

# First record of folivory in *Artibeus lituratus* (Chiroptera: Phyllostomidae) from an urban protected area in Guatemala

## Primer registro de folivoría en *Artibeus lituratus* (Chiroptera: Phyllostomidae) en un área protegida urbana de Guatemala

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*Artibeus lituratus* is primarily frugivorous, although it has been documented to supplement its diet with leaves. Leaf consumption may occur through fractionation or direct ingestion of the leaf lamina. However, observations are limited, mostly anecdotal, and there are few detailed descriptions available. We document, for the first time in Guatemala, leaf consumption by the frugivorous bat *A. lituratus*. This folivorous behavior was observed at feeding perches in Parque Nacional Naciones Unidas, in central Guatemala. Using fecal samples, fruit remains, seeds, and nibbled leaves collected from September to December 2023, we documented the consumed food resources. We identified fruits from 15 plant species and leaves from 9 species. Leaf consumption was documented from September to November, with no evidence of leaves being consumed in December. The most frequently consumed fruit genera were *Ficus*, *Solanum*, and *Spondias*, while the most common leaves belonged to the genera *Sinclairia* and *Solanum*. Leaf consumption patterns varied across different sections of the leaf (basal, apical, edge, apical-basal, vein). Basal consumption was the most frequent, with typically more than 50% of the leaf lamina consumed.

**Key words:** Feeding habits; fruit bats; leaf consumption; resource availability; Stenodermatinae.

*Artibeus lituratus* es una especie principalmente frugívora, aunque se ha documentado que complementa su dieta con hojas. El consumo de hojas puede ocurrir a través de fraccionamiento o la ingestión directa de la lámina foliar. Sin embargo, las observaciones son limitadas, mayormente anecdóticas, y hay pocas descripciones detalladas disponibles. Documentamos, por primera vez, el consumo de hojas por parte del murciélago frugívoro *A. lituratus* en Guatemala. Este comportamiento de folivoría fue observado en perchas de alimentación en el Parque Nacional Naciones Unidas, en el centro de Guatemala. Utilizando muestras fecales, restos de frutas, semillas y hojas mordisqueadas recolectadas entre septiembre y diciembre de 2023, documentamos los recursos alimenticios consumidos. Identificamos frutos de 15 especies y hojas 9 especies. El consumo de hojas se documentó de septiembre a noviembre, sin evidencia de que se consumieran hojas en diciembre. Los géneros de frutos más consumidos fueron *Ficus*, *Solanum* y *Spondias*, mientras que las hojas más comunes pertenecían a los géneros *Sinclairia* y *Solanum*. Los patrones de consumo de hojas variaron según las diferentes secciones de la hoja (basal, apical, borde, apical-basal, nervadura). El consumo basal fue el más frecuente, con típicamente más del 50% de la lámina de la hoja consumida.

**Palabras clave:** Consumo de hojas; disponibilidad de recursos; hábitos alimenticios; murciélagos frugívoros; Stenodermatinae.

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Neotropical bats are trophically diverse, including species that feed on arthropods, fruits, nectar, leaves, seeds, vertebrates, and blood (Fenton *et al.* 1992; Simmons and Conway 2003; Kunz *et al.* 2011). The use of most of these resources has been extensively documented, varying according to species-specific feeding behaviors (Patterson *et al.* 2003; Simmons and Conway 2003); however, resources such as seeds and leaves have been less studied, with limited evidence supporting their consumption (Kunz and Ingalls 1994; Kunz and Díaz 1995; Nelson *et al.* 2005; Bobrowiec and Matos 2010; Ruiz-Ramoni *et al.* 2011; Wagner *et al.* 2015; Cordero-Schmidt *et al.* 2016;

da Rocha *et al.* 2016; Villalobos-Chaves *et al.* 2016; Pellón 2022; Trujillo *et al.* 2022; Rodrigues *et al.* 2023). In the case of leaves, their consumption has been a subject of debate, as the feeding behavior of bats does not fully align with traditional definitions of true folivory (Rodrigues *et al.* 2023; Muñoz-Romo *et al.* 2025). Bats typically chew leaf fragments to extract and ingest the juices, discarding the fibrous material (Kunz and Ingalls 1994; Kunz and Díaz 1995; Nelson *et al.* 2005; Bobrowiec and Matos 2010; Ruiz-Ramoni *et al.* 2011; Cordero-Schmidt *et al.* 2016; da Rocha *et al.* 2016; Rodrigues *et al.* 2023). Nevertheless, as reports of bat folivory have become more frequent, along with

anecdotal observations of bats consuming mature leaves in their entirety without discarding any part; it is increasingly recognized that frugivorous bats may occasionally exhibit specific folivorous behaviors (Rodrigues *et al.* 2023; Muñoz-Romo *et al.* 2025). To date, folivory has been documented in five species within the genera *Artibeus*, *Platyrrhinus*, and *Carollia* (Rodrigues *et al.* 2023).

Folivory in Neotropical fruit bats has been documented since 1957 (Greenhall 1957) and continues to be an active area of research, with several key findings that have enhanced our understanding and led to hypotheses regarding leaf consumption (Kunz and Ingalls 1994; Kunz and Díaz 1995; Nelson *et al.* 2005; Bobrowiec and Matos 2010; Ruiz-Ramoni *et al.* 2011; Cordero-Schmidt *et al.* 2016; da Rocha *et al.* 2016; Rodrigues *et al.* 2023). Initially, evidence of leaf consumption was gathered through the analysis of discarded material, such as partially consumed leaves and oral pellets, and was further supported by direct observations of bats feeding (Zortéa & Mendes 1993; Kunz & Ingalls 1994; Kunz & Díaz 1995; Nogueira & Peracchi 2003; Ruiz-Ramoni *et al.* 2011; Cordero-Schmidt *et al.* 2016; Duque-Márquez *et al.* 2019). The use of complementary research methodologies, such as camera devices to monitor colonies and feeding roosts, has also made significant contributions to our understanding of this behavior (Silvestre *et al.* 2016; da Rocha *et al.* 2016; Pereira *et al.* 2017; Muñoz-Romo *et al.* 2025). Experimental tests have also provided additional insights into the folivorous habits of bats (Nelson *et al.* 2005).

The factors driving folivory in fruit-eating bats remain poorly understood (Rodrigues *et al.* 2023; Muñoz-Romo *et al.* 2025). Some studies suggest that nutritional needs, such as carbohydrates, proteins, and minerals lacking in fruits, may drive this behavior (Kunz and Ingalls 1994;

Kunz and Díaz 1995; Nelson *et al.* 2005; Bobrowiec and Matos 2010). Other factors, including water scarcity in dry habitats (Cordero-Schmidt *et al.* 2016; Rodrigues *et al.* 2023) and fruit availability tied to plant phenology (da Rocha *et al.* 2016), have also been proposed. It is important to note that none of these factors influencing folivory in bats is mutually exclusive; rather, folivory can result from a combination of all three. However, much of the existing literature remains descriptive and lacks detail (Ruiz-Ramoni *et al.* 2011; Duque-Márquez *et al.* 2019), highlighting a significant knowledge gap that requires further investigation.

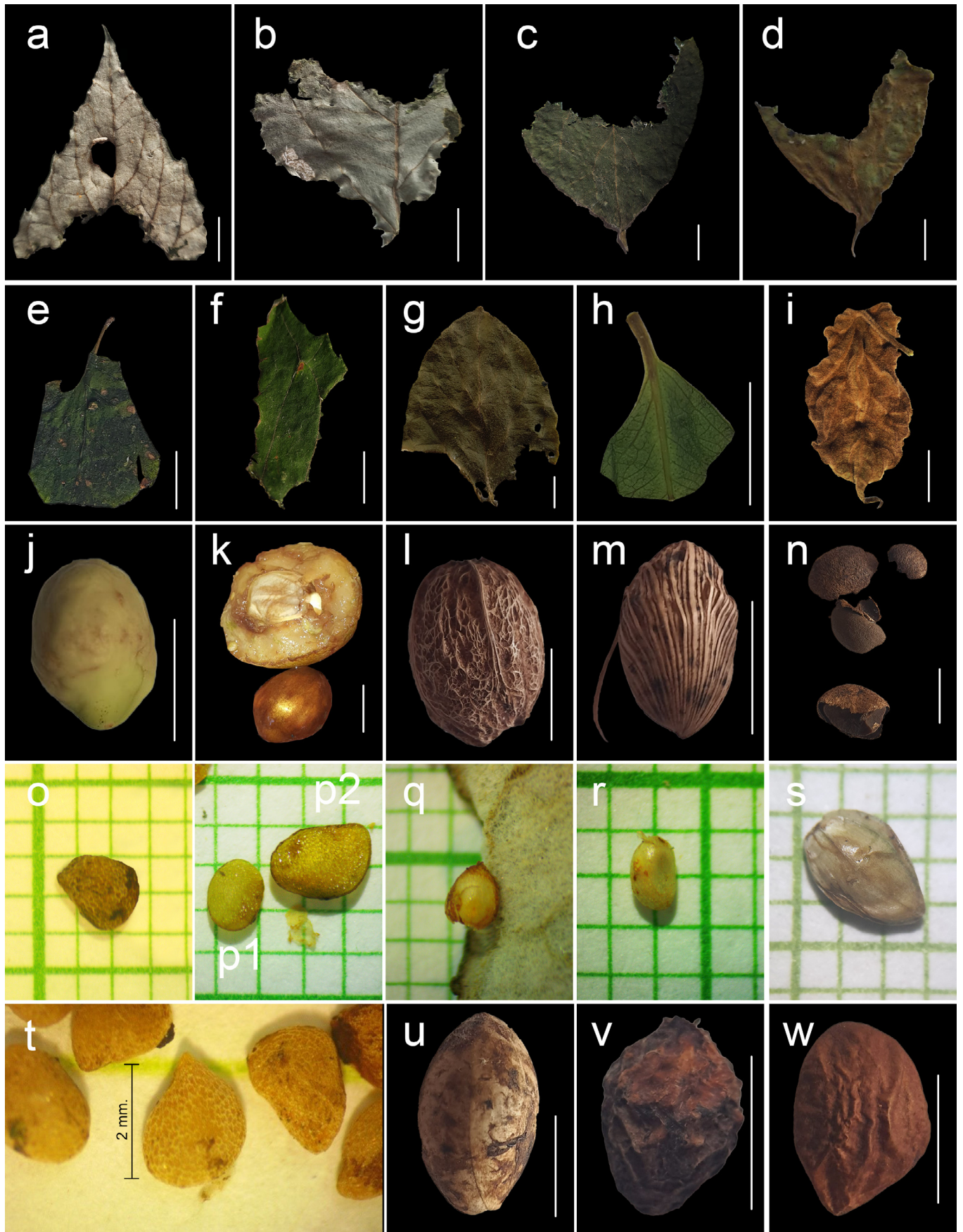
This study aims to report, for the first time, leaf consumption by *Artibeus lituratus* in Guatemala, documenting the diversity of food resources consumed at feeding perches in Parque Nacional Naciones Unidas (PNNU) in central Guatemala, a region where this behavior has not been previously recorded.

Parque Nacional Naciones Unidas (PNNU), located between the municipalities of Villa Nueva and Amatitlán in central Guatemala, spans 372 ha with elevations ranging from 1,190 to 1,330 m. The region receives annual rainfall between 1,100 and 1,349 mm, with temperatures typically ranging from 20 to 23 °C. PNNU is part of ecosystems classified as Premontane Humid Forest Ecosystem, which has predominantly pine-oak species associations (IARNA-URL 2018). The area has been significantly impacted by anthropogenic activities, leading to considerable changes in its forest structure. In most areas, native vegetation has been replaced by plantations intended for forest restoration, featuring non-native species such as cypress (*Hesperocyparis lusitanica*), eucalyptus (*Eucalyptus* sp.), casuarina (*Casuarina* sp.), pine (*Pinus* sp.), and various fruit trees and shrubs (CONAP 2005).



**Figure 1.** a) Feeding perches documented in Parque Nacional Naciones Unidas. b) Table placed under the feeding perch for sample collection. c) Table under the feeding perch with a plastic cover to receive samples.





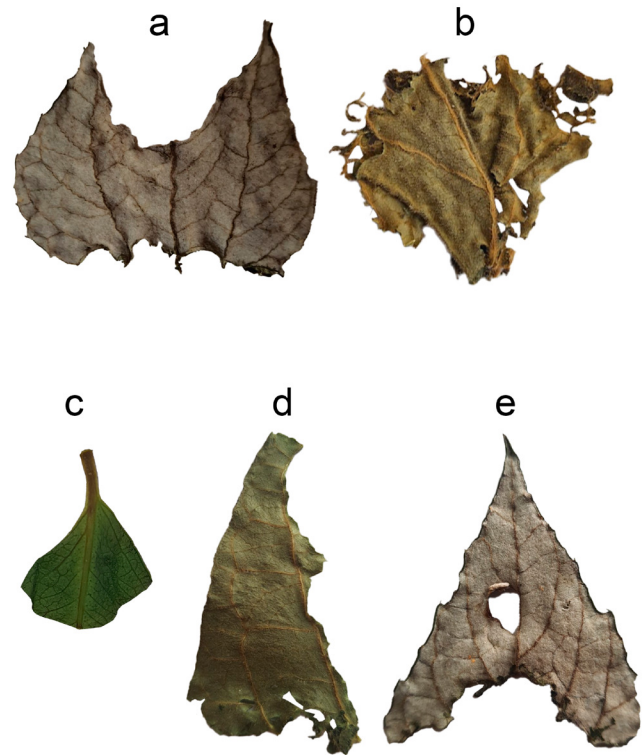
**Figure 2.** Items found at sampling sites throughout the study. a) *Sinclairia sublobata*, b) *Solanum* sp. 1, c) *Solanum* sp. 2, d) *Lycianthes* sp., e) Morphospecies 1, f) Morphospecies 2, g) Morphospecies 3, h) Morphospecies 4, i) Morphospecies 5. Seeds: j) *Casearia* sp., k) *R. bibas*, l) *S. purpurea*, m) *Areca* sp., n) *S. jambos*, o) *Solanum nigrum*, p1) *Solanum* sp.1 p2) *Solanum* sp.2, q) *Ficus cotinifolia*, r) *Panicum* sp., s) *Ficus costaricana*, t) *Lycianthes arrazolensis*, u) Morphospecies 1, v) Morphospecies 2, w) Morphospecies 3. Scale bar (white line): 1 cm.

**Table 1.** Occurrence of digested and non-digested seeds, as well as chewed leaf species, observed at feeding perches in Parque Nacional Naciones Unidas from September to December 2023. The symbol “x” denotes the record of items for each month.

	Family	Species	Sep	Oct	Nov	Dec	Native/ Introduced
Seeds							
Tree	Salicaceae	<i>Casearia</i> sp.	x				Native
	Moraceae	<i>Ficus cotinifolia</i>	x	x	x	x	Native
		<i>Ficus costaricana</i>	x	x	x	x	Native
	Rosaceae	<i>Rhaphiolepis bibas</i>	x	x			Introduced
	Anacardiaceae	<i>Spondias purpurea</i>	x	x	x	x	Native
	Myrtaceae	<i>Syzygium jambos</i>	x	x	x	x	Introduced
Shrub	Solanaceae	<i>Lycianthes arrazolensis</i>		x			Native
		<i>Solanum nigrum</i>		x	x		Native
		<i>Solanum</i> sp1	x	x	x		Mostly native
		<i>Solanum</i> sp2	x	x	x	x	Mostly native
Other	Arecaceae	<i>Areca</i> sp.	x				Introduced
	Poaceae	<i>Panicum</i> sp.	x				Mostly native
	NA	Morphospecies 1		x			NA
	NA	Morphospecies 2		x			NA
	NA	Morphospecies 3			x		NA
Leaves							
Shrub	Asteraceae	<i>Sinclairia sublobata</i>	x	x			Mostly native
	Solanaceae	<i>Lycianthes</i> sp.			x		Mostly native
		<i>Solanum</i> sp. 1	x	x	x		
		<i>Solanum</i> sp. 2	x	x			Mostly native
Other	NA	Morphospecies 1	x				NA
	NA	Morphospecies 2	x	x			NA
		Morphospecies 3	x	x			NA
	NA	Morphospecies 4			x		NA
	NA	Morphospecies 5			x		NA

Fruit, seed, and nibbled leaf samples were collected from feeding perches frequented every night by *A. lituratus*, where evidence such as leaf and fruit pellets, seed and fruit remains, and partially nibbled leaves were found on tables below the perches (Figure 1). Sampling was conducted twice a week, early in the morning, from September to December 2023. Each sample was rinsed with water, disinfected with 70% alcohol, dried, and then placed in a waxed paper envelope for preservation (Morales-Pizarro et al. 2023).

Seed identification was conducted using the ‘Index Seminum’ seed reference collection from the Botanical Garden at Universidad de San Carlos de Guatemala (Portal de Biodiversidad de Guatemala 2025). For leaf identification,



**Figure 3.** Leaf ingestion patterns. a) Apical-basal, b) Edge, c) Apical, d) Vein, e) Basal.

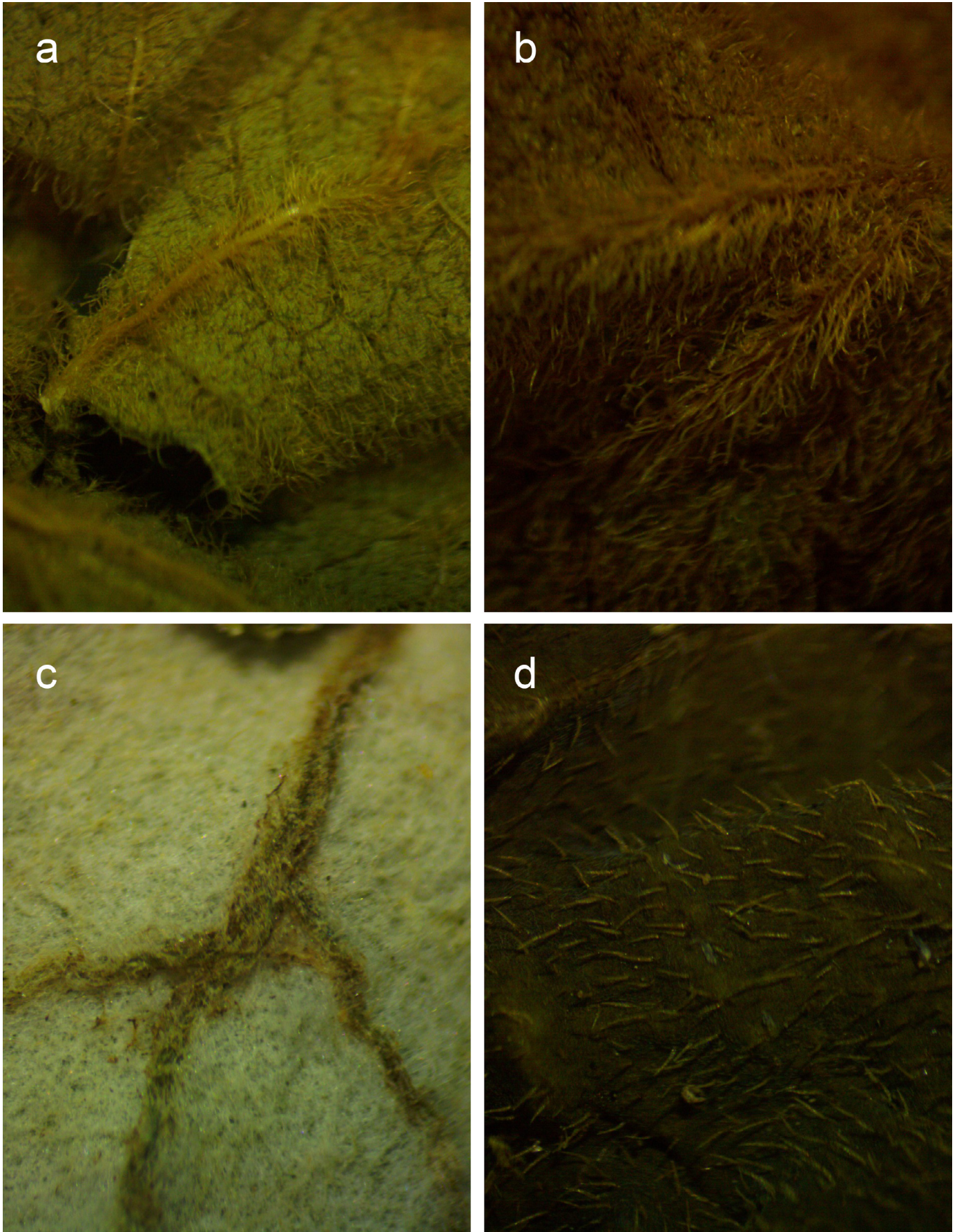
**Table 2.** Percentage of leaf consumed, and consumption patterns observed at feeding perches in Parque Nacional Naciones Unidas from September to December 2023.

Species	Percentage of leaves consumed	Leaves consumption pattern	Trichomes
<i>Liabum</i> sp.	> 50	Apical, apical-basal, basal, edge, and midrib and others	Yes
<i>Solanum</i> sp. 1	> 50	Basal, edge, and midrib and others	Yes
<i>Solanum</i> sp. 2	< 50	Basal	Yes
<i>Lycianthes</i> sp.	> 50	Basal	Yes
Morphospecies 1	< 50	Basal	No
Morphospecies 2	> 50	Edge and midrib and others	Yes
Morphospecies 3	> 50	Apical, basal, edge, and midrib and others	Yes
Morphospecies 4	> 50	Apical	No
Morphospecies 5	> 50	Apical-basal	Yes

diurnal surveys were conducted to collect plants whose leaves were potentially consumed by the bats. Bats were identified through multiple direct observations of individuals perching on the feeding perches, which were consistently used each night. To confirm these observations, bats were also captured using mist nets set up around the feeding perches. Species identification was conducted using regional field guides (Medellín et al. 2008; Reid 2009).

To assess the diversity of fruits and leaves consumed at the feeding perches, we analyzed the collected samples, categorizing the remains of each identified food item. Leaf consumption was classified into five distinct patterns: basal, apical, edge, apical-basal, and vein. In the basal pattern,





**Supplemental material 1.** Leaves with trichomes. a) *Solanum* sp. 2 (lower surface), b) Morphospecies 5 (lower surface), c) *Liabum* sp., (lower surface) d) *Solanum* sp. 2 (upper surface).



bites are concentrated at or along the leaf base; in the apical pattern, bites occur at or along the leaf apex. The edge pattern involves bites along the entire leaf margin, while the apical-basal pattern features bites at both the apex and base, sparing the middle and margins. The vein pattern includes bites along the midrib and adjacent areas of the lamina. To quantify the proportion of each leaf consumed, we classified the patterns based on whether less than or greater than 50% of the leaf was consumed.

A total of 24 food items were documented at nocturnal feeding perches within PNNU, consisting of leaves of 9 species and seeds of 15 species (Table 1; Figure 2). October exhibited the highest species richness, with leaves of 7 species and seeds of 11 species, while December had the lowest diversity, with only seeds of 4 species and no leaf consumption.

Among the fruit species observed, *Spondias purpurea*, *Syzygium jambos*, *Ficus* sp., and *Solanum* sp. were consistently present across all months. *Rhaphiolepis bibas* was exclusive to September and October. Other seeds, including *Areca* sp., *Casearia* sp., *Panicum* sp., and Morphospecies 1–3, were recorded in only one month. The 9 leaf species observed included those from the genera *Sinclairia*, *Solanum* and *Lycianthes*, along with other species cataloged as Morphospecies (Morphospecies 1–5). Leaf consumption was documented from September to November, with no evidence of leaves being consumed in December. Leaves of *Solanum*, *Sinclairia* and Morphospecies 3 were the most frequently consumed (Figure 2).

The number of nibbled leaves by *A. lituratus* varied across months, with the highest number in October ( $n = 24$ ), followed by September ( $n = 11$ ) and November ( $n = 3$ ). Five distinct leaf-ingestion patterns were identified (Figure 3), with the basal pattern being the most predominant (Table 2). The proportion of the leaf consumed varied among species, with consumption exceeding 50% in 7 of the 9 leaf species. Most of the consumed leaves shared a smooth and pubescent surface, with trichomes arranged in various configurations. Of the 9 leaf species, 7 exhibited trichomes in varying densities on both surfaces (Supplemental material 1).

This study provides novel insights into the feeding ecology of *A. lituratus* in Guatemala, highlighting its dietary plasticity and ability to exploit resources underutilized by other frugivorous bats. Notably, *Sinclairia sublobata* leaves were recorded for the first time as a dietary resource for any bat species. Furthermore, the frequent consumption of *Solanum* leaves, previously documented in the diet of *A. lituratus* (Duque-Márquez et al. 2019; Rodrigues et al. 2023), extends the knowledge of the consumption of leaf species from this genus into the region.

A distinct pattern of leaf consumption was observed, with a preference for the basal section (Figure 2 and Table 2). This is consistent with previous studies, which suggest that the higher concentrations of nutrients and water,

combined with lower fiber content, make the basal portion more attractive to frugivorous bats (Zortéa and Mendes 1993; Kunz and Diaz 1995; Ruiz-Ramoni et al. 2011; Cordero-Schmidt 2016; Duque-Márquez et al. 2019). The uneven distribution of nutrients and water, typically higher at the base, likely drives this preference (Sandars et al. 2010). In the case of the 9 leaf species, 7 exhibited trichomes on both surfaces, with densities varying across species. These structures, commonly developed by some plants to prevent herbivory (São-João and Raga 2016; Karabourniotis et al. 2020), seem to have no effect on *A. lituratus*.

The evidence of feeding behavior by *A. lituratus* in the PNNU showed consistent fruit consumption over the four months of observation, whereas leaf consumption was observed in only three of those months. Notably, the evidence of leaf consumption indicated a gradual decline over time; however, the available observations are insufficient to establish this as a pattern. Among the fruits, species from the families Solanaceae (*Solanum* sp.), Moraceae (*Ficus* sp.), and Anacardiaceae (*Spondias purpurea*) were the most frequently consumed, while for leaves, the families Solanaceae (*Solanum* sp.) and Asteraceae (*Liabum* sp.) were the most common.

*Artibeus lituratus* is exploiting plant species that were once part of the restoration programs in the PNNU, including exotic plants such as *Areca* sp. (Arecaceae), *R. bibas* (Rosaceae), and *S. jambos* (Myrtaceae), which were intentionally introduced to support the park's biodiversity (CONAP 2005). The recovery zone, primarily resulting from human-mediated ecological restoration, now provides these resources. The findings from this study offer evidence of the integration of biodiversity within these restoration efforts and highlight the species' flexibility in utilizing both native and non-native resources.

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