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FEEDING AND POTENTIAL SEED DISPERSION BY BATS AT VALE DO TABOCAS FARM, A CLOUD FOREST ENCLAVE IN THE BRAZILIAN CAATINGA

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Abstract: This study investigated the feeding patterns of fruit bats in a fragment of cloud forest enclave located in the Brazilian semiarid Caatinga and evaluated the role of bat species as potential seed dispersers. Bats were captured with mist nets during six nights each month between April 2015 and March 2016, and fecal samples were collected for content analysis. The physical integrity of the seeds was also confirmed by observing broken and intact seeds. A total of 703 bat specimens belonging to the family Phyllostomidae, including nine genera and 12 species, were captured during the fieldwork. At least 50 species of fruit-bearing plants that can be used by bats were identified, which together fruited for 12 months. Among the fruit bats, 512 fecal samples were found, of which 466 contained fruits, 44 contained insects, and two contained pollen grains. An analysis of fecal samples indicated a predominance of fruits with endozoochorous seeds (80%) in the bats' diet, which explored at least 31 different items, primarily from pioneer plants such as *Ficus*, *Cecropia*, and *Solanum*, even when other food sources were available. There was significant variation among bat species in the consumption of different items, except for the three *Artibeus* species, which had similar diets. Only 23 of the 243 (approximately 10%) fecal samples analyzed here contained damaged seeds; only one broken seed was found in each sample. The consumption of fruits from diverse plant species, the production of mixed seed rain, the release of intact seeds, and the predominance of fruits with endozoochorous seeds in the bats' diet reflect the importance of the frugivorous guild for the reproduction of diverse plant species. The concentration of the diet on fruits of pioneer plants weighing less than 5 g, whose small seeds are ingested together with the pulp, reinforces their role in the restoration of degraded areas and, in turn, in the regeneration of cloud forest enclaves found in the Brazilian semiarid region.

Keywords: chiropterochory; cloud forest enclaves; diet; Phyllostomidae; pioneer species; zoochory

INTRODUCTION

The Neotropical zone is one of the most biologically diverse regions on Earth (Williams et al. 1997). The reproductive success of many Neotropical plant species is dependent on the ecological services provided by vertebrates, including bats, which feed on both nectar and fruit, and thus act as pollinators and seed dispersers (Ramírez-Fráncel et al. 2021, Florez-Montero et al. 2022). Fleming (1987) estimated that 50–90% of the woody plants of tropical forests are dispersed by animals and that 20–50% of the bird and mammal species that inhabit these forests consume fruit during at least part of the year. Zoochoric seed dispersal may enable the plant to reduce natural enemies, such as pathogenic fungi and seed predators, and reduce intraspecific competition for space in proximity to the mother plant, thereby facilitating the colonization of novel habitats (Fleming 1988). Zoochoric dispersal is also an essential mechanism of gene flow (Jordano et al. 2006) and determines the dispersal potential and geographic distribution of many plant species (Heithaus 1982, Altringham 1996).

Worldwide, approximately a quarter of the 1,500 existing bat species are known to be phytophagous (Bredt et al. 2012, Simmons & Cirranello 2025). One important group is the Neotropical bats of the family Phyllostomidae, which are known to play an important role in the seed dispersal of more than 500 plant species distributed in 68 families (Lobova et al. 2009, Florez-Montero et al. 2022) and, in particular, in the ecological succession of the vegetation in degraded areas (Muscarella & Fleming 2007, Bredt et al. 2012). At least 186 bat species occur in Brazil (Abreu et al. 2025, Garbino et al. 2024), and 22% of these species are known to feed on fruit (Bernard et al. 2012), ranging from exclusively frugivorous to opportunistic frugivorous, with diets including food items such as nectar, insects, and vertebrates (Mello 2007, Reis et al. 2017). In addition to this natural variation, the diets of these frugivorous bats may include resources obtained from commercial plantations (Hill & Smith 1984, Luz et al. 2015, Florez-Montero et al. 2022) and introduced species (Fabián et al. 2008, Bredt et al. 2012). The principal plant families exploited by frugivorous bats in South America include Fabaceae, Solanaceae, Moraceae, Piperaceae, Malvaceae, Myrtaceae, Arecaceae, Cactaceae, Urticaceae, and Sapotaceae (Fabián et al. 2008, Florez-Montero et al. 2022). The relative contributions of these different families to the diet of bats may vary considerably depending on the region and local conditions (Bredt et al. 2012).

The available evidence indicates that bats and birds may be responsible for up to 80% of seed dispersal in some forests and savannas (Galindo-González et al. 2000). These ecological services appear to be complementary, given that bats disperse primarily the seeds of pioneer plants, whereas birds tend to disperse more secondary and climax species (Muscarella & Fleming 2007).

In the scrub forests of the semi-arid Caatinga domain of northeastern Brazil, cloud forest enclaves, locally known as *brejos de altitude*, present a notable diversity of plants and animals, which are threatened by deforestation, illegal hunting and unregulated exploitation of water resources (Pereira Filho et al. 2020). These wetlands act as humid islands in the middle of an arid environment, with distinct ecological characteristics, including a milder climate, high humidity and high biodiversity, including endemic and relict species of Atlantic origin (Tabarelli et al. 2000). In addition to representing biogeographic refuges, wetlands play a fundamental role in ecological connectivity and in providing ecosystem services such as water regulation and carbon storage (Silva et al. 2017). However, these areas have historically been neglected in conservation policies, despite their importance for maintaining regional biodiversity.

Seed-dispersing organisms play a fundamental role in nutrient cycling in these environments, the recruitment of plants, and the succession of impacted habitats. These cloud forest enclaves are widely distributed in the Caatinga (Andrade-Lima 1982) and are typically found on high plateaus at altitudes of 500–1,100 m above sea level (Andrade-Lima 2007, Nascimento 2016). These enclaves are formed by a seasonal and semi-deciduous montane forest, which is typical of the Brazilian Atlantic Forest domain (Veloso et al. 1991). The composition of the vegetation reflects the past influence of the flora of the Amazonian domain (Prance 1982) and the Atlantic Forest of southern and southeastern Brazil (Andrade-Lima 1960, 1982), which is quite distinct from the Atlantic Forest of northeastern Brazil.

The analysis of zoochoric seed dispersal involves the assessment of a range of parameters, including the morphological and ecological characteristics of the animals, the fruit, and their seeds, together with climatic conditions, and the structure of local habitats. The efficiency of the process also depends on the dispersal distance, the viability of the seeds, and the characteristics of the habitat in which the seeds are deposited (Jordano et al. 2006). As frugivorous bats are known to adapt their feeding preferences to the local availability of fruit (Fleming 1986, Luz et al. 2015), the present study examined feeding patterns in terms of the characteristics of the fruit exploited by bats in a cloud forest enclave in the Caatinga, and the potential for seed dispersal (seed damage and viability). We used these data to evaluate the potential contribution of local bats to maintaining the plant community of this unique ecosystem.

MATERIAL AND METHODS

Study area

The study was conducted at Vale do Tabocas Farm (FVT: 08º14’52.58” S, 36º22’41.58” W), a farm in the municipality of Belo Jardim, state of Pernambuco, Brazil. The study area is adjacent to the Tabocas reservoir, which supplies Belo Jardim with drinking water during periods of scarcity. The local climate is hot and dry, with lower temperatures during the rainy season, which typically begins in April and lasts until August or September. The annual precipitation ranges from 650 mm to 1000 mm, while the mean temperatures exceed 23°C (CPRM 2008). The FVT has a total area of 204.3 ha, with altitudes ranging from 648 m to 1148 m above sea level (Figure 1), and is located within the Brazilian semi-arid zone. The area is covered with montane forest typical of a *brejo de altitude* of the Caatinga domain (Andrade-Lima 1982). In addition to some well-preserved areas of natural habitat, there are anthropogenic habitats, including orchards, farmlands, pastures, and secondary forests.

Bat capture

We divided the study area into three vegetation zones for the collection of bat specimens – (Site I) the most impacted zone, which included plantations, orchards, secondary forests, and disturbed forests, (Site II) an area of forest (riparian forest) surrounding springs and a stream; and (Site III) a small area of forest with orchards (Figure 1). We captured the bats over two consecutive nights per month in each zone, with a total of six nights of sampling per month between April 2015 and March 2016. We used 10 mist nets (12 m × 2.5 m, with a 36 mm mesh) each night, set up at distances ranging from 1 m to 200 m, depending on the availability of fruit in each area.

We set the mist nets just after sunset in the proximity of bodies of water, trails, open areas, and within the forest, as well as in the vicinity of fruiting plants, both cultivated and native, and inspected them at 20-minute intervals. We closed the nets after six hours, that is, at approximately midnight. We removed each bat captured from the net and placed it in an individual, numbered cotton bag until it defecated.

Once processed, we released the bats at the original capture site, except for a pair of individuals of each species, which were retained as voucher specimens and deposited in the reference collection of the Zoology Teaching Laboratory (LABEZoo) at the Federal University of Agreste of Pernambuco (UFAPE), located in Guaranhuns, Pernambuco, Brazil. We used the taxonomic keys of Gardner (2007) and Díaz et al. (2016) to identify the species. We verified the conservation status of each species by consulting the IUCN Red List (IUCN 2025) and

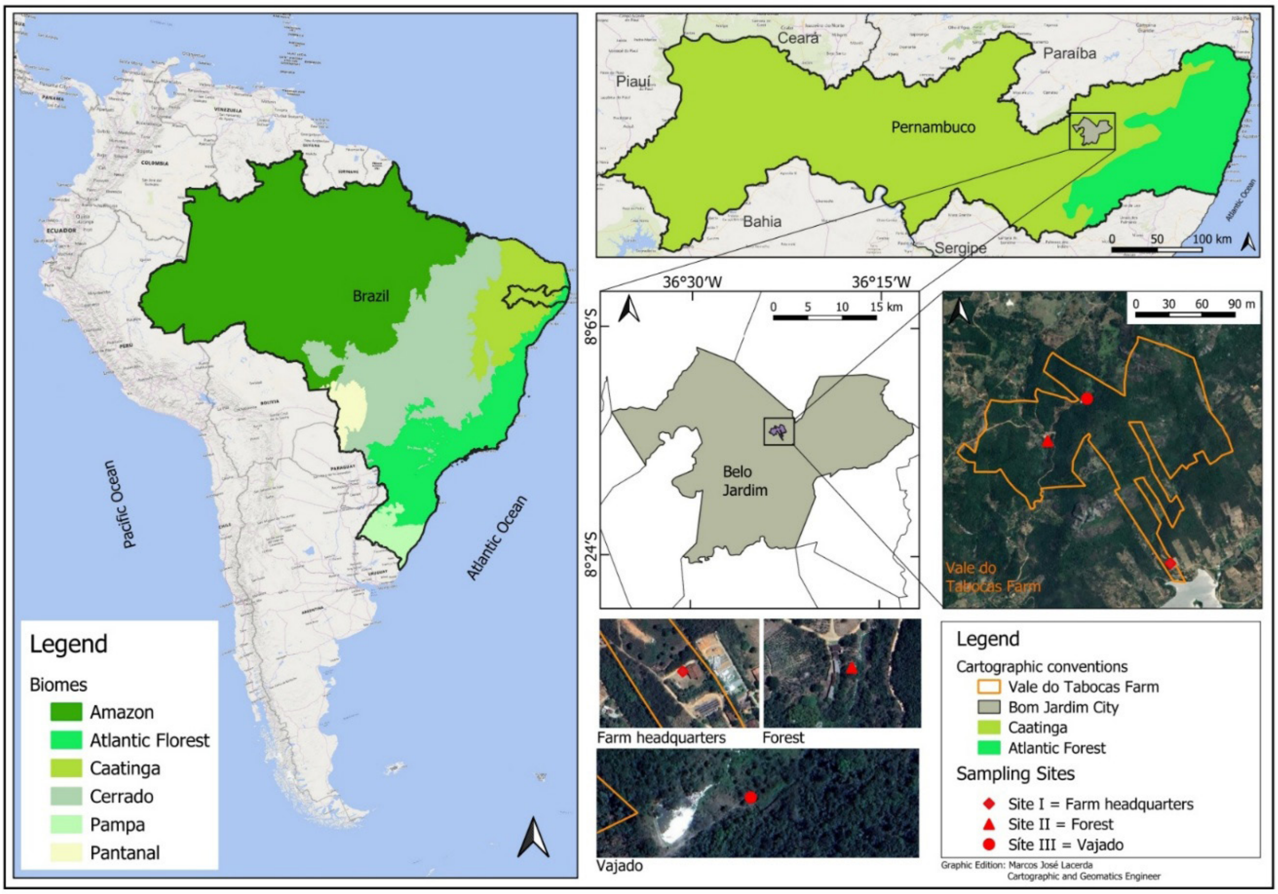

Figure 1. Map of the study area including the sample sites at the Vale do Tabocas Farm, located at Belo Jardim in the state of Pernambuco, Brazil, and the Brazilian biomes.

the Sistema de Avaliação do Risco de Extinção da Biodiversidade – SALVE (ICMBio 2025).

All handling protocols were approved by the Ethics Committee on the Use of Animals of the Federal Rural University of Pernambuco (CEUA, abbreviation in Portuguese; process #062/2016) in Recife city. All capture and collecting procedures were performed under permit number 49350-1, provided by the Sistema de Autorização e Informação em Biodiversidade – SISBIO of the Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio, Brazil.

Seed reference collection

We monitored the study area monthly for the identification of plants bearing fruit or flowers (the same plants were monitored monthly). Fruits suitable for bat consumption were collected, weighed with a dynamometer, and measured with a caliper (10 fruits per species when possible). Ripe fruits were collected from fruiting plants, below them, and attached to mist nets. The number and size of the seeds found in each fruit were also determined. We stored the seeds extracted from the sample fruits in paper envelopes, which were used as voucher specimens for the identification of the seeds found in the bat feces. All procedures described were performed in the field.

Composition of the diet

To identify the diet of the frugivorous bats, fecal samples from the individuals during handling and in the holding bags were collected for analysis. The fecal samples were removed from the cloth bags where the bats were kept and placed in paper bags labeled with the date and species of bat. The seeds were identified using a stereomicroscope (Yaxun Yx-ak11) and compared with a reference collection of seeds previously collected from fruits existing in the study area (Supplementary material Table

S2). The main fruits consumed by the bats were weighed and measured, their seeds were counted and measured, and their color and plant habits were observed (adapted from Fleming 1988). To standardize the analyses and facilitate comparisons among individuals, fruits were classified into three weight categories. Since there are no specific references for the species under study or widely accepted values in the literature (Almeida et al. 2015, De Salvador et al. 2006), a custom criterion was adopted based on the distribution of fruit weights observed in the sample. The fruits were classified as light (< 10 g), medium (11–50 g), or heavy (> 51 g). This categorization has an operational nature and aims solely to organize and enable the comparative interpretation of data within this study.

Seeds recovered from fecal samples, which passed through the bats' digestive tract, were classified as endozoochorous (Van der Pijl 1982, Bianconi et al. 2006). Conversely, the transport of fruits without seed ingestion was classified as synzoochorous (Van der Pijl 1982, Jordano 2000). Samples containing only *Mangifera indica* L. and *Syagrus* sp. fruit pulp were identified based on the coloration, texture, and odor of the material at the moment of defecation.

For analysis, the frequency of each species or type of seed was determined by the number of fecal samples in which it was identified (Passos et al. 2003, Tsukada et al. 2020). The samples were organized in a similar way when different types of fruit pulp were found in the feces. The records were organized by bat species and month.

To verify the viability of the defecated seeds, their physical condition (intact or damaged) was determined by examination under a stereomicroscope. The seeds were considered damaged when they were broken and intact when they were not broken.

Data analysis

We performed a multivariate Permutational Analysis of Variance (PERMANOVA) to evaluate differences in diet composition among bat species, considering bat species as the independent variable and the consumption of food items as the response variable. Analyses were based on a Bray–Curtis dissimilarity matrix constructed from abundance data (frequency of occurrence of each food item in fecal samples), with 9,999 permutations. We also applied a Similarity Percentage Analysis (SIMPER) to identify the food items that contributed most to the observed dissimilarities among bat species. All analyses were conducted using PAST, version 2.17c (Hammer et al. 2001). Additionally, a Chi-square test was used to compare the frequency of fecal samples containing pulp and seeds among bat species.

RESULTS

Bats sampled

A total of 703 bats (phytophagous and omnivorous) were captured at FVT during the present study, all of which belonged to the family Phyllostomidae, arranged in five subfamilies, nine genera, and 12 species (Supplementary material Table S1). The most speciose subfamily was Stenodermatinae (n = 5 species), followed by Glossophaginae and Phyllostominae (n = 2 species). Except for *Lonchophylla mordax* Thomas, 1903, which is considered to be Near Threatened (NT) by the IUCN (Sampaio et al. 2016), and Data Deficient (DD) in Brazil (Bernard et al. 2023), all the species collected during the present study are listed as Least Concern (Supplementary material Table S1). A comparison of the captures of phytophagous species at the three sites revealed that the species richness at Site I was 11 species, at Site II was 12 species, and at Site III was eight species. Supplementary material (Table S1) shows the abundance of species captured at each site during ten months of capture (excluding months of unforeseen capture events, such as rain).

Fruiting of the main plant species in the sampled areas

At least 50 fruit-bearing plant species that can be used by bats were identified at Vale do Tabocas Farm (Supplementary material Table S2- no nuts were taken into account). The main plant species in zones 1, 2 and 3 were:

The three *Solanum* species provided fruit all year round, with *S. paniculatum* and *S. stipulaceum* fruiting for 11 months, S. asperum fruiting for 10 months, and *F. mexiae* individuals fruiting for nine months, with individuals showing asynchronous fruiting. *Cecropia pachystachya* bore fruit for 11 months. Jackfruit and castanet fruited for ten months, guava and banana for nine months, jerivá for eight months, fig for seven months, mango, pitombeira, acerola, and coffee for six months, cajazeira and papaya for five months, seriguela and cashew for four months, murici and araçá for three months, and jamelão and jabuticaba for two months.

Diet, characteristics of the fruits consumed and potential for dispersal

A total of 512 fecal samples were obtained from the bats captured in the present study, of which 466 (91 %) contained fruit (seed, pulp, and/or peels), 44 (8.6 %) included insects, and two (0.4 %) contained pollen (Supplementary material Table S3). The bats feed primarily on small fruits weighing less than 5 g (Table 1), with seeds that are ingested together with the pulp, such as *F. mexiae* (mean weight = 4.0 g), *S. paniculatum* and *S. stipulaceum* (mean weight = 1.8 g), and *S. asperum* (mean weight = 2.0 g). Overall, 240 of the fecal samples with fruit contained seeds of pioneer plant species, including the five species most consumed by the bats: *F. mexiae*, *C. pachystachya*, *S. stipulaceum*, *S. asperum*, and *S. paniculatum*. Eight bat species provided mixed feces samples, containing two or three food items. *Carollia perspicillata* provided 14 mixed samples, five of which contained seeds (2 - *S. stipulaceum* + *S. asperum*; 1 – Sp.1 + *Solanum* sp.; 1 - *S. stipulaceum* + *Solanum* sp.; 1 - *F. mexiae* + Sp.1; 1 - *S. stipulaceum* + *M. tinctoria*), and seven containing seeds and insects, pulp of different colors and pulp and insects. *Artibeus fimbriatus* provided even samples, three of which contained seeds (2 - *C. pachystachya* + *F. mexiae*; 1 - *S. stipulaceum* + *F. mexiae*), whereas the others contained seeds and insects or pulp and insects. *Phyllostomus discolor* provided eight samples, all containing seeds and insects or pulp and insects.

The bats exploited at least 31 different food items, including identified species and unidentified fruit pulp, insects, and pollen. Overall, 24 of the 25 plant species identified in the bats' diet were considered dispersible by bats caught in the area. Mangifera indica was not considered dispersible, as it cannot be transported due to its mass. Of the 25 plant species identified in the diet of bats, 80% had their seeds ingested and were classified as endozoochorous, while the fruits of the remaining four species had large seeds and were not eaten. *Mangifera indica*, *Syzygium cumini* (L.) and *Syagrus* sp. were identified by the pulp (Supplementary material Table S3). The analysis of the 466 fecal samples containing fruit remains indicated that 263 (56.4%) contained endozoochorous seeds for the bat species identified in the area, whereas 203 (43.6%) contained only pulp. Only eight of the pulp samples could be identified reliably, of which five were *Syagrus* sp., two were *M. indica*, and one was *Syzygium cumini* (L.) Skeels.

Few samples (n = 7) containing pulp or seeds from cultivated fruits were identified in the bats' feces. Two samples of *M. indica*, three of *P. guajava*, and one of *S. cumini* were identified. One fruit of *A. occidentale* was found in the mist net with teeth marks.

When analyzed per bat species (Table 2), differences were found in the proportion of fecal samples containing pulp or seeds in *Artibeus fimbriatus* Gray, 1838, *Artibeus lituratus* (Olfers, 1818), *Sturnira lilium* (E. Geoffroy, 1810), and *Platyrrhinus lineatus* (E. Geoffroy, 1810), all of which defecated more samples containing seeds, and only *Carollia perspicillata* (Linnaeus, 1758) produced more fecal samples containing pulp than seeds. *Carollia perspicillata* consumed at least 22 different dietary items, *A. fimbriatus* 13 items, *S. lilium* 14 items, and *A. lituratus* (Olfers, 1818) ten items (Supplementary material Table S3). The diets of medium-sized bats, such as *C. perspicillata* and *S. lilium*, were concentrated on plants of the *Solanum genus*, whereas those of large bats of the genus *Artibeus* were concentrated on the fruits of *F. mexiae* and *C. pachystachya*.

At least 24 food items were consumed in the dry season and 18 were consumed in the wet season. Fecal samples containing seeds were more abundant in the dry season (n = 109) than in the rainy season (n = 83), and at least 14 items were present in both seasons (Supplementary material Table S4). The consumption of the different plants peaked in distinct months. *Solanum stipulaceum* was the only species for which consumption peaked in the rainy season (April), whereas the consumption of *F. mexiae* (December), *S. asperum* (September), and *C. pachystachya* (March) peaked during the dry season.

The PERMANOVA results indicated significant variation in the diet composition among bat

Table 1. Characteristics of the fruits consumed by the phytophagous bats recorded at Vale do Tabocas Farm, Belo Jardim, state of Pernambuco, northeastern Brazil. Fruit classes: Light < 10 g, Medium = 11-50 g, Heavy > 51 g. *Piece weighing 1.5 g.

Species	Habitus	Fruit color	Weight	Seed size (mm)*	Mean number of seeds per fruit	Fruits consumption index	
						N	%
SYNZOOCHORIC							
Anacardiaceae							
Anacardium occidentale L.	Arboreal	Red/ yellow	Medium/ Heavy	30.0–40.0	1	1	0.4
Mangifera indica L.	Arboreal/ exotic	Green/ yellow	Heavy	63.1–108.8	1	2	0.8
Arecaceae							
Syagrus sp.	Arboreal	Yellow	Medium	16.0–22.0	1	5	2.1
Myrtaceae							
Syzygium cumini (L.) Skeels	Arboreal/ exotic	Purple	Light	15.0–20.0	1	1	0.4
ENDOZOOCHORIC							
Moraceae							
Ficus mexiae Standl.	Arboreal/ pioneer	Green	Light	1.2–1.9	90	73	30.5
Maclura tinctoria (L.) D. Don ex. Steudel	Arboreal/ pioneer	Green	Light	3.2–3.4	60	3	1.2
Myrtaceae							
Psidium guajava L.	Arboreal/ pioneer	Green/ yellow	Medium/ Heavy	4.2–4.4	>100	3	1.2
Piperaceae							
Piper sp.	Shrub/ pioneer	Green	Light	1.6–1.8	>500	3	1.2
Solanaceae							
Solanum cf. asperum Rich.	Shrub/ pioneer	Green	Light	3.0–4.8	28	22	9.2
Solanum paniculatum L.	Shrub/ pioneer	Green	Light	3.2–4.0	37	17	7.1
Solanum stipulaceum Roem. & Schult	Shrub/ pioneer	Green	Light	2.4–2.8	116	46	19. 2
Urticaceae							
Cecropia pachystachya Trécul	Arboreal/ pioneer	Brown	Medium	1.9–2.2	272*	63	26.4
Total						**239**	**100%**

species (F = 30.39, p = 0.0001), with no significant differences detected among the three species of the genus *Artibeus* (Table 3). Pairwise PERMANOVA comparisons based on Bray–Curtis dissimilarities revealed significant differences in diet composition among most species pairs (Table 3). According to the SIMPER analysis, the food items that contributed most to the observed dissimilarities among bat species were *Ficus mexiae*, followed by *Cecropia pachystachya*, *Solanum stipulaceum* and *S. asperum*

Table 2. Results of the Chi-square test (χ^2), degrees of freedom (DF) and probability values (p) for the comparison of fecal samples containing pulp and seeds ingested by the different bat species, pair to pair: Cp – *Carollia perspicillata*, Af – *Artibeus fimbriatus*, Sl – *Sturnira lilium*, Al – *Artibeus lituratus*, Pl – *Platyrrhinus lineatus*, Ap – *Artibeus planirostris*, recorded at Vale do Tabocas Farm, Belo Jardim, state of Pernambuco, northeastern Brazil.

	Cp	**Af**	**Sl**	**Al**	**Pl**	**Ap**
Seed	76	64	57	25	17	12
Pulp	83	40	35	11	4	7
X^2	0.308	5.538	5.261	5.444	8.048	1.316
DF	1	1	1	1	1	1
(p)	0.5788	0.0186	0.0218	0.0196	0.0046	0.2513

Table 3. Pairwise PERMANOVA p-values assessing differences in the consumption of food items among bat species recorded at Vale do Tabocas Farm, Belo Jardim, Pernambuco State, northeastern Brazil. Each cell shows the p-value for the comparison between the species in the corresponding row and column. Species codes: Cp = *Carollia perspicillata*; Af = *Artibeus fimbriatus*; Sl = *Sturnira lilium*; Al = *Artibeus lituratus*; Pl = *Platyrrhinus lineatus*; Ap = *Artibeus planirostris*; Gs = *Glossophaga soricina*. No significant differences (p > 0.05) are highlighted in bold.

	Cp	**Af**	**Sl**	**Al**	**Pl**	**Ap**	**Gs**
Cp		0.0001	0.0104	0.0001	0.0001	0.0007	0.0001
Af	0.0001		0.0001	**0.0954**	0.0001	**0.2228**	0.0001
Sl	0.0104	0.0001		0.0001	0.0001	0.0003	0.0001
Al	0.0001	**0.0954**	0.0001		0.0006	**0.2477**	0.0001
Pl	0.0001	0.0001	0.0001	0.0006		0.0003	0.0001
Ap	0.0007	**0.2228**	0.0003	**0.2477**	0.0003		0.0002
Gs	0.0001	0.0001	0.0001	0.0001	0.0001	0.0002	

(Table 4). Dietary frequency data indicate that *Carollia perspicillata* and *Artibeus fimbriatus* were the species that most frequently consumed these key fruit resources (Supplementary material Table S3). No significant seasonal variation was detected in the diet composition for most species, except for *Artibeus planirostris* ($F = 3.256$, $p = 0.0409$). Overall dissimilarity among samples was primarily caused by *F. mexiae* (34.0%), insects (26.8%), and fruit pulp (20.0%).

The plant species most consumed by bats were *C. pachystachya* (nine species), *F. mexiae* (eight species), and *S. stipulaceum* (three species) (Supplementary material Table S3). Only 23 of the 243 (approximately 10%) fecal samples analyzed here contained damaged seeds; only one broken seed was found in each of the samples. For F. mexiae, nine of the 73 (12,3%) fecal samples collected contained damaged seeds. Similarly, five of the 46 samples (11.6%) of S. stipulaceum contained damaged seeds. *Carollia perspicillata* and *A. fimbriatus* were the species responsible for the majority of the damaged seeds found in the samples, with nine and seven samples, respectively. These were the species that provided the most fecal samples containing seeds, 78 and 64, respectively. Durante o período de estudo 452 indivíduos de sete espécies foram marcados. Dos indivíduos anilhados, 155 foram da espécie *C. perpicillata*, 123 *A. fimbriatus*, 83 *S. lilium*, 49 *A. lituratus*, 15 *P. lineatus*, três *P. discolor* e um *P. recifinus*.

DISCUSSION

Most of the plants exploited by the bats in the present study had small fruits that could be carried by the bats from the mother plant to a nearby perch. In many cases, these small fruits contained many small seeds that were ingested together with the fruit and remained intact after their release. In other cases, only fruit pulp was found in the fecal sample, which may reflect either (i) the consumption of

Table 4. Results of the SIMPER (Bray–Curtis analysis of the dissimilarity of the food items consumed by the different species of phytophagous bats recorded at Vale do Tabocas Farm, Belo Jardim, state of Pernambuco, northeastern Brazil, indicating the taxon of each food item, average dissimilarity (Av. dissim), percentage contribution to dissimilarity (Contrib. %), cumulative percentage (Cumulative %), and mean abundance of each item for species 1 (Mean abund. 1) and species 2 (Mean abund. 2).

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean abund.1	Mean abund. 2
Ficus mexiae Standl.	23.81	52.75	52.75	0.0494	0.95
Cecropia pachystachya Trécul	6.313	13.99	66.74	0.0864	0.325
Solanum stipulaceum Roem. & Schult	5.394	11.95	78.69	0.247	0.175
Insects	3.729	8.262	86.95	0.21	0.1
Solanum cf. *asperum* Rich.	1.851	4.101	91.15	0.16	0
Solanum sp.	1.017	2.253	93.3	0.0617	0.05
Sp. 1	0.8932	1.979	95.28	0.0988	0
Solanum paniculatum L.	0.7279	1.613	96.89	0.0864	0
Maclura tinctoria (L.) D. Don ex. Steudel	0.3966	0.8788	97.77	0.0247	0.025
Syzygium cumini (L.) Skeels	0.2572	0.5699	98.34	0	0.025
Piper sp.	0.2434	0.5393	98.88	0.037	0
Syagrus sp.	0.1449	0.321	99.2	0.0247	0
Pollen	0.1449	0.321	99.52	0.0247	0
Mangifera indica L.	0.1497	0.321	99.84	0.0247	0
Psidium guajava L.	0.07031	0.1558	100	0.0123	0
Unidentified pulp	0	0	100	1	1
Anacardium occidentale L.	0	0	100	0	0

fruits with large seeds that were not ingested, (ii) the consumption of fruits with small seeds that were spat out or (iii) the seeds that were ingested but had been defecated previously. The fruits with large seeds were of two types, those that were too large to be carried by the bats (e.g., *M. indica*) and were consumed by the mother tree, and those that could be removed to a perch to be consumed (e.g., *Syagrus* sp. and *S. cumini*).

Even though the orchards within the study area were planted with many exotic fruiting plants – e.g., jackfruit, mango, banana, papaya, fig, castanets and olive, cultivated fruit plants and various wild fruits, the bats focused primarily on native fruits and pioneer plants with small seeds. There are records of bats consuming fruit grown in orchards (Zórtea & Chiarello 1994, Hayashi 1996, Reis et al. 2007, Fabián et al. 2008, Lobova et al. 2009, Bredt et al. 2012), such as mango, pine cone, guava, soursop, cashew, papaya, persimmon, avocado, jackfruit, jabotica and others (Fabián et al. 2008, Lobova et al. 2009, Bredt et al. 2012), as well as other exotic plants, such as chestnut, *Terminalia catappa* L., (Fabián et al. 2008, Bredt et al. 2012, Guedes et al. 2020). *Ficus mexiae* and *C. pachystachya* had their fruit consumed by all the frugivorous species captured, whereas the plants of the *Solanum* genus had more restricted use, with fruit consumed by *C. perspicillata*, *S. lilium* and *A. fimbriatus*, or only *C. perspicillata* and *S. lilium*, which showed a preference for these plant species, as observed in other studies (Charles-Dominque 1986, Muller & Reis 1992, Zórtea & Chiarello 1994, Pedro & Passos 1995, Sipinski & Reis 1995, Garcia et al. 2000, Mikich 2002, Passos et al. 2003, Pinto & Hortêncio-Filho 2006, Silva 2007, Carvalho 2008). This may be related to the fruiting pattern, since these *Solanum* species provide few ripe fruits each night and have extended fruitfulness, whereas *F. mexiae*, for example, provides thousands of fruits during each fruiting period (Charles-Dominique 1986, Fleming 1988) or nutritional questions (Fleming 1986, Fleming 1988). The greater richness of phytophagous bats at Sites I and II reflects a greater abundance of fruiting plants in these areas, attracting bats, which may visit several feeding sites each night (Bredt et al. 2012, Heithaus & Fleming 1978).

Diet analysis showed that bats of the genus *Artibeus* and *C. perspicillata* concentrate their diets on different food items, showing that their roles in the seed dispersal process may be complementary, as seen in birds and bats (Galindo-González et al. 2000). Although the bats concentrated their diet on the fruits of *Solanum*, *Cecropia*, and *Ficus*, they consumed a variety of other food items when these fruits were available. The mixed fecal samples indicate that species visit more than one food item per night, potentially increasing foraging distances and consequently seed dispersal in highland wetlands (Fleming & Heithaus 1981). Furthermore, the concentration of the species' diet on the fruits of pioneer plants that contain hundreds of endozoochoric seeds, even during periods of availability of exotic and cultivated fruits, reinforces the importance of the fruit bat community in the maintenance and restoration of degraded areas (Charles-Dominique 1986, Galindo-González et al. 2000).

In the present study, a total of 29 different food items derived from fruit were identified, in addition to pollen and insects. The feeding habits of the bats were also dominated by small fruits, even when larger-sized options were available. The size of the fruit has a direct influence on its transportation by bats (Heithaus et al. 1975), given the marked correlation between the body size of the bat and the maximum size of the fruit it can carry when flying. Given this, relatively small fruits (< 100 g) predominate in phyllostomid feeding habits (Fleming 1986), and the preference for fruits that can be transported to feeding perches away from the mother tree may be a strategy to avoid predators (Bredt et al. 2012).

The bats consumed a wide range of fruits containing seeds that could be transported, including 20 species with endozoochorous seeds. In the Caatinga of Pernambuco, Silva (2007) recorded the consumption of 16 species of endozoochorous fruit in cloud forests and 17 species in the Caatinga scrub. In two remnants of seasonal semi-deciduous forest in the southern Brazilian state of Paraná, Mikich (2002) and Pinto and Ortêncio-Filho (2006) recorded the consumption of the fruit of nine endozoochorous species by bats, whereas in a remnant of the Atlantic Forest in São Paulo, Passos et al. (2003) recorded the exploitation of 23 species. This exploitation of different zoochorous species highlights the importance of bats as potential dispersers in different environments.

The most consumed plant species were *F. mexiae*, *C. pachystachya*, and those of the genus *Solanum*, as observed in previous studies of Neotropical bats (Fleming 1986, Zórtea & Chiarello 1994, Pedro & Passos 1995, Sipinski & Reis 1995, Garcia et al. 2000, Mikich 2002, Passos et al. 2003, Pinto & Hortêncio-Filho et al. 2006, Silva 2007). These plants represent an important feeding resource for the local bat populations, particularly by providing fruit throughout the year, which could favor the occurrence of frugivorous bats within the study area. *Ficus* trees, for example, provide large quantities of mature fruit each night, attracting large concentrations of foraging bats. In contrast, *Solanum* produces smaller crops, and fewer mature fruits are available on a given night (Galetti & Morellato 1994).

The higher consumption of food items during the dry season is consistent with data collected by Silva, 2007. In Santa Rosa, Costa Rica, *C. perspicillata* had a broader diet during the dry season, with 13 seed types (species) found, compared with nine during the wet season. During the dry season, fruit availability is lower (Fleming 1988), forcing the species to seek other food sources each night. This result is consistent with predictions of the ideal diet model (MacArthur & Pianka 1966).

The PERMANOVA results indicated significant variation in the consumption of different items among all the bats, however, species of the same genus or subfamily had similar diets, such as the three *Artibeus* species, which had highly similar diets and, together with *Platyrrhinus*, were the main dispersers of *F. mexiae*. In other studies, fig trees have been observed as the main items consumed by stenodermatids (Muller & Reis 1992, Korine et al. 2000, Mikich 2002, Passos & Graciolli 2004, Silva 2007, Ríos-Blanco & Pérez-Torres 2015, Pereira et al. 2019). *C. perspicillata* and *S. lilium* are the primary dispersers of *Solanum* species (Fleming 1988, Muller & Reis 1992, Hayashi 1996, Mikich 2002, Silva 2007, Reis et al. 2013). The fruiting pattern, energetic characteristics and specialization of the species probably explain these divisions (Fleming 1986, Fleming 1988).

Although some fecal samples with Piper seeds were detected, no plants of this genus were found on the farm. The general absence of plants of the genus Piper, an important component of the diet of *C. perspicillata* (Fleming 1988), from the study area may have been the key factor determining the predominance of *Solanum* in the diet of this bat species. In addition, bats may seek out fruit from different species each night as a way of supplementing their diet and achieving an adequate energy balance, since *Solanum* is rich in protein, and plants such as *Ficus*, *Cecropia* and *Spondias* are rich in carbohydrates (Fleming 1988). The consumption of insects over the months reflects the search for food with a high protein content (Fleming 1988).

This may have been one of the key factors determining the amplitude of the diet of *C. perspicillata*, which not only consumed a wide variety of fruit, but also pollen and insects, contributing to the dissimilarity of its diet in comparison with that of *S. lilium*. In the present study, the diversity of plants in the diets of the different bat species, particularly *C. perspicillata*, probably reflects the availability of fruit in the study area. *Carollia perspicillata* typically feeds on a number of different types of fruit during a night, thus producing a highly diverse seed shower, as seen by Fleming & Heithaus, 1981. According to Silva (2007), in Brejo da Madre de Deus, *C. perspicillata* and *S. lilium* concentrated their diet on *S. stipulaceum*, including 14 and 11 food items in their diets, respectively. *Artibeus* fimbriatus consumed 12 food items, and *A. lituratus* six, both concentrating their diet on *C. pachystachya*. The variety of seeds found in the feces of bat species in both studies indicates that these bats may play a key role in maintaining plant diversity in the cloud forest enclaves within the semi-arid Caatinga.

Fleming & Sosa (1994) defined a legitimate seed disperser as a frugivore that defecates intact seeds. In the present study, only few quantities of ingested seeds were damaged in comparison with the large numbers of intact seeds. In addition, the consumption primarily of fruits of pioneer plants, such as *Solanum*, *Cecropia*, and *Ficus*, reinforces the potential role of bats in the process of secondary succession in many different types of environments (Charles-Dominique 1986, Gorchov et al. 1993, Medellín & Goana 1999, Garcia et al. 2000, Muller & Reis 2002). The input of local bats is essential for the recuperation of degraded areas, such as those found at the study site, and this contribution is favored by their habit of flying over open areas (Mikich et al. 2003, Passos et al. 2003), where the seed shower is often most intense (Morawetz & Lindner 2006).

Together, *Solanum*, *C. pachystachya*, and *F. mexiae* were the principal sources of food for the frugivorous bats throughout the study period. The prolonged fruiting of *Solanum* species and *C. pachystachia*, the asynchronous fruiting of *F. mexiae* trees and various other plant species bearing fruit throughout the year, results in an abundance of fruit over long periods, allowing a number of bat species, such as *C. perpicillata*, *S. lilium*, *A. lituratus* and *A. fimbriatus*, to persist in the study area, as well as attracting other species, especially when their preferred resources are abundant. In the specific case of *Platyrrhinus recifinus* (Thomas, 1901), for example, the presence of the species was associated with the availability of *F. mexiae* fruit. Fleming (1986) and Harten et al. (2024) concluded that the spatial-temporal availability of a fruit is probably the principal determinant of its selection by frugivorous bats.

These findings reveal the importance of cloud forests for the maintenance of the frugivorous bat community. These cloud forest enclaves represent important refugees within the semi-arid zone of the Northeast Brazil, where the dry season typically lasts for more than half of the year. The distinct conditions and abundant feeding resources of these forests attract many species of frugivorous bats, which, in turn, contribute to the regeneration of these cloud forest enclaves within the semi-arid zone. By transporting thousands of seeds during the fruiting seasons, these bats contribute to the reproductive success of a wide range of plant species, particularly pioneers, increasing the diversity and dynamics of these relict altitudinal forests that have a distinct biota, are rarely studied and are thus threatened by anthropogenic activities (Pereira Filho et al. 2020). The study of these interactions may provide important insights into the functioning of these ecosystems in the Atlantic

Forest, contributing to the development of effective conservation strategies for these environments.

Despite the important results obtained in this study concerning the local bat community and its interactions with plants (frugivory), more studies are needed to better understand the movement and foraging dynamics of frugivorous species in search of food between the marsh and Caatinga areas, since long-distance movements favor the seed dispersal process.

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