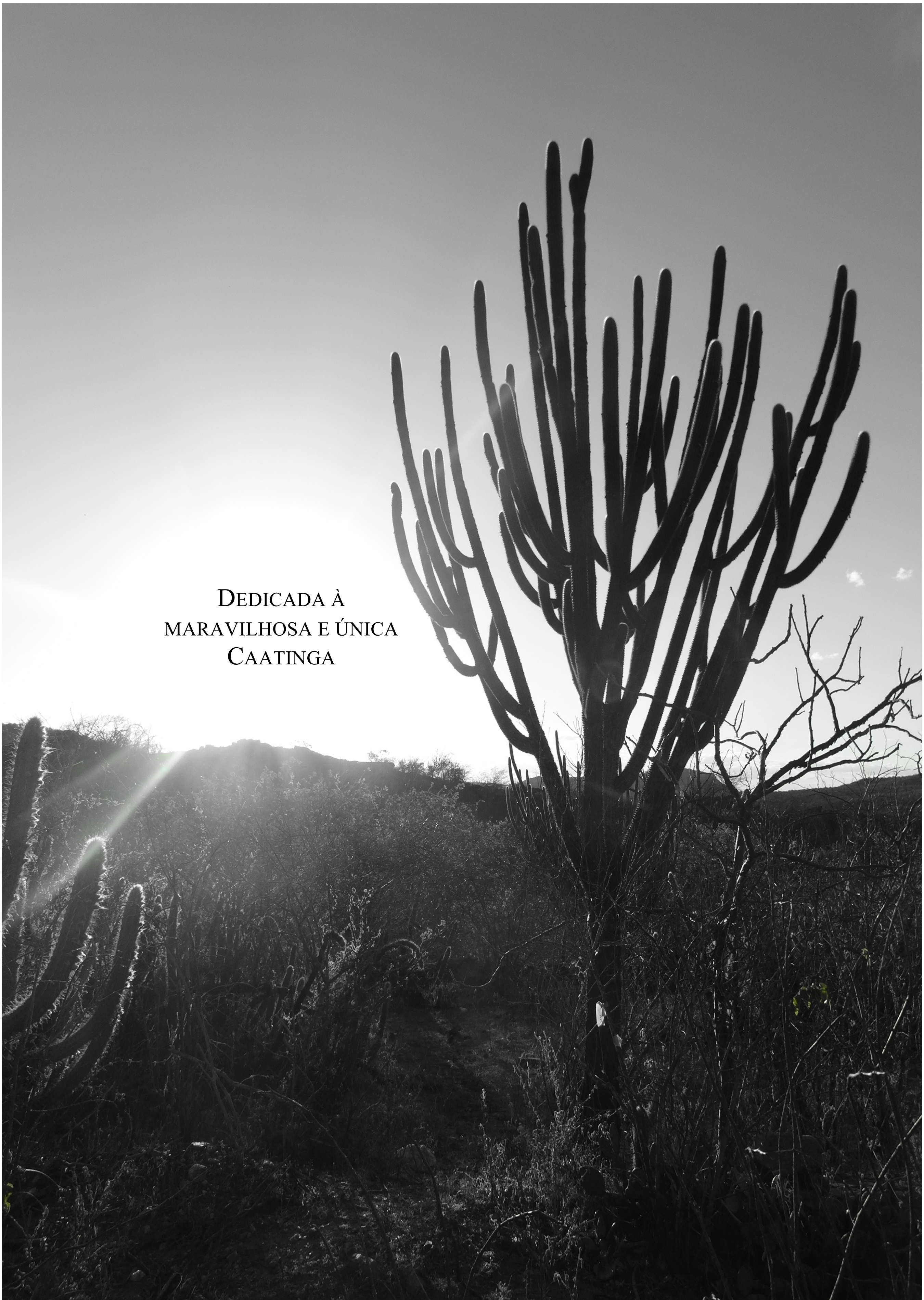

Dedicada à
maravilhosa e única
Caatinga

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CONTENTS

RESUMO: A Caatinga é uma formação florestal esclerófila, decídua e espinhosa. Situa-se em uma região semi-árida, com cerca de 730 000 km2, exclusiva do território brasileiro. Este ambiente apresenta grande variação de tipos de vegetação que foram atribuídas à variações em larga escala no clima, padrões de geomorfologia e diferenças de pequena escala em relevo e solos. A precipitação escassa e flutuante das regiões áridas e semi-áridas, exercem um forte controle sobre: histórias de vida, características fisiológicas e composição de espécies de sua biota. Pelo menos 77 espécies de morcegos das 178 espécies presentes no Brasil são encontrados na Caatinga, dos quais 13 são frugívoros e cinco nectarivorous incluindo o endémica Xeronycteris vieirai. Os morcegos são conhecidos por desempenharem papéis importantes no controle de pragas, polinização e dispersão de sementes. No entanto, pouca informação foi gerada sobre o papel ecológico dessas espécies em um ambiente como Caatinga. Em geral, esse habitat é o ecossistema brasileiro mais negligenciado em termos de pesquisa e conservação da sua biodiversidade. Especificamente no caso dos morcegos, o Rio Grande do Norte possui uma das maiores lacunas de conhecimento no Brasil. Os dados aqui apresentados, representam uma das primeiras pesquisas formais com morcegos na Caatinga do Rio Grande do Norte. Foram geradas informações sobre a estrutura aninhada e assimétrica da rede mutualística entre morcegos nectarívoros e espécies-chave de plantas para a manutenção da comunidade de morcegos nectarívoros nesta região. Além disso, a primeira evidência de folivoria de pelo menos 16 espécies de plantas pelo morcego frugívoro Artibeus planirostris foi documentada. Isto representa o primeiro registro para um ambiente semi-árido e o primeiro registro para a espécie. Finalmente, o primeiro "insight" para aspectos biológicos do morcego endêmico *X. vieirai*, incluindo dieta, poleiros e dados de reprodução, assim como a extensão de sua distribuição a nível nacional.

ABSTRACT: Caatinga is a deciduous thorny woodland and sclerophyllous vegetation, encountered in a semi-arid region of around 730 000 km2 entirely within the Brazilian territory . This environment presents high variation of vegetation types that have been attributed to large-scale variations in the climate, geomorphology patterns, and small-scale differences in topography and soils. The sparse and fluctuation precipitation of arid and semiarid regions is believed to exert strong control over life histories, physiological characteristics, and species composition of their biotas.

At least 77 bat species of the 178 species present in Brazil are found in Caatinga, of which 13 are frugivorous and five nectarivorous including the endemic *Xeronycteris vieirai*. Bats are known play important roles in pest control, pollination and seed dispersal, nonetheless little information has been generated regarding the ecological role these species play in an environment like Caatinga. In general, this habitat is the most neglected Brazilian ecosystem in terms of investigation and conservation of its biodiversity. Specifically in the case of bats, Rio Grande do Norte is one of the biggest knowledge gaps in Brazil. The data presented here represent one of the first formal investigations with bats in the Caatinga in Rio Grande do Norte. Information on the nested and asymmetric structure of the mutualistc network between nectarivorous bats and plants was generated, with data on key plant species for the maintenance of the community of nectar-feeding bats in this region. Also, the first evidence of folivory of at least 16 plant species by the fruit-eating bat Artibeus planirostris was documented, representing the first record for a semi arid enviroment and the first record for the bat species. Finally, the first insight to biological aspects of the endemic X. vieirai including diet, roosts and reproduction data were registered as well the extention of its range distribution at a national level.

GENERAL INTRODUCTION

Caatinga is a deciduous thorny woodland and sclerophyllous vegetation, encountered in a semi-arid region of around 730 000 km2 entirely within the Brazilian territory (Leal *et al.,* 2003). This environment presents high variation of vegetation types that have been attributed to large-scale variations in the climate, geomorphology patterns, and small-scale variations in topography and soils (da Costa *et al.,* 2007). Meteorological parameters are extreme here, with high solar radiation, low cloudiness, high annual average temperature, low rates of relative humidity, high evapotranspiration, and especially, the low and very irregular precipitations, limited, in most of the area, in a short period in the year (Bullock *et al.,* 1995; Leal *et al.,* 2003). The sparse and variable precipitation of arid and semiarid regions is believed to exert strong control over life histories, physiological characteristics, and species composition of their biotas (Chesson *et al.,* 2004). Floral resources and rewards in the Caatinga's vegetation are very diversified as well as the pollination syndromes despite all climatic restrictions (Machado and Lopes, 2004).

The Caatinga ecosystem plays an important role in maintaining regional macro-ecological processes and indirectly supports regions with greater diversity and endemism in Brazil and the world (Leal *et al.,* 2003). At least 77 bat species of the 178 species present in Brazil are found in Caatinga, representing 44.7% of the mammal species in this habitat (Oliveira *et al.,* 2003; dos Reis *et al.,* 2007; Bernard *et al.,* 2012; Nogueira *et al.,* 2014). Bat pollination in Caatinga accounts for at least 13.1% of plants species belonging to 9 families (Machado and Lopes, 2004).

The most diverse family of bats in the Neotropics is Phyllostomidae with160 species distributed in tropical and subtropical areas of the Americas (Simmons, 2005). It is also the most diverse family in Brazil with 92 species (Nogueira *et al.,* 2014), of which 39 are present in Caatinga (Paglia *et al.,* 2012). This family stands out due to its unique diversity in high feeding specializations. Phyllostomid bats feed on insects, blood, small vertebrates, fruits, nectar and pollen (Datzmann *et al.,* 2010). These variety of diets are reflected in the environmental services they provide. They play important roles in pest control, pollination and seed dispersal (Fleming 1993; Kunz *et al.,* 2011). Nectarivorous and frugivorous bats are responsible for gene flow within and between plant populations, through pollination and seed dispersal (Horner *et al.,* 1998; Lobova *et al.,* 2009).

Among the Phyllostomid bat species present in Caatinga, there are 13 frugivorous species and 5 nectarivorous, of which two are endemic to this biome, one frugivoruous (*Chiroderma vizottoi*) and other nectarivorous (*Xeronycteris vieirai*) (Paglia *et al.,* 2012). Little information has been generated regarding the ecological role these species play in an environment like Caatinga. In general, this habitat is the most neglected Brazilian ecosystem in terms of investigation and conservation of its biodiversity (Zanella and Martins, 2008). According to Bernard *et al.,* (2010) only a very low percentage of Catinga's total area has been minimally sampled regarding bats, the authors emphasized that Rio Grande do Norte as a whole is one of the biggest knowledge gaps in Brazil.

The data presented here represent one of the first formal investigations with bats for the Caatinga in Rio Grande do Norte. This dissertation is divided into three chapters focusing mainly on the interactions between plants and Phyllostomid bats from a feeding perspective as well as a chapter focused on the Caatinga's endemic species, *Xeronycteris vieirai*.

The first chapter "Structure of mutualistic networks between nectar-feeding bats and plants in a semiarid Caatinga forest of Rio Grande do Norte, Brazil", discusses the structure of the interactions network between nectarivorous bats and the plants they feed on. The aim was to understand how these relationships are structured and their stability. Besides an inquiry into the possible existence of differences in the use of plants within different species of nectar-feeding bats and differences in their diet over a period of six months was performed.

The second chapter "Are leaves a good option in Caatinga's menu? First record of folivory in *Artibeus planirostris* (Phyllostomidae) in the semiarid forest, Brazil", here data of the first evidence of folivory by the fuit-eating bat *Artibeus planirostris* is presented. This is also the first record of this feeding strategy for a semi arid environment like Caatinga. These findings were submitted to the Journal Acta Chiropterologica in partnership with the MSc. Maricélio Medeiros Guimarães who during his fieldwork in the Caatinga of Bahia also found evidence of folivory in *A. planirostris*, making possible to characterize this feeding strategy in a more complete way.

Finally, in the third chapter "First insight to the biological aspects and range extension of the Brazilian endemic Vieira's Flower Bat (*Xeronycteris vieirai* Gregorin and Ditchfield, 2005)", aspects of natural history of the endemic species of Caatinga *X.*

vieiriai are presented. This species is cataloged as Data Deficient by the IUCN. The information about its reproduction, roost, diet and range extension presented here depict a step closer in the understanding of the species basic requirements in this poorly studied and highly impacted habitat.

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CHAPTER I

STRUCTURE OF MUTUALISTIC NETWORKS BETWEEN BATS AND PLANTS IN A SEMIARID CAATINGA FOREST OF RIO GRANDE DO NORTE, BRAZIL.

Photo: Luciana Rocha

Structure of mutualistic networks between nectar-feeding bats and plants in a semiarid Caatinga forest of Rio Grande do Norte, Brazil.

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ABSTRACT

Biodiversity encloses not just different species but also the interactions among them. Ecological networks seek for patterns with a strong representation of the interactions between species highlighting their global interdependence. The study of these networks represents a conceptual and methodological challenge in highly diversified communities with several interactions. Bats exhibit high degrees of functional, compositional and structural diversity. Sixteen of the total 178 bat species occurring in Brazil are nectar-feeding bats and at least five of these species co-occur in the semi arid Caatinga ecosystem. Mutualistic networks between nectar-feeding bats and plants in semi arid environments have not been broadly studied. Our main objective was to describe the network of mutualistic interactions between nectar-feeding bats and plants in a semi arid forest in Caatinga of Rio Grande do Norte, to understand how these interactions varied according to resource use between bat species and resources availabilities temporally. As expected this network presented a pattern of nestedness and asymmetry. Showing this is a cohesive and resilient system where differences between the plants species used by bats varied among the bat species and among the sampled months.

KEY WORDS: Nestedness, Diet, Chiropterophily, Resource use, Pollen types, Cactaceae

INTRODUCTION

Biodiversity encloses not just different species but also the interactions among them. However, the study of biodiversity has typically been focused on species diversity and genetic diversity, leaving aside the ecological interactions (Magurran, 2004; McCann 2007; Bascompte, 2009). Ecological networks look for patterns with a strong representation of the interactions between species (nodes) highlighting their global interdependence (Bascompte, 2009; Guimarães *et al.,* 2011). From a more applied, conservation-minded perspective, an understanding of the ecological networks can be used to measure the stability (resilience and resistance) of the ecosystems and to explore and predict functional responses of ecosystems to structural changes such as the biodiversity loss due to different human activities (Dunne *et al.,* 2002; Bascompte *et al.,* 2006a; Ives and Carpenter 2007; Okuyama and Holland 2008).

Ecological networks can be subdivided into three types: traditional trophic networks, host- parasite networks and mutualistic networks (Okuyama and Holland 2008; Ings *et al.,* 2009; Bascompte, 2010). Mutualistic networks refer to the mutually beneficial interactions between animals and plants such as seed dispersal, pollination and ant–plant interactions. In the past ten years more attention has been paid to the study of mutualistic networks (Bascompte *et al.* 2003, 2006b; Vázquez and Aizen, 2004; Thompson, 2006). Several general characteristics have been described for this type of network: nestedness, asymmetry and heterogeneity regardless of the type mutualism, of the region in which the community was studied and of species composition. This general pattern has potentially important consequences for ecological and co-evolutionary processes. The nestedness represents a system that is more redundant, meaning that if some interactions are lost, the system may generate alternative interactions that limit the damage from a perturbation (Bascompte *et al.,* 2003; Jordano et al, 2006; Rezende *et al.,* 2007; Burgos *et al.,* 2007). The asymmetric interactions are where the most specialist species tend to interact with the most generalist ones (Vázquez and Aizen, 2004; Bascompte *et al.,* 2006a), as the heterogeneous distribution is where the links per species show few extreme “generalists” and many “specialists” (Jordano *et al.,* 2003). Both asymmetric and heterogeneous distribution may provide a mechanism for the persistence of rare, specialist species (Bascompte, 2009).

These network patterns seem to be common regardless the species composition, geographic location and other factors (Bascompte *et al*. 2003, 2006b; Memmott *et al.* 2004, 2007; Okuyama and Holland 2008, Tylianakis *et al*., 2008). Nonetheless, it is a conceptual and methodological challenging to address this type of research in highly diversified communities with several interactions (Olesen *et al.,* 2007). Bats represent an example of this type of situation because they exhibit high degrees of functional, compositional and structural diversity. Bats account for at least 1200 species around the world, representing 22% of the total number of mammal species of the world (Simmons, 2005) and are found throughout the globe in a broad geographic distribution (Kunz and Parsons, 2009). Bats play an important role in pollination, seed dispersal and pest control (Fleming 1993; Kunz *et al.,* 2011). Nectar-feeding bats are known to pollinate ecologically and economically important group of plants classified in 28 orders, 67 families and about 528 species of angiosperms in the Neotropics (Flemming *et al.,* 2009). Nectar-feeding bats are mainly attracted to large inflorescences or large single flowers with wide opening, long and numerous stamens, high nectar and pollen production and light colored corollas with unpleasant odors (Muchhala and Jarrin 2002) this pollination syndrome is called chiropterophily. Non-the less, it has also been demonstrated that bats also visit flowers that do not present this specific chiropterophily characteristics (Vogel *et al.,* 2004).

One of the main characteristics of arid and semi arid environments is that resources are supplied in pulses due to the limited and variability in precipitation, exerting adaptation challenges to both, plants and animals (Chesson *et al.,* 2004). The seasonal pattern of resource availability seems to be a key factor controlling species composition and therefore it also influences the niche dynamics and coexisting patterns of consumer populations (Kneitel and Chase, 2004). Up to six species of nectar-feeding bats, can be found coexisting in a tropical dry forest (Santos and Arita, 2002). Neotropical semi arid and arid lands are especially rich in bat-pollinated species and previous research in arid and semi arid regions of Mexico and South America indicates that certain species of columnar cacti depend heavily on pollination by one or more species of phyllostomid bats (Meffe, 1998). Sixteen of the total 178 bat species occurring in Brazil are nectar-feeding bats (Nogueira *et al.,* 2014; Moratelli and Dias, 2015), and at least five of these nectarivorous bat species are distributed in the Caatinga ecosystem. Caatinga consists of patches of seasonal dry forest and sclerophyllous vegetation covering a Semiarid region of around 730 000 km2 in northeastern Brazil (Leal *et al.,* 2003).

Mutualistic networks between nectar-feeding bats and plants in semi arid environments have not been broadly studied. Ecological attributes, such as the specific resource dependence of glossophagines suggest that this group of bats might be more susceptible to extinction than other neotropical bats (Meffe, 1998). Making them an interesting and important group for the study of their interaction network from the standpoint of stability and resilience of the communities of bats and plants. Our main objective was to (1) describe the network of mutualistic interactions between nectar-feeding bats and plants in a semi arid forest in Caatinga of Rio Grande do Norte by first characterizing the assembly of nectarivous bats and the plants they feed on, to understand how these interactions varied according to resource use (2) between bat species and resources availabilities (3) temporally.

We expect to find (1) a network pattern characterized by nestedness and asymmetry in the mutualistic network of interactions between nectarivorous bats and the plants from which they feed, in this semiarid ecosystem. On the other hand, we expect (2) differences between the plant species used by the different nectar-feeding bat species, and (3) we expect a temporal variation related to the use and resource availability by months. For both (2) and (3), we expect to find central plant species characterized to be very abundant and used by all species of bats in a high frequency, there will also be species of plant less abundant but used by most of the bat species and finally there will be species that regardless of their abundance and availability wont be used by bats.

MATERIALS AND METHODS

Study site

Lajes, located in the central portion of the state of Rio Grande do Norte (RN), in the vegetation region of Planalto da Borborema. This area is the best-preserved portion of Caatinga in Rio Grande do Norte. The eco-region is characterized by dry weather, very hot and semi-arid. The rainy season lasts from February to May, and the average annual rainfall varies from 400 to 650 mm. Vegetation ranges from open spiny shrubby areas to arboreal the dry forests with abundant bromeliads and columnar cactus (Velloso *et al.,* 2002).

Five sampling sites, with at least 4.5 km between each other, were selected (Fig. 1). They are located either inside or in the border of the largest fragment of Caatinga of RN, with an approximate area of 53,500 hectares.

Site 1. Sitio Santa Rosa (S 05º49'56.2"- W36º12'16.0").- Located at 310 meters of altitude. On the site there a depression of the basin of a river (which has been dry for around 5 years) that ends in an artificial "açude" of around 20 by 20 meters, it is filled with water only during the rainy season. About 10 years ago the place was used to remove wood to make charcoal and there was also livestock.

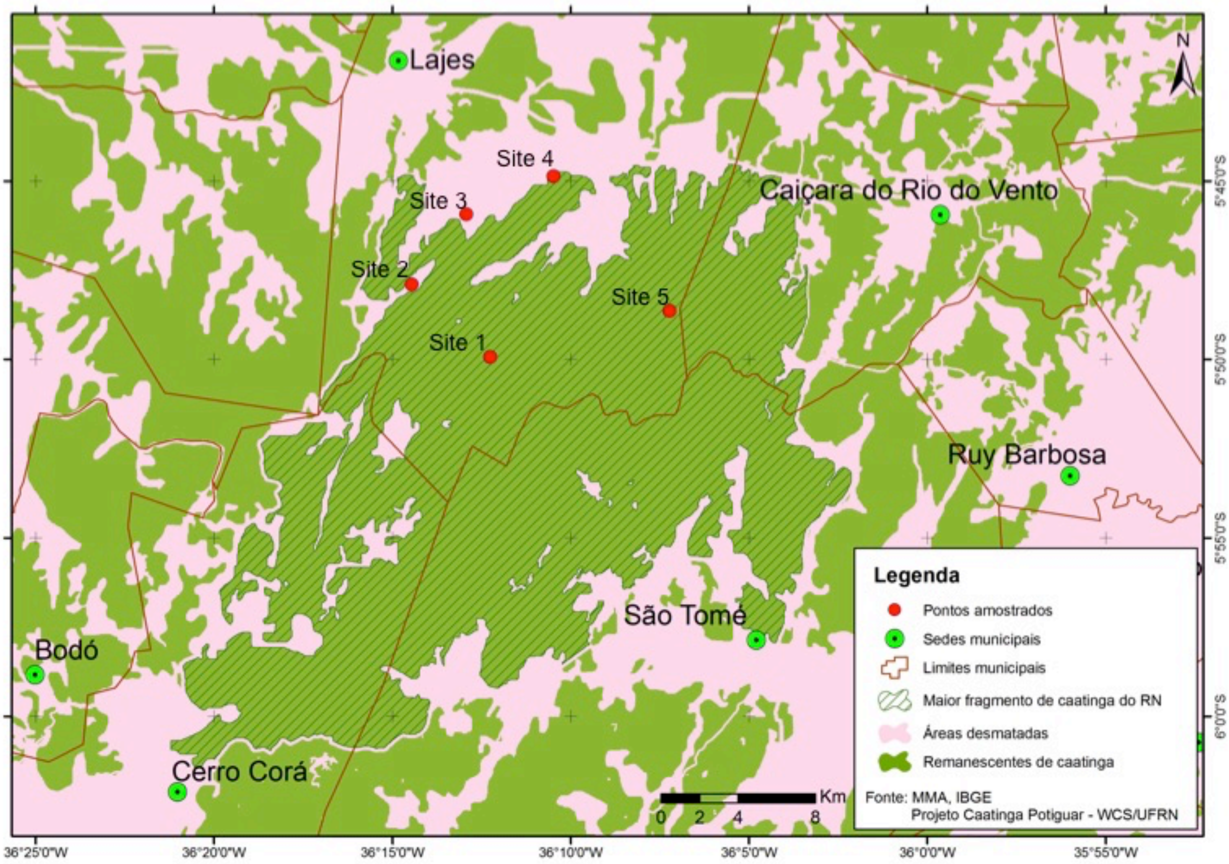
Site 2. Fazenda Santo Antonio (S05º47'53.7"-W36º14'28").- Located at 332 m of altitude. It is a private property where the forest is intact; it is only crossed by a road used to transport limestones. There is a small cave that is been used as roosts for at least three species bats. People visit this cave occasionally.

Site 3. Sitio Joazeiro (S05º45'55.7"-W36º12'55.7").- Located at 230 meters of altitude. It lies at the foot of the "Serra do Feiticeiro". It is a place that has the characteristic "caatinga baixa". Occasionally there are cattle present. In the past, part of the forest was cut to grow cotton. It is crossed by a river basin that has been dry for more than five years.

Site 4. Serra do Feiticeiro (S05º44'52.0"-W36º10'29.3").- Located at 350 meters of altitude. It is near the top of the "Serra do Feiticeiro". Thirty years ago mining was practiced in this place, about 15 years ago this activity stopped leaving around six different sizes abandoned mines. These abandoned mines are being used by at least 5 species of bats as roosts. This is the place where the wind power parks will be installed.

Site 5. Sitio Bonfim (S05º48'37.9"-W36º07'14.0").- Located at 270 meters of altitude. Site crossed by a river that has been dry more than five years. A mining company, currently active, is located at 4 kilometers from our sampling site. There is a street crossing our site that is used as one option to as one of the options to access the mining company.

It is a region recognized by its importance for mineral exploration and with a potential for installation of wind power turbines, especially in the regions near the Serra do Feiticeiro where one of the biggest Wind Parks in Latin America will be installed.



Fonte: MMA, IBGE
Projeto Caatinga Potiguar - WCS/UFRN

Fig. 1 Map showing the five sampling sites in the largest fragment of Caatinga of RN, Lajes.

Bat assembly

Data collection began in May with a pilot visit of 4 nights, here the sampling sites were recognized and bats were captured. Data collection was conducted until October. Mist nets were placed for 5 nights per month, trying to avoid when possible full moon, which affects foraging behavior of bats. Mist nets are an effective method for capturing frugivorous and nectarivorous bats because they are active in the lower levels of the forest and have little ability to detect mist nets (Kunz and Parsons, 2009). At least 80 meters of mist nets were placed each night, for six and a half hours (from dusk until midnight). The mist nets were relocated every month in order to cover as much microhabitats and available resources at the time and in each of the sites. The sampling effort was calculated by multiplying the mist-net area (length x width) installed by the quantity of hours they remained opened, resulting in an effort unit of m^2h (Straube and Bianconi, 2002).

Sampled bats were identified in the field using several systematic keys and species diagnosis (Gregorin and Taddei, 2002, Gardner, 2007; dos Reis *et al.,* 2007; Miranda *et al.,* 2011; Araújo and Langguth, 2012; dos Reis *et al.,* 2013).

Bats were sexed, weighed with 100 g Pesola and forearm length measured. In addition, the reproductive phase was determined through the observation of secondary sexual characteristics. The abdomens of the females were palpated to detect pregnancy and lactating females (hardened nipples, hairless around and / or secreting milk) were indentified according to the criteria of Fleming *et al.* (1972). In the case of males, the presence of obvious exposed scrotums was considered as reproductively active.

Those individuals impossible to identify in the field or that represented a new report for the area, were collected for later catalog and they were preserved in the mammal collection of the Museum of the Universidade do Rio Grande do Norte. The survey and collection of specimens were allowed by the Brazilian environmental agency (SISBIO license number 48325-2 MMA e IBAMA and ICMBIO).

Plant assembly and phenology

In each of the five sampling sites, a 200 meters long and 10 meters wide transects were established. During the first month, the species of trees, shrubs, cacti and bromeliads were identified and individuals of each species were counted for abundance estimation in each transect.

The main characteristics of the flowers that attract bats (chiropterophily) are large inflorescences or single flowers, the flower opening is wide, the stamens are numerous and long, possess lots of nectar and pollen, the corollas are light colored with unpleasant odors (Quiroz *et al.,* 1986; Altringham, *et al.,* 1996; Tschapka and Dressler 2002; Muchhala and Jarrıín 2002).

Phenological data was taken in each of these transects once a month, during five months (June to October). For the phenological data, up to 10 individuals of each species (when possible) in each transect were tagged with fluorescent flagging tape with the number of each individual and the common name noted. Data collected for each individual is: % of new leaves, % leaves droped, number of flower buds, number of open flowers, anthesis, flower color, inmature fruits, ripe fruits and color of ripe fruit.

Botanical samples of each of the species were collected for proper identification and deposited in the herbarium of the Universidade Federal do Rio

Grande do Norte. Pollen samples were collected directly from the flowers available during the sampling period with jelly-glycerin cubes in order to make a pollen collection for reference.

Structure of the mutualistic interaction networks

Pollen samples

For each captured bat, inspection for pollen was done all over its body. Pollen was collected with a sticky jelly cube (3-4 mm) prepared with glycerin, phenol and safranine for preservation and coloring respectively (Voigt *et al.,* 2009). Each cube of glycerine jelly was deposited in a microtube in a cooler to prevent them from melting. For pollen analysis were considered only identification of pollen grains present in microscope slides. The microscope slide were prepared by melting each glycrine jelly cube per bat sample and analysed under a light microscope (Leica DM500).

Pollen types were identified by comparison with a reference collection from the Palynotheca of the LAMIV/UEFS (Plant Micromorphology Laboratory/Feira de Santana State University), which is a representative collection of the pollen flora of the Caatinga vegetation from north-eastern Brazil. Relevant pollen catalogues were used for auxiliary identification, published by Chávez et al. (1991), Roubik and Moreno (1991), Santos *et al.* (1997), Carreira and Barth (2003), and Melhem et al. (2003). Photos of the pollen grains were taken using an Olympus BX51 microscope with contrast prisms of differential interference (DIC), coupled with a DP25 camera and the program Imaging software cellSens.

Pollen grains were identified to the lowest possible taxonomic level. Pollen was scored on a presence/absence scale for each bat this information obtained for several individuals may provide an estimate of the relative use of that particular plant species within a nectar-feeding bat population. When identifying the pollen types were taken into account situations where small amounts of pollen could have contaminated the samples meaning that the specific bat species really did not feed on that plant, these pollen grains could have been deposited in the chiropterophillic flowers by other means such as air and/or insects. Criteria were established to discard some accidental pollen types: If the pollen types belonged to plant families that presented anemofilia (Poaceae for example) and if a pollen type only appeared in a single sample of one bat species.

Species accumulation curves were constructed based on nectarivorous bats captured in nets and the pollen species found in the samples of each individual to establish whether the diet sampling of nectar-feeding-bats was completed, or otherwise, to know it's representativeness of the total estimated pollen species (Moreno and Halffter, 2001; Nielsen and Bascompte, 2007).

Network analysis

Data was organized on bat resource use of plants as an adjacency matrix, with plant species listed as rows (*lower* level) and bat species listed as columns (*higher level*). Each cell was filled with the percentage of samples of bats that presented pollen of each species of plant (the number of individuals that had the specific pollen divided by the total number of the specific bat species individuals caught, times 100) and thus the matrix was weighted with standardized use of plants by bats.

Metrics were calculated in the "bipartite" (version 2.05) package of R (Dormann *et al.,* 2009). Null models were created using the method "swap.web" (N=1000). Nestedness values of the observed data and of the null matrices were calculated using the method "weighted NODF" which incorporates the weights of each link.

The function "plotweb" was used to draw a bipartite graph, in which rectangles represent species, and the width is proportional to the sum of interactions involving this species. Interacting species are linked by lines, whose width is again proportional to the number of interactions. The function "visweb" was used to draw a plot of the data matrix with shading representing number of interactions per link; the darker squares are the ones with more links. The number inside the plot refers to the percentage of interactions (as explained above).

Using the "bipartite" (version 2.05) package of R (Dormann *et al.,* 2009), with "networllevel" function the robutness coefficient was calculated following the method by Burgos *et al.* (2007). "R" value is defined as the area under the extinction curve. This analysis provides two values of R, one for the higher level (bats) and another for the lower level (plants).

Similarities between the nectar-feeding bat species and temporal similarities

To visualize and analyze whether there were differences in diet variation: 1) among species of nectar-feeding bats considering the different sampling months and 2) among the months considering the different nectar-feeding bat species, a Non Metric Multidimensional Scaling – NMDS was done using a using a Bray Curtis dissimilarity matrix. We checked the Stress, a measure of the fit between the final solution of the analysis and the original distance matrix of the community. This ordination technique has been positively evaluated even when dealing with species rich and under sampled communities (Brehm and Fiedler 2004). Analysis was performed with Analysis was performed with PAST 3.0

To test if the differences in the diet variations: 1) among species of nectar-feeding bats considering the different sampling months and 2) among the months considering the different nectar-feeding bat species an analysis of similarity (ANOSIM) was performed, which is a non parametric permutation procedure to test for significant differences among differently grouped sampling units (Clarke, 1993). To measure the similarity we used the Bray Curtis dissimilarity index. Significance levels were adjusted by a Bonferroni sequential correction. Analysis were performed with PAST 3.0

To help with the interpretation of the results obtained with the ANOSIM, a Similarity Percentages (SIMPER) analysis was done using the Bray-Curtis method. This analysis breaks down the contribution of each species of plant to the observed dissimilarity between 1) nectar-feeding bat species diets and between 2) sampling months. It allows identifying the species that are most important in creating the observed pattern of dissimilarity. Analysis was performed with PAST 3.0

The general pattern of bat community consumption and general plant availability composition in the time (months) was tested with Mantel test between the Bray Curtis dissimilarity index of bat community consumption and available plant species. Analysis was performed in PAST 3.0.

Availability and use of resources

First a “pre-selection of plant species” was done to prepare the data properly for further analysis. At the beginning there were 120 records of which 57 were eliminated following three criteria. First criteria: Plants that during the sampling period never had flowers available and were never used by nectar-feeding bats. Second criteria: Even though the plants had available flowers they were not used by any nectar-feeding bat species. Third criteria: Only one individual of one species of bat presented the pollen type in one pollen sample (the specific case of *Prosopis juliflora*) assuming that it may have been an accidental event. With these three criteria nine species of plants were removed: *Calotropis procera*, *Croton sonderianus*, *Jatropha mollissima*, *Pithecellobium diversifolium*, *Poincianella pyramidalis*, *Prosopis juliflora*, *Ruellia asperula*, *Tabebuia aurea* and *Tacinga inamoena.* With the 63 remaining records a fourth criteria was applied: Plants that have never been reported in literature to be visited by bats and were never used by nectar-feeding bats during the sampling period. With this fourth criteria, two plant species were removed form the analysis *Cynophalla hastata* and *Cereus jamacaru*.

Regression analyzes were performed for each one of four nectarivorous bat species in two ways. First with 27 records from seven plant species (*Bauhinia cheilantha*, *Cleome spinosa*, *Coursetia rostrata*, *Encholirium spectabile*, *Melocactus zehntneri*, *Pilosocereus pachycladus*, *Pilosocereus gounellei*). These 27 records are all plant species used by one of the four bat species analyzed. Second, for each bat specie, only the plant species used by himself were selected. In this analisys the number of samples was 12, but was different for *Lonchophylla sp.* (N=14). After the regression we analyzed the residual pattern to identify outliers species (outside of confidence intervals 95%). Before the analysis the number of plants with available flowers by species/months were transformed in LN+1.

RESULTS

Bat assembly

With a sampling effort of 45456.9 m^{2}h, a total of 303 individuals belonging to 16 species, 15 genera, 4 families and 4 subfamilies, representing different types of diets have been captured (Table 1). Of which only *Peropteryx macrotis, Desmodus rotundus, Diphylla ecaudata, Trachops cirrhosus, Glossophaga soricina* and *Artibeus planirostris* have been reported for Caatinga in the state of Rio Grande do Norte (Ferreira *et al.,* 2010; Garcia *et al.,* 2014), the other species are new records for the Caatinga of Rio Grande do Norte.

For purposes of this study only 4 species of nectar-feeding bats were considered, due to the low rate of capture of fruit eating bats. The nectarivorous bat *Anoura geoffroyi* was excluded from the analysis as well because only one individual was captured in September. The species considered in the analysis are *Glossophaga soricina, Lionycteris spurrelli, Lonchophylla sp.* and *Xeronycteris vieirai* (Fig. 2). Lonchophylla's individuals captured were identified to genus level only as during sampling, in July, a new species was described, *Lonchophylla inexpectata* (Moratelli and Dias, 2015). The authors mention the fact that it is easily confused with *L. mordax* and both species may occur in the same area.

Table 1. Number of bats captured per month from May to October (Sampling effort of 45456.9 m^{2}h) in Lajes, Rio Grande do Norte. Nomenclature according to Gardner (2007)

TAXA	Diet	May	June	July	Aug	Sep	Oct	Total
Family Emballonuridae								
Peropteryx macrotis (Wagner, 1843)	Insectivore	3	0	0	0	0	0	**3**
Family Phyllostomidae								
Subfamily Desmodontinae								
Desmodus rotundus (E. Geoffroy, 1810)	Hematophage	6	18	10	4	1	1	**40**
Diphylla ecaudata (Spix, 1823)	Hematophage	0	2	0	1	1	3	**7**
Subfamily Glossophaginae								
Anoura geoffroyi (Gray, 1838)	Nectarivore	0	0	0	0	1	0	**1**
Glossophaga soricina (Pallas, 1766)	Nectarivore	9	4	13	21	1	0	**48**
Lionycteris spurrelli (Thomas, 1913)	Nectarivore	3	0	2	1	2	4	**12**
Lonchophylla sp. (Thomas, 1903)	Nectarivore	6	8	7	5	1	0	**27**
Xeronycteris vieirai (Gregarin and Ditchfield, 2005)	Nectarivore	11	2	9	10	1	1	**34**
Subfamily Phyllostominae								
Micronycteris megalotis (Simmons and Voss, 1998)	Insectivore	1	0	1	0	0	0	**2**
Micronycteris schmidtorum (Sanborn, 1935)	Insectivore	0	0	0	0	1	0	**1**
Phyllostomus discolor (Wagner, 1943)	Omnivore	4	0	0	1	0	0	**5**
Tonatia bidens (Spix, 1823)	Insectivore/Carnivore	2	17	0	2	1	1	**23**
Trachops cirrhosus (Spix, 1823)	Carnivore	1	5	2	2	2	0	**12**
Subfamily Stenodermatinae								
Artibeus planirostris (Spix, 1823)	Frugivore	12	1	15	26	15	15	**84**
Family Noctilionidae								
Noctilio albiventris (Desmarest, 1818)	Insectivore/Piscivore	1	0	0	0	0	0	**1**
Family Molossidae								
Neoplatymops mattogrossensis (Vieira, 1942)	Insectivore	1	0	1	0	0	0	**2**
		60	57	60	73	27	26	**303**

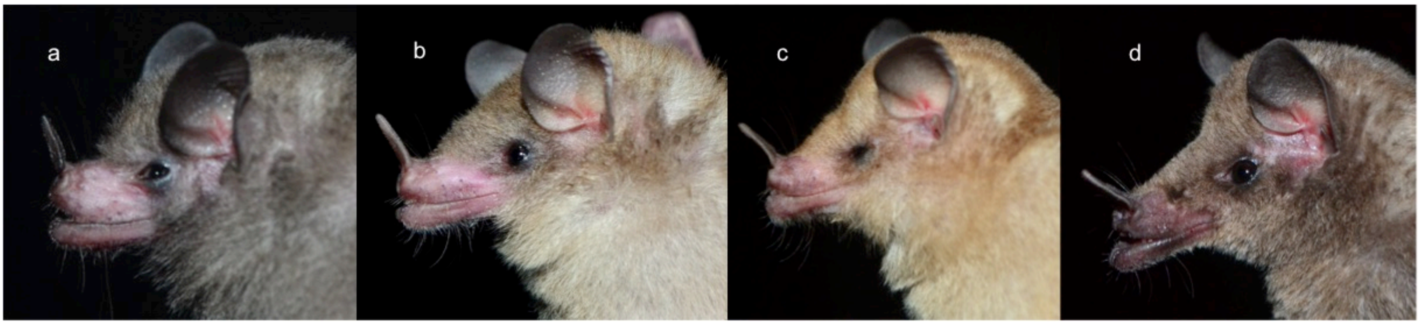


Fig. 2 Nectar-feeding bats considered for all the analysis. a)*Glossophaga soricina*, b) *Lionycteris spurrelli*, c) *Lonchophylla sp.,* d) *Xeronycteris vieirai*. Photos: Juan Carlos Vargas Mena.

Plant assembly and phenology

Phenological data from 25 species of plants belonging to 12 families of angiosperms were taken (Table 2). Most species belong to the family Fabaceae (8 species) followed by Cactaceae (5 species). In all transects, cacti were the most abundant plants, showing different growth types such as globose (*Melocactus. zehntneri*), flattened-padded (*Tacinga. inamoena*), shrubby (*Pilosocereus gounellei*) and columnar (*Cereus jamacaru* and *Pilosocereus pachycladus*). Of the sampled plant species only five have bats as recognized as pollinators (Table 2) and nine species presented chiropterophily features in their flowers (Fig. 3). Most sampled plants had flowers throughout the study period. (Table 2).

Table 2. Plant species sampled in five transects Lajes, RN for a period of May to October with known data on their pollinators. ✓ = Presented flowers.

Taxa	**Known pollinators**	**Estimate abundance in all transects**	**Individual with phenology data**	**June**	**July**	**Aug**	**Sep**	**Oct**
Acanthaceae								
Ruellia asperula	Hummingbird	1	1	✓	✓	✓	✓	✓
Apocynaceae								
Aspidosperma pyrifolium	Moth	27	16					
Asclepiadaceae								
Calotropis procera	Bee	4	4	✓	✓	✓	✓	✓
Bignoniaceae								
Tabebuia aurea	Bee	10	10					✓
Bromeliaceae								
Bromelia laciniosa	?	255	32					
Encholirium spectabile	Hummingbird/Bat/ Opossum	149	8	✓	✓			
Burseraceae								
Commiphora leptophloeos	Bee	8	6	✓				
Cactaceae								
Cereus jamacaru	Moth	5	3	✓	✓			
Pilosocereus gounellei	Hummingbird/Moth /Bat	1149	32	✓		✓		
Pilosocereus pachycladus	Hummingbird/Bat	305	37	✓	✓	✓	✓	✓
Melocactus zehntneri	Hummingbird	1	1					
Tacinga inamoena	Hummingbird	478	28	✓	✓	✓	✓	✓
Capparaceae								
Cynophalla hastata	?	4	4			✓	✓	
Cleomaceae								
Cleome spinosa	Bat	32	12	✓	✓	✓	✓	
Combretaceae								
Combretum leprosum	Bee	7	7					
Euphorbiaceae								
Croton sonderianus	Bee	147	29	✓	✓			
Jatropha mollissima	Bee	267	29	✓	✓	✓	✓	✓
Fabaceae								
Anadenanthera colubrina	Bee	5	3					

Bauhinia cheilantha	Hummingbird/Bat	3	1			✓		
Coursetia rostrata	?	51	11	✓	✓	✓	✓	✓
Mimosa tenuiflora	Bee	119	29				✓	✓
Poincianella pyramidalis	Bee	315	31		✓	✓		
Piptadenia stipulacea	Bee	10	4					
Pithecellobium diversifolium	?	2	2		✓			
Prosopis juliflora	Insects	299	26			✓	✓	✓

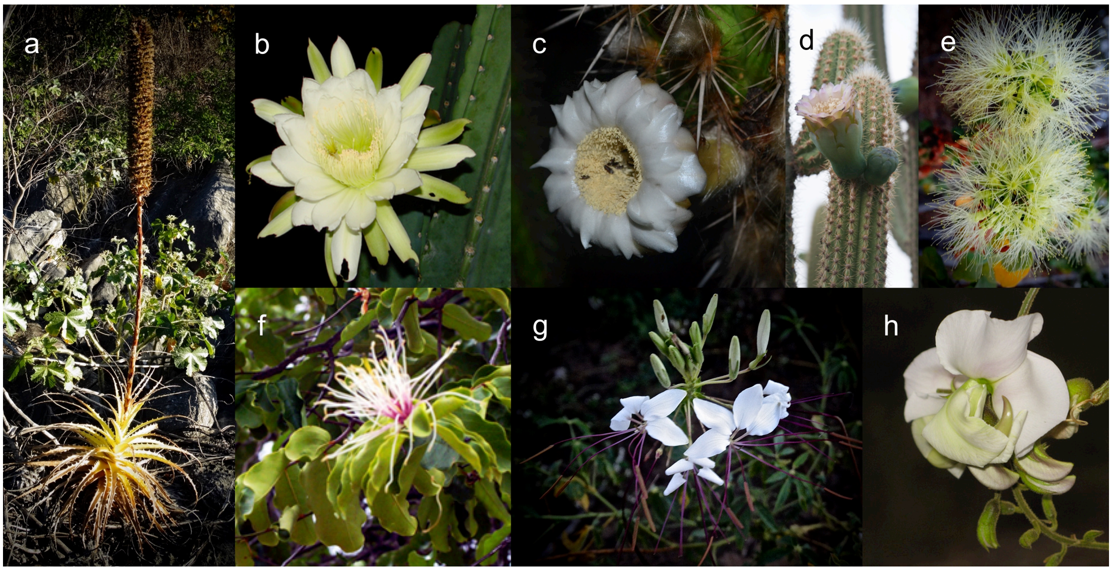


Fig. 3 Plants with chiropterophily features included in the sampled transects a) *E. spectabile,* b) *C. jamacaru* (Photo: E. Duarte), c) *P. gounellei*, d) *P. pachycladus* (Photo: A. Taemi), e) *P. diversifolium*, f) *C. hastata* (Photo: R. Soares Neto), g) *C. spinosa* and h) *C. rostrata* (Photo: D. Cardoso).

Structure of the mutualistic interaction network

Twenty-one pollen types from seven families of angiosperms were identified (Fig. 4) in 91 samples of pollen taken from the fur of the four species of nectarivorous bats. *G. soricina* (38 samples) *L. spurrelli* (12), *Lonchophylla sp.* (21) and *X. vieirai* (20). The accumulation curve of pollen types and bat species (Fig. 6) showed that none bat species reaches asymptote, there still is a growing trend indicating that sampling of pollen types for different species of bats was incomplete, specially for *L. spurrelli* .

The families Acanthaceae and Cactaceae presented more pollen types in the samples, each represented by three pollen types. *P. pachycladus* (Cactaceae) type appeared in 91% of the samples being the most abundant in samples of the four nectar-feeding bats, followed by *E. spectabile* (Bromeliaceae) in 30% of samples and *C. spinosa* (Cleomaceae) in 24%.

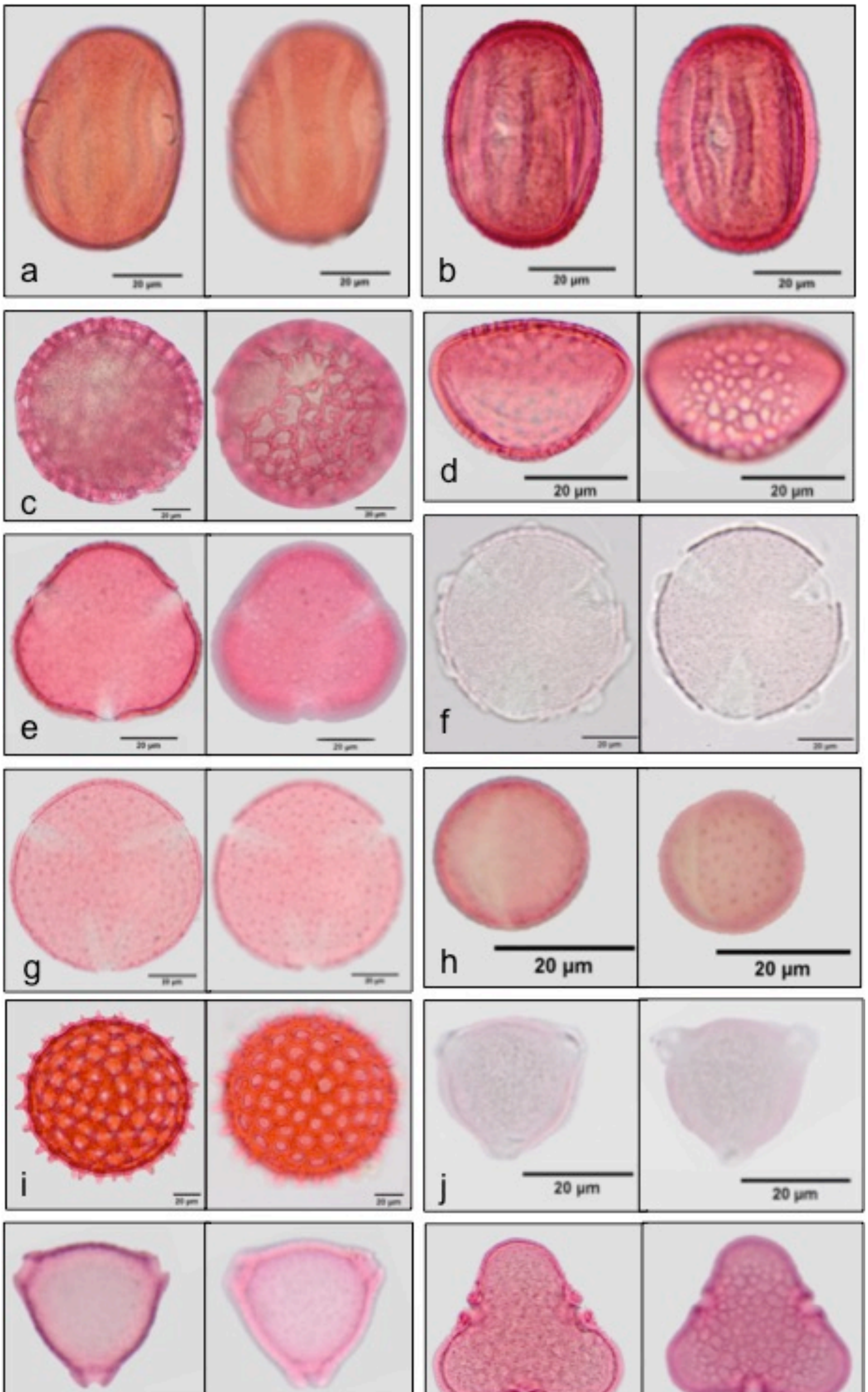


Fig 5. Fig. 4 Pollen types from seven families of angiosperms that appeared most frequently in the fur of four species of nectarivorous bats in Lajes, Rio Grande do Norte. Acanthaceae a) *Thyrsacanthus sp,.* b)Acanthaceae type 1 and c)*Dicliptera sericea* . Bromeliaceae d) *Encholirium spectabile*. Cactaceae e) *Pilosocereus pachycladus,* f) *Melocactus zehntneri* and g) *Pilosocereus gounellei*. Cleomaceae h) *Cleome spinosa.* Convolvulaceae i) *Ipomea sp.* Fabaceae j) *Coursetia rostrata*.

Malvaceae k) *Helicteres sp.* and l) *Pseudobombax sp.* All photos were taken with 40x lens, scale bar 20 μm.

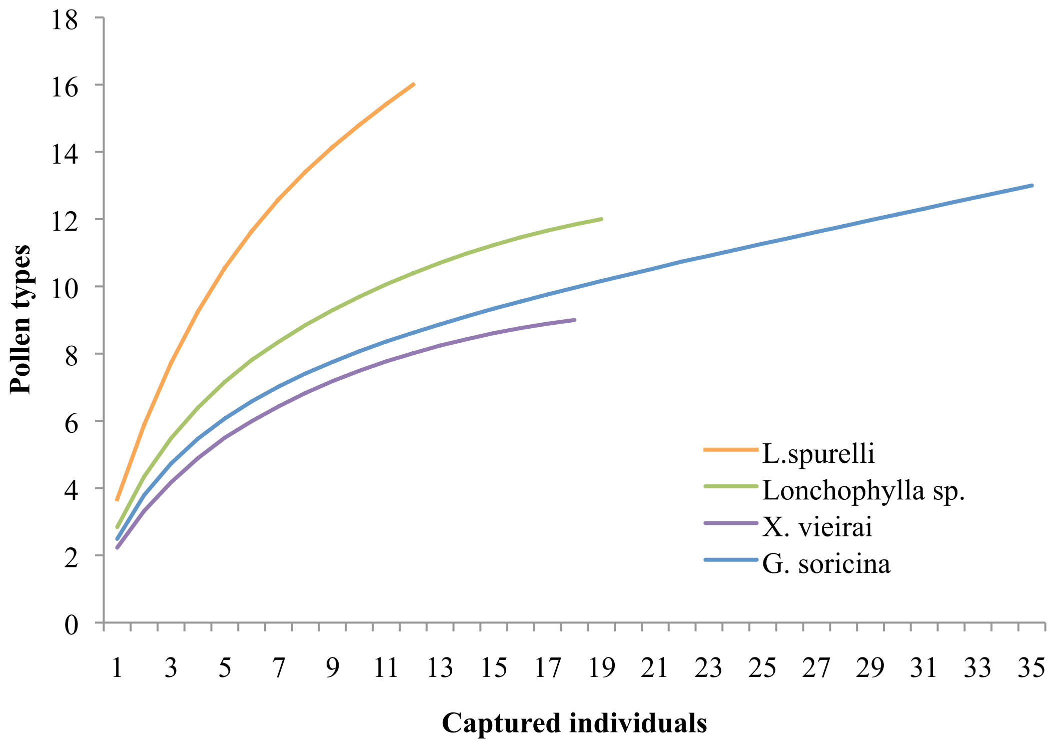
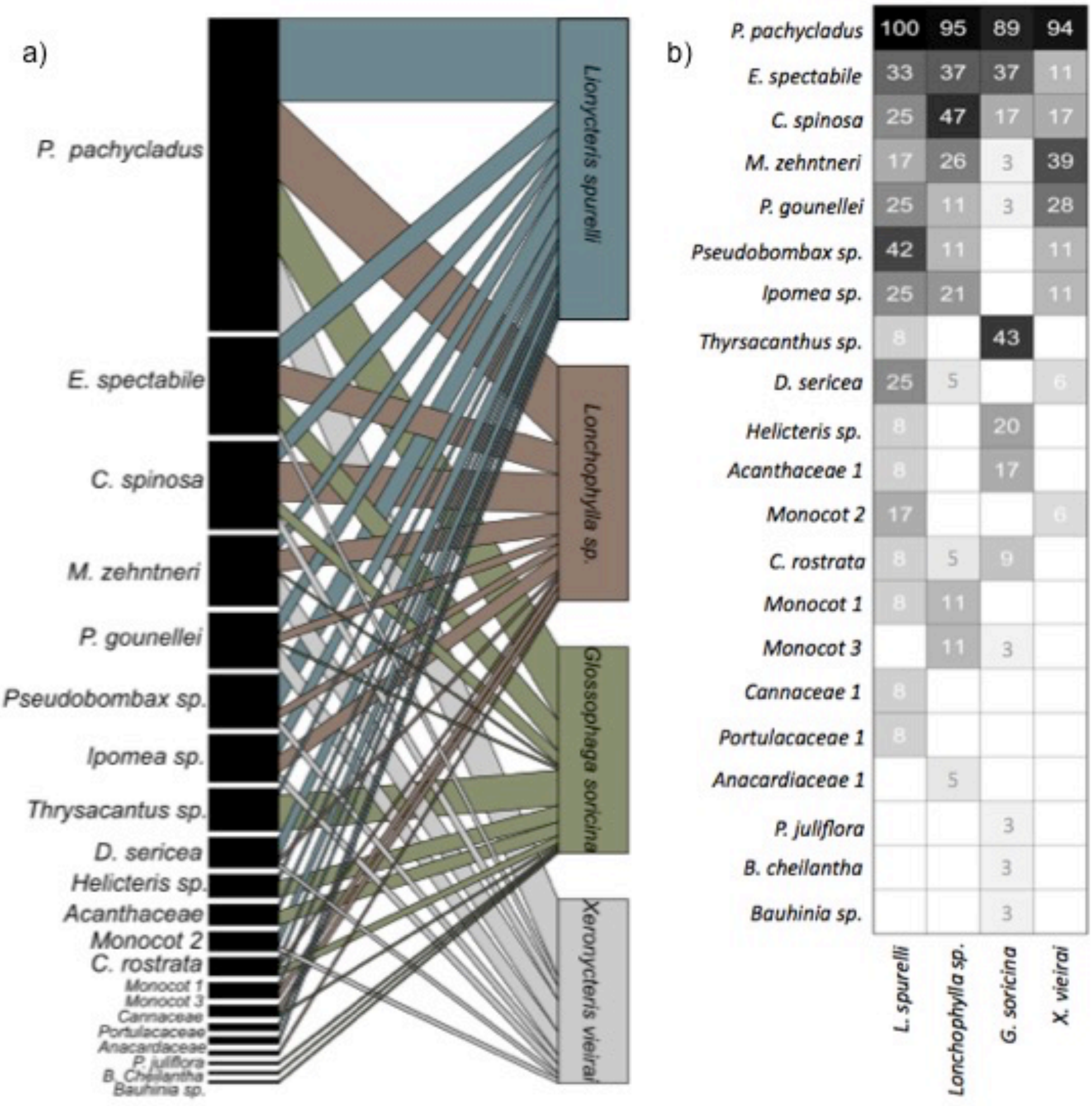


Fig 6. Accumulation curve of pollen types for each nectarivorous bat species.

The nestedness analysis of the interaction network between nectarivorous bats and plants in this Caatinga region is highly nested when compared to the null expectation (NODF= 59,04, Z =4,00, P < 0.001). The results show that the nectar-feeding bats and the plants they feed on, form a highly cohesive network, where all species are attached to the network and non-isolated compartments are presented (Figure 7a). These nested interactions can be visualized as well in a double entry qualitative and quantitative matrix describing the percentage of the interactions between the four species of nectar-feeding bats and the 21 species of plants they use as feeding resources. The different rows and columns are organized from the most generalists to the most specialists (Figure 7b). The species that stands out as core food resource is the columnar cacti *P. pachycladus*, not only because it is used by the four species of nectarivorous bats, but also because it is used much more frequently than any other plant.

The robustness coefficient for the higher level (bats) was R= 0,944 and R=0,744 for the lower level (plants). Both robustness coefficients are close to the value R=1, which corresponds to a curve that decreases very mildly until the point at which almost all bat species are eliminated. This is consistent with a very robust system in which most of the plant species survive even if a large fraction of bat species is eliminated and vice versa.

The species that interacted with more plant species was *L. spurrelli* (16 species) on the other hand; the one that had fewer interactions was *X. vieirai* (9 species).



	L. spurelli	Lonchophylla sp.	G. soricina	X. vieirai
P. pachycladus	100	95	89	94
E. spectabile	33	37	37	11
C. spinosa	25	47	17	17
M. zehntneri	17	26	3	39
P. gounellei	25	11	3	28
Pseudobombax sp.	42	11		11
Ipomea sp.	25	21		11
Thyrsacanthus sp.	8		43	
D. sericea	25	5		6
Helicteris sp.	8		20	
Acanthaceae 1	8		17	
Monocot 2	17			6
C. rostrata	8	5	9	
Monocot 1	8	11		
Monocot 3		11	3	
Cannaceae 1	8			
Portulacaceae 1	8			
Anacardiaceae 1		5		
P. juliflora			3	
B. cheilantha			3	
Bauhinia sp.			3	

Fig 7. a) Interaction network of nectar-feeding bats and plants in the Caatinga of Lajes. The widths of the rectangles and linking lines are proportional to the number of interactions involving the species. b) Interactions matrix between nectar-feeding bats and plants. The numbers inside the plot refer to the percentage of the samples that presented those interactions between the species.

Similarities between the nectar-feeding bat species

The sizes of the minimum convex polygon in the NMDS indicate how the diet of each nectar-feeding bat species varied in time (Fig. 8). Along the first axis, which accounted for 36% of total variation, it is possible to observe differences between *G. soricina* and *X. vieirai*. Along the second axis (32% of total variation) the species that varied it's diet the less was *X. vieirai*. The results of NMDS ordination have significant distortion to represent the original Bray Curtis dissimilarity index in two dimensions (Stress 0.28).

The ANOSIM (Table 3) revealed significant differences between the four species of nectar-feeding bats (R = 0.1568, p = 0.0003). *G. soricina* is different from the other species. The average dissimilarity between the bat species was 55.87% (Table 4). *E. spectable*, *C. spinosa*, *M. zehntneri* , *P. gounellei* and *Thrysacanthus sp.* were the main species to explain the dissimilarities. They contributed over 57.2% (accumulated) of the to dissimilarities between the diets of the bat species. *G. soricina* was the specie that fed the most of *C. spinosa* and *Thyrsacanthus sp.* and he fed the less of *M. zehntneri* and *P. gounellei* compared with the other species of bats. It is also worth mentioning that *P. pachycladus* is the species of plant that is most commonly used by all bats and this is why this plant explains only 7.7% of the dissimilarity between the diets of the bat species (Table 4).

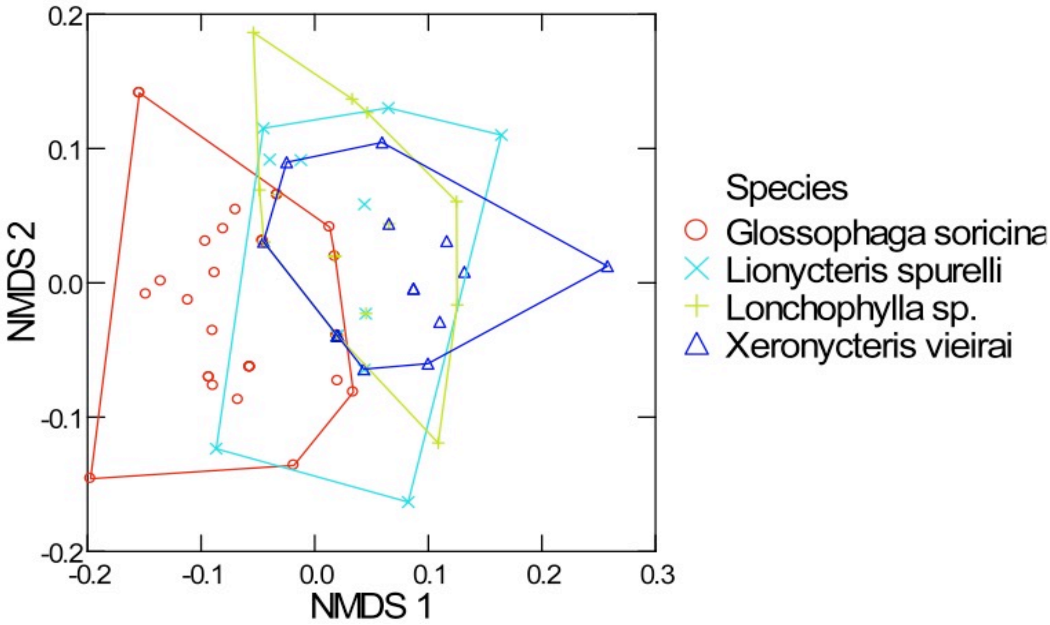


Fig 8. Graphic representation of the first two axes of a NMDS performed for all species of nectar-feeding bats diet. First axis explained 36% of total variation and second axis 32% Stress = 0,28.

Table 3. ANOSIM for significant differences in diet composition among the different nectar-feeding bat species.

R values

	Glossophaga soricina	*Lionycteris spurrelli*	*Lonchophylla sp.*
Lionycteris spurrelli	**0.2543**		
Lonchophylla sp.	**0.1521**	0.07236	
Xeronycteris vieirai	**0.1998**	0.1388	0.04025

Values in bold $p<0.05$

Prob, sequential Bonferroni significance

	Glossophaga soricina	*Lionycteris spurrelli*	*Lonchophylla sp.*
Lionycteris spurrelli	**0.0016**		
Lonchophylla sp.	**0.0039**	0.1169	
Xeronycteris vieirai	**0.001**	0.0229	0.133

Table 4. Plant species consumed by the nectar-feeding bats and its relative contribution to the Bray-Curtis dissimilarity index; values calculated by the SIMPER method. Values for each species are mean abundances.

Taxon	Av. dissim	Contrib. %	Cumulative %	*Glossophaga soricina*	*Lionycteris spurrelli*	*Lonchophylla sp.*	*Xeronycteris vieirai*
Encholirium spectable	8.275	14.81	14.81	0.382	0.333	0.368	0.111
Cleome spinosa	7.443	13.32	28.13	0.176	0.25	0.474	0.167
Melocactus zehntneri	6.05	10.83	38.96	0.0294	0.167	0.263	0.389
Thyrsacanthus sp.	5.834	10.44	49.4	0.441	0.0833	0	0
Pilosocereus gounellei	4.356	7.795	57.2	0.0294	0.25	0.105	0.278
Pseudobombax sp.	4.02	7.194	64.39	0	0.417	0.105	0.111
Ipomea sp.	3.345	5.987	70.38	0	0.25	0.211	0.111
Pilosocereus pachycladus	2.963	5.303	75.68	0.912	1	0.947	0.944
Helicteres sp.	2.615	4.681	80.36	0.206	0.0833	0	0
Acanthaceae 1	2.156	3.858	84.22	0.176	0.0833	0	0
Dicliptera sericea	1.989	3.559	87.78	0	0.25	0.0526	0.0556
Coursetia rostrata	1.457	2.607	90.39	0.0588	0.0833	0.0526	0
Monocot 3	1.333	2.387	92.77	0.0294	0	0.105	0
Monocot 2	1.128	2.019	94.79	0	0.167	0	0.0556
Monocot 1	0.9357	1.675	96.47	0	0.0833	0.105	0
Anacardiaceae 1	0.4107	0.7351	97.2	0	0	0.0526	0
Prosopis juliflora	0.3689	0.6603	97.86	0.0294	0	0	0
Cannaceae 1	0.3477	0.6223	98.48	0	0.0833	0	0
Portulacaceae 1	0.3477	0.6223	99.11	0	0.0833	0	0
Bauhinia sp.	0.266	0.4761	99.58	0.0294	0	0	0
Bauhinia cheilantha	0.2339	0.4186	100	0.0294	0	0	0

Overall average dissimilarity = 55.87

Temporal similarities

Considering the diet of the four nectar-feeding bats in the six sampled months, the NDMS ordination showed differences between their diets in some of the months (Fig. 9). Apparently all nectar-feeding bats species are eating what it is available monthly, presenting overlapping in their diets. July and August are the months where the nectarivorous bats varied their diet the most in both Axis (Axis1 36.6%, Axis2 34.8%).

The ANOSIM (Table 5) revealed significant differences between months (R=0.1055 p=0.0053). Bonferroni sequential significance showed differences between August and October, May and October and between June and May. The plant species used by nectar-feeding bats were similar in June, August and September.

The similarity of percentages (SIMPER) presented an average dissimilarity between months of 55.3% (Table 6). The plants that explained most of the dissimilarity percentages between the months of August and October were *C. spinosa* and *Thrysacanthus sp.*, because they were not consumed at all in October. Between May and October the main plant species explaining the dissimilarity was *E. spectable* which was not consumed at all in May. Finally between June and May, *Thrysacanthus sp.* was not consumed in June and *C. spinosa* was consumed twice the amount in June than in May. Once again it is demonstrated that *P. pachycladus* is essential for the nectarivorous bat community, been consumed monthly. The general pattern of bat community consumption is highly correlated to general plant availability composition (rMantel= 0.66; p= 0.017).

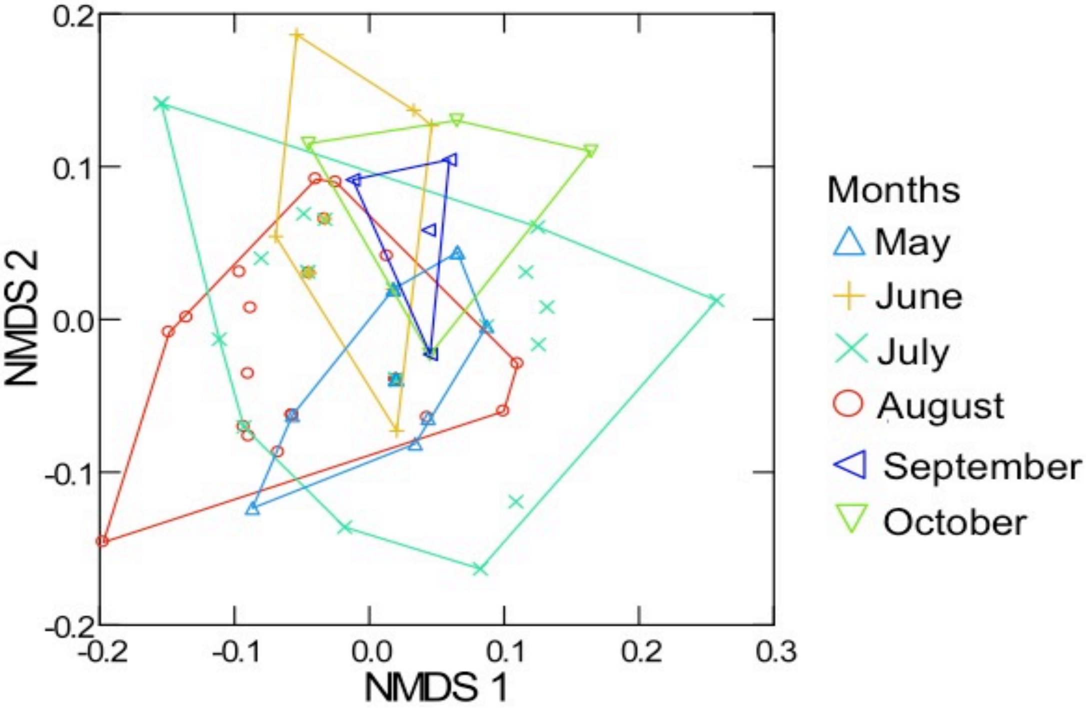


Fig 9. Graphic representation of the first two axes of a NMDS performed for all species of nectar-feeding bats diet for six months (May-October). First axis explained 36.6% of total variation and second axis 34.8% Stress = 0.29.

Table 5. ANOSIM for significant differences in diet composition among the different nectar-feeding bat species for six months (May-October).

R values

	October	September	August	July	June
September	0.151				
August	**0.4708**	0.2447			
July	0.1811	0.09996	0.07497		
June	0.3936	0.1799	0.1731	0.03689	
May	**0.6598**	0.3507	0.02755	-0.05589	**0.2717**

Values in bold p <0.05

Prob, sequential Bonferroni significance

	October	September	August	July	June
September	0.2344				
August	**0.0006**	0.0263			
July	0.1273	0.2489	0.0117		
June	0.006	0.1282	0.0188	0.2988	
Mayo	**0.0003**	0.0199	0.2741	0.7763	**0.0017**

Table 6. Plant species consumed by the nectar-feeding bats and its relative contribution to the Bray-Curtis dissimilarity index in six months (May-October); values calculated by the SIMPER method. Values in months are mean abundances.

Taxon	Av. dissim	Contrib. %	Cumulative %	October	September	August	July	June	May
Encholirium spectable	8.497	15.36	15.36	0.5	0.25	0.32	0.296	0.7	0
Cleome spinosa	7.681	13.89	29.25	0	0.75	0.24	0.0741	0.6	0.308
Thyrsacanthus sp.	6.141	11.1	40.35	0	0	0.48	0.0741	0	0.154
Melocactus zehntneri	5.351	9.674	50.03	0.5	0	0.08	0.222	0.2	0.231
Pseudobombax sp.	3.957	7.155	57.18	0.75	0.75	0.04	0.0741	0	0
Pilosocereus gounellei	3.732	6.748	63.93	0	0	0.16	0.148	0.1	0.154
Ipomea sp.	3.05	5.514	69.44	0.5	0.25	0.04	0.111	0.2	0
Pilosocereus pachycladus	2.972	5.373	74.82	1	1	0.96	0.889	0.9	1
Helicteres sp.	2.619	4.736	79.55	0	0	0.16	0.148	0	0
Acanthaceae 1	2.359	4.265	83.82	0	0	0.24	0	0	0.0769
Dicliptera sericea	2.137	3.864	87.68	0.75	0.25	0	0	0.1	0
Coursetia rostrata	1.743	3.151	90.83	0	0	0	0.037	0.3	0
Monocot 3	1.298	2.348	93.18	0	0	0	0.0741	0	0.0769
Monocot 2	0.9142	1.653	94.83	0	0	0.04	0.037	0	0.0769
Monocot 1	0.8611	1.557	96.39	0	0	0	0.037	0.2	0
Prosopis juliflora	0.3874	0.7005	97.09	0	0	0	0.037	0	0
Cannaceae 1	0.36	0.6508	97.74	0.25	0	0	0	0	0
Portulacaceae 1	0.36	0.6508	98.39	0.25	0	0	0	0	0
Anacardiaceae 1	0.3255	0.5886	98.98	0	0	0	0.037	0	0
Bauhinia sp.	0.3007	0.5436	99.52	0	0	0.04	0	0	0
Bauhinia cheilantha	0.2639	0.4771	100	0	0	0.04	0	0	0

Overall average dissimilarity = 55.31

Availability and use of resources

The linear regressions for each nectar-feeding bat species considering the available resources and the used resources (Table 7) was done first with the pre selected plants available (See Methodology) and second only with the plants bats used. The regression with the pre-selected plants was not significant for *L. spurrelli*, even without the outlier (*P. gounellei*). When performing regressions only for plants that were used by the nectar-feeding bats, the regressions were significant for *G. soricina*, *L. spurrelli* and *X. vieirai;* for *Lonchophylla sp.* the regression was significant only after removing the outlier value.

Table 7. Linear regressions of the used available resources by nectar-feeding bats. N = plant species used for analysis in different months.

Species	Pre-selected plant species				All used plants by bats			
	R^2	Std. coeff	N	p-value	R^2	Std. coeff	N	p-value
Glossophaga soricina	0.108	0.328	27	0.095	0.341	0.584	12	0.046
Glossophaga soricina (no outlier*)*	0.169	0.411	26	0.037				
Lionycteris spurrelli	0.004	-0.065	27	0.746	0.343	0.585	12	0.046
Lionycteris spurrelli (no outlier*)*	0	-0.002	26	0.991				
Lonchophylla sp.	0.14	0.375	27	0.054	0.202	0.449	14	0.107
Lonchophylla sp.(no outlier)	0.195	0.441	26	0.024	0.514	0.717	13	0.006
Xeronycteris vieirai	0.126	0.355	27	0.069	0.465	0.682	12	0.015
Xeronycteris vieirai (no outlier)	0.202	0.45	26	0.021				

After plotting the standardized residuals from the regressions for the values in bold in Table 7 we can see positive and negative residuals based on the expected utilization of each plant species by bats. In a Fig. 10 we can observe that *G. soricina* used more than expected the plants *C. spinosa* and *P. pachycladus*, the other species that was used within the expected intervals was *E. spectabile*. On the other hand *C. rostrata* was used less than expected by chance by *G. soricina*. *Lonchophylla sp.* presented a very similar pattern to that of *G. soricina* where the main plants in its diet were *C. spinosa* and *P. pachycladus*. *X. vieirai* had two species that were very representative in its diet, *P. pachycladus*, and *E. spectabile*. *C. spinosa* during a specific time of the sampling period was used more than expected by chance, but in another time that species was used much less than expected. Another species that is worth highlighting for *X. vieirai* is *M. zehntneri* which was not expected to be widely used by the species, yet we can see that at one time of the sampling period this species was used much more than expected by chance. Finally for *L. spurrelli* the species used more than expected were *P. pachycladus* and *E. spectabile,* and *C. rostrata* was used less than expected by chance.

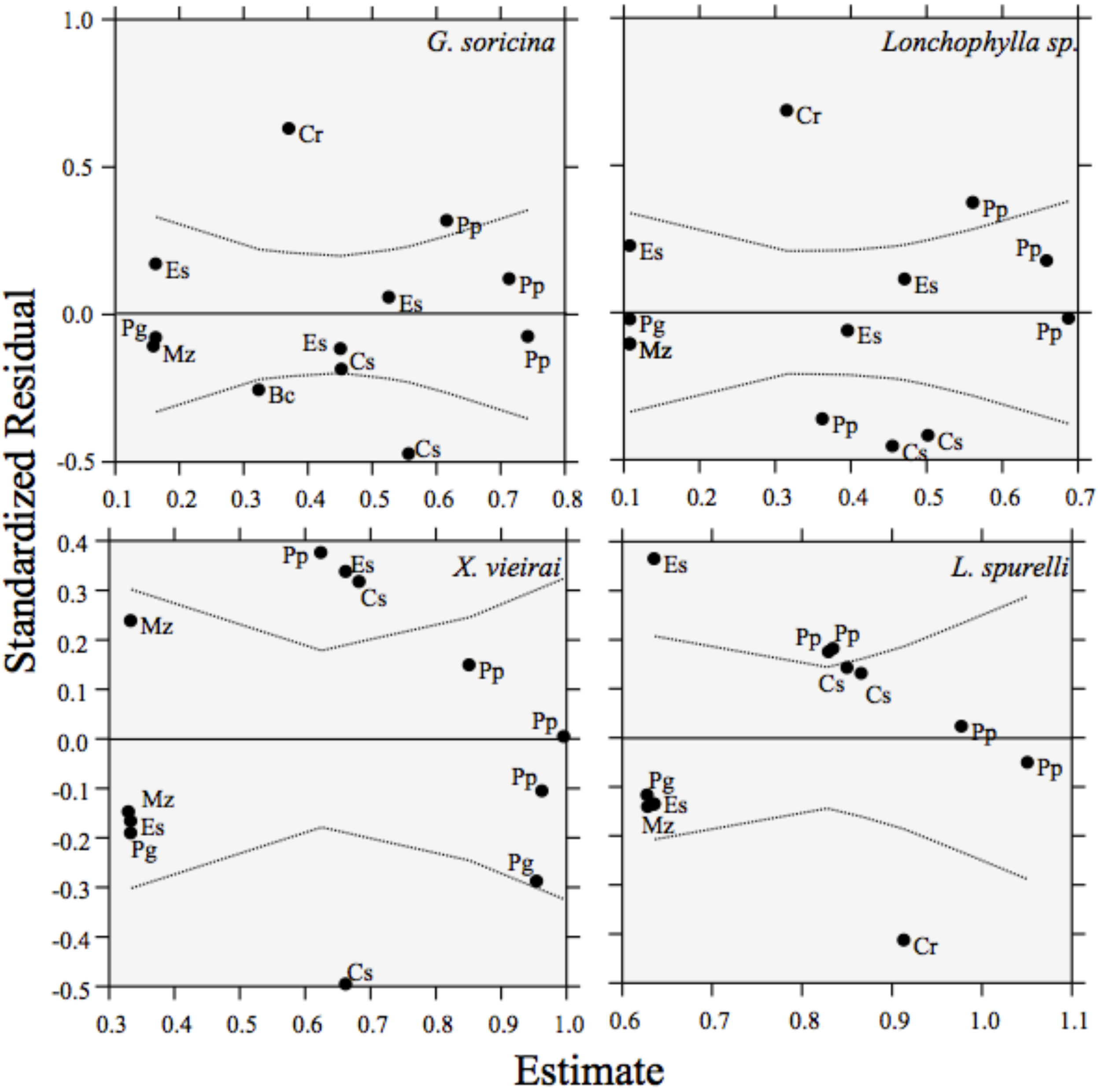


Fig 10. Standardized residuals from the regressions based on the expected utilization of each plant species by bats. The dotted line indicates the 95% confidence intervals. Pp= *Pilosocereus pachycladus*, Pg= *Pilosocereus gounellei*, Mz=*Melocactus zehntneri,* Es= *Encholirium spectabile*, Cs= *Cleome spinosa*, Cr=*Coursetia rostrata* and Bc= *Bauhinia cheilantha.*

DISCUSSION

Structure of the mutualistic interaction network

The analysis of interactions between the four species of nectar bats and the twenty-one species of plants proved to be significantly nested when compared to the null model, the interactions between nectar bats and plants in this Caatinga area are not random. A cohesive network and asymmetry is observed. There is a core of more generalist species of bats (*L. spurrelli* and *Lonchophylla sp.*) that feed on generalist plants (*P. pachycladus*, *E. spectabile* and *C. spinosa*), forming a dense nucleus where more specialist species adheres (Fig. 7).

In a nested network, specialization is asymmetric. Specialist species of one of the assemblies (bats in this case) tend to interact only with other generalist species from the other assembly (plants). This phenomenon provides greater opportunity of specialist species to persist, because the generalists species from which they depend often are more abundant and less fluctuating, since they have many different resources (Bascompte and Jordano 2008).

Another way to understand this type of network is viewing it as a robust core of bat species and plants in a resilient system that when some of their interactions are lost due to extinction of some of its species, alternative routes are found to keep the system working. The network here exposed high robustness values at both plants level (R = 0.744) and at bats level (R = 0.944). If the extinction of species was given randomly in a robust network the system would remain stable, even if a large fraction of species were eliminated; since, randomly, the more likely species to be removed are the specialists and the less likely to be eliminated are the generalists species.

These generalist species are the ones bringing together the entire network and are the ones giving stability to the system (Bascompte *et al.,* 2006a; Ives and Carpenter 2007. Blüthgen *et al.,* (2008) warned about being cautious when performing more detailed analysis of networks interaction, such as measuring the specialization level, the interaction strength asymmetry among other metrics, because they are quite affected by sampling intensity and biased by incomplete sampling, as for rarely observed species for example. Considering this and the results of our accumulation curve of pollen types for each nectarivorous bat species (Fig. 6), we decided not to go further on the analysis. A more complete sampling is needed for a better characterization of the network for nectar-feeding bat species, mainly for *L. spurrelli*. Nevertheless, from a biological perspective there is valuable data to be discussed here.

Bat assembly

The local nectar-feeding bat assembly at our study site consisted of five species (Table 1). *G. soricina* was the most abundant in our study, as expected, due to its wide distribution and general abundance in different environments (Reid, 2009). The next most abundant species was *X. vieirai*, followed by *Lonchophylla sp.* and finally *L. spurrelli.* Something observed for all species, except for *L. spurrelli*, is that the number of captures decreased in the last two sampling months despite having kept the sampling effort equal throughout field data collection. This variation in abundance of nectar-feeding bats has been shown to be common in environments that are subjects to variation in precipitation during annual cycles because of the fact that flowering is tightly synchronized with the seasonal water availability (Sperr *et al.,* 2011). To be able to confirm if the observed trend in the abundances of nectar-feeding bats species is a real patter where *G. soricina*, *Lonchophylla sp*. and *X. vieirai* decrease in abundance when the peak of the dry season begins (October to November) and instead *L. spurrelli* and *A. geoffroyi* increase their abundance, it would be necessary to sample for at least one full year to be able to depict a complete cycle. It has been documented that in some regions the community of nectar-feeding bats are divided into resident species (present all year) and non-residents (presents only part of the year) (Tschapka, 2004), this could be happening in this region.

Plant assembly and phenology

Based on phenological data obtained in this study it would be impetuous to characterize a pattern of resource availability determined by water availability. However, a decrease in the availability of flowering species can be seen during the last two months. In the same way as discussed for sampling bats, phenological data should be taken for at least one year.

The study area can be characterized by being dominated by plants of 4 families: Cactaceae, Bromeliaceae, Facabecae and Euphorbiaceae according to the abundances of plant species in our transects. Species composition in semi arid forest and their relative abundance are determined by both biotic factors (abundance of pollinators and seed disperser for example) and abiotic factors (rain and soil nutrients)

(Ribeiro *et al.,* 2015). The utilization of feeding resources in the study area will be discussed later.

Similarities between the nectar-feeding bat species

As to the difference in diet between the four species of nectar-feeding bats based on the analyzes of NMDS and ANOSIM, it was detected that *G. soricina* is the species with significantly different diet. Compared with the other three species, it is the best studied regarding its diet (Bredt *et al.,* 2012). Among nectar-feeding bats, this species is cataloged as typical generalists showing great feeding plasticity, using not only nectar and pollen but also fruits and insects to supplement their diet in situations of resource scarcity (Alvares *et al.,* 1991; Reid, 2009; Gonzalez *et al.,* 2012). By using other feeding resources in our study area we could explain the fact that this species did not present the highest number of interactions with flowering plants (Fig. 7). During the study period feces samples were collected to identified if the species were using other feeding resources in addition to nectar (see Supplementary material 1), only *G. soricina* and *Lonchophylla sp.* presented insects remains. Previous studies in another Caatinga area, demonstrated that, morphologically, these two species are very similar and their strategy to reduce competition was by *G. soricina* feeding almost exclusively on fruit (Willig, 1986). In this study no differences were observed in the content of their feces samples, but there were differences between some of the plant species they used. For example, *G. soricina* was the only species who used *Thrysacanthus sp.* and that used less frequently *C. spinosa*, *M. zehntneri*, *P. gounellei* and that did not used at all *Pseudobombax sp.* and *Ipomea sp.* which were important for *Lonchophylla sp.* Now, the low frequency use of *P. gounellei* by *G. soricina* is an interesting situation to discuss based on the morphological differences between bat species. There was a differentiated use of this resource in our study, the species that most commonly used this plant was *X. vieirai* and the species that used it the least was *G. soricina*. The most obvious morphological character in nectar-feeding bats is the elongated rostrum, which varies from moderate elongation in the generalist *Glossophaga* species to extreme elongation in specialists (Tschapka *et al.,* 2008). Despite the fact that no morphological measurements were taken systematically in this study, the rostrums of few individuals of both species were measured. *X. vieirai* exhibits a more elongated snout (13.5 mm) compared to that of *G. soricina* (7.6 mm). The morphological difference in snout length is related to the fact that not all species of bats manage to reach the nectar of deep flowers (Gonzalez *et al.,* 2012). The flowers of *P. gounellei* have been characterized by the production of less pronounced odor, lower nectar production and a narrower and more elongated floral tube in comparison to other species of *Pilosocereus* (Roncha *et al.,* 2007). Possibly because of the size of its snout, *X. vieirai* was the species that most frequently used this floral resource.

M. zehntneri is a small globose cactus that is found almost at ground level; so far the only pollinator species recognized are hummingbirds (Machado and Lopes, 2004, Rocha *et al.,* 2007). Although hummingbirds seem to be the most important pollinators of *Melocactus*, other taxa including small bees and butterflies have been proposed as alternative pollen vectors (Nassar and Ramirez, 2004). Its ornithophilous characteristics and small globular size and hence its low height is what took us by surprise when finding this pollen type in 39% of samples of *X. vieirai* followed by 26 % in the samples of *Lonchophylla sp.* due to the fact that another limitation represented by the morphology in bats is their ability to fly at different heights, their agility and maneuverability (Norberg, 1987). These species are probably likely to have greater agility and maneuverability to fly at such low altitudes (about 20-30 cm from the ground) than *G. soricina*.

Temporal similarities

The general pattern of bat community consumption is highly correlated to the general plant availability. This suggests synchronic variation between consumption and resource availability in the analyzed months.

Precipitation rates varied very little throughout the sampling period, so this data was not included in the analyzes (Supplementary material 2). But observing the precipitation data in a finer scale (rain per day) may help understand changes in diet that took place during the months of July and August. The capture rate of nectar-feeding bats during these two months was the highest (Table 1). In July it rained before, during and after the sampling nights. There are plant species in semiarid regions that respond quickly to sporadic rainfalls, making resources available in some cases (Schwinning and Sala, 2004). We assumed that the rain that fell sporadically during the month of July had an effect on the availability of floral resources in some plant species during July and August. Based on this assumption, the bigger size of the minimum convex polygon in Fig. 8 observed for July and August reflects a higher availability of different resources in comparison to the other months.

Availability and use of resources

Based on the expected utilization of each plant species by bats, four species of plants stood out. *Pilosocereus pachycladus* is a columnar cactus with documented vulnerability due to small populations in some areas of Caatinga and widespread in other areas (Ribeiro *et al.,* 2015). In our study site it was the second most abundant species (Table 2). It is a species that produces 1288-1997μm nectar (accumulated volume in 14 hours) with a sugar concentration of 11-17% (Rocha *et al.,* 2007). This value is within the range reported for bats, which is of around 17%; in comparison to other pollination systems this is considered a dilute nectar as a strategy that obligates bats to consume more nectar per night, thus the plant ensures that the individual will visit more flowers (Tschapka and Dressler, 2002). Its flowering and fruiting period is asynchronous intraspecifically, which may represent a consequence of the competition for dispersers and/or pollinators in the same area (Rocha *et al.,* 2007). The high specialization to bat pollination observed in most of the tropical columnar cacti in Mexico and Venezuela (Valiente-Banuet et al, 1996; Nasar *et al.,* 1997) might be a response of long and stable coexistence in arid and semi arid environments (Rojas-Martínez *et al.,* 1999). Under these characteristics and by data generated in this study we can safely point out that the columnar cacti *P. pachycladus* is a keystone species for the support of the community of nectar-feeding bats in this region of Caatinga. Other studies have also demonstrated the importance of this species for the maintenance of local wildlife such as birds, bees, moths, ants and beetles (Rocha *et al.,* 2007).

The second species with the highest importance to the community of nectar-feeding bats was the bromeliad *E. spectabile* as it was the second species with the highest frequency of use. Recently it was reported that this species has a system of mixed pollination by hummingbirds, bats and a marsupial (Queiroz *et al.,* 2016). The flowers of this species were used as food resource primarily by *G. soricina*, *Lonchophylla sp.* and *L. spurrelli* for all sampling months, except in May, which coincides with the phenological data exposed by Queiroz *et al.,* (2016). The authors documented that the flowering period goes from June to October, it is an attractive and reliable resource since different individuals open their flowers each night and for 30 consecutive days (Queiroz *et al.,* 2016). Plants have different strategies to ensure its pollination, *E. spectabile*'s strategy is presented as well in other plants with chiropterophily characteristics (in Cactaceae eg) where each individual open one or a few flowers per night (Rocha *et al.,* 2007). These strategies have been associated with nectar-feeding bats with a trapliner behaviour, consisting in foraging along regularly used feeding routes (Alvarez *et al.,* 1991, Sazima *et al.,* 1999).

Cleome spinosa is a species that has already been reported to be used by bats as food resources, not only for nectar-feeding bats but also for the omnivorous bat *P. discolor*, butterflies, bees, sphingids, and hummingbirds (Machado *et al.,* 2006; Tschapka *et al.,* 2008). According to Machado *et al.,* 2006, this species provide nectar with a sugar concentration of 15.56% ± 4.75 and its flowering period is during the rainy season (February to May), nonetheless in our study site individuals of these species presented flowers until September. This species represented an important resource for *X. vieirai* and *L. spurrelli* (Fig. 10).

Finally, *Coursetia rostrata* was a species with significant importance in the diet of *G. soricina* and *Lonchophylla sp.*, unfortunately no information about the biology of this species was found. In our field sampling we observed flowers for at least five months (June to October). Fruits were observed simultaneously with flowers; both available in periods where the individuals were completely leafless. Bees were observed visiting its flowers during the day and bats at night bats. This is the first record of nectarivorous bats visiting flowers of *C. rostrata.*

In this study we present four plant species with new records of bat visitation: *Melocactus zehntneri, Coursetia rostrata, Thyrsacanthus sp* and *Dicliptera sericea*. None of them have typical chiropterophily features, except for *C. rostrata* that at least presented white coloration and night anthesis (pers. obs.). There is growing evidence of unspecialized nectar-feeding bat species opportunistically learning to use non-coevolved plants with accessible and large pollen or nectar supplies, this could be explained by high behavioral flexibility that has been selected due to the ephemeral characteristics of their resources (Tschapka, 2003).

CONCLUSIONS

(1) The network structure of mutualistic interactions between nectar-feeding bats and plants in a semi arid forest in Caatinga of Rio Grande do Norte presented a pattern of nestedness and asymmetry with high robustness as expected. Showing this is a cohesive and resilient system.

(2) There were differences between the species of plants consumed by nectar-feeding bats in the area and also differences in the frequency of use of some plant species.

(3) There was a temporal variation related to the use and resource availability as expected, in general, the community of nectarivorous bats consume the available plant species, but some preferences occurs for some species.

(4) *P. pachycladus* was detected as the central keystone species for the support of the nectar-feeding bat community present in this Caatinga area of Rio Grande do Norte during the sampled months. This species presented high abundance and its resources were the most used by all species of nectar bats. *P. pachycladus* must be taken into account in decision making related to important areas for conservation in Caatinga.

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CHAPTER II

ARE LEAVES A GOOD OPTION IN CAATINGA'S MENU? FIRST RECORD OF FOLIVORY IN *ARTIBEUS PLANIROSTRIS* (PHYLLOSTOMIDAE) IN THE SEMIARID FOREST, BRAZIL

Photo: Juan Carlos Vargas Mena

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Are leaves a good option in Caatinga's menu? First record of folivory in Artibeus planirostris (Phyllostomidae) in the semiarid forest, Brazil

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KEY WORDS: Bats, Phyllostomidae, caves, feeding habits, folivory, Pteropodidae, Caatinga

ABSTRACT

Folivory can be defined as the consumption of foliage, including leaves, stems and leaf content. This trophic strategy has been documented in two families of bats, Pteropodidae (Old World fruit bats) and Phyllostomidae (New World leaf-nosed bats). Existing folivory hypothesis for bats suggest this behavior as a dietary supplement of protein and other essential minerals due to deficiency of these in a frugivore diet. The Caatingas have seasonaly deciduous tropical dry forest where during the extended dry season most of the vegetation is leafless and dormant. Here we present the first evidence of folivory in bats for the Brazilian Caatingas, records for the phyllostomid Artibeus planirostris using at least 16 species of plants as a food item in its diet, and a bibliographic review about bat folivory in the tropics. Additionally, we propose a new hypothesis on folivory in bats for this semiarid environment.

INTRODUCTION

Folivory can be defined as the consumption of foliage, including leaves, stems and leaf content (Kunz and Ingalls, 1994). From an evolutionary perspective, folivory is not as simple as it sounds since not all animals can manage to digest foliage, because it involves several biochemical and morphological specializations (dentition and gut) and the help of certain intestinal microbes to be able to extract nutrients and energy from plant fibers (Kunz and Diaz, 1995). However, fruit-eating bats have managed to avoid these biochemical and morphological specializations by masticating, extracting and swallowing the nitrogen-rich liquid fraction and finally discarding fibrous pellets (Lowry, 1989). Some authors have proposed a term for this eating strategy, "leaf fractioning" (Kunz and Ingalls, 1994).

This trophic strategy has been documented in two families of bats, Pteropodidae (Old World fruit bats) and Phyllostomidae (New World leaf-nosed bats). There are different hypothesis for explaining this feeding strategy in different species (see Table 1), but something that all the species with documented folivory have in common is that they are all primarily fruit eaters. Furthermore, bat folivory has mainly been documented in tropical rain forests, tropical savanna and high altitude cloud forests (Zortéa and Mendes, 1993; Kunz and Diaz, 1995; Tan *et al.*, 1998; Aguiar, 2005; Nelson *et al.*, 2005), but never for a semiarid environment.

The Brazilian Caatingas consists of a semiarid region of 730 000 km2 in northeastern Brazil and contains patches of seasonal dry tropical forest and sclerophyllous and xerophytic vegetation, dominated by Fabaceae trees, and species of Bromeliaceae and Cactaceae (Lima-Araújo *et al.*, 2007; Santos *et al.,* 2011). Leaves and flowers are produced during a short rainy season and during the extended dry season most of the vegetation is leafless and dormant (Leal *et al.*, 2003). The Caatingas has an extreme climate. According to Köppen classification, the climate in the region is BShw (hot and dry), with a lower annual rainfall of 800 mm (Alvares *et al.*, 2013). However, in this region there are at least 77 bat species of the 178 species present in Brazil (Oliveira *et al.*, 2003; Reis *et al.*, 2007; Paglia *et al.*, 2012; Nogueira *et al.*, 2014). Among the species of bats in the Caatinga, 12 species are frugivorous. Nevertheless, this region is the most neglected Brazilian ecosystem in terms of the conservation, probably due to its semiarid characteristics (Santos *et al.*, 2011).

One of the species of bats present at the Caatinga is *Artibeus planirostris*. *A. planirostris* is a species of fruit-eating bat that ranges from southern Colombia and southern Venezuela to northern Argentina and to eastern Brazil in altitudes from sea level to 1660 m.a.s.l. (Hollis, 2005). In Brazil it inhabits forested and forest fragments ranging from moist Amazonian and Atlantic forests to xeromorphic areas in Caatingas and Cerrado (Reis *et al*., 2013). *Artibeus planirostris* roost in hollow trees and caves in groups ranging from 5-40 individuals in a harem structure (Beguelini *et al*. 2013). *A. planirostris* has been characterized by its high diet plasticity, it feeds mainly on fruits but also supplements it diet with nectar, pollen and insects (Hollis, 2005).

It is important to know the type of food resources that sustain the populations of *A. planirostris* in semiarid environments, where an evident seasonal resource fluctuation occurs. Here we present the first evidence of folivory for the phyllostomid bat, *A. planirostris* based on observations of dry leaf pellets and bitten leaves of at least 16 species of plants in six day and night roosts in the Caatingas of two states, Bahia (BA) and Rio Grande do Norte (RN) in northeastern Brazil.

MATERIALS AND METHODS

We observed folivory in *A. planirostris* (Spix, 1823) in six caves in five municipalities (Fig. 1): Campo Formoso-BA (Toca do Morrinho), in Lajes-RN (Caverna do Serrote Preto), in Felipe Guerra-RN (Caverna Carrapateira), two in Governador Dix-Sept Rosado-RN (Caverna Lajedo Grande and Caverna da Pedrada) and finally one in Caraúbas-RN (Gruta Casa de Homens). In Toca do Morrinho throughout the month of January of 2013, we visited a colony that raged from 51 to 120 individuals every day. We also made monthly visits to the Serrote Preto Cave from May to October 2015 were the colony was composed of at least six individuals, who remained present for six months, but the colony size varied up to a maximum of 30 individuals in September. We made one visit to the remaining five caves between August and September 2015, and the colonies observed varied from 10-40 individuals. In all caves, we captured some individuals to take biometric measurements and to record their reproductive status.

We collected the partially eaten leaves and dry leaf pellets below the roosts for identification and to check the prevalence of folivory throughout the months. The identification of the leaves was carried out with the aid of botanists from the Universidade Federal do Rio Grande do Norte, Universidade Federal da Paraiba and Universidade Federal do Vale do São Francisco. Since most of the samples collected were only fragments of leaves, it was impossible to identify some of them to species level. Five were identified only at family level and six were classified as morphotype.

To gather the hypotheses proposed so far and identify in which habitats folivory has been documented and determine what type of information has been collected on this type of feeding behavior (e.g. casual observations, persistent observations and chemical analyses of plants), we conducted a bibliographic review on folivory in bats. This review included Old World fruit bats and New World leaf-nosed bats, and we synthesize the major conclusions of this published information (articles and notes). The survey was conducted in the major academic databases such as Periódico Capes, Google Scholar, Web of Science, Science Direct and ResearchGate using the keywords “folivory” and “bats”.

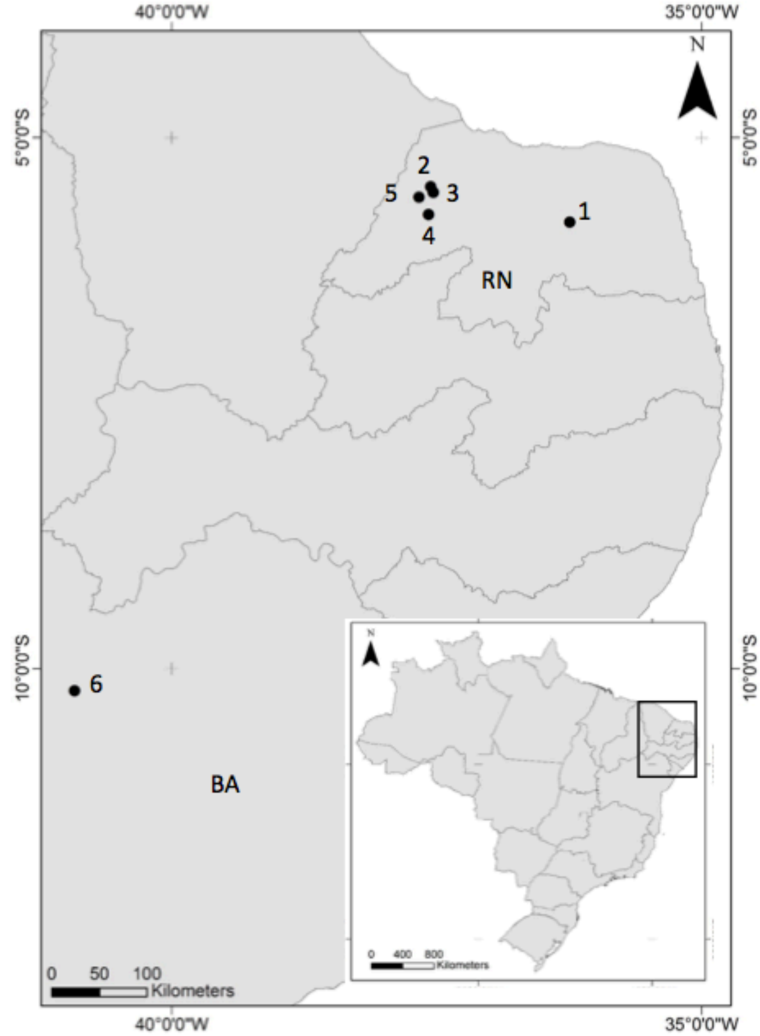

Fig 1. Map of the six surveyed caves in this study located in the Caatinga Biome: five in the state of Rio Grande do Norte 1.Caverna do Serrote Preto; 2. Caverna Lajedo Grande; 3. Caverna da Pedrada; 4. Gruta Casa de Homens; 5. Caverna Carrapateira and one in the state of Bahia 6. Toca do Morrinho.

RESULTS

The prevalence of leaf pellets and partially eaten leaves occurred in 15 of the 29 days monitored in Toca do Morrinho and during the six months of observation at Serrote Preto Cave. This high number of repeated observations suggests that leaves are an important diet component for *A. planirostris* both when bats were reproductively active (pregnant and lactating females and evidence of scrotum in males) and when they were not reproductively active.

Bats of Toca do Morrinho used leaves from six plant species (*Prosopis juliflora*; Euphorbiaceae sp^1; Euphorbiaceae sp^2; Euphorbiaceae sp^3; Moraceae sp^1, and Moraceae sp^2). In Serrote Preto Cave we identified leaves of *Cynophalla hastata* and the other leaves were classified into two morphological types (Fig. 2). In the other caves, we observed and collected oral dry pellets and partially eaten leaves from at least nine plant species of which only *Cynophalla hastata, Carica papaya, Mangifera indica,* and *Poincianella* sp. could be identified, the other leaves were classified in four different morphotypes (Fig. 2). One remarkable observation was that the majority of the leaves were eaten at the base, leaving the apex intact.

Additionally, leaf pellets and partially eaten leaves were also observed in five other caves located in northern Bahia state (R. Ferreira, personal observation). Including the two biggest caves in Brazil, Toca da Boa Vista (10°09'37"S, 40°51'40"O) and Toca da Barriguda (10°08'26"S, 40°51'08"O). Other observations occurred in Toca do Pitu (10°07'44"S, 40°50'16"O) and Lapa do Convento (10°02'56"S, 40°43'37"O) and finally in Toca dos Ossos (10°55'51"S, 41°03'27"O). All observations were made under roost of *A. planirostris* colonies, indicating that this behavior was common and persistent in the area (from year 1991 to 2005). Unfortunately, leaves were not collected nor identified for those caves; therefore, the data was not included in either the map or in the discussion.

We found seventeen references on folivory (including articles and notes) in the literature (Table 1) seven of which reported folivory in Old World bats and ten in New World bats. Only four publications conducted chemical analyzes on the composition of leaves, and three addressed the issue from the standpoint of behavior (hours of foraging, foraging time, and adaptive behavior after environmental disasters). Of the remaining publications, two were field observations made during a specific event (casual observations) and the other eight were observations during an extended period of time (persistent observations).

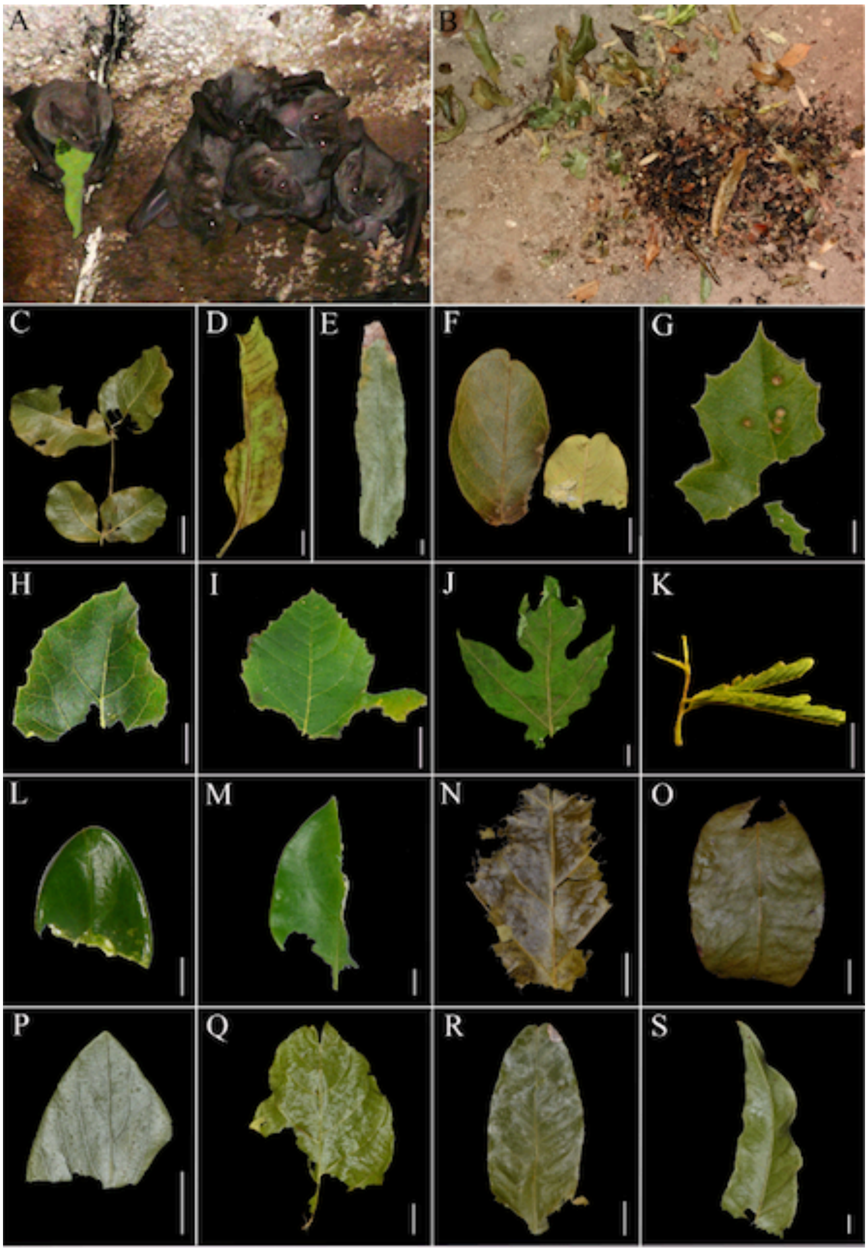

Fig 2. Folivory evidence: a) *Artibeus planirostris* eating a leaf in Toca do Morrinho. b) Partially eaten leaves and dry leaves pellets below the roosts in Gruta Casa de Homens. c) *Poincianella sp.* d) Immature leaf of *Mangifera indica* e) Mature leaf of *Mangifera indica* . f) *Cynophalla hastata.* g) Euphorbiaceae sp¹. h) Euphorbiaceae sp² i) Euphorbiaceae sp³. j) *Carica papaya.* k) *Prosopis juliflora.* l) Moraceae sp¹. m) Moraceae sp². n) Morphotype1. o) Morphotype2. p) Morphotype3. q) Morphotype4. r) Morphotype5. s) Morphotype6. Scale bar: 1 cm.

Table 1. Summary of the bibliographic review about folivory in Old World and New World bats.

Bat species	**Type of habitat**	**Type of information**	**Hipothesis**	**Conclusions**	**Reference**
Old World fruit bats					
Pteropus samoensis *Pteropus tonganus*	Islands of Savai'I in Western Samoa and Tutuila and Ofu in American Samoa	Behavior	Dietary complement of protein. First available resource after stochastic event (Cyclonic storms)	Leaves generally have higher protein content than fruit, switching to folivory following a cyclone is highly adaptive	(Pierson et al., 1996)
Cynopterus brachyotis	Disturbed lowland dipterocarp forest,Malaysia. Univestity campus.	Persistent observations	Dietary complement of protein, minerals and steroids	Fruits provide an energy source (carbohydrates) to phytophagous bats, and leaves ansource of protein, minerals, and steroids	(Tan et al., 1998)
Cynopterus brachyotis	Disturbed lowland dipterocarp forest, Malaysia	Chemical analyses of leaves	Dietary complement of protein and calcium. Suply calcium demands during pregnancy and lactation	Chemical composition of leaves meet daily protein and calcium requirements, especially during late pregnancy and lactation	(Rajamani et al., 1999)
Cynopterus sphinx	Campus of St. Johns College, Palayamkottai, India	Chemical analyses of leaves.	Dietary complement of protein and calcium	Relatively high concentrations of protein and calcium in leaves, important dietary sources for this plant-visiting bat	(Ruby et al., 2000)
Cynopterus sphinx	University campus, Madurai, India	Behavior	Suply protein, minerals and nutrient demands during pregnancy and lactation	Temporal differences in nightly foraging behavior. First obtain water and carbohydrate (fruits), then protein and minerals for important for reproduction from leaves (later hours of the night)	(Elangovan et al., 2001)
Pteropus samoensis *Pteropus tonganus*	Tutuila, American Samoa, island dominated by lowland and montane rain forests	Chemical analyses of leaves	Dietary complement of protein, zinc, manganese and calcium	Leaves are a rich source of protein for fruit bats. Leaves are rich in zinc, manganese and calcium.	(Nelson et al., 2005)
Ptenochirus jagori	Northwest Peninsula of Panay Island, Philippines. Primary Rain Forest	Chemical analyses of leaves	Dietary complement of higher protein content than fruits	Balanced diet with folivory. Leaves are chosen by their nutritional composition (not a specific nutrient)	(Reiter and Tomaschewski, 2003)
New World fruit bats					

Artibeus jamaicensis	Rain Forest, Puerto Rico	Persistent observations	Dietary complement of protein. Suply protein demands during pregnancy and lactation	Folivory may provide important source of protein during pregnancy and lactation for females	(Kunz & Diaz, 1995)
Artibeus concolor	Neotropical Rain Forest, Brazil	Casual observation	Dietary complement of protein. Suply protein demands durin pregnancy and lactation	Folivory is supplementary source of protein, specially during reproductive stages	(Bernard,1997)
Artibeus fimbriatus	Atlantic Forest, Brazil	Persistent observations	Dietary complement of protein	Maintenance of protein balance	(Esberard et al., 1998)
Artibeus lituratus	Atlantic Forest, Brazil	Casual observation	Dietary complement of protein	Bats get proteins from other food sources, so as insects and leaves	(Passos & Passamani, 2003)
Platyrrhinus lineatus	Cerrado, Brazil	Persistent observations	Dietary complement of protein	Leaves have high nitrogen-rich (protein) content that suplements their low-protein fruit diet. Females protein resource before reproduction period	(Aguiar, 2005)
Artibeus lituratus	Atlantic Forest (Urban area), Brazil	Persistent observations	Useful energetic resource. Potential detoxfying effect	Leaves are energetic resource in low fruit rich habitats as in urban areas. Potential detoxifying effect because of type of plant consume rgistered in the study	(Novaes & Nobre, 2009)
Artibeus lituratus	Cerrado (urban area), Brazil	Behavior.	Dietary complement of protein. Suply protein demands during pregnancy and lactation	Liquid fractions from leaves contains a reliable source of dietary protein and may provide important source of protein during pregnancy and lactation for females	(Bobrowiec, & Cunha, 2010)
Artibeus amplus	Andes, Venezuela	Persistent observations	Non-seasonal phenomenon	Nutriotional role of some leaf species consumed all year round.	(Ruiz-Ramoni et al., 2011)
Platyrrhinus lineatus	Atlantic Forest, Brazil	Persistent observations	Dietary complement of protein	Maintenance of protein balance	(Zortéa, 1993)
Artibeus lituratus	Atlantic Forest, Brazil	Persistent observations.	Dietary complement of protein and	Folivory among frugivorous phyllostomids is due to protein deficiency, since insects protein are eaten only occasionally	(Zortéa & Mendes, 1993)

DISCUSSION

Several hypotheses have attempted to explain folivory in frugivore bats (Table 1). Kunz and Diaz (1995) proposed that leaves provide a rich source of protein during periods of pregnancy and lactating in females. However, leaves and dry pellets were found even though captured females showed no evidence of lactation and/or pregnancy. In addition, fruit eating bats benefit from zinc, manganese and calcium contained in the liquid part of the leaves (Nelson *et al.*, 2000). Insects are also a protein supplement for frugivore bats; however, feeding on leaves is energetically more effective than feeding on insects as less energy is spent foraging for leaves because leaves are abundant and therefore easier to find (Kunz and Diaz 1995; Tan *et al*., 1998). This is the first report of folivory in a semiarid environment of Caatinga where water deficit during a large part of the year is a factor that conditions the vegetation. Resources, such as fruits, are supplied in pulses due to the limited and variable precipitation exerting adaptation challenges to both animals and plants (Chesson *et al*., 2004).

Herein, we would like to propose a simple, but as far as we know (Table 1), new hypothesis about folivory in bats the water supply hypothesis. Water is a quintessential resource for any living organism, and under some environmental conditions water stress can be quite relevant. It is well known that many desert species depend on their food to maintain their water balance (Schmidt-Nielsen 1997). This can be the case for bats living in arid and semiarid regions, like the Caatinga, where bodies of water are hard to find except after energy demanding long-distance travelling.

Literature has continuously referred the conspicuous deciduous phenology of the Brazilian Caatinga where most of the species of plants lose their leaves during the dry season while few species retain them year round (Machado *et al*., 1997). Phenological data taken in Lajes, RN near Serrote Preto Cave showed that most plants drop their leaves in September. We observed that during the transition from the rainy to the dry season (May-October), leaves are an abundant and potential food choice, but a remaining question is if this is a year-round nutritional strategy applied by *A. planirostris* populations given the loss of leaves by most plants in Caatinga during the long dry season and also during the wet season when more fruits are available.

Apparently, most of the species would be using this resource in a seasonal way (Kunz and Diaz, 1995), but at least for *Artibeus amplus* in the Venezuelan Andes, folivory has been proven to be a non-seasonal phenomenon (Ruiz-Ramoni *et al*., 2011). In the study area of Felipe Guerra (RN), bats were also feeding on perennial plants such as *Carica papaya* and *Magifera indica*. These plants are abundant in some cultivated areas and could be offering a food alternative throughout the year for different species of animals (Florentino *et al*., 2007), but something that should be taken into consideration is that bats would have to travel greater distances to feed on cultivated plants probably meaning a greater energy expenditure.

Moreover, it has been proven that the selection of leaves that have been consumed was unrelated to protein content (Reiter and Tomaschewski, 2003). Based on this finding, it is worth considering the hypothesis mentioned by Kunz and Ingalls (1994), that bats eat leaves to either stimulate or inhibit reproductive activity (also see Kunz and Díaz, 1995), as well as to prevent parasite infections. From the plants that we were able to identify in the study, information on the chemical composition of *Carica papaya*, *Magifera indica* and *Prosopis juliflora* was found. All three species are known for their multiple uses in both human and animal consumption as well as their importance as remedies for various illnesses. For example, extracts from *P. juliflora* seeds and leaves have piperidine alkalids that is thought to have antibacterial, antifungal and anti-inflammatory properties (Silva *et al.*, 2007). Both *C. papaya* and *M. indica* contains tannins in their leaves know to exhibit antiviral, antibacterial and anti-tumor effects (Aiyelaagbe and Osamudiamen, 2009; Otsuki *et al.*, 2010). Unfortunately, none of these properties have been tested for bats. In fact the hypotheses related to possible benefits and/or impairments of the ingestion of certain secondary metabolites and tannins has not been explored in detail yet (Kunz and Díaz, 1995; Nogueira and Peracchi, 2008).

In relation to the observation that the majority of the leaves were eaten at the base, leaving the apex intact (Fig. 2). Studies on the composition and concentration of some nutrients and minerals in leaves have shown there is a difference in the concentration depending of the section of the leaf (Rios *et al.*, 2012). The preference of bats for the base of the leaves suggest that this might be the part of the leaf where the greatest concentration of nutrients and/or other chemical components important for bats are deposited. Additionally, the water supply hypothesis that we propose here could also explain this specific behavior of *A. planirostris* because water content tends to be higher in the basal portion of the leaves (Sandars *et al.*, 2010).

Based on the bibliographic review, folivory in bats seems to happen at a Pantropical scale. In the Paleotropics within the pteropodids and in the Neotropics only on phyllostomids mostly in Brazil (Amazon and Atlantic forests) and in Puerto Rico (Table 1). However, the occurrence of folivory is not exclusive of low land rain forest since it also has been reported for Venezuelan Andes (Ruiz-Ramoni *et al.*, 2011) and in the Brazilian savannas (Cerrado) (Aguiar, 2005; Bobrowiec and Cunha, 2010).

Greenhall (1957) registered for the first time folivory in bats for *Artibeus lituratus* on *Ficus religiosa* in the island of Trinidad. Years later, Tuttle (1968) found beneath an *Artibeus jamaicensis* roost in Chiapas (Mexico), discarded leafs that appeared to be chewed and partly eaten. Gardner (1977) mentioned these two observations in a bibliographic review on feeding habits of phyllostomid bats. However, these authors presented neither hypothesis nor discussion on folivory.

Phyllostomid bats of the genus *Artibeus* showed folivory in five species: *A.amplus* (Ruiz-Ramoni *et al*., 2011), *A.concolor* (Bernard, 1997), *A. fimbriatus* (Esberard *et al*., 1998) *A.jamaicensis* (Kunz and Diaz, 1995), and *A.lituratus* (Passos and Passamani, 2003; Novaes and Nobre, 2009; Bobrowiec and Cunha, 2010) making this the genus with the largest number of reports with this diet strategy. This study adds one more species with folivory for Artibeus bats. Therefore, from the five species of *Artibeus* registered for Brazil (Nogueira *et al*., 2014), four species are now reported as folivorous. As for the totality of the genus, for the existing 12 species described so far (Solari and Martínez-Arias, 2014) six species (50%) have reported folivory. Although, it is unknown if folivory happens in the totality of the genus since observations have been done mainly on common species in the areas where they occur and are easily captured liked *A.jamaicensis*, *A.lituratus* and now with *A.planirostris*. Data gathered herein suggests that leaves are a recurrent food option for bats at least within the genus. However, detailed studies are necessary to determine water content in the leaves of species eaten by *A. planirostris,* as well as chemical and nutrient composition analysis to better understand folivory in bats in this semiarid environment.

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CHAPTER III

FIRST INSIGHT TO THE BIOLOGICAL ASPECTS AND RANGE EXTENSION OF THE BRAZILIAN ENDEMIC VIEIRA'S FLOWER BAT (*XERONYCTERIS VIEIRAI* GREGORIN AND DITCHFIELD, 2005).

Photo: Juan Carlos Vargas Mena

First insight to the biological aspects and range extension of the Brazilian endemic Vieira's Flower Bat (*Xeronycteris vieirai* Gregorin and Ditchfield, 2005)

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KEY WORDS: Caatinga, Nectar-feeding bat, Reproduction, Roost, Ectoparasite, Geographic distribution

ABSTRACT

Xeronycteris vieirai is an endemic bat species recently described by Gregorin and Ditchfield in 2005. Five specimens have been collected to date. Currently there is little information regarding this species and its ecological requirements are poorly known and only speculations have been made about its nectarivorous diet. *X. vieirai* apparently has a restricted distribution to Caatinga (semi-arid region), an habitat that has been deeply deteriorated. Data presented here provide not only the first information generated about the species reproduction, roost, nocturnal activity, ectoparasite, and diet but also a range extension.

INTRODUCTION

Xeronycteris vieirai, Vieira's Flower Bat, is an endemic nectarivorous bat recently described by Gregorin and Ditchfield in 2005. *X. vieirai* was described based on four specimens, all of them from the northeast region of Brazil. Holotype (MZUSP 29777) is from Fazenda Espírito Santo, municipality of Soledade state of Paraíba (07°05 S, 36°21 W). The other specimens are from the states of Bahia, municipality of Cocorobó (MZUSP 14170 adult female, MZUSP 14173 subadult male), Pernambuco, municipality of Exu (MZUSP 29777 adult male) and the most recent report from of Minas Gerais, Jaíba region, (ALP 6824) (Nogueira *et al.,* 2014).

Sixteen of the total 179 bat species occurring in Brazil are nectar-feeding bats (Nogueira *et al*., 2014; Moratelli and Dias, 2015; Gregorin *et al*., 2016), and at least five of these nectarivorous bat species are distributed in the Caatinga ecosystem, including *Xeronycteris vieirai.* Its distribution is apparently restricted to this the Brazilian Caatinga which consists of a semi-arid region of 826 411 km^2 in northeastern Brazil (MMA/IBAMA, 2011) and contains patches of seasonal dry tropical forest and sclerophyllous and xerophytic vegetation, dominated by leguminous trees, and species of Bromeliaceae and Cactaceae (Lima-Araújo *et al.,* 2007; Santos *et al.,* 2011). Leaves and flowers are produced during a short rainy season and during the extended dry season most of the vegetation is leafless and dormant (Leal *et al.,* 2003).

The Caatinga has an extreme climate. According to Köppen classification, the climate in the region is BShw (hot and dry), with a lower annual rainfall of 800 mm (Alvares *et al.,* 2013). This unique region is proportionally the least studied among Brazilian natural regions, it is also the less protected. Approximately 7.4% of its territory is preserved under some category of protection (integral protection or sustainable use) and it is distressingly going through an extensive change process and environmental deterioration (MMA/IBAMA, 2011).

Knowledge about *X. vieirai* is scarce. There are articles that mention the species from a systematic perspective and comparisons with closely related species (Lira *et al.,* 2006; Woodman and Timm, 2006; Mantilla-Meluk, 2007; Sá-Neto and Marinho-Filho, 2013; Dias *et al.,* 2013; Nascimento *et al.,* 2013; Parlos *et al.,* 2014; Solari and Arias, 2014). However, there are only two articles exclusively on this species, including the description of it by Gregorin and Ditchfield (2005) and another one about the emended diagnosis and record of polydontia (Nogueira *et al.,* 2014). There are no publications on the biological aspects of this species.

This is the first study with information on the biology of the species. *X. vieirai* it is listed as Vulnerable in the Red List of Brazilian Threatened Species (MMA, 2014) and as Data Deficient in the IUCN (2016), more biological surveys and revision of specimens in museums have been suggested. The information presented here was generated as part of a larger project that aimed to understand the interaction between plants and nectar-feeding bats, and among bats and ectoparasites in the Caatinga of northeastern Brazil. We also aimed to generate information about poorly known bat species present in the Caatinga, such as the endemic *X. vieirai*. Here we describe for the first time the roost of *X. vieiriai*, their diet, nocturnal activity, ectoparasites, and notes about its reproduction. Our findings take us a step closer to understanding the biology of this endemic and unknown species.

MATERIALS AND METHODS

Study area

Data were collected in two states in northeastern Brazil, Pernambuco (PE) and Rio Grande do Norte (RN). The Catimbau National Park (hereafter CNP) has an area of 62.292 hectares and includes the municipalities of Buíque, Tupanatinga and Ibimirin in the state of Pernambuco (MMA, 2002; ICMBio, 2015). This park is a priority area for Caatinga biome conservation due to the ecological value and to rare and endemic species occurrence (MMA, 2002). Rainfall in the region is concentrated between the months of April to June, with an annual average ranging from 300 mm to 500 mm (SUDENE, 1990; Rodal *et al*., 1998; Silva, *et al*., 2011). The CNP is elevated from 600 m to 1000 m a.s.l. and has a vegetation mosaic, varying from non-prickly arboreal habitats to xeric habitats, where prickly shrubs predominate (Rodal *et al*., 1998; Figueirêdo *et al*., 2000; Andrade *et al*., 2004).

Lajes, located in the central portion of the state of Rio Grande do Norte (RN), in the Caatinga’s vegetation region of Planalto da Borborema. This area is the best-preserved portion of Caatinga in RN. Five sampling sites, with at least 4.5 km between each other, were selected. They are located either inside or on the border of the largest fragment of Caatinga of RN, with an approximate area of 53,500 hectares. It is a region recognized by its importance for mineral exploration and with a potential for installation of wind power turbines, especially in the regions near the Serra do Feiticeiro where one of the biggest Wind Parks in Latin America will be installed. Both regions are marked by strong rainfall irregularity and may have long periods of drought.

Data collection

Field sampling in CNP (PE) was conducted from June 2014 to May 2015. Mist nets were placed for two nights per month, except in August 2014 (four nights) and in January 2015 (one night). In Lajes (RN) sampling was conducted from May to October 2015. Here, mist nets were placed for 5 nights per month.

Mist nets ranging from 80 to 120 meters were placed for six hours (from dusk until midnight). The mist nets were relocated monthly in order to cover as many microhabitats and available resources at the time and in each of the sites. The sampling effort was calculated by Straube and Bianconi (2002).

The specimens were identified as *X. vieirai* according to Gregorin and Ditchfield (2005) and Nogueira *et al*. (2014). Bats were sexed, weighed with 100 g Pesola, forearm length measured, and the capture time was recorded. In addition, the reproductive phase was determined through the observation of secondary sexual characteristics (Fleming *et al.,* 1972). Finally, individuals were inspected to find ectoparasites.

Two adult females from Lajes (RN) were collected and deposited in the Museum of the Universidade Federal do Rio Grande do Norte. Five individuals from CNP (PE) were collected and deposited in the Mammal Collection of the Universidade Federal de Pernambuco, of which three were males (two juveniles) and two adult females.

Observations on the available resources were taken in Lajes (RN). In each of the five sampling sites, 200 meters long and 10 meters wide transect was established to record resource availability (flowers and flower buds). Data were collected for 25 species (up to 10 individuals per species), including trees, shrubs, cacti and bromeliads.

Pollen samples were collected directly from the flowers available during the sampling period with jelly-glycerin cubes in order to make a pollen collection for reference.

Pollen analysis

For each captured bat in Lajes (RN), inspection for pollen was done all over its body. Pollen was collected with a sticky jelly cube (3-4 mm) prepared with glycerin, phenol and safranine for preservation and coloring respectively (Voigt *et al.,* 2009). Each cube of glycerine jelly was deposited in a microtube in a cooler to prevent them from melting. For pollen analysis were considered only identification of pollen grains present in microscope slides. The microscope slide were prepared by melting each glycrine jelly cube per bat sample and analysed under a light microscope (Leica DM500).

Pollen types were identified by comparison with a refence collection from the Palynotheca of the LAMIV/UEFS (Plant Micromorphology Laboratory/Feira de Santana State University), which is a representative collection of the pollen flora of the Caatinga vegetation from north-eastern Brazil. Relevant pollen catalogues were used for auxiliary identification, published by Chávez et al. (1991), Roubik and Moreno (1991), Santos *et al.* (1997), Carreira and Barth (2003), and Melhem et al. (2003).

Fecal samples

Because bats have a fast transit time of food ingestion-defecation (Dumont, 2003; Muscarella and Fleming, 2007), each captured bat in Lajes (RN) was kept in a cloth bag for a maximum time of 30 min to obtain fecal samples. Fecal samples were placed in microtubes for preservation and subsequent analysis. The contents of each fecal sample were categorized by the presence or absence of seeds, pollen, plant material, pulp-peels, insects and unidentifiable content with a stereoscope (Olympus sz40 Zoom 6.7-40x).

Ectoparasite samples

For each bat specimen captured in CNP (PE), ectoparasites were collected using forceps and conserved in vials with 70% ethanol for future identification. The vials were labeled individually for each bat host. Flies were identified under stereomicroscope, according to Wenzel (1976) and Guerrero (1995). In order to describe host-parasite associations, we used prevalence, mean intensity infestation (Bush *et al*., 1997), and aggregation (Poulin, 1993). All analyses were carried out in the program Quantitative Parasitology 3.0 (Rózsa *et al*., 2000). Bats were marked using non-toxic ink to prevent recapture during the same sample period, and released at the capture site.

RESULTS

Captures, body measurements, and activity

With a total sampling effort of 86,856.9 m^2.h a total of 62 individuals of *X. vieirai* were captured. Of which 34 were captured in Lajes (RN) with a sampling effort of 45,456.9 m^2.h, 14 were males and 20 females. And 28 individuals were captured in CNP (PE) with a sampling effort of 41,400 m^2.h, 10 were males and 18 females (Table 1). The average capture was 1.1 individual per night sampled, ranging from 0-11. The species was captured in all intervals sampled hours but showed two highest activity peaks at 18:30 h. and at 23:30 h. However, no nets were placed after midnight so we do not know if there is a peak after this period.

The month with the highest number of captures was July 2014 (in CNP) and May 2015 (in Lajes). Only in September 2014 and April 2015, no individuals were captured. During the last two months of sampling (September and October) the rate of captures declined to one individual per month in Lajes.

The mean size of the forearm for adult males is 37.0 mm (35.9-38 mm; sd = 0.75; n=24) and the mean weight of 11.5 g (8-14 g; sd =1.4, n= 38). Adult females have a mean size of the forearm of 37.8 mm (36.8-39.2 mm, sd = 0.5) and mean weight of 13.0 g (9-16 g; sd = 1.6). Adult females have a significantly larger forearm than adult males (t = 4.4; p = 0,0001) and are significantly heavier (t = 3.5; p = 0,001).

Table 1. Data from the 62 individuals of *Xeronycteris vieirai* captured from July 2014 to October 2015 in Catimbau National Park (CNP), Pernambuco and Lajes, Rio Grande do Norte, northeastern Brazil.

Date	**Site**	**Sex**	**Age**	**RS**	**FA (mm)**	**W (g)**
July 2014	CNP, Buíque	**M	J	NR	37.1	12
July 2014	CNP, Buíque	F	A	LA	38.6	13
July 2014	CNP, Buíque	**M	J	NR	36.9	12
July 2014	CNP, Buíque	F	J	NR	37.4	12
July 2014	CNP, Buíque	F	J	NR	38	15
July 2014	CNP, Buíque	M	J	NR	37.8	15
July 2014	CNP, Buíque	M	J	NR	37.1	13
July 2014	CNP, Buíque	M	A	E	37.9	10
July 2014	CNP, Buíque	M	A	E	36.1	8
July 2014	CNP, Buíque	F	A	PR	37.4	13
August 2014	CNP, Buíque	F	J	NR	40.1	15
August 2014	CNP, Buíque	**F	A	NR	38.3	15
October 2014	CNP, Buíque	**F	A	NR	37.7	12
October 2014	CNP, Buíque	F	A	PR	37.1	13
November 2014	CNP, Buíque	F	A	LA	37.3	13
November 2014	CNP, Buíque	F	C	NR	31.7	6

November 2014	CNP, Buíque	M	A	E	35.9	12
December 2014	CNP, Buíque	F	A	LA	38.2	13
December 2014	CNP, Buíque	M	A	E	36.1	11
December 2014	CNP, Buíque	F	A	LA	37.6	15
December 2014	CNP, Buíque	F	A	LA	38.2	16
January 2015	CNP, Buíque	M	A	E	37.9	12
January 2015	CNP, Buíque	F	A	LA	38.7	15
January 2015	CNP, Buíque	F	A	LA	36.8	15
February 2015	CNP, Buíque	F	A	PL	37.5	13
February 2015	CNP, Buíque	F	J	NR	37.4	12
March 2015	CNP, Buíque	F	A	LA	37.4	16
May 2015	CNP, Buíque	**M	A	E	37	14
May 2015	Fazenda Santo Antônio, Lajes	F	A	NR	37.9	9
May 2015	Fazenda Santo Antônio, Lajes	F	A	NR	38.1	13
May 2015	Fazenda Santo Antônio, Lajes	F	A	NR	38	12
May 2015	Fazenda Santo Antônio, Lajes	F	A	NR	38.3	13
May 2015	Fazenda Santo Antônio, Lajes	M	A	E	37.1	10
May 2015	Fazenda Santo Antônio, Lajes	M	A	E	37.4	12
May 2015	Fazenda Santo Antônio, Lajes	M	A	E	37.7	12
May 2015	Fazenda Santo Antônio, Lajes	M	A	E	36.3	12
May 2015	Fazenda Santo Antônio, Lajes	M	A	E	37.2	12
May 2015	Fazenda Santo Antônio, Lajes	M	A	NR	38	12
May 2015	Fazenda Santo Antônio, Lajes	M	A	NR	37	11
June 2015	Fazenda Santo Antônio, Lajes	M	A	E	37.5	13
June 2015	Sítio Joazeiro, Lajes	M	A	E	37.3	11
July 2015	Fazenda Santo Antônio, Lajes	M	A	NR	37.9	12
July 2015	Fazenda Santo Antônio, Lajes	F	A	PL	37.9	13
July 2015	Fazenda Santo Antônio, Lajes	F	A	NR	37.8	12
July 2015	Fazenda Santo Antônio, Lajes	F	A	NR	39.2	9
July 2015	Fazenda Santo Antônio, Lajes	F	A	NR	38	12
July 2015	Fazenda Santo Antônio, Lajes	F	A	PL	38	13
July 2015	Fazenda Santo Antônio, Lajes	F	A	PL	38	13
July 2015	Sítio Joazeiro, Lajes	M	A	E	36.1	10
July 2015	Sítio Joazeiro, Lajes	M	A	E	36.7	12
August 2015	Fazenda Santo Antônio, Lajes	F	A	L	37.7	18*
August 2015	Fazenda Santo Antônio, Lajes	F	A	NR	38.6	13.5
August 2015	Fazenda Santo Antônio, Lajes	F	A	NR	38.3	11
August 2015	Fazenda Santo Antônio, Lajes	F	A	NR	38.8	11.5
August 2015	Fazenda Santo Antônio, Lajes	F	A	NR	38.1	14
August 2015	Fazenda Santo Antônio, Lajes	F	A	NR	37.4	13
August 2015	Fazenda Santo Antônio, Lajes	M	A	E	37.1	11
August 2015	Fazenda Santo Antônio, Lajes	M	A	NR	38	14
August 2015	Santa Rosa, Lajes	F	A	E	37.1	12.5
August 2015	Santa Rosa, Lajes	F	A	NR	37.2	14
Setember 2015	Fazenda Santo Antônio, Lajes	**F	A	PL	37.4	15
October 2015	Fazenda Santo Antônio, Lajes	**F	A	NR	38	13

M = Male, F = Female, A = Adult, J = Juvenile, C = Calf, RS = Reproductive status, NR = Non Reproductive, E = Obvious scrotum, PL = Post-lactating, LA = Lactating, PR = Pregnant, FA = Forearm, W = Weight, *Weight of female plus calf, **Collected individuals.

Reproduction

Individuals of all the different reproductive phases were captured throughout the sampling period (Fig. 1). Two pregnant females were captured, in July and October 2014 in CNP (PE). Two females with a calf were captured (Fig. 2c), one in November 2014 in CNP (PE) and another in August 2015 in Lajes (RN). A total of 8 lactating females were captured in July (1 female), November (1), December (3), January (2) and in March (1). Five post-lactating females were captured in February (1), July (3) and in September (1). Of the 24 males captured, 17 had obviously exposed scrotums (reproductively active) in July (2 males) and the periods from November to January (3) and from May to August (12).

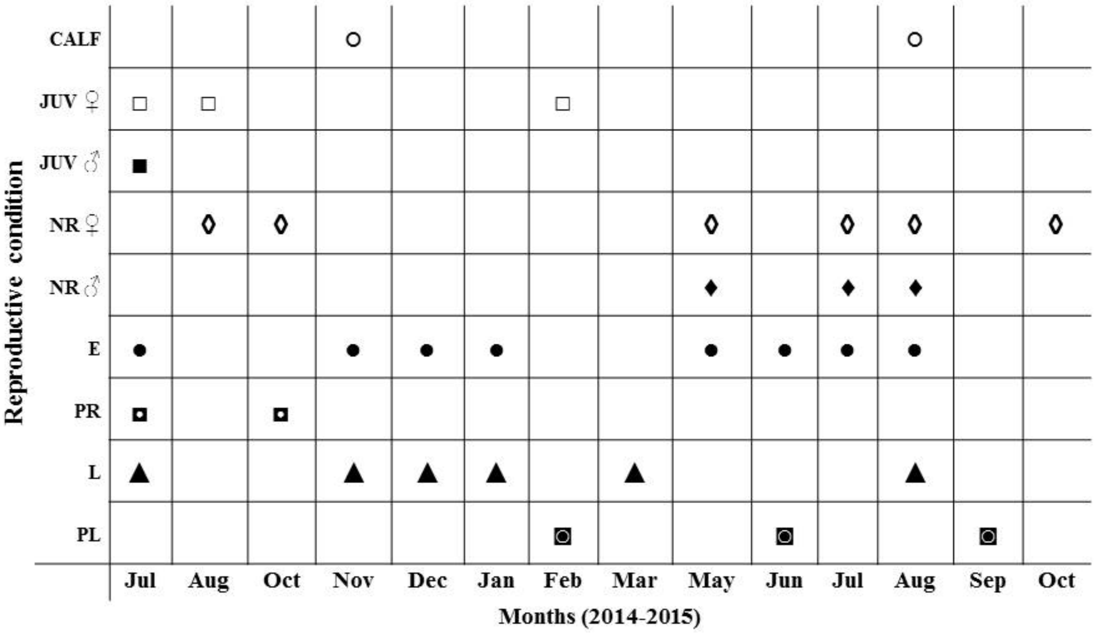

Fig. 1. Reproductive conditions of the captured individuals from July 2014 to October 2015 in Catimbau National Park, Pernambuco and Lajes, Rio Grande do Norte, northeastern Brazil (n=62).

Roost

A colony of around 20 individuals of *X. vieirai* (Fig. 2e-f) were found in a cave (marble lithology) located at Fazenda Santo Antônio in the municipality of Lajes (RN). It is a medium-sized cave with multiple entries (at least 5 of different sizes), which makes it a very ventilated and bright cave. The colony was roosting in an open and illuminated area of the cave. *X. vieirai* shared the cave with at least five other bat species – *Artibeus planirostris, Glossophaga soricina*, and *Tonatia bidens* (Phyllostomidae); *Peropteryx macrotis* (Emballonuridae); *Furipterus horrens* (Furipteridae). This cave was visited monthly, but individuals of *X. vieirai* were only observed during the months of August and October. In the CNP (PE) diurnal roosts were not found.

Diet

After inspecting 17 feces samples, 70.5% had pollen grains and 47% had what was categorized as "other plant material", which could not be properly identified. No insect remains nor pulp and peels were found in the feces samples.

Eighteen microscope slides with pollen samples from the bat's body were analyzed, from which nine pollen types were identified (Fig. 3). *X. vieirai* feeds on at least one species of columnar cacti, *Pilosocereus pachycladus* (in 17 samples), one species of shrubby cacti, *Pilosocereus gounellei* (5) and one species of globular cacti, *Melocactus zehntneri* (7). The other pollen types identified are *Cleome spinosa*, Cleomaceae (3 samples), *Encholirium spectabile*, Bromeliaceae (2), *Ipomoea sp.*, Convolvulaceae (2), *Pseudobombax sp.*, Malvaceae (2), *Dicliptera sericea*, Acanthaceae (1), and finally a monocot unidentified.

Fig. 2. *Xeronycteris vieirai*. a) Close-up of an adult male. b) Hairless forearm. c) Hanging adult female, d) Adult female with calf. e-f) Colony in a cave.

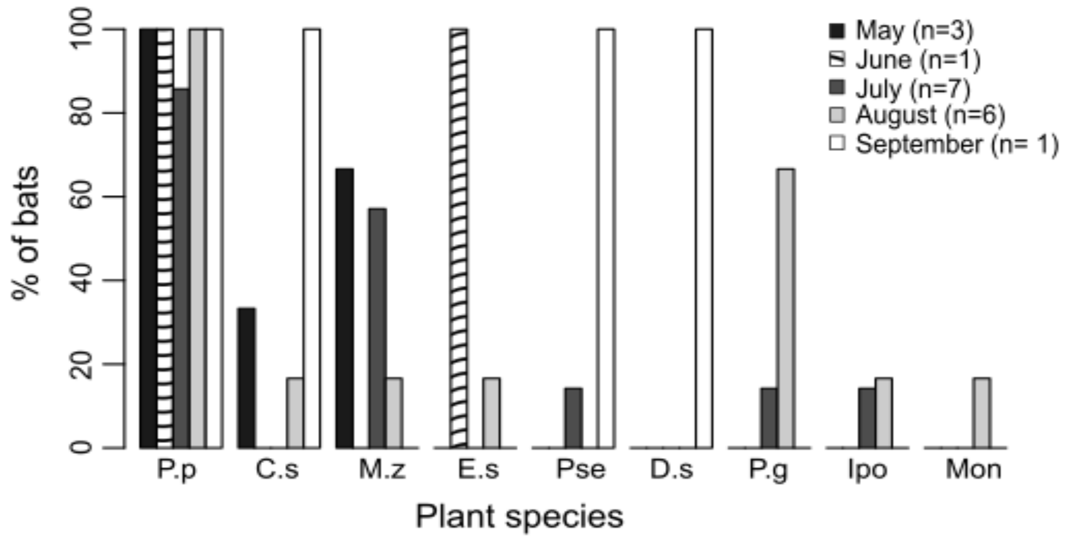

Fig. 3. Percentage of *Xeronycteris vieirai* individuals with pollen types found monthly in their fur. Pollen types: P.p: *Pilosocereus pachycladus,* C.s: *Cleome spinosa*, M.z: *Melocactus zehntneri*, E.s: *Encholirium spectabile*, Pse: *Pseudobombax sp*., D.s: *Dicliptera sericea*, P.g: *Pilosocereus gounellei*, Ipo: *Ipomea sp.,* Mon: Monocot.

Ectoparasites

Ectoparasitic flies from the Streblidae family (Diptera), genus *Tricobius*, were collected. From the 28 captured bats in CNP (PE), 24 were infested by *Trichobius* sp. resulting in a prevalence of 85.7%. Females were less parasitized (88%) compared to males (90%). The mean intensity infestation was 4.6 flies per host, ranging from 1 to 20. The aggregation was 0.46 (Poulin's discrepancy index).

Distribution and range extension

This is the first record for the species in the Caatinga of Rio Grande do Norte in Northeastern Brazil (Fig. 4), it represents the new northern end of the distribution of the species. The nearest locality where the species was captured previously is where the holotype was collected, in Fazenda Espírito Santo, municipality of Soledade state of Paraíba (07°05 S, 36°21 W). It is located at about 145 km in a straight line from the new records sites presented here. We also present here a new record for the Catimbau National Park in Pernambuco.

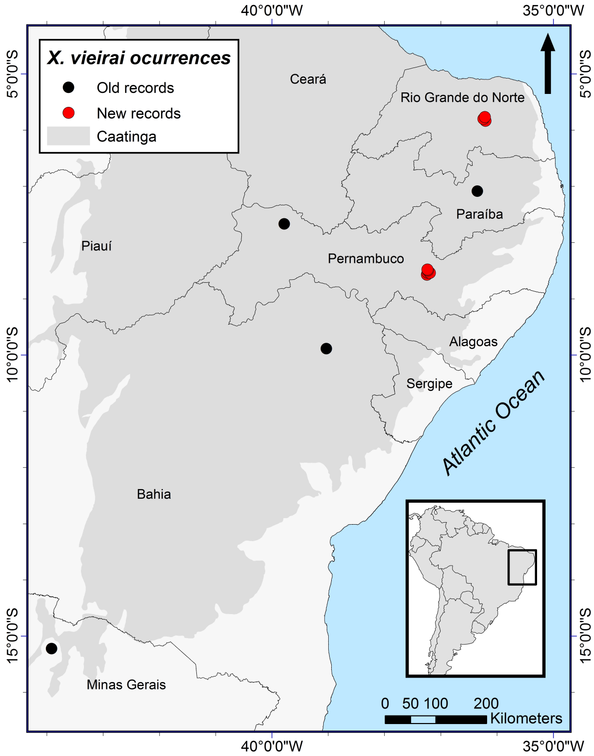

Fig. 4. Map of recorded localities for *Xeronycteris vieirai*, including old and new records (this study) all in Caatinga, Brazil.

DISCUSSION

The capture of these 62 individuals represent the fieldwork with the highest number of captures for the species so far. The Caatinga vegetation, where *X. vieirai* was captured is characterized as a tree or shrub forests, comprising mainly low shrubs and trees many of which have thorns, small leaves and some xerophytic characteristics. It is also characterized by having plenty of succulent plants, mainly from the Cactaceae and Bromelaceae family (Prado, 2003). The sampled sites where most of the individuals were captured presented high abundance of the columnar cacti, *Pilosocereus pachycladus* F. Ritter*, Cereus jamacaru* DC. and the shrubby cacti *Pilosocereus gounellei* (F.A.C. Weber) Byles and Rowley*,* also less abundant but considerably numerous are two species of bromeliads, *Bromelia laciniosa* Mart. Ex Schhult and Schult. f. and *Encholirium spectabile.*Mart. Ex Schhult and Schult. f. *Xeronycteris vieirai* presented two peaks of activity, with most pronounced in the first hour after the beginning of the catch. This pattern was also observed in *G. soricina*, another nectarivorous bat (La Val, 1970; Aguiar and Marinho-Filho, 2004).

This intense activity in the early hours after sunset can be related to the competition for the food resources (e.g., Heithaus *et al*., 1975; Pedro and Taddei, 2002), in addition to the extended period of fasting which bats are exposed (e.g., Thies *et al*., 2006). Moreover, factors such as climatic conditions, predation risk, and endogenous causes (e.g., Morrison, 1978; Erkert, 1982; Lee and McCracken, 2001; Thies *et al*., 2006; Stevens, 2013) may also interfere with this behavior. In this way, many factors linked to bat ecology can be elucidated with information about its activity and interaction with the environment (Pianka, 1969).

Other nectarivorous bat species were captured in the same sites where we recorded *X. vieirai – Anoura caudifer*, *G*lossophaga *soricina*, and *Lonchophylla* sp. in CNP, and *G. soricina*, *Lonchophylla sp*. and *Lionycteris spurrelli* in Lajes. The floral resources available in the sampled sites may be allowing the coexistence of these species (Fischer, 1992; Tschapka, 2004).

We thought that the decline in the number of captured individuals in the last two sampling months could be related to precipitation rates and resource availability. With two defined seasons throughout the year, the rainy season (4-6 months) and dry season (8-6 months) that vary in length depending on the year, the Caatinga shows variation in the availability of floral and fruit resources (Machado *et al.,* 1997). For animals and plants to be able to live under these conditions it often involves adaptations. In the case of mammals in Caatinga no pronounced physiological adaptations have been found, but adaptations and changes in the behavior of small and medium-sized mammals have been reported (Albuquerque *et al.,* 2012). In other groups of animals for example, in some species of birds (Ruiz-Esparza *et al.,* 2011; Las-Casas *et al.,* 2012.), moths (Junior and Schlindwein, 2005) and bees (Freitas *et al.*, 2007); another kind of adaptation has been demonstrated: local migration (short distance) within the Caatinga ecosystem. This could be the case for *X. vieirai*. Nonetheless, to be able to have a proper conclusion about this, a long-term study with the species population should be done.

The capture of the female with her calf in August and November may suggest that during these months resource options had good quality and were not scarce. It has been documented that lactating and pregnant females have special nutritional requirements (amino acids, calcium and proteins) that they manage to obtain by including other feeding resources such as fruits, insects or even pollen (Tschapka, 2005). The dry season in Caatinga goes from June to December (Machado *et al.,* 1997). Previous phenology studies in Caatinga observed that flowering at community level occurred through the year, but showed a peak early in the rainy season, this way pollinators may have a continuous supply of flowers, but they are reduced to a few species of plants during the dry season (Machado *et al.,* 1997). Post-lactating females captured in July and males with obvious scrotums from May to August suggest that a breeding period of the species occurs during the period of the year when the transition between the rainy and the dry season are taking place.

The colony of *X. vieirai* was observed in the cave only in August and October, suggesting that this species changes roosts momentarily, which could be related to the availability of food resources, maybe due to short distance migrations, as commented previously. However, this cave is visited by humans as trash and remains of old campfires were found on the inside as well as drawings and graffiti on its walls, these factors could also have caused the momentary abandonment of roost.

August was the month where the captured individuals of *X. vieirai* presented the highest number of pollen types, followed by July (Fig. 3). No insects, seeds nor pulp were observed in their feces. Nonetheless, pollen was observed in most of the feces samples indicating they could complement their diet with this item but not necessarily in relation to their reproductive stage. Pollen in feces was observed in both male and females not been reproducibly active.

The "plant material" found in 47% of feces samples raised speculations regarding the diet of *X. vieirai*. This plant material could be part of leaves, part of the cactus flowers (pericarp) or even part of cacti skin. Being a repetitive element in several feces suggests that it is not an accidental event and that these bats could be using some of these suggested plant parts to supplement their nectarivorous diet. On the other hand, no insect remains, nor seeds or pulp was found in their feces. As mentioned by Gregorin and Ditchfield (2005) the lingual characters and the extreme reduced dentition of Vieira's Flower Bat, could indicate that the species may have a predominantly liquid diet, such as nectar, as opposed to the other glossophagines that are known to have the capability to complement their diet with insects and fruit in addition to nectar.

The pollen types found in *X. vieirai*'s fur indicated central species for its diet. From May to September the main feeding resource was the columnar cacti *P. pachycladus*. Neotropical semiarid and arid lands are especially rich in bat-pollinated species and previous research in semiarid regions of Mexico and South America indicated that certain species of columnar cacti depend heavily on pollination by one or more species of phyllostomid bats (Valiente-Banuet *et al.,* 1996; Meffe, 1998). Two other species particularly captured our attention. *Melocactus zehntneri* due to its small size and globular habit and the fact that the only known pollinators so far are hummingbirds (Rocha *et al.,* 2007) and *P. gounellei* which is a shrubby cacti know to be visited and pollinated only by hawkmoths. Rocha *et al.* (2007) discussed that bats were not observed visiting this flowers due to the fact that *P. gounellei*'s flowers have a less pronounced odor, produces less nectar and have a narrower and elongated floral tube in comparison to other *Pilosocereus* species in a Caatinga area. Apparently, *X. vieirai* has a snout and tongue long enough to access the nectar of *P. gounellei* in comparison to other nectar-feeding bats in Caatinga. Finally Rocha *et al.,* (2007) mentioned that *P. gounellei*'s flowers are sometimes very close to the ground making their access by bats difficult. The fact that *X. vieirai* is feeding on flowers of *M. zehntneri* and *P. gounellei* indicates that it is a species that has the ability to fly near to the ground. The other plant species that appeared in *X. vieirai*'s fur have already been documented to be visited by other nectar-feeding bat species. *Cleome spinosa* Jacq., actually *Tarenaya spinosa* (Jacq.) Raf., is pollinated by *Glossophaga soricina* and *Phyllostomus discolor* (Machado *et al.,* 2006). *Encholirium spectabile* Mart. ex Schult. & Schult.f., recently reported presenting mixed pollination between bats, opossums, and hummingbirds (Queiroz *et al.,* 2016). The genus *Ipomoea* L. and *Pseudobombax* Dugand both are known to be pollinated by bats as well (Gribel and Gibbs, 2002; Queiroz *et al.,* 2015). Finally, *Dicliptera sericea* Ness, actually *Dicliptera squarrosa* Nees, is a species known to be pollinated by hummingbirds (Murcia and Feisinger, 1996), nonetheless other Acanthaceae species with similar characteristics as *Dicliptera* Juss. has also been reported to be visited by bats (Vogel *et al.,* 2004; Tripp and Manos, 2008). All the species of plants reported here represent the first insights of *X. vieirai*'s diet.

In Brazil, *Trichobius* is the genus with the highest number of species (n = 26) in Streblidae family (see Graciolli, 2015). This genus consists of several species complexes (see Dick and Graciolli, 2008), many of them difficult to taxonomic distinction. *Trichobius* sp. collected on *X. vieirai* belongs to the "*dugesii*" complex, which is composed of 12 other species. In fact, the species resembles *T. dugesii*, primary parasite of *G. soricina*. However, the main differences are in the bristles pattern of the occipital lobes and mesonotum, and in the size of the antescutellar setae row. Morphological studies with specimens collected from different regions can elucidate questions about regional variations or even cryptic species.

Trichobius sp. had high indices prevalence and mean intensity infestation in this study. Studies with *Trichobius* spp. in other environments (e.g., Atlantic Forest and Cerrado) have not found values of prevalence above 60% and mean intensity infestation greater than 3.5 (e.g., Komeno and Linhares, 1999; Bertola *et al*., 2005; Eriksson *et al*., 2011; Santos *et al*., 2013). In order to determine if this is a pattern to Caatinga, further studies involving bats and ectoparasitic flies must be developed.

The distribution range extension presented here is the new northern end of the distribution of the species, representing a range extension at a sub national level (Rio Grande do Norte state) and a new record of bat species for the Catimbau National Park in Pernambuco.

In order to establish conservation strategies and to understand the role of *X. vieirai* in this unique Brazilian habitat, it is important to know the species basic requirements such as roosts and the food resources they depend on, as well as their distribution. This paper represents one step closer to accomplishing this.

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SUPPLEMENTARY MATERIAL 1

Data on feces samples collected from bats during the sampling period (May-October).

Each captured bat was inspected in search of fruit remains or seeds in the mouth and body. If found, they were deposited in microtubes for further identification. Because bats have a fast transit time of food ingestion-defecation (Dumont, 2003; Muscarella and Fleming, 2007), each bat was kept in a cloth bag for a maximum time of 30 min to obtain fecal samples. Fecal samples were placed in Eppendorf tubes for preservation and subsequent analysis. The contents of each fecal sample were categorized by the presence or absence of seeds, pollen, plant material, pulp-peels, insects and unidentifiable content with a stereoscope (Olympus sz40 Zoom 6.7-40x).

A total of 70 feces samples belonging to six bat species have been collected and analyzed (Fig. 1). In relation to the seeds found in the samples, the identification of what appeared to be pieces of a larger seed in the feces of *P. discolor* was not possible, to overcome the doubt if they were pieces of a larger seed or small seeds, they were placed to germinate without getting any success (Fig. 2a). On the other hand the seeds found in the feces of *Artibeus planirostris* was identified as *Pilosocereus pachycladus subsp. pernambucoensis*, Cactaceae (Fig. 2c).

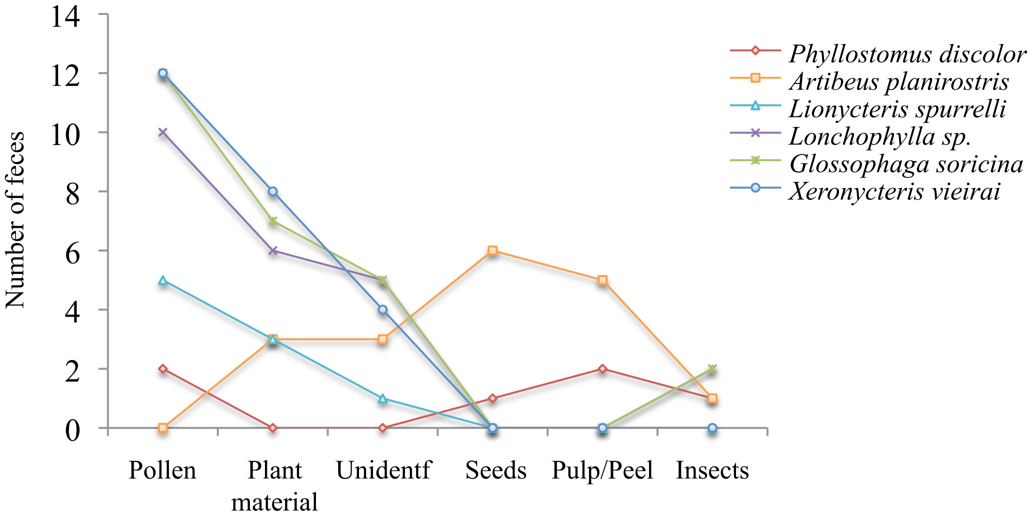

Fig 1. Food items found in 70 feces samples of six species of bats captured from May to July in Lajes, Rio Grande do Norte.

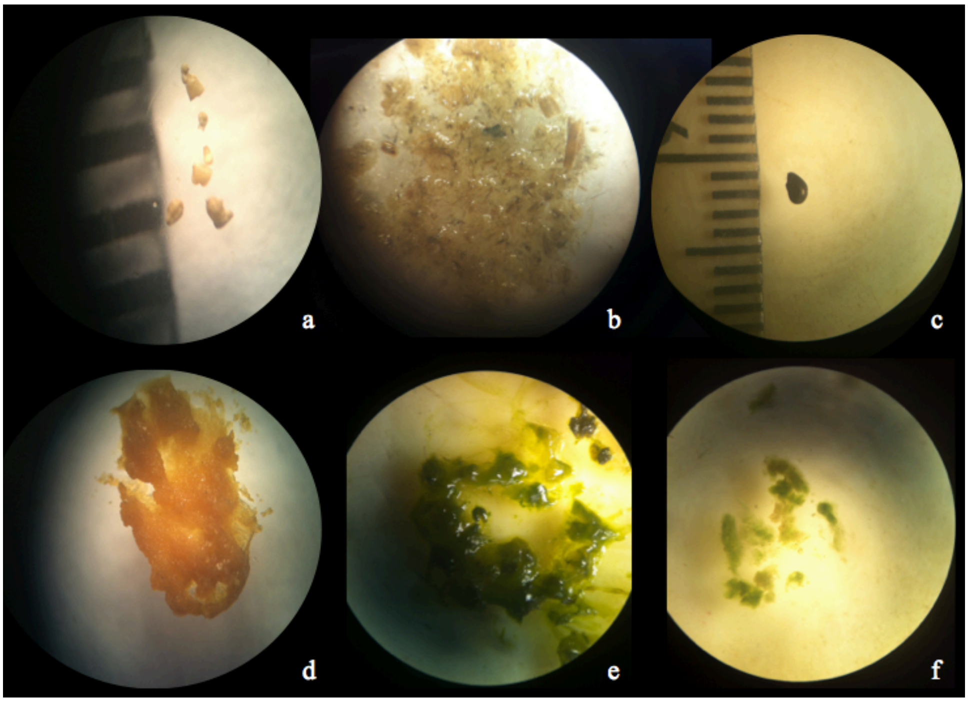

Fig. 2 Feces samples in stereoscope. a) Seed pieces, *P. discolor.* b) Pulp and vegetal material, *P. discolor.* c) Facheiro seed, *A. planirostris.* d) Pollen, *L. spurrelli.* e) Plant material, *X. vieirai.* f) Plant material, *Lonchophylla sp.*

In sampling Site 2 (Fazenda Santo Antonio), a group of six *Artibeus planirostris* were observed in their roost (cave), during the three months of sampling. A detailed search of seeds was made beneath their roosting site. More seeds of Facheiro cacti were found. Also several empty shells of *Prosopis juliflora* (Algaroba) were found. It was not possible to determine if *Artibeus planirostris* predated the seeds or just the fruit and after dropping it, secondary predation of seeds happened.

In relation to the four nectar-feeding bats species, speculations were raised about the “plant material” found in 45% of feces samples. This plant material could be part of leaves, part of the cactus flowers (pericarp) or even part of cacti skin. Being a repetitive element in several feces suggests that it is not an accidental event and that these nectar feeding bats could be using some of these suggested plant parts to supplement their nectarivorous diet (Fig.1, Fig. 2 e,f). None of this has been documented in the literature; we were not able to properly identify this vegetal material.

SUPPLEMENTARY MATERIAL 2

Precipitation data Provided by the Prefecture of the Municipality of Lajes, RN and EMPARN (Empresa de Pesquisa Agropecuária do Rio Grande do Norte). No information was provided on the equipment used for the measurements.
* = Field sampling days

Precipitation Data

Municipality of Lajes / EMPARN

DAY	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT
1	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
2	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
3	0,00	0,00	0,00	0,00	5.00	0,00	1.0	0,00	0,00	0,00
4	0,00	0,00	0,00	0,00	0,00	0,00	*0,00	0,00	0,00	0,00
5	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
6	0,00	0,00	0,00	29.0	0,00	0,00	4.3	0,00	0,00	0,00
7	0,00	0,00	0,00	3.3	0,00	0,00	0,00	0,00	0,00	0,00
8	0,00	0,00	0,00	51.2	0,00	0,00	0,00	0,00	0,00	0,00
9	0,00	0,00	10.07	0,00	*0,00	0,00	0,00	0,00	0,00	0,00
10	0,00	0,00	0.0	0,00	*0,00	0.0	0,00	0,00	0,00	0,00
11	0,00	0,00	0,00	0,00	*0,00	0,00	0,00	0,00	0,00	0,00
12	0,00	0,00	0,00	0,00	*0,00	0,00	0,00	0,00	0,00	0,00
13	0,00	0,00	0,00	0,00	*0,00	0,00	0,00	0,00	0,00	0,00
14	0,00	0,00	0,00	0,00	0,00	0,00	*0,00	0,00	0,00	* 0,00
15	0,00	0,00	0,00	0,00	0,00	0,00	*0,00	0,00	*0,00	*0,00
16	0,00	0,00	0,00	0,00	0,00	0,00	*5.6	0,00	*0,00	*0,00
17	0,00	0,00	0,00	0,00	0,00	*0,00	*5.3	0,00	*0,00	*0,00
18	0,00	8.4	0,00	0,00	0,00	*0,00	*0,00	0,00	*0,00	*0,00
19	0,00	0,00	1.6	0,00	0,00	*0,00	0,00	*0,00	*0,00	0,00
20	0,00	5.6	0,00	0,00	0,00	*0,00	0,00	*0,00	0,00	0,00
21	0,00	0,00	10,00	0,00	0,00	*0,00	0,00	*0,00	0,00	0,00
22	0,00	0,00	10,00	0,00	0,00	0,00	0,00	*0,00	0,00	0,00
23	0,00	0,00	36,4	0,00	0,00	0,00	0,00	*0,00	0,00	0,00
24	0,00	0,00	0,00	18.2	0,00	31.04	0,00	0,00	0,00	0,00
25	0,00	10.8	0,00	2.1	0,00	0,00	0,00	0,00	0,00	0,00
26	0,00	15.2	0,00	0,00	0,00	3.2	0,00	0,00	0,00	0,00
27	0,00	0,00	0,00	0,00	0,00	0,00	1.4	0,00	0,00	0,00
28	0,00	0,00	0,00	0,00	0,00	0,00	4.5	0,00	0,00	0,00
29	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
30	0,00	0,00	0,00	0,00	0,00	0,00	1.4	0,00	0,00	0,00
31	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
TOTAL (mm)	**0,00**	**40,00**	**68,7**	**103,8**	**5,00**	**34.24**	**23.5**	**0,00**	**0,00**	**00.0**

Natal, RN, 2016