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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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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 hypotheses for bats suggest this behavior provides a dietary supplement of protein and other essential minerals due to a deficiency of these in a frugivorous diet. The Caatinga is a seasonally deciduous tropical dry forest where most of the vegetation is leafless and dormant during the extended dry season. Here we present the first evidence of folivory in bats from the Brazilian Caatinga, with evidence for the phyllostomid *Artibeus planirostris* ingesting the leaves of at least 16 species of plants. We include a bibliographic review of bat folivory in the tropics. Additionally, we propose a new hypothesis on folivory in bats for this semiarid environment.

Key words: Phyllostomidae, caves, feeding habits, folivory, Pteropodidae, Caatinga

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 digest foliage. This ability 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 fractionation" (Kunz and Ingalls, 1994: 665).

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 several hypotheses for explaining this feeding strategy in different species (see Table 1), but notably, all are frugivores. 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 in a semiarid environment.

The Brazilian Caatinga consists of a semiarid region of 730,000 km^2 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 have an extreme climate. According to Köppen classification, the climate in the region is BShw (hot and dry), with a mean annual rainfall less than 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 Caatinga species, 12 are frugivorous. Nevertheless, this region is the most neglected Brazilian ecosystem in terms of the conservation, probably due to its semi-arid characteristics (Santos *et al*., 2011).

One of the species of bats present at the Caatinga is *Artibeus planirostris* — a species of fruit-eating bat that ranges from southern Colombia and southern Venezuela to northern Argentina and eastern Brazil at elevations from sea level to 1,660 m.a.s.l. (Hollis, 2005). In Brazil it inhabits forests and forest fragments ranging from moist Amazonian and Atlantic forests to xeromorphic areas in Caatinga and Cerrado (Reis *et al*., 2013). *Artibeus planirostris* roosts in hollow trees and caves in groups ranging from 5–40 individuals in a harem structure (Beguelini *et al*., 2013). This species has been characterized by its high diet plasticity; it feeds mainly on fruit, but also supplements its 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 Caatinga in two states, Bahia (BA) and Rio Grande do Norte (RN) in northeastern Brazil.

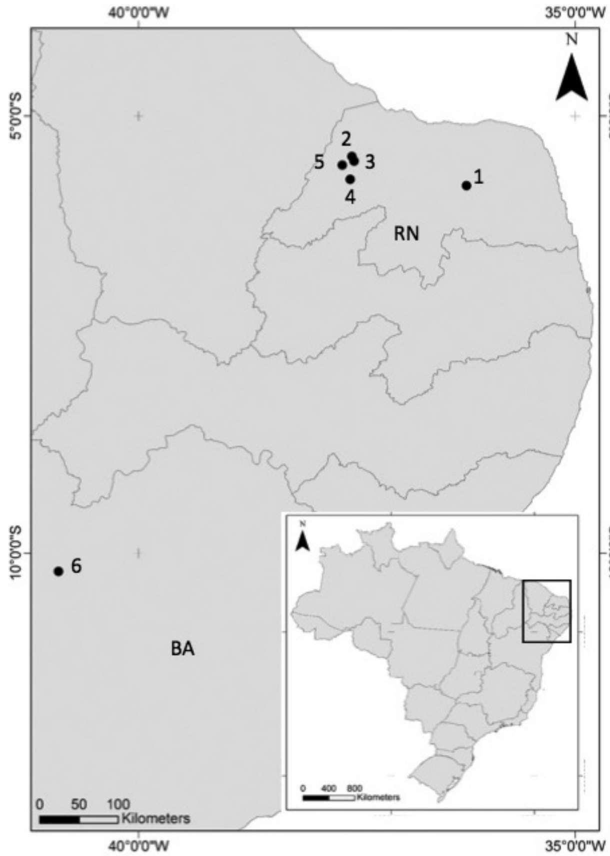

Fig. 1. Map of the six surveyed caves in this study located in the Caatinga biome: five in the state of Rio Grande do Norte 1 — Caverna do Serrote Preto, 2 — Caverna Lajedo Grande, 3 — Caverna da Pedrada, 4 — Gruta Casa de Homens, 5 — Caverna Carrapateira and one in the state of Bahia; 6 — Toca do Morrinho

Materials and Methods

We observed folivory in *A. planirostris* (Spix, 1823) in six caves at five municipalities (Fig. 1): Campo Formoso-BA (Toca do Morrinho), Lajes-RN (Caverna do Serrote Preto), 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 ranged from 51 to 120 individuals every day. We also made monthly visits to the Serrote Preto Cave from May to October 2015 where the colony was composed of at least six individuals that 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 sampled 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 to family level and six were classified as morphotypes.

To gather the hypotheses previously proposed, we conducted a bibliographic review on folivory in bats with which we identified habitats in which folivory has been documented and determined what type of information has been collected on this type of feeding behavior (e.g., casual observations, sustained observations, chemical analyses of plants). In this review we included both Old World fruit bats and New World leaf-nosed bats, and we synthesized 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'.

Results

Leaf pellets and partially eaten leaves occurred in samples from 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* during the reproductive period (pregnant and lactating females and appearance of scrotal testes in males) as well as 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 *C. 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 only at the base, leaving the apex intact.

Additionally, leaf pellets and partially eaten leaves were 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”W) and Toca da Barriguda (10°08’26”S, 40°51’08”W). Other records were stated in Toca do Pitu (10°07’44”S, 40°50’16”W) and Lapa do Convento (10°02’56”S, 40°43’37”W) and finally in Toca dos Ossos (10°55’51”S, 41°03’27”W). All observations were made under roosts at *A. planirostris* colonies, suggesting that this behavior was common and consistent in the area (from year 1991 to 2005). Unfortunately, leaves were neither collected nor identified at those caves; therefore, the data were not included in the map or discussion.

We found 17 references on folivory (including articles and notes) in the literature (Table 1), seven of which reported folivory in Old World bats and 10 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 (sustained observations).

Discussion

Several hypotheses have attempted to explain folivory in frugivorous 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 frugivorous bats; however, feeding on leaves is energetically more effective than feeding on insects — these bats are poorly adapted to insect capture, whereas leaves are abundant and easily accessed (Kunz and Diaz, 1995; Tan *et al*., 1998). This is the first report of folivory in a semiarid environment such as the Caatinga where water deficit during a large part of the year is a major factor that restricts the availability of vegetation. Resources such as fruits are supplied in pulses due to the limited and variable precipitation, therefore exerting adaptive challenges to both animals and plants (Chesson *et al*., 2004).

Herein, we would like to propose a 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). In the specific case of bats, water is gained by direct drinking, from food and by the production of metabolic water from the oxidation of nutrients (Bassett *et al*., 2009). Nonetheless, gained water is lost in several ways, by pulmonary and cutaneous evapotranspiration, urination and defecation and in females during lactation (Bassett *et al*., 2009). In environments characterized by high temperatures and low relative humidity bats may lose as much as 15–30% of their body mass through evaporative water during diurnal roosting; replenishment of part of this water can be achieved by drinking in water sources (Adams and Thibault, 2006) or by ingesting water rich fruits (Studier *et al*., 1983). However in this semiarid region of Caatinga, free water and fruit sources are scarce in dry season forcing frugivorous bats to obtain water in leaves.

In the literature it is clear that in the Brazilian Caatinga 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. During the transition from the rainy to the dry season (May–October), we observed that

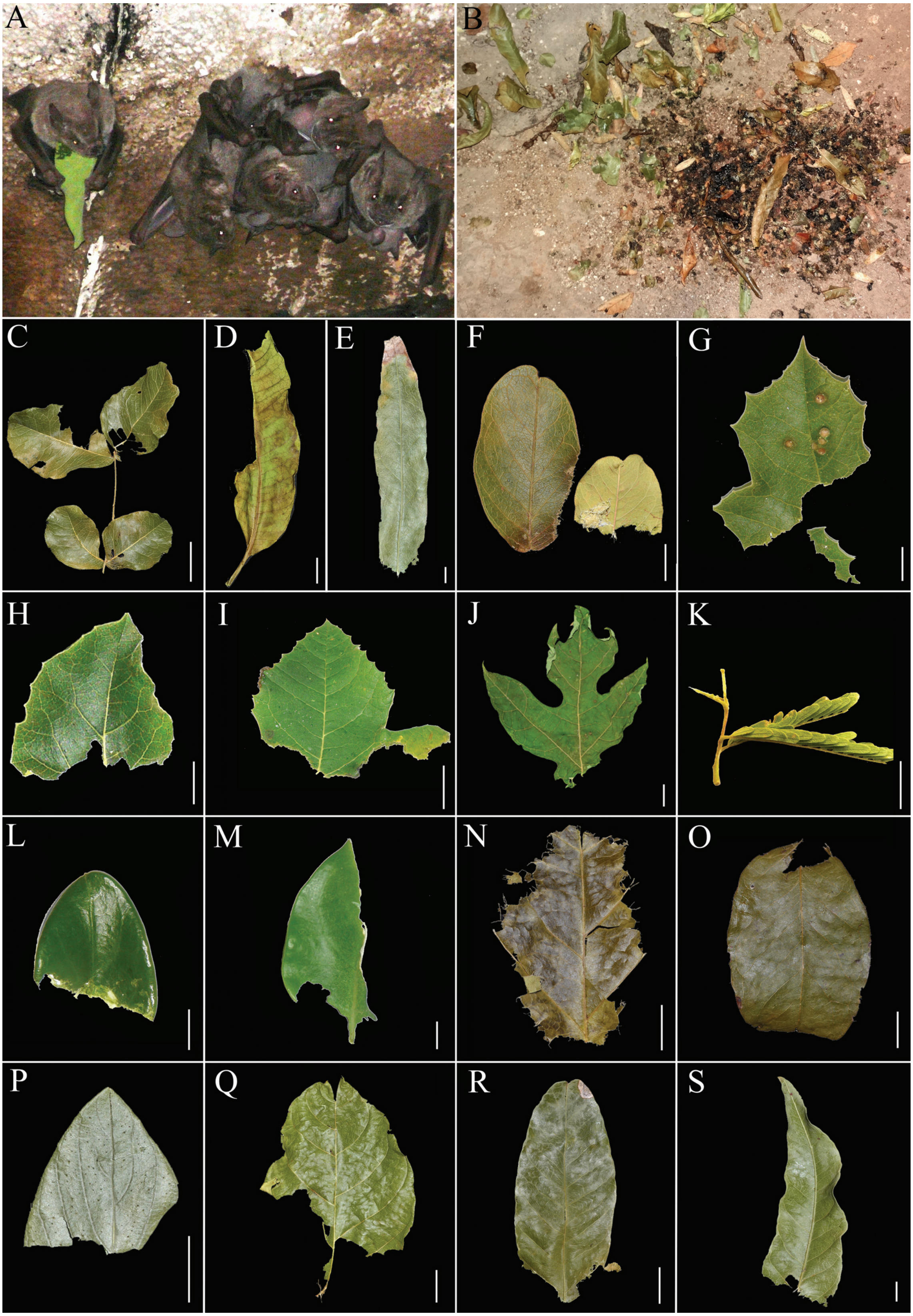

FIG. 2. Folivory evidence: A — *Artibeus planirostris* eating a leaf in Toca do Morrinho; B — Partially eaten leaves and dry leaves pellets below the roosts in Gruta Casa de Homens; C — *Poincianella* sp.; D — Immature leaf of *Mangifera indica*; E — Mature leaf of *M. indica*; F — *Cynophalla hastata*; G — Euphorbiaceae sp.[1]; H — Euphorbiaceae sp.[2]; I — Euphorbiaceae sp.[3]; J — *Carica papaya*; K — *Prosopis juliflora*; L — Moraceae sp.[1]; M — Moraceae sp.[2]; N — Morphotype1; O — Morphotype2; P — Morphotype3; Q — Morphotype4; R — Morphotype5; S — Morphotype6. Scale bar: 1 cm

leaves are an abundant and potential food choice, but the question remains whether or not this is a year-round nutritional strategy of *A. planirostris* populations given the loss of leaves by most plants in the Caatinga during the long dry season and also during the wet season when more fruits are available.

Apparently, most of the bat species that feed on leaves would be using this resource in a seasonal

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

Bat species	Type of habitat	Type of information	Hypothesis	Remarks	Reference
Old World fruit bats					
Cynopterus brachyotis	Disturbed lowland dipterocarp forest, University campus, Malaysia	Sustained observations	Dietary complement of protein, minerals and steroids	Fruits provide an energy source (carbohydrates) to phytophagous bats, and leaves a source of protein, minerals, and steroids	Tan *et al*. (1998)
C. brachyotis	Disturbed lowland dipterocarp forest, Malaysia	Chemical analyses of leaves	(1) Dietary supplement of protein and calcium* (2) Supply 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)
C. 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 the bat	Ruby *et al*. (2000)
C. sphinx	University campus, Madurai, India	Behavior	Supply protein, minerals and nutrient demands during pregnancy and lactation	Temporal differences in nightly foraging behavior. First, water and carbohydrate (fruits), then protein and minerals important for reproduction from leaves (later hours of the night) of the night)	Elangovan *et al*. (2001)
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)
Pteropus samoensis, *P. tonganus*	Islands of Savai'I in Western Samoa and Tutuila and Ofu in American Samoa	Behavior	(1) Dietary complement of protein (2) 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)
Pteropus samoensis, *P. 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. They are rich in zinc, manganese and calcium	Nelson *et al*. (2005)
New World fruit bats					
Artibeus amplus	Andes, Venezuela	Sustained observations	Non-seasonal phenomenon	Nutritional role of some leaf species consumed all year round	Ruiz-Ramoni *et al*. (2011)
A. concolor	Neotropical rain forest, Brazil	Casual observation	(1) Dietary complement of protein (2) Supply protein demands during pregnancy and lactation	Folivory is supplementary source of protein, especially during reproductive stages	Bernard (1997)

TABLE 1. Continued

Bat species	Type of habitat	Type of information	Hypothesis	Remarks	Reference
A. jamaicensis	Rain forest, Puerto Rico	Sustained observations	(1) Leaves provide micronutrients and vitamins not available in fruits; (2) Insures rich-protein diet for males to reduce cost of harem defense; (3) Supply protein demands for females during pregnancy and lactation; (4) Harem males takes metabolites of leaves that stimulates reproduction activity; (5) Females takes metabolites from leaves as hormones precursor for reproduction timing; (6) Individuals select low metabolite leaves which at higher concentrations could inhibit food digestion	Folivory may be common and widespread among frugivorous bats, because fruits are low in protein	Kunz and Diaz (1995)
A. fimbriatus	Atlantic forest, Brazil	Sustained observations	Dietary complement of protein	Maintenance of protein balance	Esberard *et al*. (1998)
A. lituratus	Atlantic forest, Brazil	Sustained observations	Dietary complement of protein	Folivory among frugivorous phyllostomids is due to protein deficiency; insect's protein is eaten only occasionally	Zortéa and Mendes (1993)
A. lituratus	Atlantic forest, Brazil	Casual observation	Dietary complement of protein	Bats get proteins from other food sources, such as insects and leaves	Passos and Passamani (2003)
A. lituratus	Atlantic forest (urban area), Brazil	Sustained observations	(1) Useful energetic resource (2) Potential detoxifying effect	Leaves are energetic resource in low fruit rich habitats as in urban areas. Potential detoxifying effect because of type of plant consume registered in the study	Novaes and Nobre (2009)
A. lituratus	Cerrado (urban area), Brazil	Behavior	(1) Dietary complement of protein (2) Supply 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 and Cunha (2010)
Platyrrhinus lineatus	Atlantic forest, Brazil	Sustained observations	Dietary complement of protein	Maintenance of protein balance	Zortéa (1993)
P. lineatus	Cerrado, Brazil	Sustained observations	Dietary complement of protein	Leaves have high nitrogen-rich (protein) content that supplements their low-protein fruit diet. Females protein resource before reproduction period	Aguiar (2005)
Artibeus planirostris	Caatinga, Brazil	Sustained observations	Water supply due to scarcity of fruits and water	The Caatinga has long periods of scarcity of fruits and drinkable water during dry season	This study

* — Tested hypothesis

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 *C. papaya* and *M. 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 of 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 *C. papaya*, *M. indica* and *P. 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 suggests 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 on a Pantropical scale, both in the Paleotropics (pteropodids) and Neotropics (phyllostomids) (Table 1). However, the occurrence of folivory is not exclusive to lowland 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 Trinidad. Years later, Tuttle (1968) found beneath an *A. 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.

Folivory has been documented in five species of phyllostomid bats of the genus *Artibeus*: *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). 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. Thus half the known species of this genus practice folivory. The species of known folivores are common and easily observed and thus have produced most of the known data on folivory. The other six, less common, may also be folivores, and should be subjected to further research. There is only one report of folivory in another genus, *Platyrrhinus lineatus* (Zortéa, 1993; Aguiar, 2005). Data gathered herein suggests that leaves are a recurrent food option for bats at least within this genus. We believe that multiple factors determine the use of leaves as a dietary item for *A. planirostris*. The most important factors in the Caatinga environment are likely related to nutrient supplements and water stress. However, detailed studies are necessary to determine water content in the leaves of species eaten by *A. planirostris*, as well as analyses of chemical and nutrient composition, to better understand folivory in bats in this semiarid environment.

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