

ORIGINAL ARTICLE

Relationships between nectarivorous bats (Phyllostomidae: Glossophaginae, Lonchophyllinae) and plants in an area of environmental preservation in Southeastern Brazil

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ABSTRACT

Bats play a crucial role as floral visitors in the Neotropical Region, and are responsible for pollinating a variety of plant species. However, there is a lack of studies on this topic, particularly regarding interactions between these organisms. The objective of this study was to identify nectar-feeding bat species inhabiting the National Park Cavernas do Peruaçu (NPCP) and examine the temporal variation of these relationship. Plant species visited were identified by analyzing the pollen carried by bats. The study was conducted in the NPCP between December 2008 and November 2009, with four expeditions, one for each season, each lasting 20 nights. Pollen on the fur and skin of nectar-feeding bats was collected using double-sided tape and examined under an electron microscope in the laboratory. A total of 174 nectar-feeding bats from six different species were captured. The most abundant bat species was *Glossophaga soricina* (118 individuals), followed by *Anoura caudifer* (21), *Lonchophylla* cff. *mordax* (15), *L. cff. dekeyseri* (13), *A. geoffroyi* (4), and *Lionycteris spurrelli* (3). Nineteen distinct pollen types were collected from the nectar-feeding bats in the NPCP, with *Bauhinia forficata* being the most prevalent and present in 71 individuals. Pollen types associated with chiropterophily, such as from *Hymenaea* spp., *Caryocar brasiliense*, and *Pseudobombax* spp. were also common. The utilization of floral resources by nectar-feeding bats was consistent within the NPCP. Variation in the pollen load on bats was noted across the seasons, coinciding with differing phenological patterns of the visited plants. Analyzing the pollen present in the bats serves as an effective tool to enhance our understanding of the use of floral resources by the nectar-feeding bats.

INTRODUCTION

The diversity of pollination systems is a result of the evolutionary history of pollen-dispersing plants and animals, a relationship marked by mutual benefits. This dynamic has been identified as one of the factors shaping Earth's plant and animal biodiversity (Bascompte & Jordano 2007, Rohr et al. 2014, Moreira-Hernández & Muchhala 2019). The importance of animal-mediated pollination in maintaining biodiversity is shown by the estimate that 98–99% of angiosperms in tropical forests are pollinated by biotic vectors (Bawa 1990, Bascompte & Jordano 2007, Gamba & Muchhala 2023). Vertebrates play a pivotal role as pollinators in tropical and subtropical regions due to their ability to cover substantial distances and facilitated by their large body size for effective pollen adhesion (Fleming et al. 2009). In particular, Neotropical bats stand out among pollinators for their relatively large body size and strong flying capabilities, which enable them to traverse considerable

distances (González-Gutiérrez et al. 2022). Nectar-feeding behavior evolved in two bat families: Pteropodidae, found in the Paleotropics, and Phyllostomidae, exclusive to the New World (Fleming et al. 2009).

In the Neotropics, there are 60 known species of nectar-feeding bats that belong to the subfamilies Glossophaginae and Lonchophyllinae (Simmons & Cirranello 2025). Both subfamilies exhibit morphological and physiological adaptations for nectar consumption (Helversen & Winter 2003, Diniz & Aguiar 2023a, 2023b), such as an elongated rostrum and tongue, reduced dentition, pollen-adapted fur, and tongues with grooves and long filiform papillae (Howell & Hodgkin 1976, Freeman 1995, Diniz & Aguiar 2023a, 2023b), aiding in the capture of food resources from flowers during their visits. Most species of glossophagines and lonchophyllines weights between 6–15 g, with few species reaching up 20–30g. However, it is important to distinguish between floral visitors and effective

pollinators. While nectar-feeding bats are often considered key pollinators due to their ability to carry pollen over long distances, not all floral visits result in successful pollination. Some interactions may involve resource robbing, where bats consume nectar or pollen without effectively transferring pollen between flowers (Tschapka 2004). This distinction is particularly relevant for understanding the ecological roles of bats in plant reproduction. Additionally, genera from other subfamilies such as *Carollia*, *Phyllostomus*, and *Artibeus* are also reported as floral visitors (Buzato & Franco 1992, Fischer 1992, Vieira & Carvalho-Okano 1996, Diniz & Aguiar 2023a), even though they predominantly exhibit frugivory, insectivory, and omnivory. These bats may occasionally visit flowers for nectar but are less likely to act as effective pollinators compared to specialized nectar-feeding species.

The effectiveness of bats as pollen vectors depends on plant reproductive strategies and pollinator foraging patterns (Heithaus et al. 1974, Stewart et al. 2022). Phyllostomidae commonly exhibit trapline foraging behavior, which consists of flying along a repeated route, visiting specific plants in search of nectar-bearing flowers (Fleming et al. 2009), which requires spatial memory to locate flowers. According to Sazima et al. (1999), the trapline behavior of nectar-feeding bats promotes cross-pollination and pollen exchange between neighboring populations. Floral traits exploit bats' sense of smell, vision, and echolocation (Helvesen & Winter 2003). Characteristics of the chiropterophily syndrome include white to greenish flowers, nocturnal anthesis, copious nectar capable of sustaining bats' endothermic metabolism, and exposed flowers for mid-flight visitation (Baker 1961, Helvesen & Winter 2003, Stewart et al. 2022). The plant families rich in chiropterophilous species include Fabaceae, Cactaceae, Malvaceae, Bignoniaceae, and Caryocaraceae, the latter being a primary bat-pollinated family in Neotropics (Fleming et al. 2009, Parolin et al. 2016, Pellón et al. 2021).

Thus, bats play a fundamental role in maintaining essential ecological processes, as the reproductive success and establishment of certain plants rely on the roles of these animals as both dispersers and pollinators (Bonaccorso 1979, Cordero-Schmidt et al. 2021). The devastation and fragmentation of the Cerrado and Caatinga, which are key ecosystems for preserving the remaining fragments and aiding the reforestation of degraded areas (Machado et al. 2004, MMA 2002, Myers et al. 2000) threaten these processes. Therefore, studies on bat-plant interactions, particularly aspects of flower visitation, can make significant contributions to conservation efforts.

Several studies have focused on bat pollination (Baqi et al. 2022, González-Gutiérrez et al. 2022), often centered on one or a few chiropterophilic plant species (Buzato & Franco 1992, Fischer 1992, Sanmartín-Gajardo & Sazima 2005, Sazima et al. 1999, Sazima & Sazima 1978) to understand their reproductive characteristics. Some studies have explored the dietary aspects of specific species such as *Lonchophylla dekeyseri* (Coelho & Marinho-Filho 2002) and *Leptonycteris nivalis* (Sánchez & Medellín 2007). However, community-level studies on nectarivorous bat pollination at the in Brazil remain scarce (Cordero-Schmidt et al. 2021, Diniz & Aguiar 2023a), with most research on this topic

being concentrated in Central America and northern South America (González-Gutiérrez et al. 2022).

In the present study, the evaluation of the relationships between nectar-feeding bats and plants took an unusual approach by utilizing pollen grains adhered to the fur and skin of the animals. This methodology has been minimally explored in Brazil (Coelho & Marinho-Filho 2002) and offers the practical advantage of capturing the range of plant species visited by bats while surveying bat assemblages within a specific region. This approach is intriguing because selective observations of certain botanical species do not cover the full spectrum of plants accessed by bats. This underscores the importance of analyzing pollen on pelages as a tool for studying bat feeding habits. Therefore, the study objectives were: (1) to document the nectar-feeding bat species within the National Park Cavernas do Peruaçu and (2) to identify the plant species with which nectar-feeding bats interact as floral visitors.

2 METHODS

Study area

The study was conducted in the National Park Cavernas do Peruaçu (NPCP), located in the São Francisco River Valley in northern Minas Gerais. This protected area was established in 1999 and encompasses the municipalities of Itacarambi, Januária, and São João das Missões, spanning coordinates 14°54' to 15°15'S and 44°03' to 44°22'W (Fig. 1). The total area of the NPCP is 56,448.32 ha, with elevations ranging from 500 to 750m, along the Peruaçu River (Piló & Rubbioli 2002). The NPCP features a distinct karst terrain with a significant number of natural cavities. The climate is classified as Aw according to the Köppen classification, indicating a tropical climate with humid seasons and dry winters from April to September, followed by a wet season from October to March (Alvares et al. 2013). The average annual precipitation is 832.4 mm, with 183 mm in January and only 1 mm in July. The mean annual temperature is 24°C, fluctuating between 16°C and 34°C (Brandão & Magalhães 1991).

The vegetation comprises a heterogeneous phytophysognomy consisting of mixed formations, including: 1) Cerrado stricto sensu, 2) semi-deciduous forests, 3) "Carrasco," a shrubby xeromorphic formation that sheds leaves during winter and shares characteristics with the Caatinga, 4) Tropical Dry Forest along karstic paths, and 5) hyperxeromorphic formations on rocky terrains consisting of cacti and bromeliads (Azevedo 1966, Brandão & Magalhães 1991, Fernandes 2006).

Bat captures

Four expeditions were conducted between December 2008 and November 2009, with each expedition consisting of 20 sampling nights. The summer expedition occurred from late December 2008 to January 2009, autumn expedition occurred between April and May 2009, winter expedition occurred between July and August 2009, and spring expedition occurred between October and early November 2009.

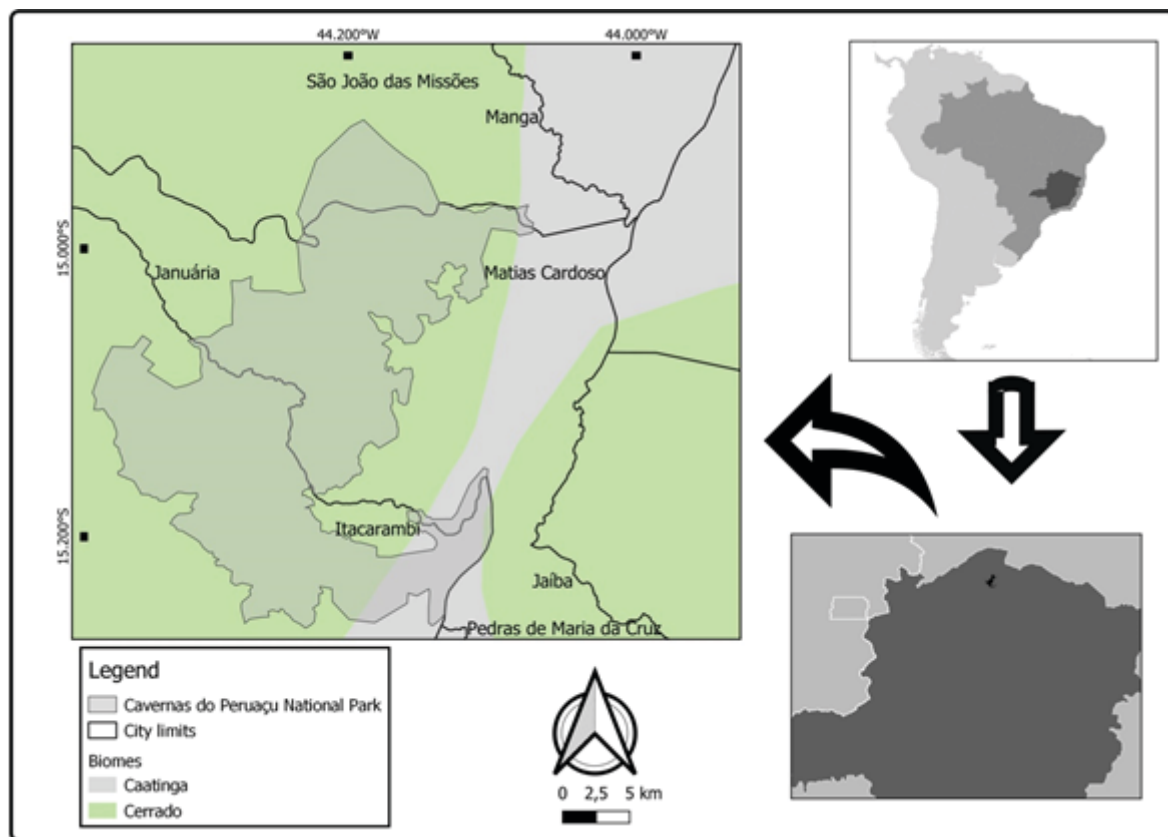


Fig. 1 - Map of the NPCP showing its relationships with the Cerrado and Caatinga biomes.

Mist nets were used to capture bats in trails, small clearings, and available spaces within the vegetation. Six nets measuring 12 meters in length and four nets measuring 7 meters in length were set up; all were positioned at a height of 2.5 meters. Typically, the nets were installed approximately 0.3 meters above the ground and left in place from dusk to dawn, with checks conducted every 30 min. After capture, individuals were tagged with aluminum rings and released at the same site. The tagging aimed to enable future recaptures, assessing movement patterns, fidelity to feeding areas, and pollen load changes over time (Esbérard & Daemon 1999). To prevent bats from learning about net locations (Esbérard 2006), each expedition avoided repeating sites. Consequently, a minimum of two months elapsed before resampling at the same site. The sampling effort was calculated by multiplying the area covered by the installed nets by the number of hours they remained active (nets were deployed for the entire night, totaling 12 hours), resulting in a total of 237,571 h.m². The distribution of sampling nights across lunar phases was even, with approximately five nights per lunar phase.

Only nectar-feeding bats belonging to the subfamilies Lonchophyllinae and Glossophaginae were considered (classification according to Baker et al. 2003). Species identification followed keys from different authors contained in Gardner (2008) and information from Reis et al. (2007). The nomenclature used followed Simmons (2005). Since the work was conducted between 2008 and 2009, the identification of species of the genus *Lonchophylla* was based on the latest available references at the time but its taxonomy is in flux (Benathar et al. 2024, Pilatti et al. 2025).

Three individuals of each bat species, along with those with uncertain identification, were euthanized and prepared as reference vouchers. These vouchers are currently housed in the Mammal Collection of the Federal University of Lavras (CMUFLA) and were obtained under the IBAMA License, process 14875-2.

Pollen collection and identification

Immediately after capture, the bats were subjected to pollen collection from their fur and skin. The pollen collection process involved applying a 5 × 5 mm double-sided tape (Bernhardt 2005) onto the head, thorax, and scapular regions of the bats. Additionally, 10 × 10 mm squares of tape were applied to the wings and body to maximize the diversity of pollen on each individual. The pollen-laden tapes were then affixed to labeled microscopy slides and stored in a cool, dry environment. These tapes were examined using an Olympus BX50 optical microscope (Olympus Corporation, Tokyo, Japan) to identify pollen grains. The illustrations of the pollen grains were digitally obtained using this microscope equipped with camera. Due to the abundance of pollen grains, a subsampling technique known as “pollen sum” was used (Ybert et al. 1992), involving the counting of approximately 300 pollen grains per tape, with each bat serving as a sample.

The term “pollen type,” used for identification, refers to distinct morphological groups of pollen that may correspond to a specific species or be shared among species within the same genus or family (Barth 1989). In cases where differentiation between these groups is impossible, the concept of pollen type establishes a connection between

the material examined and a specific taxonomic group of plants, indicating their taxonomic proximity (Lorscheitter 1989).

Pollen type identification primarily relied on a comparison with a reference pollen collection maintained at the Botanical Institute of the Environmental Secretariat of the State of São Paulo. Catalogs by Melhem et al. (1984) and Roubik & Moreno (1991), as well as specific works by Barth (1970a, 1970b, 1970c, 1970d, 1989), were essential for this process. Additional data from vegetation surveys conducted during the creation of the NPCP Management Plan (MMA 2005) and in the Januária region of Minas Gerais, as reported by Lombardi et al. (2005), were also utilized. Apart from these surveys, a third exploration was undertaken by our team during the inaugural expedition to identify the plants potentially visited by bats.

At the time of the study, the APG II system (Judd et al. 2007) was the most widely adopted classification for botanical families. However, to ensure taxonomic accuracy, we later consulted the updated APG IV system (2016) to verify and update plant family names where necessary. The collected botanical and pollen samples were stored in the ESAL Herbarium of the Federal University of Lavras (UFLA) and the pollen collection of the Botanical Institute of the Environmental Secretariat of the State of São Paulo, ensuring preservation and accessibility for future research. To account for temporal variations in bat-plant interactions within the NPCP, field expeditions were distributed across the four seasons.

Data Analysis

The classification of pollen abundance was based on the quartile distribution of interaction frequencies observed in our dataset. Pollen types with up to two interactions corresponded to the first quartile and were classified as rare, those with 3 to 14 interactions fell within the interquartile range and were considered common, and types with 15 or more interactions represented the upper quartile, thus being categorized as abundant. This data-driven approach provides an objective criterion for identifying abundance patterns (Zar 1999).

Pollen load, defined as the number of pollen types per individual, was assessed throughout the year and among species. This analysis employed the Kruskal-Wallis ANOVA test followed by the post hoc Student-Newman-Keuls (SNK) test (Corder & Foreman 2009, Zar 1999). Treatment levels with five or fewer samples were omitted to avoid statistical bias. Kruskal-Wallis and SNK tests were performed using BioEstat version 5 (Ayres et al. 2007). All statistical tests were performed considering a significance level of 0.05 ($\alpha = 5\%$), corresponding to a 95% confidence level.

RESULTS

A total of 174 nectar-feeding bat individuals from the subfamilies Glossophaginae and Lonchophyllinae were captured, representing six species with no recaptures. Among the captured species, *Glossophaga soricina* was the most abundant, with 118 captures, followed by *Anoura*

caudifer, with 21 captures. *Lonchophylla* cff. *mordax* and *Lonchophylla* cff. *dekeyseri* showed 15 and 13 captures, respectively. The least abundant species were *A. geoffroyi*, recorded four times, and *Lionycteris spurrelli*, recorded three times (Table 1). The highest abundance was observed during winter and autumn, while summer exhibited a lower count, with spring showing no significant differences from the other seasons ($H = 9.74$; $p = 0.02$). *Anoura geoffroyi* was observed exclusively during autumn, while *L. spurrelli* was documented in winter and spring. The other four species were present throughout the study period. Notably, pollen from *Bauhinia forficata* was identified in a single individual of *Phyllostomus hastatus* during the winter, representing an uncommon record for this typically omnivorous/animalivorous species.

A total of 86 pollen samples were collected, yielding 23,723 pollen grains from 19 pollen types belonging to 12 plant families (Table 1, Fig. 2, and Fig. 3). Although Malvaceae presented the highest pollen types (five), Fabaceae showed the highest interactions (four types). The other families presented only one pollen type each. Brazilian orchid tree *Bauhinia forficata* was the most abundant pollen type, found in 71 individuals, followed by pequi or souari nut *Caryocar brasiliense* (32 individuals) and *Hymenaea* (30 individuals) (Table 2). *Pseudobombax* and *Passiflora* were considered common, occurring in 14 and 13 individuals, respectively. Pollinia were detected in 12 individuals, while the *Calliandra* type appeared in 11 individuals. The remaining 12 pollen types were recorded fewer than 10 individuals. The *Brosimum* and *Cecropia* types required cautious because they were observed in only one individual during summer, each with three and two pollen grains, respectively.

Temporal variation in pollen interaction frequency was evident across seasons. However, due to the limited sample size in summer, this season was excluded from the analysis. Comparisons among the other three seasons revealed significant differences between all pairs. *Caryocar brasiliense*, was the main contributor to spring, while courbaril *Hymenaea* and *B. forficata* were associated with autumn and winter, respectively. During spring, 92% of the samples contained *C. brasiliense*, with 36% showing only this pollen type and 56% in combination with other pollen types. *Bauhinia forficata* was detected in 48% of the samples, always combined with *C. brasiliense*. In winter, *B. forficata* was present in 100% of the samples, while *Hymenaea* appeared in 48%. *Calliandra* and Bromeliaceae type 1 were recorded in 27% and 21% of the samples, respectively. In autumn, *B. forficata* occurred in 91% of the samples, with 48% also containing *Hymenaea*, and 48% showing pollinia.

The average pollen load was 2.5 ± 1.31 pollen types per individual, with a maximum of eight types recorded in a single *G. soricina* individual during autumn. Only 25.6% of the individuals carried a single pollen type. Pollen load significantly varied across seasons, with autumn and winter showing higher loads compared to spring ($H = 7.72$; $p = 0.02$). No differences in pollen load were detected among bat species, ($H = 0.99$; $p = 0.80$), excluding *A. geoffroyi* and *L. spurrelli*.

Table 1 - Pollen types observed in the pelage of nectarivorous bats in the NPCP throughout the seasons (S - summer, A - autumn, W - winter, Sp - spring, Ab - abundant, Co - Common, Ra - rare). Pollen types with up to two interactions were classified as rare, those with 3 to 14 interactions as common, and those with 15 or more as abundant. The values in parentheses indicate the number of samples for each season.

Pollen Type/Season	S (5)	A (33)	W (23)	Sp (25)	Total (86)	Status	Família (APG IV)
1. Pollinia	0	11	1	0	12	Co	Orchidaceae ou Apocynaceae (subf. Asclepiadoideae)
2. <i>Anacardium</i>	0	1	0	0	1	Ra	Anacardiaceae
3. Bromeliaceae type 1	0	2	7	0	9	Co	Bromeliaceae
4. Cactaceae type 1	1	0	1	0	2	Ra	Cactaceae
5. <i>Caryocar brasiliense</i>	4	4	1	23	32	Ab	Caryocaraceae
6. <i>Aparisthium</i>	0	1	0	0	1	Ra	Euphorbiaceae
7. <i>Anadenanthera</i>	0	0	2	0	2	Ra	Fabaceae (subf. Caesalpinioideae)
8. <i>Bauhinia forficata</i>	3	21	33	14	71	Ab	Fabaceae (subf. Cercidoideae)
9. <i>Calliandra</i>	0	0	9	2	11	Co	Fabaceae (subf. Mimosoideae)
10. <i>Hymenaea</i>	2	12	16	0	30	Ab	Fabaceae (subf. Detarioideae)
11. Bombacoideae type 1	0	1	4	0	5	Co	Malvaceae (subf. Bombacoideae)
12. <i>Cavanillesia</i>	0	0	4	0	4	Co	Malvaceae (subf. Bombacoideae)
13. <i>Chorisia</i>	0	0	1	0	1	Ra	Malvaceae (subf. Bombacoideae)
14. <i>Ochroma pyramidale</i>	0	1	1	1	3	Co	Malvaceae (subf. Bombacoideae)
15. <i>Pseudobombax</i>	0	9	5	0	14	Co	Malvaceae (subf. Bombacoideae)
16. <i>Brosimum</i>	1	0	0	0	1	Ra	Moraceae
17. <i>Passiflora</i>	1	0	4	8	13	Co	Passifloraceae
18. <i>Roupala</i>	0	3	0	0	3	Co	Proteaceae
19. <i>Cecropia</i>	1	0	0	0	1	Ra	Urticaceae

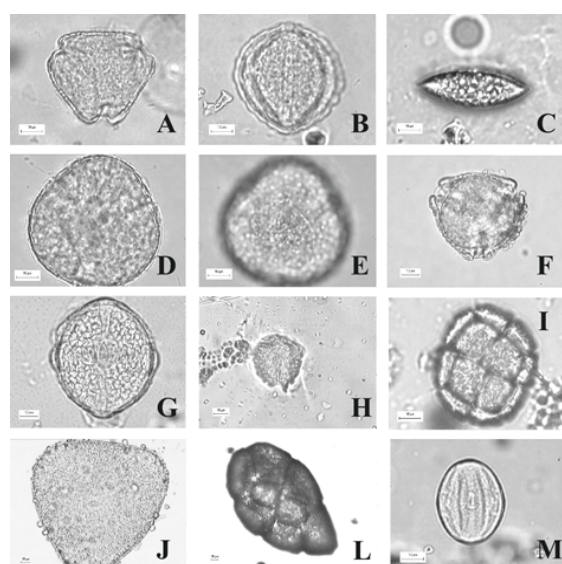


Fig. 2 - Photomicrographs of pollen collected in the hairs of nectarivorous bats in the NPCP. **A**: Anacardiaceae, *Anacardium*, polar view. **B**: Anacardiaceae, *Anacardium*, equatorial view. **C**: Bromeliaceae type 1. **D**: Cactaceae type 1, polar view, optical section. **E**: Cactaceae type 1, polar view, surface. **F**: Caryocaraceae, *Caryocar brasiliense*, polar view. **G**: Caryocaraceae, *Caryocar brasiliense*, equatorial view. **H**: Euphorbiaceae, *Aparisthium*. **I-M**: Fabaceae. **I**: *Anadenanthera*. **J**: *Bauhinia forficata*, polar view. **L**: *Calliandra*. **M**: *Hymenaea*, equatorial view. Scales in figures = 10 μ

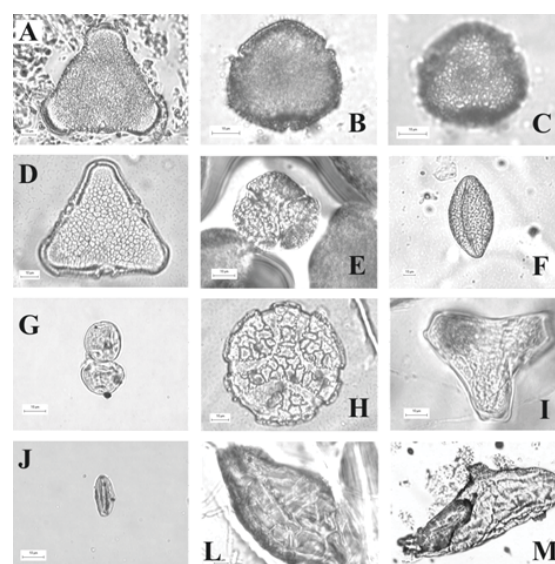


Fig. 3 - Photomicrographs of pollen collected in the hairs of nectarivorous bats in the NPCP. **A-F**: Malvaceae/Bombacoideae. **A**: *Cavanillesia*, polar view. **B**: *Ochroma pyramidale*, polar view, optical cut. **C**: *Ochroma pyramidale*, polar view, surface. **D**: *Pseudobombax*, polar view. **E**: Bombacoideae type 1, polar view. **F**: Bombacoideae type 1, equatorial view. **G**: Moraceae, *Brosimum*, two pollen grains together. **H**: Passifloraceae, *Passiflora*, polar view. **I**: Proteaceae, *Roupala*, polar view. **J**: Urticaceae, *Cecropia*. **L-M**: Pollinia. Scales in figures = 10 μ

Table 2 - Interaction matrix between nectarivorous bats and pollen types with the amounts of interactions in the NPCP. Values in parentheses indicate the number of samples for each species. The values between square brackets indicate the number of occurrences of pollen types. Gs: *Glossophaga soricina*; Ac: *Anoura caudifer*; Ld: *Lonchophylla* cff. *dekeyseri*; Lm: *Lonchophylla* cff. *mordax*; Ls: *Lionycteris spurrelli*; and Ag: *Anoura geoffroyi*

Pollen type/Taxon	Gs (49)	Ac (9)	Lm (12)	Ld (12)	Ls (3)	Ag (1)
<i>Caryocar brasiliense</i> [32]	15	3	6	5	2	1
<i>Bauhinia forficata</i> [71]	43	6	11	10	1	0
<i>Hymenaea</i> [30]	22	2	2	3	0	1
<i>Passiflora</i> [13]	2	1	5	4	1	0
<i>Calliandra</i> [11]	6	1	1	2	1	0
Pollinia [12]	6	2	4	0	0	0
<i>Pseudobombax</i> [14]	8	5	0	0	0	1
Bromeliaceae type 1 [9]	7	0	1	1	0	0
<i>Cavanillesia</i> [4]	2	1	0	0	1	0
Bombacoideae type 1 [5]	4	0	1	0	0	0
<i>Roupala</i> [3]	0	2	0	0	0	1
Cactaceae type 1 [2]	0	1	0	1	0	0
<i>Ochroma pyramidale</i> [3]	3	0	0	0	0	0
<i>Anadenanthera</i> [2]	2	0	0	0	0	0
<i>Anacardium</i> [1]	1	0	0	0	0	0
<i>Aparisthium</i> [1]	1	0	0	0	0	0
<i>Brosimum</i> [1]	0	0	1	0	0	0
<i>Chorisia</i> [1]	0	1	0	0	0	0
<i>Cecropia</i> [1]	0	0	1	0	0	0

DISCUSSION

Our study revealed a remarkable diversity of nectar-feeding bats in the study area, with six identified species representing 60% of the known nectarivorous bat species in the Cerrado and 67% in the Caatinga (Aguiar et al. 2016, Cordero-Schmidt et al. 2021, Silva et al. 2018). This richness is noteworthy when compared to the average nectar-feeding bat species richness in the Neotropical Region, which is 3.1 ± 0.3 species per habitat, ranging from one to six species (Fleming et al. 2005). Similar patterns are observed in Brazil, with an average of 3.2 ± 0.9 species per habitat (Bernard & Fenton 2002, Cordero-Schmidt et al. 2021, Diniz & Aguiar 2023a).

The methodology used here, particularly the application of double-sided tape to collect pollen from bat surfaces, provided valuable insights into the foraging activities of nectar-feeding bats. However, it is important to acknowledge potential limitations related to the pollen reference bank used for identification. While the reference collection at the Botanical Institute of the Environmental Secretariat of the State of São Paulo, along with catalogs and specific works (e.g., Melhem et al. 1984, Roubik & Moreno 1991, Barth 1970a, 1970b, 1970c, 1970d, 1989), allowed us to identify 19 pollen types, the completeness of this reference bank may have influenced our results. For example, pollen grains that were not represented in the reference collection or

that could not be distinguished at the species level (e.g., *B. forficata*, which comprises multiple species in the NPCP area) may have led to an underestimation of the true diversity of plant species visited by bats. Additionally, the use of the “pollen sum” subsampling technique (Ybert et al. 1992), where approximately 300 pollen grains were counted per tape, may have overlooked rare pollen types present in smaller quantities. This could further contribute to an underestimation of the diversity of interactions. Future studies could benefit from complementary methods, such as DNA barcoding of pollen (Bell et al., 2016), to improve the accuracy of identification and provide a more comprehensive picture of bat-plant interactions.

Similarly, a significant diversity of floral species, potentially forming a diet of bats, was identified, encompassing 19 pollen types. Other studies focusing on bat-flower interactions have revealed diverse pollen types. For instance, Heithaus et al. (1975) identified 21 pollen types in phyllostomid bats within a Costa Rican deciduous forest. Diniz & Aguiar (2023a) found 35 types in a Cerrado area in Brazil. Muchhala & Jarrín-V (2002) detected 13 pollen types in nectar-feeding bats in cloud forest, Ecuador, and Cordero-Schmidt et al. (2021) reported 30 pollen types in nectar-feeding bats in Caatinga, northeastern Brazil. Coelho & Marinho-Filho (2002) examined the specific diet of *L. dekeyseri* in the Cerrado of the Federal District, Brazil, recording its interactions with seven plant genera. Sánchez

& Medellín (2007) assessed *Leptonycteris nivalis* in Mexico and documented the presence of 10 pollen types. Cordero-Schmidt et al. (2017) analyzed the diet of *Xeronycteris vieirai* and identified nine pollen types. However, it is important to note that the richness might have been even higher if pollen separation had been achieved at the species level. This challenge is exemplified by the pollen of *B. forficata*, which comprises approximately nine species in the NPCP area, with five cataloged during the floristic inventory conducted in this study. Therefore, richness might have been underestimated because of the limitations of the taxonomic units used.

Among the identified pollen types, *B. forficata* emerged as the most abundant, persisting throughout the year, except during summer. The interaction between nectar-feeding bats and plants of this genus has been well documented (Coelho & Marinho-Filho 2002, Sánchez & Medellín 2007, Diniz & Aguiar 2023a). In the NPCP, *B. forficata* plays a pivotal role in the dietary preferences of nectar-feeding bats. While the prevalence of this data relies on the distribution of botanical species throughout the region, it aligns with studies from Costa Rica, where the genus *Bauhinia* ranked second in observations (Heithaus et al. 1975). Additionally, when analyzing the diet of *L. dekeyseri* in the Federal District, Coelho & Marinho-Filho (2002) observed *Bauhinia* as its most frequent food item.

The pollen type *Caryocar brasiliense* was detected throughout the year, with a marked increase in spring, coinciding with its peak flowering period (Vilela et al. 2008). Its pollination by bats is well documented in the Cerrado (Gribel & Hay 1993, Diniz & Aguiar 2023a), and occasional records of flower visits by *Chiroderma villosum* in the Amazon suggest that even non-nectarivorous bats may interact with its flowers (Martins & Gribel 2007). However, such behavior was not observed in our study, even during peak flowering. Notably, *C. brasiliense* was the only species visited by all nectar-feeding bat species recorded in the NPCP, highlighting its central role as a key food resource structuring the nectarivorous bat community in the region.

Hymenaea spp. the third most abundant pollen type, was primarily recorded during the dry season (winter and autumn), suggesting that bat interactions occurred during this period. Although little information exists about the phenology of *Hymenaea* species in the Cerrado, it is known that *H. stigonocarpa* can flower during the rainy season (Bulhão & Figueiredo 2002). Distinct phenological patterns may result from geographic variations, abiotic factors, and ecological interactions (Ollerton & Dafni 2005). González-Gutiérrez et al. (2022) identified *G. soricina* as a specialist for *H. stigonocarpa* in the Americas.

The discovery of pollinia attached to bat fur is remarkable. These structures, composed by a waxy mass packaging the pollen grains, are transported by attaching to bird beaks and insect bodies. When these pollinators visit another flower of the same species, the pollinia remains intact, minimizing pollen loss. However, the absence of bat pollination in orchids is due to the lack of suitable surfaces for pollinia adhesion (Dressler 1981). This study suggests that nectar-feeding bats in the NPCP might be pollinating these flowers to some extent, as pollinia were observed, although they

appeared to be broken. The presence of broken pollinia raises questions about the effectiveness of bats as pollinators in these interactions. While bats may visit flowers to consume nectar or pollen, the observed damage to pollinia suggests that resource plundering—where bats exploit floral resources without providing effective pollination services—may be occurring. This behavior has been documented in other bat-plant systems, where bats consume nectar or pollen without facilitating pollen transfer (Tschapka 2004). In such cases, the plant may not benefit reproductively, even though the bat gains a nutritional reward. This highlights the need to differentiate between floral visitors and effective pollinators, as not all interactions contribute equally to plant reproduction. Nevertheless, other adhesion mechanisms exist in plants, such as the tongue adhesion of *Microloma sagittatum* (Asclepiadoideae) pollinia to pollinating birds, a rare case (Pauw 1998), and pollinia transfer in *Disa* orchids through the feet of pollinating birds (Johnson & Brown 2004). These examples illustrate the diversity of strategies plants use to ensure effective pollen transfer, even in the absence of specialized pollinators.

Pollen from *Calliandra* was found in five of the six nectar-feeding bat species recorded in the NPCP. MacQueen (1992) documented visits of frugivorous bats to *C. calothyrsus* flowers in Honduras, with *Glossophaga soricina* acting as the primary pollinator. Similarly, Lemke (1984) reported pollen theft by *G. soricina* from *C. laxa* in Colombia, noting more frequent predation on anthers than nectar collection. These observations suggest that the role of nectar-feeding bats in *Calliandra* pollination may vary depending on species and region. Therefore, further direct observations are needed to clarify the nature of the interaction between *Calliandra* and bats in the NPCP.

Subfamily Bombacoideae exhibited the highest diversity of pollen types during the study. This subfamily prominently displays the chiropterophilous syndrome, spanning a total of 24 genera, with 18 found in the New World, particularly in arid and semi-arid Neotropical regions like the NPCP (Fleming et al. 2009). Although chiropterophily is commonly associated with this group, the occurrence of these pollen types in nectar-feeding bats was limited, accounting for just 31% of the studied individuals. In instances like *Ceiba pentandra* and *Pseudobombax munguba* within the Amazon, *Phyllostomus* spp. were the primary pollen vectors (Gribel & Gibbs 2002, Gribel et al. 1999). Despite the presence of abundant non-nectar-feeding phyllostomid bats in the NPCP, no Bombacoideae pollen was detected on their fur.

An intriguing observation relates to the *Ochroma pyramidale* pollen type found in three individuals of *G. soricina* captured at different times and nearby locations. There is a history of nectar-feeding bats consuming plants of this genus, as noted by Heithaus et al. (1975) and Tschapka (2005) for *Glossophaga*, and Tschapka (2004) for *Lichonycteris*. However, Fleming et al. (2009) reported that *O. pyramidale* is primarily visited by bats not specialized in nectarivory. Additionally, other mammals, such as *Cebus capucinus*, have been observed as floral visitors (Ferrari & Strier 1992). Although *O. pyramidale* has an Amazonian distribution, it is commonly utilized as an ornamental plant. Thus, while not directly observed, it may have been introduced to the region.

The observed variation in the abundance of interactions between nectar-feeding bats and pollen types among seasons underscores the fluctuation in resource availability throughout the year (Quirino & Machado 2014). This variation reflects the phenology of different plants visited by the bats, with spring standing out due to the prevalence of *C. brasiliense* in the bats' diet. The lower nectar-feeding bat abundance during summer supports the idea of reduced floral resource availability, suggesting a connection between nectar-feeding bat abundance and the flowering periods of plants (Quirino & Machado 2014). It is important to highlight that many nectar-feeding bat species may include other items in their diet, such as fruits and insects, especially during periods of floral scarcity. For example, studies have shown that species like *G. soricina* and *A. caudifer* may increase fruit consumption during summer when flower availability is reduced (Tschapka 2004). This dietary flexibility allows bats to adapt to seasonal changes in resource availability and may influence their spatial foraging patterns, leading them to explore different habitats in search of resources. While these bats are specialized for nectarivory, their ability to exploit alternative food sources highlights their ecological versatility and resilience in dynamic environments.

While our study focused on nectar-feeding bats of the subfamilies Glossophaginae and Lonchophyllinae, other pollinators play similar ecological roles. Pteropodid bats, for example, are key pollinators in Paleotropical regions, visiting large, sturdy flowers, while the smaller and more specialized Glossophaginae and Lonchophyllinae interact with nocturnal, nectar-rich plants (Fleming et al. 2009, Helversen & Winter 2003). Nectar-feeding birds, such as hummingbirds, also serve as long-distance pollen vectors but differ in foraging strategies: while they prefer brightly colored, tubular, diurnal flowers, bats visit pale, nocturnal flowers with exposed reproductive structures (Fleming et al. 2009). These differences reflect adaptations to their distinct flight capabilities, metabolism, and sensory perception.

The pollen load found on bats represents the resource utilization by an individual during its capture night. Pollen found on bats corresponds to the current foraging night, given frequent grooming behavior (Fleming et al. 2009). Pollinators carrying pollen from various species can detrimentally affect plant reproduction (Bell et al. 2005, Fishbein & Venable 1996). In this context, our study suggests that nectar-feeding bats carried fewer pollen species during spring, coinciding with *C. brasiliense* flowering period. This dominant plant might have attracted and monopolized bats' visits, reducing their interactions with other flowers. In autumn and winter, the observed pollen load remained similar and relatively high. However, plants employ strategies to counter this issue by utilizing different pollen deposition sites on pollinators (Brown & Kodric-Brown 1979).

CONCLUSION

The NPCP plays a key role in supporting nectar-feeding bat communities due to its environmental heterogeneity and seasonal resource availability. Our study documented a diverse fauna of six nectar-feeding bats (*G. soricina*, *A. caudifer*, *L. cff. mordax*, *L. cff. dekeyseri*, *A. geoffroyi*, and *L. spurrelli*), highlighting the importance of this Cerrado-

Caatinga ecotone region for bat conservation.

Glossophaga soricina and *A. caudifer* were the most abundant species, occurring across all seasons, along with *L. cff. dekeyseri* and *L. cff. mordax*. This temporal variation in bat abundance and richness is closely tied to the availability of floral resources, with peaks during the dry season when plants like *B. forficata* and *Hymenaea* sp. dominate the bats' diet. During the rainy season, *C. brasiliense* emerged as a key resource, visited by all recorded nectar-feeding bat species.

The use of double-sided tape to collect pollen from bat fur and skin provided a unique snapshot of their foraging activities, revealing the diversity of plant species visited in a single night. However, the observed pollen load also underscores the challenges of accurately quantifying bat-plant interactions, particularly when rare pollen types or species-level identifications are involved. Future studies could benefit from complementary methods, such as DNA metabarcoding, to further refine our understanding of these interactions.

In summary, our findings emphasize the influence of seasonal resource availability on nectar-feeding bat communities and their interactions with plants. The NPCP serves as a critical habitat for these bats, with certain plant species playing a pivotal role in sustaining the community during periods of resource scarcity. These insights have important implications for local-scale conservation, highlighting the need to preserve both floral resources and the pollinators that depend on them in dynamic ecosystems like the Cerrado and Caatinga.

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