Roost Structure, Modification, and Availability in the White-throated Round-eared Bat, Lophostoma Silvicolum (Phyllostomidae) Living in Active Termite Nests¹

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ABSTRACT

We studied roost structure, modification, and availability in *Lophostoma silvicolum* (Phyllostomidae), an insectivorous gleaning bat, on Barro Colorado Island (BCI), Panamá. Collection of nest material beneath termitaria and infrared video filming indicated that males of *L. silvicolum* excavate and maintain cavities inside active termite nests. A binary logistic regression analysis showed that to be suitable as roosts, termite nests have to be larger than 30 cm in diameter and taller than 30 cm, well shaded, with few transecting branches, and freely accessible from below. Use of active termite nests as roosts may provide several benefits to *L. silvicolum*, including reduction of competition for roost sites with sympatric bat species, reduced parasite load and a suitable microclimate. A comparison of number of all termite nests in selected forest plots with number of termite nests that are potentially suited as bat roosts and number of termite nests that are actually used by bats suggests that *L. silvicolum* may not be roost-limited on BCI in spite of its highly specialized roost choice.

RESUMEN

Se estudió la estructura, modificación y disponibilidad de la percha para Lophostoma silvicolum (Phyllostomidae), un murciélago insectívoro en la Isla Barro Colorado (BCI), Panamá. La colección de material de las perchas debajo de los termitarios y la filmación con vídeocámara infrarroja, indica que los machos de L. silvicolum excavan y mantienen cavidades en el interior de los nidos activos de la termita. Un análisis con regresión logística binaria demostró que para ser adecuados como perchas, los nidos de la termita deben ser más de 30 cm en diámetro y 30 cm de altura, con buena sombra y pocas ramificaciones que se crucen, así como ser fácilmente accesibles desde abajo. El uso de nidos activos de la termita como percha puede proporcionar algunos beneficios a L. silvicolum, incluyendo la reducción de la competencia para perchas con especies de murciélagos simpátricas, la reducción en la carga de parásitos y un microclima adecuado. Una comparación del número total de los nidos de la termita en porciones selectas de bosque, con el número de nidos que potencialmente pueden utilizarse como perchas y el número de ellos que en realidad están siendo usados, sugiere que las poblaciones de L. silvicolum pueden no estar limitadas a las perchas en BCI, a pesar de su altamente especializada preferencia por las perchas.

Key words: Barro Colorado Island; Chiroptera; Lophostoma; Phyllostomidae; roost availability; roost structure; roost modification; termites.

ROOSTS ARE CRUCIAL FOR THE SURVIVAL AND REPRODUCTION of many animals. Bats, in particular, strongly depend on suitable shelters to protect them from predators and climate fluctuations. Most bat species are closely associated with specific roost types and frequently show site preferences within roosts (Rodriguez-Duran 1998, Lausen & Barclay 2002). Both observational and experimental evidences show that roost selection is driven by a variety of factors including structure of social systems, predator avoidance, thermoregulation, and reproductive condition (Kunz 1982, Lewis 1995).

Diversity of roost types as well as roost selection and availability are important factors contributing to the high ecological diversity of bats, particularly in tropical lowlands where bats use many more types of roosts than in temperate zones and are often highly specialized in their roost choice (Kunz & Lumsden 2003). However, specialization may also constrain bats if they rely on only one roost type. It is, therefore, important to learn how dependent bat species

are on specific roost types, which factors influence roost selection, and whether availability of roosts could be a limiting factor. This knowledge is particularly important for conservation efforts, due to anthropogenically driven decline of roosting opportunities, such as tree cavities in old growth forest (Kunz & Lumsden 2003).

Most bats roost in a wide variety of pre-existing natural and man-made structures (Kunz 1982) for example, *Neoplatymops matogrossensis* (Molossidae) whose flat skull permits it to roost in fine rock fissures (Handley, pers. obs.). Another species, *Thyroptera tricolor* (Thyropteridae), which roosts head-up on the flat surface inside rolled musoid leaves (Riskin & Fenton 2001, Vonhof & Fenton 2004) has developed suction disks to cling on to leaves. Another type of specialization is the construction of roosts by bats themselves, which is known from about 20, mostly frugivorous species that modify leaves or other plant material into tent-like shelters (Kunz & Lumsden 2003, Kunz *et al.* 1994).

The Neotropical genus *Lophostoma* (formerly *Tonatia*; Lee *et al.* 2002) provides an unusual example of roost making in bats. These insectivorous gleaners roost exclusively in excavated live arboreal

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termite and probably also in ant nests (McCarthy et al. 1983, 1992; Q1 Kalko et al. 1999, Dechmann et al. 2005). This roost choice is rather common in several groups of birds (Brightsmith 2000), but among bats only one flying fox (Hodgkison et al. 2003) and possibly one vespertilionid bat (Clague et al. 1999) roost in termite nests. Previously, it had been proposed that Lophostoma silvicolum might modify bird-made cavities (Kalko et al. 1999); However, size and opening of the cavity inhabited by L. silvicolum indicated that they might be constructed by the bats. The cavities were dome shaped with smooth walls and an opening at the bottom; none of them showed any sign of a former side entrance, which would be typical for bird-made cavities. Thus, we hypothesized that instead of using abandoned bird cavities, L. silvicolum may actively make roosts by excavating termite nests.

We wanted to verify that L. silvicolum excavates termite nests, because roost making by bats is so rare in spite of the strong dependence on suitable shelters (Kunz 1982). Termite nests are made from predigested wood and are very hard (Dietz & Snyder 1924) and thus we assume that time and energy are required to excavate them. However, if the excavation of termite nests results in access to a large number of roosts for which L. silvicolum does not have to compete, this investment may be justified, especially in combination with other potential advantages, such as greater flexibility of roost site selection or proximity to food sources (Kunz & Lumsden 2003). As termite nests vary greatly in shape, position on host trees, and a number of other parameters, not all nests may be suitable for excavation by the bats.

We studied a large number of termite nests on Barro Colorado Island (BCI) in Panamá to determine which termite nests are used by L. silvicolum, and whether and how the bats create cavities in the termitaria. We visually looked for the presence of bats in nests, collected discarded nest material beneath occupied and unoccupied excavated termite nests, and recorded the behavior of bats inside cavities by infrared video. In addition, we conducted an extensive nest census in predetermined areas on BCI with standardized protocols, recorded the characteristics of termite nests used by bats, and compared numbers of excavated roosts with availability of all termite nests that could potentially be used by L. silvicolum, to determine whether roost limitation occurs for this species.

MATERIAL AND METHODS

STUDY SITE, PERIOD, AND STUDY SPECIES.—The study was conducted on BCI, a field station of the Smithsonian Tropical Research Institute. BCI is a 1560 ha island in Gatun Lake (0°09'N, 79°51′W) bordering the Panama Canal in the central Panamá. The island is covered with semideciduous, moist, tropical lowland forest (Foster & Brokaw 1982) ranging in age from 80 yr to 600 yr (Piperno 1992). Rainfall averages 2600 mm per year, about 90 percent of which falls during the rainy season from May to December (Windsor 1990). For more details see Leigh (1999). Most data collection took place from September 1998 to February 1999 and from October 2001 to June 2003. Actual time in the field covered 6.5 mo during three dry seasons and 9.5 mo during three wet seasons. Our

study species was the white-throated round-eared bat L. silvicolum, a medium-sized (FA 52.5 mm; mass 31 g), gleaning insectivorous, New World leaf-nosed bat (Phyllostomidae), which occurs in lowland rainforests of Central and South America (Reid 1997). On BCI, L. silvicolum is rather common (Kalko et al. 1996) and the only resident of the genus Lophostoma.

DATA COLLECTION.—Bat roosts were found either by searching the forest visually and checking arboreal termite nests with a flashlight for an opening at the bottom or by radio tracking. L. silvicolum was identified visually in the cavities by its distinct size, fur color, and ear shape and confirmed by captures from roosts (see Kalko et al. 1999, Dechmann et al. 2005).

PRESENCE OF BATS AND SAMPLING OF NEST MATERIAL.—We regularly observed accumulation of dislodged nest material beneath termitaria that contained a cavity with an opening at the bottom. We observed six termite nests for 6 weeks (15 October-30 November 1998) and collected all discarded material in traps placed beneath the roost entrance to associate accumulation of nest material with absence or presence and number of bats. Traps consisted of PVC frames (50 \times 50×85 cm) that were covered with fine plastic mesh. Traps were emptied every 5-6 d and the accumulated nest material was weighed after being dried for 3 d at 60°C. We then correlated maximum and mean number of animals per week with the weekly mass of material collected under each nest.

OBSERVATIONS AND RECORDINGS WITH INFRARED VIDEO AT THE ROOSTS.—To observe bat behavior inside excavated termite nests, we illuminated selected roosts with custom-built LED arrays and filmed the cavity with infrared video cameras installed about 2-4 m beneath the entrance, which was situated 3-5 m above ground. During the first part of the study (1998-1999) we used an analog system (Dark Invader, 50 mm lens, F/1.3) to study one roost in Q3 detail and during the second part of the study (2001–2003) a digital system for detailed observations of two cavities (Sony system, for details see Dechmann et al. 2004). For analysis, the video sequences were displayed on a TV monitor.

NEST SUITABILITY AND AVAILABILITY.—We recorded nest height and width, cavity diameter and depth, position of nest, height above ground, amount of vegetation above, through, and below termite nests, as well as the presence or absence of termites for nests occupied by bats in order to identify the main characteristics, which determine suitability of termite nests for L. silvicolum. These nests were distributed over the entire island Barro Colorado, including two nests, which were on the two census plots, where we assessed nest availability (see below). We used a laser-operated distance meter (Leica) to measure height of termite nests as well as cavity depth and height of nests above ground. Nest and cavity widths were estimated visually, while vegetation above and below the nest was classified between 0 (no vegetation) and 3 (dense cover). Further, we counted number of branches transecting the nest. A few termites were collected from each nest to determine host specificity of the bats.

We conducted a census of all termite nests on two selected plots to assess roost availability. The first plot was in old forest (400- $600 \, \mathrm{yr}$) and measured $400 \times 400 \, \mathrm{m}$. The second plot was in younger forest (70–100 years) and its size was 100×200 m. We searched the areas visually by walking in 10 × 10 m squares in every direction, thus making sure we discovered as many termite nests as possible. We may have overlooked some nests located higher than 25 m because they might have been obscured by the canopy. However, as high nests were generally rather rare and as mist netting data on BCI indicate that L. silvicolum flies mostly in the forest understory, we excluded high nests from our data base. We then compared data of nests occupied by bats with that of all available termite nests from the census on the two plots to find the variables determining suitability for excavation by the bats. For this purpose, we tested the influence of various nest parameters on use as roosts by the bats in a logistic regression embedded in the generalized linear model procedure of the software SAS (SAS Institute Inc., USA). The dependent binary variable was roost use (presence or absence of a bat made cavity) and the independent factors were nest height and width, meters above ground, vegetation below and above, and number of branches. We applied a type III model with contrasts that are a linear function of the model parameters and that involve the parameters of the effect and any interactions with that effect. The model used a logit link function.

RESULTS

OBSERVATION OF BAT PRESENCE AND EVIDENCE OF ROOST MODIFI-CATION FROM COLLECTION IN TRAPS.—We found small, irregularly shaped pieces of nest wall material with diameters of about 5-10 mm in the traps on a daily basis under the six nests but only when L. silvicolum was present in the roost. The number of L. silvicolum individuals in occupied roosts varied from 1 to 19. The shapes of the collected pieces, which were smooth on one side and rough on the other, indicated that they were actively broken off the wall lining the cavity. A Kruskal-Wallis test revealed that mass of discarded material, as well as mean and maximum numbers of animals in the nest per week were significantly different between roosts. Consequently, we decided to test each roost separately for a correlation between mass of nest material and number of animals. However, we found no influence of either maximum or mean number of animals and the amount of nest material beneath each roost in a series of Spearman Rank correlations (R^2 varied from -0.4 to 0.5, with P values between 0.2 and 1).

In one case, we monitored the progress of a new cavity in a rather small termite nest (50 × 50 cm), which did not contain a cavity upon its discovery during a census. Twenty-four days later, we noticed a small cavity that was about 30 cm deep and 10 cm wide at the bottom of the termitarium. A single L. silvicolum was present in this roost on five occasions during daily checks over an ensuing 2-mo period. The bat abandoned the nest at the end of this period because the termitarium had cracked, water was seeping into the cavity during heavy rainfall, and the termites had left or died. Furthermore, the bat had been unable to continue enlarging the cavity because a branch obstructed the center of the cavity. We observed fresh tooth marks on the branch, which we took as evidence that the bat attempted to chew through it.

L. silvicolum roosted only in active nests of Nasutitermes corniger although other termite species with arboreal termitaria were present on BCI. We found evidence that the termites close their nest once the bats abandon the termitarium. In two cases, we observed that large cavities in active termite nests that had been temporarily used by L. silvicolum, were closed by the termites within 1 week and in the second case within 3 mo after the bats had left. After another termitarium with a roost cavity had remained empty for a month, the termites began to add new layers of nest material inside the cavity. Within 2 weeks, an area of 20 × 40 cm was covered with a 3 cm layer of fresh nest material. Five days later, all of the fresh material was removed again and was found beneath the roost (80.4 g). The cavity was restored by the bats to its previous size and shape and regularly used by two to six L. silvicolum in the following weeks.

EVIDENCE OF ROOST MODIFICATION ON INFRARED VIDEO RECORDINGS.—We observed for the first time in 1998 an individual L. silvicolum working on the cavity on seven out of 13 nights of continuous filming in a roost. The bat crawled up and down and bit into the wall in 1-2 min intervals, using mostly its incisors and the edges of its canines. It dislodged pieces of wall material with its teeth and dropped them. To break off hard pieces, the bat pushed itself off the wall with the help of its wrists and thumbs. Twice it lost its balance and fell out of the roost, only to return and continue its work immediately. Surprisingly, the activity of the bat did not provoke any noticeable reaction of the termites, which were generally only rarely seen inside the cavities. In another roost, a branch of about 2 cm diameter, which had grown through the middle of the cavity, had been severed by a bat at both ends and the working individual repeatedly spent long intervals chewing the remaining stubs on each side (Fig. 1). As the working individual from the first termitarium copulated with females that entered the roost during three of our observation nights, we conclude that it must have been a male. Time spent working on the walls of a cavity ranged between 1 and 34 min per night and one single male was once observed working on the walls of a cavity continuously for more than 90 min.

NEST SUITABILITY AND AVAILABILITY.—We compared characteristics of active termite nests from our census on BCI with a total of 44 nests we found occupied by bats to identify the most important parameters determining roost selection by L. silvicolum (Tables 1 & 2). Inactive nests and nests with cavities made by birds, such as trogons or parakeets were excluded from this analysis as they were not used by the bats. Of the active nests, we used 142 for which data were available in the GLM. We found several parameters, in which nests excavated by L. silvicolum differed from unused nests. These included, in particular, nest height and width, vegetation above and below the nest, and number of branches leading through the nest (Table 1). Nests had to be larger than 30 cm in diameter and taller than 30 cm, active, shaded, without many branches inside, and free from obstructing vegetation immediately below the nest.

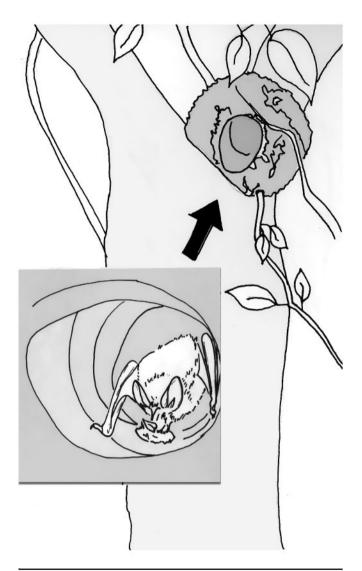


FIGURE 1. Lophostoma silvicolum working inside the cavity of an arboreal termitarium on BCI biting into the stump of a branch that had transected the nest. Drawing by Dechmann based on a video image.

All of these variables had a significant influence in the model (Table 2). Even when we corrected for interactions, each independent variables retained a significant influence on selection by the bats (see last two columns of Table 2). The fact that nests were

not selected randomly according to their occurrence is illustrated by the example of Figure 2, where we plotted nest height against nest width, showing that large nests were selected by the bats.

Regarding possible roost limitation, we found on the selected plots on BCI that there were more termitaria available with appropriate dimensions than were actually used by the bats. We counted 23 nests (14 active and 9 dead) on our 100 × 200 m census plot in young forest. Seven were large enough for the bats. Of those, only one contained a bat- and one a bird-made cavity. The lower part of the nest with the bird-made cavity was crisscrossed by many branches, which rendered it unsuitable for bats. Four of the remaining nests had no vegetation above and were probably too exposed to the sun. In our 400×400 m census in old forest, we counted a total of 185 nests. Of those, 160 were active and 25 inactive. In 27 cases, activity was unknown, because we could not reach the nests. Nevertheless, because of their intact outer covering we assumed these nests to be active. Of the total of 86 active nests that were large enough to serve as potential bat roosts, only 37 were accessible from below. Four of the latter nests had a bat-made cavity and one a bird-made cavity. This means that the bats used less than 15 percent of the potentially suitable nests on the selected plots on BCI.

DISCUSSION

Active roost making is extremely rare in bats (Kunz & Lumsden 2003) and it appears to occur only under particular, species-specific circumstances. The rarity of shelter making was partially responsible for the assumption that the bats of the genus Lophostoma reuse bird-made cavities in termite nests (Kalko et al. 1999). Instead, we present compelling evidence that L. silvicolum excavates and maintains the nests it occupies. Most of the cavities we observed were completed by the time we found them. Thus, we cannot make any quantitative statement about the overall removal rate of nest material or the investment during excavation. Time and energy need to be invested, however, to break off the termite nest material consisting of hard, predigested wood, and also to maintain cavities because the termites quickly fill in cavities when bats are absent for more than a few days. Interestingly, although we only found nest material whenever bats were present in an excavated termitarium, quantity of discarded material was not correlated with the number of bats inside the roost. These observations support the results of Dechmann et al. (2005), as well as our initial observation in 1998

TABLE 1. Average, minimum, and maximum of five parameters that differ between termite nests used as roosts by Lophostoma silvicolum (N=44) and the nests from the census on two plots on BCI (N=142) in brackets. Number of branches refers to small branches transecting the termite nest. Density of "vegetation below" and "vegetation above" was determined with a scale between 0 (no vegetation) and 3 (dense cover).

Used (census)	Number of branches	Nest width (cm)	Nest height (cm)	Vegetation below	Vegetation above
Average	1.6 (2.6)	45.9 (31.4)	65.2 (41.2)	0.7 (1.0)	2.5 (1.4)
SD	2.2 (2.7)	10.5 (15.2)	22.2 (24.0)	0.8 (1.2)	0.9 (1.3)
Min	0.0 (0.0)	30.0 (7.0)	30.00 (0.2)	0.0 (0.0)	0.0 (0.0)
Max	9.0 (7.0)	95.0 (100.0)	120.0 (150.0)	2.0 (3.0)	3.0 (3.0)

TABLE 2.	Results of logistic regression testing for the influence of number of branches growing through nest, nest width, nest height, vegetation below and above nests, and
	distance of nest entrance from ground on use of nests by bats (N $=$ 44) versus available nests (N $=$ 142). The last two columns show the logistic regression
	statistics of the type III analysis, which corrects for interactions.

Independent variable	df	Estimate	SE	Chi-square	Pr	Chi-square (type III)	Pr (type III)
Intercept	1	-4.73	0.94	25.34	< 0.0001	÷	-
Nest width	1	0.06	0.02	6.81	0.0090	7.50	0.0062
Nest height	1	0.03	0.01	8.90	0.0029	9.38	0.0022
Meters above ground	1	-0.33	0.09	14.06	0.0002	22.33	< 0.0001
Vegetation below	1	-0.63	0.31	4.16	0.0413	4.52	0.0334
Vegetation above	1	1.48	0.32	21.63	< 0.0001	32.64	< 0.0001
Number of branches	1	-0.48	0.14	11.13	0.0008	14.85	0.0001

indicating that only single adult males work on the cavity. The social system of L. silvicolum corresponds to resource defense polygyny (McCracken & Wilkinson 2000) with males offering roosts as a resource to females, thereby siring more than 45 percent of the pups of the females, who join them in their roost (Dechmann et al. 2005). This high reproductive success may have contributed to the evolution of this rare and presumably costly behavior by the males.

Additional benefits may be protection against rain, predators, and a reduction of ectoparasite load. Preliminary data show much lower ectoparasite load of L. silvicolum in comparison with other, ecologically similar and closely related species, in particular Trachops cirrhosus and Tonatia saurophila that roost in tree cavities (E. Kalko et al. pers. comm., Kalko et al. 1996). Bats living in active termite nests also may indirectly benefit form their host's regular use of chemical defenses (Prestwich 1988), which may reduce parasite

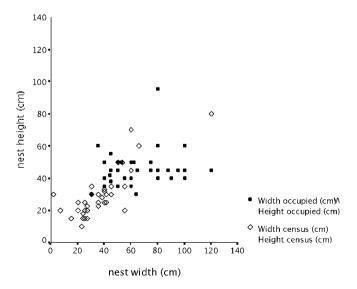


FIGURE 2. Width and height of active termitaria on BCI with (filled, N =44) and without cavities (open, N = 142) used by L. silvicolum.

loads or the risk of fungal diseases. Further, comparisons of temperature measurements in bat-made cavities in active termite nests with similar-shaped dead termite nests and tree cavities show that cavities in active termite nests provide a warmer and stable temperature regime (Dechmann et al. 2004), which is likely to be particularly beneficial for reproduction.

Avoidance of competition with other bat species is another advantage of the highly specialized roost selection by L. silvicolum. With more than 70 species of bats co-occurring on BCI (Kalko et al. 1996, pers. comm.), adequate roost sites, in particular tree cavities that are heavily sought by many bat species, are likely to become limited resources in species-rich assemblages with high numbers of individuals. Unlike most other bats that use common roost types (Kunz & Lumsden 2003), L. silvicolum may only compete with a few bird species. On BCI, L. silvicolum is the only resident species of the genus. It is unclear whether species of Lophostoma sp. may roost together where they co-occur. We coincidentally found two termite nests excavated by two species of Lophostoma in a close proximity during a stay at the field station of the German Primate Center (Deutsches Primatenzentrum, Göttingen) near Iquitos, Peru. One nest was occupied by L. silvicolum, the other by the much smaller species L. brasiliense (8 g). The size difference of the bats was well reflected in the size of their cavities. Both bats occupied large, active termite nests that were about 60-70 cm wide and 60-70 cm high. However, the roost entrance of L. silvicolum was about 10 cm in diameter with a cavity depth about 44 cm in comparison to L. brasiliense with a roost entrance of only 6 cm in diameter and a cavity depth of about 28 cm.

The only species that we repeatedly found roosting together with L. silvicolum in modified termite nests (McCarthy et al. 1983; pers. obs.) is the much larger and partially carnivorous Phyllostomus hastatus (Phyllostomidae) against which L. silvicolum probably cannot defend its roost. However, as P. hastatus is known to use a wide range of roost types including tree cavities, caves, and manmade structures (e.g., Kalko et al. 1996), it clearly does not depend on termite nests as a main roost type and joins L. silvicolum only temporarily. Also, there is no evidence that P. hastatus modifies or maintains termite nests.

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We found that the bats selected nests that were larger than 30×30 cm, which have few or no branches growing through them and nests that are well shaded and hidden by vegetation from above and freely accessible from below. Although we registered quite a number of termite nests that were potentially suited as roosts at both of our study plots, only a small fraction were actually used by L. silvicolum, in spite of the high densities at which these bats occur on BCI (e.g., Kalko et al. 1996). Thus, roosts do not appear to be a limiting resource locally, in spite of the high degree of specialization found in this bat. Similarly, roosts of the suckerfooted bat Thyroptera tricolor were also not limited in a study area in Costa Rica (Vonhof & Fenton 2004). We cannot exclude the possibility, however, that other parameters not evident to the human observer, such as distance to foraging areas, also may influence selection by the bats. L. silvicolum is a perch hunter with small home ranges and short commuting distances (Kalko et al. 1999), and requires high abundances of large insects such as katydids and beetles (e.g., Belwood 1988, Giannini & Kalko 2004).

The fact that L. silvicolum only excavates nests of N. corniger, and the absence of reliable records of L. silvicolum using any other type of roost suggest that the geographical distribution of L. silvicolum may be limited by the occurrence of its termite host. Nasutitermes corniger is common and widely distributed throughout Central and South America, tolerating a broad range of climate regimes (Nickle & Collins 1992), and roost availability for Lophostoma sp. may not be as strong as one might expect based on its highly specialized roost selection. There is even some evidence that naturally occurring forest islands in the Savanna areas of Bolivia and Brazil harbor termitaria occupied by L. silvicolum (Aguirre et al. 2003, Bernard & Fenton 2003).

This favorable situation may change in areas where severe human-induced habitat disruption leads to habitat fragmentation and degradation. Changes in land use are likely to enhance vulnerability of bats with rather specialized ecological requirements. For instance, in the Biological Dynamics Forest Fragmentation Project (BDFFP) near Manaus, Brazil, insectivorous and carnivorous gleaners, in particular L. silvicolum are very rare or even absent in the small 1 ha fragments (Sampaio et al. 2003, E. Kalko pers. comm.). Together with a general reduction in resource availability, limitation in roost availability is likely to be among the main factors leading to the observed loss of diversity in the fragments.

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Queries

- Q1 Author: Reference Dechmann et al. (2005) has not been listed. Please check.
- Q2 Author: Reference Clague et al. (1999) has not been listed. Please check.
- Q3 Author: Please provide manufacturer's detail for "Dark Invader."
- Q4 Author: The reference Belwood (1988) has not been listed. Please check.
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