



# BATS AND TERMITE NESTS: ROOSTING ECOLOGY OF *Lophostoma brasiliense* (CHIROPTERA: PHYLLOSTOMIDAE) IN COLOMBIA

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**ABSTRACT.** Interactions of bats with their roosts have played an important role in bat evolution. These interactions are well-known in frugivorous bats, where it has been found that several morphological characters may be associated to specific roosts, as in tent-roosting species from subtribes Vampyressina and Artibeina or foliage-roosting bats Stenodermatina. However, data on interactions between bats and roosts are scarce for several other groups. This is the case for *Lophostoma* species and termite nests, which are the preferred shelters for this genus. Herein we provide new data on roosting ecology of the bat *Lophostoma brasiliense*, along with information on diet and activity patterns. We additionally compiled data on use of termite nests by these bats. *L. brasiliense* consumed 11 food items, mainly Coleoptera and Heterocera and were more active between 00:00 and 02:00 h. According to our results *L. brasiliense* and *L. silvicolum* are strongly associated with termite nests and each of these species appears to have particular roost requirements. The use of termite nest is currently documented for 15 bat species with a high frequency in *Lophostoma* species, but evolutionary mechanisms that generated the use of this type shelter remain unknown.

**RESUMEN.** Murciélagos y termiteros: ecología del refugio de *Lophostoma brasiliense* (Chiroptera: Phyllostomidae) en Colombia. Las interacciones de los murciélagos con sus refugios han jugado un rol importante en la evolución de estos organismos. Estas interacciones son bien conocidas en murciélagos frugívoros, donde se ha encontrado que varios caracteres morfológicos pueden estar asociados a refugios específicos, como en las especies de las tribus Vampyressina y Artibeina que construyen tiendas de campaña en hojas o de la tribu Stenodermatina que se refugian en el follaje. Sin embargo, datos sobre interacciones entre murciélagos y sus refugios son escasos para otros grupos. Este es el caso para las especies de *Lophostoma* y los termiteros, los cuales son el refugio preferido por este género de murciélagos. Aquí, nosotros proveemos nuevos datos sobre la ecología del refugio del murciélago *Lophostoma brasiliense*, incluyendo información sobre dieta y patrones de actividad. Adicionalmente, compilamos datos sobre el uso de termiteros por murciélagos. *L. brasiliense* consumió 11 ítems alimenticios, principalmente Coleoptera y Heterocera y presentó una mayor actividad entre las 00:00 y 02:00 h. De acuerdo a los resultados, *L. brasiliense* y *L. silvicolum* están fuertemente asociados a los termiteros y cada una de estas especies parece tener requerimientos particulares de refugio. El uso de termiteros es documentando para 15 especies de murciélagos con una mayor frecuencia en las especies de *Lophostoma*, pero los mecanismos evolutivos que generaron el uso de este tipo de refugios permanecen desconocidos.

**Key words:** natural history, Pygmy Round-eared Bat, roost bats, termite nest

**Palabras clave:** historia natural, murciélago de orejas redondas pigmeo, refugios de murciélagos, termiteros.

## INTRODUCTION

The availability of food and roosts are key factors that limit the distribution, population density and reproductive biology of bat species (Dechmann & Kerth 2008). The importance of diurnal roosts for bats has been long known (Kunz 1982), but the evolutionary mechanisms underlying the interactions between bats and their roosts are still poorly studied. Recent evidences from fruit-eating bats, showed correlations between the use of foliage and leaf tents as roosts, with morphological and ecological attributes, considering pelage patterns, group size and social organization (Santana et al. 2011; Garbino & Tavares 2018; Tavares et al. 2018).

Most bats may compete for the use of roosts and many species do not actively build them (Kalko et al. 2006). There are, currently, more than 1386 bat species known (Burgin et al. 2018) and only approximately 35 species use structures modified by themselves to roosting, such as leaves, stems, parts of plants (Kunz & McCracken 1996; Kunz & Lumsden 2003), and ant and termite nests (Dechmann et al. 2009; Chaverri & Kunz 2010). Both modification and use of termite nests is rare among bats, and only three species has been documented to have this roosting habits: *Lophostoma silvicolum* d'Orbigny, 1836, *Lophostoma carrikeri* (Allen 1910) and *Lophostoma brasiliense* Peters, 1867 (York et al. 2008; Voss et al. 2016).

It is known that males of *L. silvicolum* use their teeth to modify active termite nests and use them as roost, suggesting adaptations to roost excavation. Besides, these adaptations could represent advantages for reproductive success of the male, because females use termitaries as maternity roosts (Dechmann et al. 2009). Thus, the ability of males to modify and use termite nest appears to be a behavior selected by females (Dechmann & Kerth 2008). Although such interactions with termite nests have been explored in *L. silvicolum*, the roosting ecology is poorly understood for other species of *Lophostoma*.

There are reports of roosting *L. brasiliense*, in termite nests, from several sites along its neotropical distribution, including Belize (Reid 1997), Brazil (Peracchi & Albuquerque 1993), Costa Rica (York et al. 2008), Panama (Handley 1966), Peru (Kalko et al. 2006; Voss et al. 2016), Trinidad and

Tobago (Goodwin & Greenhall 1961), and Venezuela (Robinson & Lyon 1901; Handley 1976). Nevertheless, they are based on occasional encounters and do not provide details about social organization, architecture and size of termite nests that are used by the bats, which allows us to see possible patterns in their choice as shelter. Also, there is not a comprehensive compilation of records of bats in termite nests to serve as a base to analyzing variations on the roosting behavior of termite nest's bats.

We herein report observations on the use of termite nests by *Lophostoma brasiliense* in Colombia, including information on both diet and activity patterns. Also, we conduct a comprehensive compilation of records on associations between termite nest and bats, in order to investigate the frequency of use of this shelter type by Chiroptera.

## MATERIAL AND METHODS

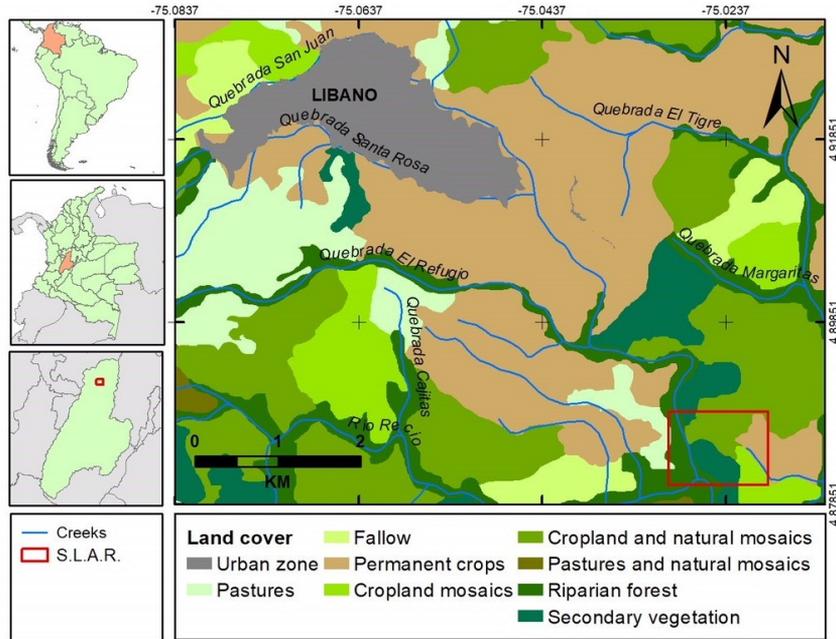
### Study area

The study was conducted at Santa Librada Agroecological Reserve (SLAR), in El Líbano municipality, on department of Tolima over the central cordillera of Colombia, at 800 m elevation (4.8758 N; 75.0225 W; Fig. 1). The area encompasses 52 ha of secondary forest in distinct stages of succession, mixed in a mosaic of coffee and cacao plantations, as well as native species, such as *Anacardium excelsum*, *Annona cherimola*, *Carludovica palmata*, *Cecropia peltata*, *Cedrela montana*, *Erythrina fusca*, *Heliconia bihai*, *Lafoesia acuminata* and *Ochroma pyramidale*. The average annual temperature is 23°C and the average annual rainfall ranged from 1500 to 2000 mm.

### Roost and group/colony characterization

We made one observation per each shelter of *L. brasiliense* (two termite nests and one underneath houses basement), in January 2016 and January 2018, for a total of six observations. We recorded width, length, height, and diameter measurements for each of the termite nest, using a one-meter professional measuring rule. To count the number of individuals, present in each shelter and in every visit, we capture the individuals using an entomological net and mist-nets placed around the nests.

Each captured individual was sexed, identified, measured with a 0.01 mm-accuracy digital caliper, weighed, photographed, and reproductive status was determined based on the presence / absence of nipples, the size and position of the testicles and the degree of ossification of the metacarpals (Morris 1972). We collected two specimens which were deposited in the mammal collection of Museo de Historia Natural de la Universidad Distrital Francisco José de Caldas, under catalogue numbers MUD 1140 and



**Fig. 1.** Location of the roosts of *Lophostoma brasiliense* in the Santa Librada Agroecological Reserve, El Líbano, department of Tolima, Central Andes in Colombia.

MUD 1141. The taxonomic identification follows Gardner (2007) and Díaz et al. (2016).

## Diet

The diet was inferred from fecal samples, left by the bats in the cloth bags and collected under each shelter. Parts of insects collected were separated, identified and quantified by the number of wings, legs and exoskeleton of prey that were found, with the help of a Leica EZ4 HD stereoscope. Parts of arthropod wings were cleaned using a 10%phenol solution, being later dried and photographed. We followed Warren et al. (2013) for the taxonomic determination and had the collaboration of experts for some confirmations. The food items were identified to the lowest possible taxonomic level, mostly to the level of order. Additionally, we built a reference collection of specimens, mainly of Coleoptera, Diptera and Lepidoptera, that were captured 10 meters around the shelter's sites, for later comparison with the fragments found in the feces. For this proposal, we used Van Someren-Rydon, entomological nets and light traps. We also include data about composition and abundance of insects present in SLAR, that were collected between 2017 and 2018 (Valenzuela et al. 2019). The frequency of consumption of each prey item was calculated by the number of parts containing such item over the total number of analyzed samples.

## Activity patterns

Once identified, a female and a male that were located underneath a house's basement, were studied by direct

observations, in order to know the activity patterns of these individuals. The observations were made during three nights (January 15-17, 2018, during the Moon's new phase), in which two researchers seated 10 meters away of the bat's shelter-that had a unique exit-at different places, they counted the number of entry and exit of the bats to the shelter each night, as well as the duration of these movements. The activities were classified, according to the number of departures, as follows: low activity (less than five exits per hour), average activity (between five and 10 exits per hour) and high activity (more than 10 exits per hour). It was not possible to discriminate the number of exits for each sex (male and female).

## Bats and Termite nests database compilation

To determine the frequency of use of this type of shelter, among Chiroptera, we conducted a literature review on termite nests used by bats, by using several tools, such as Google Scholar (<https://scholar.google.com/>), ISI Web of Knowledge (<http://www.webofknowledge.com>), Scopus (<https://www.scopus.com>), Biodiversity Heritage Library (<https://www.biodiversitylibrary.org/>) and institutional repositories. For these searches, we used keywords in Spanish, English and Portuguese for the terms "termites", "termite mounds", "ant nests", "termite nests", "termitaria", "use of termite nest", "bats", "Chiroptera", and "*Lophostoma*". Our compilation also included unpublished roosting data and photographs of different authors which unambiguously allowed the identification of these species.

## RESULTS

### Roosting ecology of *Lophostoma brasiliense*

We collected information on the roosting ecology from three *L. brasiliense* colonies, two of them occupying termite nests and one roosting on a shelter (underneath house's basement). All shelters were found inside human-made structures.

Shelter 1: On January 25<sup>th</sup>, 2016, we recorded seven individuals of *L. brasiliense* hanging inside an active termite nest. The termite nest built by *Nasutitermes* spp. (Isoptera: Termitidae), was 57 cm height, 44 cm width, presenting two cavities. The first cavity, which was used by bats, was 28.8 cm deep with 9 cm of diameter, while second cavity, not occupied by bats, was 24 cm deep with a diameter of 5.8 cm (Fig. 2). This termite nest, at 2.5 meters above ground, was located on the roof of an abandoned house. Bats were not the only animals using the termite nest: juveniles and adults of *Blaberus giganteus* (Blattodea: Blaberidae) cockroach occupied the second cavity, while the *Pheidole* spp. (Hymenoptera: Formicidae) was occupying both cavities of the nest. The presence of *Pheidole* spp. and *Nasutitermes* spp., seemed not to bother the bats, which even had some of these organisms in their bodies. The social group of *L. brasiliense* consisted of four females (three adults and one juvenile), two males (adult and juvenile) and another individual that we were not able to capture. Two years later, we visit again this termite nest, but termitaria did not have bats, termites or ants.

Shelter 2: We found this shelter on January 12<sup>th</sup>, 2018. It was occupied by three individuals and located in an abandoned house, at two meters above ground. This termite nest showed no signs of the presence of termites or ants. It was 50 cm high and 42 cm wide, and had a single cavity with 5.1 cm diameter and 20 cm depth. Bats shared this cavity with a juvenile *Blaberus giganteus*. This social group of *L. brasiliense* was composed of two adult females, and one adult male.

Shelter 3: We captured and identified two adult bats, a female and a male, of *L. brasiliense* in a shelter that was located underneath house's basement, on January 15<sup>th</sup>, 2018. Bats were hanging at <40 cm distance from the ground. This site only had one exit and it was the only shelter located in this inhabited house.

In Table 1, we summarize these termite nests measurements and compared them to the measurements made by Kalko et al. (2006) and York et al. (2008).

### Diet of *Lophostoma brasiliense*

From analyses of fecal samples, we found remains of wings, legs, antennae, mouth parts, and other fragments, totaling 185 parts of preys, corresponding to six orders of insects. Coleoptera, Heterocera and Hymenoptera were the most frequently consumed preys (respectively, 26.5%, 20% and 14.6%), while Blattodea and Orthoptera were the least consumed (Table 2). Dietary composition included those insects species more close to the nest with a high frequency of beetles (Melolonthidae) and moths (Heterocera).

### Activity patterns

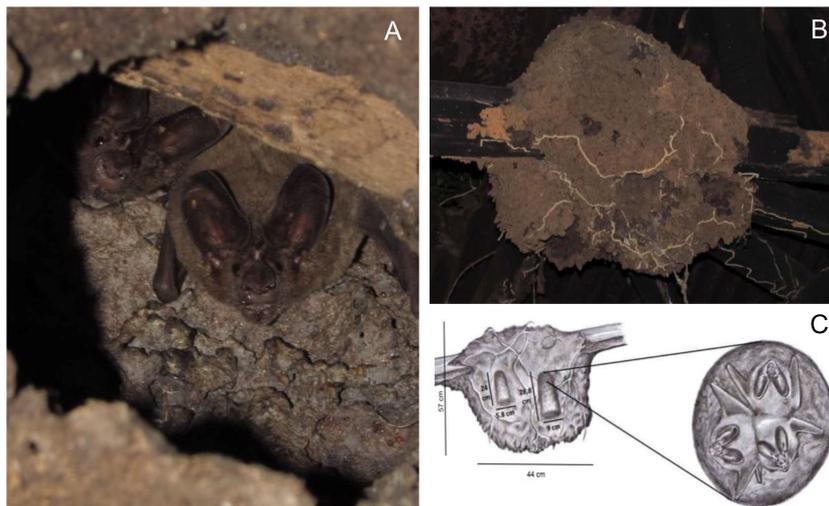
We recorded a moderate activity between 17:30 and 19:30 h. Bats' activities were low, with five exits in this period, and the individual flights out of the termite nets did not last more than five minutes. Between 19:30 and 00:00 h the activity dropped even more and we only observed two sporadic flight outs. The most intense activity was observed between 00:00 and 02:00 h, with more than 25 exits, each lasting for approximately two minutes. After this time, activity was low, with less of five flight outs until dawn.

### Bats and use of termite nest

We compiled a total of 55 records of termite nests used by 15 bat species from five families in 25 localities around the world, including our own data. Our compilation showed that termite nests were used by bats from the families: Phyllostomidae (10 species), followed by Emballonuridae (2), Vespertilionidae (1), Pteropodidae (1), and Nycteridae (1). It is noteworthy that 87.3% of the records is associated with species of subfamily Phyllostominae, and 78.2% is related to species of the genus *Lophostoma* (*L. brasiliense*, N = 19; *L. carrikeri*, N = 2; *L. evotis*, N = 2; *L. kalkoae*, N = 1; *L. silvicolum*, N = 19), showing a high preference of such shelters by species of this genus (Table 3).

## DISCUSSION

The nests we observed have similar measurements to those reported by other authors. Our termites nest were located at a similar height, had the same depth, but were smaller and narrower than those reported by Kalko et al. (1999) in Peru. York et al. (2008) did



**Fig. 2.** Termite nest used by *Lophostoma brasiliense* in Central Andes, El Libano-Tolima, Colombia. A. Bats roosting inside termite nest, B. Termite nest in abandoned houses roof and C. Graphic representation of termite nest with bats inside.

**Table 1**  
 Termite nest measurements used by *Lophostoma brasiliense*.

	Kalko et al. (2006)	York et al. (2008)	Nest 1 cavity 1	Nest 1 cavity 2	Nest 2
Height nest	60-70	-	57	57	50
Width nest	60-70	-	44	44	42
Depth entrance	28	20	28.8	24	20
Diameter entrance	6	-	9	5.8	5.1
Height above ground	-	2.5 m	2.5 m	2.5 m	2 m
Number of individuals	5	5	7	0	3

not offer measures of the termitaria in Costa Rica and only described a termite nest with about 20 cm of depth and therefore shallower than ours.

*L. brasiliense* has been reported using termite nests of *Microcerotermes arboreus* and *Nasutitermes* spp. (Isoptera: Termitidae) in Trinidad and Costa Rica respectively (Goodwin & Greenhall 1961) and in shelters located between 1.5-2.5 meters above ground as recorded by several authors (Handley 1966; Peracchi & Albuquerque 1993; York et al. 2008).

Records of individuals of *L. brasiliense* roosting in termite nests vary from a single individual to groups with up to five individuals. Peracchi & Albuquerque (1993) and York et al. (2008) found five individuals occupying the same nest at once, while Rojas-Rojas-Rojas et al. (2015) and Goodwin & Greenhall (1961) found groups of four individuals. Here, we reported the largest group currently found with seven individuals occupying a same nest which

is remarkable due to space constraints offered by termite nest.

Activity patterns of *L. brasiliense* are little known (Mangolin et al. 2007) and have been hypothesized to be similar to *L. silvicolum* patterns, which has a somewhat sedentary behavior and appears to stay close to its roost and foraging at distances from 200 to 500 m (Kalko et al. 1999). Our observations suggest that *L. brasiliense* may also be a sedentary hunter, moving away from its roosts for short distances. Mangolin et al. (2007) reported a high and constant activity of *L. brasiliense* late at night, when the bats used to leave their roosts for brief periods, whose were shorter than those reported to the species *L. silvicolum* by Kalko et al. (1999).

### Termitaria as nest sites for bats

Our compilation on the use of termite nests by bats is the first review on the subject. We have shown that most bats using termite nests are insectivores

**Table 2**Diet of *Lophostoma brasiliense* in Santa Librada Agroecological Reserve, El Líbano-Tolima, Colombia.

ORDER	SUBORDER/FAMILY	SPECIES	CONSUMPTION FREQUENCY		PROPORTION ORDER LEVEL
			NO. PREY	% PREY	
Blattodea	-	-	1	0.54	0.54
Coleoptera	Melolonthidae	-	26	14.05	26.48
	Scarabaeidae	-	4	2.16	
	Chrysomelidae	-	1	0.54	
	Unidentified	-	18	9.73	
Hemiptera	-	-	8	4.32	4.32
Hymenoptera	-	-	27	14.60	14.60
Lepidoptera	Hesperiidae	<i>Astrartes alardus</i>	1	0.54	20.00
	Riodinidae	<i>Eurybia lycisca</i>	1	0.54	
	Saturniidae	-	1	0.54	
	Heterocera	-	34	18.37	
Orthoptera	-	-	1	0.54	0.54
Unidentified	-	-	62	33.51	33.51
Total			185	100	100

(74%), which contrasts with the prevalence of the use of modified and unmodified leaves for roosting in frugivorous bats (Garbino & Tavares 2018). Some bats can use termite nests opportunistically since this behavior has been reported for some species, such as the fruit-eating bat *Artibeus fraterculus* (Carrera et al. 2010; Hernández-Mijangos 2010), the carnivore bat *Chrotopterus auritus* (Sanborn 1932; Medellín 1989), the insectivore *Micronycteris megalotis* (Patterson 1992), *Phyllostomus hastatus* (Voss et al. 2016), the emballonurid species *Saccopteryx canescens*, and *S. leptura* (Ibañez 1981), and the old world species *Murina florium* (Clague et al. 1999) and *Balionycteris maculata* (Hodgkison et al. 2003).

Nesting inside termitaria can offer advantages for bats, such as protection against predators and a suitable micro-climate (Boonman 2000). However, not every termite nest is occupied, although this resource can be abundant or scarce. Villalobos-Chaves et al. (2016) observed a low rate of occupation of termites nests in Costa Rica (1 out of 74 nests) and Mangolin et al. (2007) only recorded two occupied termite nests out of ten in Brazil. In our study, after two visits (2016 and 2018) each one with 30 sampling days (unpublished data), we did not find more termite nests, despite the intensive searches that we carried out, suggesting the possibility that

these types of shelters are scarce in our study area. Also, the low occupation rates of termite nests can be due to low population densities and high selectivity of termite nests for this species. Kalko et al. (2006) showed that the quality of roosts, including the physical structure of the termite nests, is key to roosting choice by the bats.

Although there are some reports on the occupation of tree holes (Handley 1966), small cavities in rocks (Robinson & Lyon 1901) and human-made structures -as reported by Hice et al. (2004) and this work- the majority of data available (see Table 3) point to a noteworthy preference of termite nests by *L. brasiliense*.

Therefore, although at a first glance, the occupation of termite nests appears to be opportunistic, we herein compiled evidence to reinforce the occurrence of unique relationships between species of *Lophostoma* and termite nests. This rare roosting behavior of *Lophostoma* species in termite nests could represent constraints for species conservation, related to the very specific requirements regarding food or shelter (Sagot & Chaverri 2015) that may be enhanced by threats and concurrent effects, as given by habitat loss and fragmentation.

**Table 3**  
 Compilation on reports of bats using termite nests as roosts worldwide.

Family	Species	Country	Roost type	Reference
Emballonuridae	<i>Saccopteryx canescens</i>	Venezuela: Apure State	Termite nest	Ibañez (1981)
	<i>Saccopteryx leptura</i>	Venezuela: Apure State	Termite nest	Ibañez (1981)
Phyllostomidae	<i>Artibeus fraterculus</i>	Ecuador: Guayas, Manglares Churute Ecological Reserve	Termite nest	Carrera et al. (2010)
	<i>Artibeus lituratus</i>	Mexico: Chiapas, La Encrucijada Biosfera Reserve	Termite nest	Hernández-Mijangos (2010)
	<i>Chrotopterus auritus</i>	Bolivia: Sara Providence, Dolores river	Termite nest	Sanborn (1932); Medellín (1989)
	<i>Lophostoma brasiliense</i>	Belize: Lamanai	Termite nest	Reid (1997)
	<i>Lophostoma brasiliense</i>	Brazil: Espírito Santo State, Linhares	Termite nest	Peracchi & Albuquerque (1993)
	<i>Lophostoma brasiliense</i>	Colombia: Caldas department	Termite nest	Rojas-Rojas et al. (2015)
	<i>Lophostoma brasiliense</i>	Colombia: Caldas department	Termite nest	Rojas-Rojas et al. (2015)
	<i>Lophostoma brasiliense</i>	Colombia: Tolima, El Libano, Santa Librada Reserve	Termite nest	This work
	<i>Lophostoma brasiliense</i>	Costa Rica: Puntarenas	Termite nest	Plerson Hill 2009 (Unpublished)
	<i>Lophostoma brasiliense</i>	Costa Rica: Sarapiquí, Bijagual Ecological Reserve	Termite nest	York et al. (2008)
	<i>Lophostoma brasiliense</i>	Peru: Amazonian region	Termite nest	Voss et al. (2016)
	<i>Lophostoma brasiliense</i>	Peru: Iquitos, German Primate Center	Termite nest	Kalko et al. (2006)
	<i>Lophostoma brasiliense</i>	Trinidad: Aripo and Irois Forest	Termite nest	Goodwin & Greenhall (1961)
	<i>Lophostoma brasiliense</i>	Trinidad: Aripo and Irois Forest	Termite nest	Goodwin & Greenhall (1961)
	<i>Lophostoma brasiliense</i>	Costa Rica: Sarapiquí, Heredia Province	Termite nest	Villalobos-Chaves et al. (2016)
	<i>Lophostoma brasiliense</i>	Colombia: Antioquia: Zaragoza	Termite nest	USNM 499293-499294; captured by Peterson, N.E. 1971
	<i>Lophostoma brasiliense</i>	Trinidad and Tobago	Termite nest	Daniel Hargreaves 2016 (Unpublished)
	<i>Lophostoma brasiliense</i>	Costa Rica	Termite nest	Adriana Zuniga Castro 2017 (Unpublished)
	<i>Lophostoma brasiliense</i>	Costa Rica	Termite nest	Manuel Sánchez Mendoza 2016 (Unpublished)
	<i>Lophostoma brasiliense</i>	Nicaragua	Termite nest	Plan Conservación Murciélagos Nicaragua 2016 (Unpublished)
	<i>Lophostoma brasiliense</i>	Costa Rica	Termite nest	Juan Carlos Vargas Mena 2012 (Unpublished)
	<i>Lophostoma brasiliense</i>	Trinidad	Termite nest	Merlin Tuttle 2016 (Unpublished)
	<i>Lophostoma carrikeri</i>	Venezuela: Mocho river	Termite nest	Allen (1910)
	<i>Lophostoma carrikeri</i>	Colombia	Termite nest	McCarthy et al. (1983; 1992)
	<i>Lophostoma evotis</i>	Belize: Lamanai	Termite nest	Reid (1997)
	<i>Lophostoma evotis</i>	Belize: Toledo	Termite nest	McCarthy et al. (1993)
	<i>Lophostoma kalkoae</i>	Panama: Colón, Soberanía National Park	Ant nest	Velazco & Gardner (2012)
	<i>Lophostoma silvicolum</i>	Panama	Termite nest	Handley (1966)
	<i>Lophostoma silvicolum</i>	Peru: Amazonian region	Termite nest	Voss et al. (2016)
	<i>Lophostoma silvicolum</i>	Peru: Iquitos, Itaya river	Termite nest	Rengifo et al. (2013)
	<i>Lophostoma silvicolum</i>	Venezuela	Termite nest	Handley (1976)
	<i>Lophostoma silvicolum</i>	Panama: Gatun Lake, Barro Colorado Island	Termite nest	Kalko et al. (1999)
	<i>Lophostoma silvicolum</i>	Panama: Gatun Lake, Barro Colorado Island	Termite nest	Kalko et al. (1999)
<i>Lophostoma silvicolum</i>	Peru: Iquitos	Termite nest	Kalko et al. (2006)	
<i>Lophostoma silvicolum</i>	Peru: Iquitos	Termite nest	Díaz & Díaz & García (2012)	
<i>Lophostoma silvicolum</i>	Peru: San Juan	Termite nest	Tuttle (1970)	
<i>Lophostoma silvicolum</i>	Panama: Barro Colorado Island	Termite nest	Christian Ziegler 2010 (Unpublished)	
<i>Lophostoma silvicolum</i>	Nicaragua: Rivas	Termite nest	Tamara Pérez Rodríguez 2012 (Unpublished)	
<i>Lophostoma silvicolum</i>	Nicaragua: Rivas	Termite nest	Iveth Pérez 2012 (Unpublished)	
<i>Lophostoma silvicolum</i>	Peru: Amazonian region	Termite nest	Voss et al. (2016)	
<i>Lophostoma silvicolum</i>	Peru: Amazonian region	Termite nest	Voss et al. (2016)	
<i>Lophostoma silvicolum</i>	Peru: Amazonian region	Termite nest	Voss et al. (2016)	
<i>Lophostoma silvicolum</i>	Panama: Gatun Lake, Barro Colorado Island	Termite nest	Kalko et al. (2006)	
<i>Lophostoma silvicolum</i>	Panama: Gatun Lake, Barro Colorado Island	Termite nest	Carl koford in 1944 cited by Kalko et al. (2006)	
<i>Lophostoma silvicolum</i>	Brazil: Manaus	Termite nest	Kalko et al. (2006)	
<i>Lophostoma silvicolum</i>	Costa Rica: Sarapiquí, Heredia Province	Termite nest	Villalobos-Chaves et al. (2016)	
<i>Micronycteris megalotis</i>	Brazil: Aveiros	Termite nest	Patterson (1992)	
<i>Phyllostomus hastatus</i>	Peru: Amazonian region	Termite nest	Voss et al. (2016)	
<i>Phyllostomus hastatus</i>	Peru: Amazonian region	Termite nest	Tuttle (1970)	
<i>Phyllostomus hastatus</i>	Brazil: Manaus	Termite nest	Reis & Peracchi (1987)	
Vespertilionidae	<i>Murina florium</i>	Australia	Termite nest	Clague et al. (1999)
Pteropodidae	<i>Balonycteris maculata</i>	Malaysia: Kuala Lompat, Krau Wildlife Reserve	Termite nest	Hodgkison et al. (2003)
Nycteridae	<i>Nycteris hispida</i>	South Africa	Holes in termitaria	Monadjem et al. (2016)

## CONCLUSIONS

We reviewed evidence of the strong association between termite nest and *Lophostoma* species and we provide new data on the roosting ecology of *L. brasiliense*. Future studies should consider other interactions between bats and termites, not addressed in this review, as for example chemical responses of termites against the modification and use of its termitaria and the possible influence of termite species in bat distribution. Further studies could help to elucidate the evolutionary history and distribution patterns of the genus.

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## LITERATURE CITED

- ALLEN, J. A. 1910. Mammals from the Caura District of Venezuela, with description of a new species of *Chrotopterus*. American Museum of Natural History 28:145–149.
- BOONMAN, M. 2000. Roost selection by noctules (*Nyctalus noctula*) and Daubenton's bats (*Myotis daubentonii*). Journal of Zoology 251:385–389. <https://doi.org/10.1017/S0952836900007123>
- BURGIN, C., J. P. COLELLA, P. L. KAHN, & N. S. UPHAM. 2018. How many species of mammals are there? Journal of Mammalogy 99:1–14. <https://doi.org/10.1093/jmammal/gyx147>
- CARRERA, J. P. ET AL. 2010. Bats of the tropical lowlands of western Ecuador. Special Publications Museum of Texas Tech University 57:1–37. <https://doi.org/10.5962/bhl.title.142936>
- CHAVERRI, G., & T. H. KUNZ. 2010. Ecological determinants of social systems. Perspectives on the functional role of roosting ecology in the social behavior of tent-roosting bats. Advances in the Study of Behavior 42:275–318. [https://doi.org/10.1016/S0065-3454\(10\)42009-4](https://doi.org/10.1016/S0065-3454(10)42009-4)
- CLAGUE, C., R. COLES, O. WHYBIRD, H. SPENCER, & P. FLEMONS. 1999. The occurrence and distribution of the tube-nosed insectivorous bat (*Murina florium*) in Australia. Proceedings of the Linnean Society of New South Wales 121:175–191.
- D'ORBIGNY, A. 1836. Mammifères. Voyage dans l'Amérique méridionale (le Brésil, la République orientale de l'Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivie, la République du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830. (A. d'Orbigny, ed.). Chez Pitois-Levrault, Paris. <https://doi.org/10.5962/bhl.title.85973>
- DECHMANN, D., & G. KERTH. 2008. My home is your castle: roost making is sexually selected in the bat *Lophostoma silvicolum*. Journal of Mammalogy 89:1379–1390. <https://doi.org/10.1644/08-MAMM-S-061.1>
- DECHMANN, D., S. E. SANTANA, & E. R. DUMONT. 2009. Roost making in bats—Adaptations for excavating active termite nests. Journal of Mammalogy 90:1461–1468. <https://doi.org/10.1644/09-MAMM-A-097R.1>
- DÍAZ, M. M., & V. H. LINARES GARCÍA. 2012. Refugios naturales y artificiales de Murciélagos (Mammalia: Chiroptera) en la selva baja en el Noroeste de Perú. Gayana (Concepción) 76:117–130. <http://dx.doi.org/10.4067/S0717-65382012000300005>
- DÍAZ, M. M., S. SOLARI, L. F. AGUIRRE, L. M. AGUIAR, & R. M. BARQUEZ. 2016. Clave de identificación de los murciélagos de Sudamérica – Chave de identificação dos morcegos da América do Sul. PCMA (Programa de Conservación de los Murciélagos de Argentina) (Publicación Especial 2), Tucumán, 160 pp.
- GARBINO, G. S. T., & V. D. C. TAVARES. 2018. Roosting ecology of Stenodermatinae bats (Phyllostomidae): evolution of foliage roosting and correlated phenotypes. Mammal Review 48:75–89. <https://doi.org/10.1111/mam.12114>
- GARDNER, A. L. (ED.). 2007. Mammals of South America. Volume 1. Marsupials, Xenarthrans, Shrews, and Bats. The University of Chicago press. Chicago.
- GOODWIN, G., & A. M. GREENHALL. 1961. A review of the bats of Trinidad and Tobago: descriptions, rabies infection, and ecology. American Museum of Natural History 122:187–302.
- HANDLEY, C. O. 1966. Checklist of the mammals of Panama. Ectoparasites of Panama (R. L. WENZEL & V. J. TIPTON, eds.). Field Museum Natural History Press, Chicago. p. 753–795.
- HANDLEY, C. O. 1976. Mammals of the Smithsonian Venezuelan Project. Brigham Young University Science Bulletin 20:1–89. <https://doi.org/10.5962/bhl.part.5667>
- HERNÁNDEZ-MIJANGOS, L. A. 2010. Uso de termitero como refugio por *Artibeus lituratus* (Chiroptera: Phyllostomidae). Revista Mexicana de Mastozoología 14:59–63.
- HICE, C., P. M. VELAZCO, M. R. WILLIG. 2004. Bats of the Reserva Nacional Allpahuayo-Mishana, Northeastern Peru, with notes on community structure. Acta Chiropterologica 6:1–16. <https://doi.org/10.3161/1508110042955568>
- HODGKISON, R., S. T. BALDING, Z. AKBAR, & T. H. KUNZ. 2003. Roosting ecology and social organization of the spotted-winged fruit bat, *Balionycteris maculata* (Chiroptera: Pteropodidae), in a Malaysian lowland dipterocarp forest. Journal of Tropical Ecology 19:667–676. <https://doi.org/10.1017/S0266467403006060>
- IBÁÑEZ, C. 1981. Biología y Ecología de los murciélagos del Hato "El Frio", Apure, Venezuela. Acta Vertebrata 8:1–263.
- KALKO, E. K., D. FRIEMEL, C. HANDLEY, & H. SCHNITZLER. 1999. Roosting and foraging behavior of two neotropical gleaning bats, *Tonatia silvicola* and *Trachops cirrhosus* (Phyllostomidae). Biotropica 31:344–353. <https://doi.org/10.1111/j.1744-7429.1999.tb00146.x>
- KALKO, E. K., K. UEBERSCHAER, & D. DECHMANN. 2006. Roost Structure, modification, and availability in the White-throated Round-eared Bat, *Lophostoma silvicolum* (Phyllostomidae) Living in Active Termite Nests. Biotropica 38:398–404. <https://doi.org/10.1111/j.1744-7429.2006.00142.x>
- KUNZ, T. H. 1982. Roosting ecology of bats. Ecology of Bats (T. H. Kunz, ed.). Plenum Press, New York, pp. 1–56.
- KUNZ, T. H., & G. F. MCCracken. 1996. Tents and harems: apparent defence of foliage roosts by tent-making bats. Journal of Tropical Ecology 12:121–137.
- KUNZ, T. H., & L. F. LUMSDEN. 2003. Ecology of cavity and foliage roosting bats. Bat Ecology (T. H. Kunz & M. B. Fenton, eds.). University of Chicago Press, Chicago, pp. 3–89
- MANGOLIN, R., A. G. MOTTA, C. E. ESBERARD, & H. C. BERGALLO. 2007. Novos registros de *Lophostoma brasiliense* Peters para o sudeste do Brasil (Mammalia, Chiroptera, Phyllostomidae). Revista Brasileira de Zootecias 9:225–228.
- MCCARTHY, T. J., A. A. CADENA, & T. O. LEMKE. 1983. Comments on the first *Tonatia carrikeri* (Chiroptera: Phyllostomidae) from Colombia. Lozania 40:1–6.
- MCCARTHY, T. J., A. L. GARDNER, & C. O. HANDLEY. 1992. *Tonatia carrikeri*. Mammalian species 407:1–4. <https://doi.org/10.2307/3504304>
- MCCARTHY, T. J., W. B. DAVIS, J. E. HILL, J. K. HILL, J. K. JONES, & G. A. CRUZ. 1993. Bat (Mammalia: Chiroptera) records, early collectors, and faunal lists for northern Central America. Annals of Carnegie Museum 62:191–228.

- MEDELLÍN, R. 1989. *Chrotopterus auritus*. Mammalian Species 343:1–5. <https://doi.org/10.2307/3504232>
- MONADJEM, A. ET AL. 2016. A conservation assessment of *Nycteris hispida*. The Red List of Mammals of South Africa, Swaziland and Lesotho (M. F. Child, L. Roxburgh, S. E. Do Linh, D. Raimondo, H. T. Davies-Mostert, eds.). South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- MORRIS, P. 1972. A review of mammalian age determination methods. Mammal Review 2:69–104. <https://doi.org/10.1111/j.1365-2907.1972.tb00160.x>
- PATTERSON, B. 1992. Mammals in the Royal Natural History Museum, Stockholm, collected in Brazil and Bolivia by A.M. Olalla during 1934-1938. Fieldiana Zoology 66:1–48. <https://doi.org/10.5962/bhl.title.3551>
- PERACCHI, A. L., & S. T. ALBUQUERQUE. 1993. Quirópteros do município de Linhares, estado do Espírito Santo, Brasil (Mammalia, Chiroptera). Revista Brasileira de Biologia 53:575–581.
- PETERS, W. 1867. Fernere Mittheilungen zur Kenntniss der Flederthiere, namentlich über Arten des Leidener und Britischen Museums. Monatsbericht der Königlich-Preussischen Akademie der Wissenschaften zu Berlin 1867:672–681.
- REID, F (ED.). 1997. A field guide to the Mammals of Central America and Southeast Mexico. Oxford University Press, New York.
- REIS, N. R., & A. L. PERACCHI. 1987. Quirópteros da região de Manaus, Amazonas, Brasil (Mammalia, Chiroptera). Boletim Museu Paraense Emilio Goeldi 3:161–182.
- RENGIFO, E. M., W. CALDERÓN, & R. AQUINO. 2013. Características de refugios de algunas especies de murciélagos en la cuenca alta del río Itaya, Loreto, Perú. UNED Research Journal/Cuadernos de Investigación 5:143–150.
- ROBINSON, W., & M. LYON. 1901. An annotated list of Mammals collected in the vicinity of La Guaira, Venezuela. Proceedings of the National Museum 24:135–162. <https://doi.org/10.5479/si.00963801.1246.135>
- ROJAS-ROJAS, A., J. CORRALES-ESCOBAR, C. SAAVEDRA-RODRÍGUEZ. 2015. Observaciones reproductivas de *Lophostoma brasiliense* (Chiroptera: Phyllostomidae) en el Magdalena medio. Memorias II Congreso Latinoamericano de Mastozoología, Bogotá D.C., Colombia.
- SANBORN, C. C. 1932. Neotropical bats in the Carnegie Museum. Annals Carnegie Museum 21:171–183.
- SAGOT, M., & G. CHAVERRI. 2015. Effects of roost specialization on extinction risk in bats. Conservation Biology 29:1666–1673. <https://doi.org/10.1111/cobi.12546>
- SANTANA, S. E., T. O. DIAL, T. P. EITING, & M. E. ALFARO. 2011. Roosting ecology and the evolution of pelage markings in bats. Plos One 10:e25845. <https://doi.org/10.1371/journal.pone.0025845>
- TAVARES, V. D. C., O. M. WARSÍ, F. M. BALSEIRO, C. A. MANCINA, & L. M. DÁVALOS. 2018. Out of the Antilles: Fossil phylogenies support reverse colonization of bats to South America. Journal of Biogeography 45:859–873. <https://doi.org/10.1111/jbi.13175>
- TUTTLE, M. D. 1970. Distribution and zoogeography of Peruvian bats: with comments on natural history. University of Kansas Publications 69:45–86. <https://doi.org/10.5962/bhl.part.9197>
- VALENZUELA, D., Y. JIMÉNEZ, J. ANGULO, & K. SUBA. 2019. Caracterización preliminar de insectos de la Reserva Agroecológica Santa Librada de Libano, Tolima como estrategia pedagógica para el estudio de la taxonomía. Gobernación del Tolima, BPIN:2012000100101.
- VELAZCO, P. M., & A. L. GARDNER. 2012. A new species of *Lophostoma* (Chiroptera: Phyllostomidae) from Panama. Journal of Mammalogy 93:605–614. <https://doi.org/10.2307/41480372>
- VILLALOBOS-CHAVES, D., J. VARGAS-MURILLO, E. ROJAS-VALERIO, B. W. KEELEY, & B. RODRIGUEZ-HERRERA. 2016. Understorey bat roosts, availability and occupation patterns in a Neotropical rainforest of Costa Rica. Revista de Biología Tropical 64:1333–1343. <https://doi.org/10.15517/RBT.V64I3.21093>
- VOSS, R. S., D. W. FLECK, R. E. STRAUSS, P. M. VELAZCO, & N. B. SIMMONS. 2016. Roosting Ecology of Amazonian Bats<U+202F>: Evidence for Guild Structure in Hyperdiverse Mammalian Communities. American Museum of Natural History 3870:1–43.
- WARREN, A., K. DAVIS, M. STANGELAND, J. PELHAM, N. GRISHIN. 2013. Butterflies of America. Visited May 21, 2019. <https://www.butterfliesofamerica.com/>
- YORK, H., P. F. FOSTER, M. F. JONES, W. H. SCHWARZ, A. L. VEZEAU, & M. S. ZERWEKH. 2008. Observations of cavity-roosting behavior in Costa Rican *Lophostoma brasiliense* (Chiroptera: Phyllostomidae). Mammalian Biology 73:230–232. <https://doi.org/10.1016/j.mambio.2007.02.008>