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Tent-Use by the Bat *Rhinophylla pumilio* (Phyllostomidae: Carolliinae) in French Guiana[1]

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ABSTRACT

This is the first report of a non-Stenodermatine neotropical bat using "tents." Tents in the palm *Astrocaryum sciophilum* used by *Rhinophylla pumilio* (Carolliininae) in French Guiana, are characterized by the typical "V" shape incision in the leaf blade. Additionally, the long inferior spines were cut in the roosting area. Using radiotelemetry *R. pumilio* and *Artibeus gnomus* (Stenodermatinae), another tent-user, were monitored to determine their response to the replacement of tents by intact leaves or by new artificial tents, and to the introduction of new spines to the roosting area. No actual tent-making was observed but spine-cutting was achieved by *R. pumilio*. Judging from nocturnal observations, tent-use is interpreted as a means of protection from adverse weather and predators during feeding periods.

RESUME

Pour la première fois, une chauve-souris neotropicale ne faisant pas partie des Stenodermatinae est décrite gîtant sous des "tentes." En Guyane française, *Rhinophylla pumilio* (Carolliininae) utilise le palmier *Astrocaryum sciophilum* dont les feuilles immatures sont découpées selon deux incisions en "V." En outre, les longues épines inférieures sont sectionnées dans la partie occupée de la palme. Le suivi par radio-tracking de *R. pumilio* et *Artibeus gnomus* (Stenodermatinae), autre utilisateur de tentes, a permis de comparer les différents gîtes et d'expérimenter en remplaçant des tentes par des feuilles intactes, des feuilles artificiellement découpées, ou bien en introduisant des nouvelles épines dans des gîtes occupés. *R. pumilio* sectionne les épines, mais aucune découpe du limbe n'a pu être observée. A partir d'observations nocturnes, l'utilisation de tentes est interprétée comme une réponse aux intempéries, mais aussi aux prédateurs pendant les périodes d'alimentation.

Key words: Artibeus gnomus; *diurnal roosts; feeding roosts; French Guiana; fruit bats;* Rhinophylla pumilio; *tent-use.*

A NUMBER OF NEOTROPICAL BATS are known to modify leaves of plants into "tents" for use as daytime roosts. Barbour (1932) and Chapman (1932) were the first to describe this behavior in *Artibeus watsoni* and *Uroderma bilobatum,* respectively, two frugivorous bats of the subfamily Stenodermatinae (Family Phyllostomidae). Other genera of the subfamily Stenodermatinae, *Artibeus, Uroderma, Ectophylla, Mesophylla* and *Vampyressa* have been later described as roosting in different types of tents made in large leaves of palms, *Heliconia, Philodendron,* Rubiaceae, etc. (Foster & Timm 1976; Timm & Mortimer 1976; Koepke 1984; Timm 1984, 1987; Brooke 1987; Foster 1992; reviewed in Kunz 1982, Kunz *et al.* 1992). Two species of Old World megachiropteran *Cynopterus sphinx, C. brachyotis* and an Asian vespertilionid *Scotophilus kuhli,* have been described as occupying similar types of tents (Lekagul & McNeely 1977, Sandhu 1984, Rickart *et al.* 1989, Kunz *et al.* 1992). Tent-use has not been reported in other groups than Pteropidae and Vespertilionidae in Asia, and several species of Stenodermatinae in tropical America (Kunz *et al.* 1992). Numerous indirect observations, in particular tooth marks on the tents and the characteristics of selected leaves, confirm that these tents are made by bats (Choe & Timm 1985, Timm 1987, Brooke 1990) and are not the result of leaf bud piercing by insects as suggested by Eisentraut (1975). However, no one has directly observed the construction of these tents.

In the course of the general program "Forest regeneration, impact of seed dispersal by frugivorous vertebrates," conducted in French Guiana, we regularly observed *Rhinophylla pumilio,* a small frugivorous bat occupying tents. As these observations were the first of a non-Stenodermatinae, neotropical

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TABLE 1. *Plant species composition and numbers of roosts occupied by* Rhinophylla pumilio *and* Artibeus gnomus *(St Elie and Nouragues stations). The numbers in parentheses indicate the observations made by direct sighting. Others were located using radiotelemetry.*

	Rhinophylla pumilio		*Artibeus gnomus*
	St Elie	Nouragues	Nouragues
Atalea ataleoides intact immature leaf	2		
Atalea ataleoides tent[a]	2 (11)		
Astrocaryon sciophilum tent[a]	1	20 (12)	
Philodendron melinonii & *Philodendron ornatus*[a]	3 (1)	6 (2)	10
Rhodospatha latifolia[a]		1	
Sterculia sp.[a,b]		1	1
Astrocaryon sciophilum intact[b] sub-mature leaf		7	
Astrocaryon sciophilum adult[b] leaf + dead leaves		1	
Cecropia spp. dead leaf[b]		3	
Jessenia bataua[b]		1	
Cyclantaceae[b]		4	
Bromeliaceae[b]		1	
Total	8 (12)	45 (14)	11

[a] Leaves modified into "tent."
[b] Substitutive diurnal roosts after experimental removal of tents.

bat using tents, I invested some time to study this problem. (The old subfamilies Carolliinae and Stenodermatinae are now combined in the tribe Stenodermatini [Baker *et al.* 1989]). I asked the question if *R. pumilio* was responsible for making tents or if it only used tents made by other bat species, as noticed by Timm (1987) and Brooke (1987) for some Stenodermatinae.

METHODS AND STUDY SITES

DESCRIPTION OF *RHINOPHYLLA PUMILIO* TENTS.—*R. pumilio* is common in the Guianas (Husson 1962, Genoways & Williams 1979, Tranier & Berthier 1984, Brosset & Charles-Dominique 1990). This small frugivorous bat—body weight: 8.9 g (Range = 5.5–13, $N = 87$); forearm length: 36 mm (Range = 32–38, $N = 121$)—is restricted to intact mature forests where it has been mist netted mostly at ground level.

The following observations were made at the "Piste de St Elie" station (5°18′N, 53°04′W), and the "Nouragues" station (4°05′N, 52°40′W), both in the evergreen lowland primary rain forest (mean annual rainfall 3450 mm). Mean monthly temperatures ranged from 25° to 27°C, Lescure *et al.* 1983).

The first observations took place during the 1984–86 period, at the Piste de St Elie station where 20 roosting sites were found (Table 1). Most were typical tents constructed in immature palm leaves characterized by a large undivided terminal leaf blade. Tents (and those of the same type observed later at the "Nouragues" station) were made in young palm leaves corresponding to the stage when they were practically undivided, with no more than one to five pairs of lanceolated folioles at the proximal part of the rachis. This stage is called "immature," in comparison to older, "submature" stages described later. Tents were made in horizontal leaves, ranging from 0.60 to 2.20 m in height, in a "free" environment, *i.e.,* relatively far from the trunks, branches, or lianas as described by Brooke (1987) for the tents of *Vampyressa nymphaea.* The leaves were cut with two incisions forming a "V" shape, which produced a folding in the distal part. In the center of this shelter, which can be named the "roosting area," the intermediate parenchyma was altered between the small veins, displaying many small holes probably produced by the bats' claws or teeth. This type of tent, with a "V" shape section, is similar to the tents made by *Artibeus watsoni* in the small bifid leaves of *Geonoma* and *Bactris* (Chapman 1932, Timm 1987). They can be classified in the "bifid tents" category of Kunz (pers. comm.). In addition, at the "Piste de St Elie" station, we found *Rhinophylla pumilio* roosting in two intact *Atalea ataleoides* leaves and in four tents made in leaves of *Philodendron melinonii* and *P. ornatum* (Araceae).

These tents of a second type (in *Philodendron*) were similar to those described for *Artibeus cinereus, A. gnomus,* and *Vampyressa nymphaea* in the leaves of *Philodendron* and *Monstera* (Araceae) by Brooke

(1987) and Timm (1987) and classified as "simple apical tents" by Kunz (pers. comm.). They consisted of large undivided horizontal leaves whose lateral veins were severed near the central axis, producing a lateral folding of the proximal part of the leaf blade. These Araceae tents (and those observed later in the "Nouragues" station) were located at 2–8 m above the ground.

The second series of observations took place in the "Nouragues" station during the 1986–91 period. In this area, 120 km south of the "Piste de St Elie," *Atalea ataleoides* is practically absent, and most of the tents occupied by *R. pumilio* were located in *Astrocaryum sciophilum*. The leaves of this palm are similar in shape to *A. ataleoides,* but they bear long spines on the underside of the rachis. In addition to the "V" shape incision of the leaf blade, the spines located in the roosting area were cut at about 1–4 mm from the base of the leaf in all tents.

Possible construction of tents and responses to manipulation.—In order to locate their tent roosts, 17 *Rhinophylla pumilio* were mist netted and equipped with a 1 g radio transmitter glued on their backs (SS1 of Biotrack). Most of the bats (14) remained in the area, foraging in a small home range of 10 to 15 ha, and alternately using 3 to 5 tents. The same animal would roost alone one day, and within a group of 2 to 7 individuals the next day. In two areas, all tents where radio-equipped bats had been found, were removed, expecting that new "fresh" tents would be soon constructed. Over five successive experiments lasting from 7 to 12 days (according to the radio transmitter life span), conducted in November 1988, April 1989, November 1989, October 1990, and April 1991, no direct observations of tent-making were made. After the removal of all typical tents in *Astrocaryum, Phylodendron* and *Rhodospatha latifolia,* local bats used various substitutive shelters listed in Table 1: dry leaves of *Cecropia sciadophylla* and *C. obtusa* fallen on a liana, mature horizontal pinnately lobed palm of *Astrocaryum sciophilum* covered with dead leaves and making a kind of "roof" at 2 m height, Bromeliaceae epiphytes, Cyclantaceae epiphytes, broken folioles of a *Jessenia bataua* at 5 m height, and submature leaves of *A. sciophilum.*

The more frequent substitutive diurnal shelters were submature leaves of *A. sciophilum* (3 to 4 m long), with an undivided bifid terminal segment and 8 to 20 pairs of folioles along the rachis. *Rhinophilla pumilio* roosted in the terminal part, 2–3 m in height, but no incisions were observed in the leaf blade. Only small perforations of the parenchyma were noticed along the veins in the roosting area, probably produced by the bats' claws as observed in "true tents" made in immature leaves of a younger stage. Further observations indicated that these roosts were used regularly during the night, but it is much more difficult to find roosting bats in such situations. The first submature leaf found with roosting *R. pumilio* was observed regularly, with the expectation that it would be transformed into a tent. From 15 April 1989 this leaf had been regularly used, but no evidence of its transformation into a tent was observed until our last observation on 6 April 1991. The other submature leaves were never transformed into typical tents although they were occupied by bats.

Some months after each tent-removal experiment, new tents were observed in the area, always constructed in immature leaves.

In October 1990 and April 1991 five *Astrocaryum* tents were immediately replaced by new intact leaves of similar size. The bats came back to one of them during the four week experiment without cutting the leaf blade or the spines. After several weeks the leaves began to desiccate and probably became more difficult for bats to chew.

The following experiment consisted of making artificial tents in young palm leaves where a tent had been removed previously, and also in nearby palms (by cutting the leaf blade according to the typical "V" shape). Of 12 artificial tents made in April 1989, one was used regularly by *Rhinophylla pumilio* as a daytime roosting site in November 1989, and its spines were cut in the roosting area by this bat. In fact, this leaf was the only one showing all the characteristics of natural tents (horizontal position and isolation from the neighboring environment).

In April 1991 five new spines (inserted through the parenchyma) were added to the artificial tent. During the first five days, the tent was abandoned, then it was regularly reoccupied by the *R. pumilio,* which roosted adjacent to the spines. The spines were cut only four weeks later, probably by these bats which continued to occupy the tent.

I expected that these tents were constructed by other bat species then "used" by *R. pumilio.* Thus, several Stenodermatinae of equivalent size were radio-equipped in order to locate their roosts but none were observed using *Astrocaryum* tents. However, during a census conducted in May 1991 at the Nouragues station, a group of *Mesophylla* was observed in a typical tent constructed in a young *A. sciophilum* (A. Cockle, pers. comm.). Compared to the 23 similar tents occupied by *R. pumilio* and

found only by direct observation, without the aid of radio tracking (Table 1), this observation suggests that *Mesophylla* could be an accessory user of such roosts. Taking into account that the only species known to use the same type of palm tents with the typical "V" shape incision was the small central American *Artibeus watsoni* (Chapman 1932, Foster & Timm 1976, Timm 1987), I focused on *Artibeus gnomus*. This small 10 g bat is relatively common, and eight individuals were fitted with transmitters, leading to the discovery of 11 different roosting sites (Table 1). All of them were tents located at 3 to 15 m above the ground: 10 in *Philodendron melinonii* and *P. ornatum,* and 1 in a large leaf of *Sterculia* sp. All of these tents were of the type used by *R. pumilio* in Araceae and Sterculiaceae leaves (present study), and by *Artibeus cinereus, A. gnomus, Vampyressa nymphaea* in the leaves of *Philodendron* and *Monstera* (Brooke, 1987, Timm 1987 "simple apical tent" type of Kunz pers. comm.).

USE OF TENTS AS FEEDING ROOSTS.—Careful examination of the ground below the tents yielded evidence of food remains (*e.g.,* Piperaceae, infructescence axes, Araceae seeds, *Schlegellia surinamensis* fruit pericarps) from *R. pumilio,* indicating that this bat also uses tents as nocturnal feeding roosts. This was confirmed by placing small collectors under six tents. In addition, the activity of five radio-tagged animals was followed during the night with the aid of a directional antenna. After each flying bout, and when it was possible to approach and localize the animal (at ± 10 m, $N = 30$), it was always in an area with a tent (or with an intact postmature leaf also known to be used as a diurnal substitutive roost).

To obtain more information about the nocturnal utilization of roosts by *R. pumilio,* an electrical switch connected to a small lamp in the camp, was fitted to a *Astrocaryum sciophilum* leaf regularly used as a diurnal roost (2 to 6 individuals). Each departure and arrival of a bat induced a light bending of the leaf towards the ground, resulting in an intermittent signal. The observation of the system during six days (between 1900 and 0000) revealed an intensive use of this roost, interrupted by short 10–30 min periods of inactivity. These different observations indicate that tents are not only used as diurnal shelter but also as feeding roosts.

DISCUSSION

No evidence of tent building by *R. pumilio* could be obtained by the different experiments. The fact that this bat roosted in different tent substitutes, even in a "man-made" tent, could lead to the interpretation that this bat simply uses tents made by other species. However, in French Guiana, with one exception (*Mesophylla macconnelli*), no other bat species have yet been observed roosting in such palm tents.

My first conclusion is that it is easier to demonstrate the existence of a behavior than its nonexistence. We must remember that all evidence of bat tent-making to date is based on indirect evidence, and at present no naturalist has directly witnessed this behavior. Without the aid of radio tracking techniques and some preliminary field experiments, the present observations would have certainly led to a short note giving an additional species (and subfamily) to the list of the "tent-using" or "tent-making" bat species. However, considering all published information about tent-using behavior, we can conclude that it is highly probable that tents are made by several bat species. If *R. pumilio* is one of these species, tent-making is, at least, rarely done by this species. Following this hypothesis, most individuals would have to use tents made by conspecifics. Recently, Kunz & McCraken (pers. comm.), referring to *Artibeus jamaicensis, Uroderma bilibatum, Artibeus cinereus* and *Mesophylla macconnelli,* proposed the hypothesis that it is the harem males which make tents, in order to propose suitable roost to females. There is also the possibility that *R. pumilio* uses tents made by other bat species.

My second and last conclusion concerns the use of tents. In the literature, most descriptions of tent use and their interpretations refer to diurnal observations. This probably explains why they were only thought to serve as diurnal protection (Chapman 1932; Timm & Mortimer 1976; Foster & Timm 1976; Kunz 1982; Timm 1984, 1987; Boinski & Timm 1985; Brooke 1987). Nocturnal observations of radio-equipped *R. pumilio* and *Artibeus gnomus,* as well as the collection of food remains from beneath their tents, indicate that they also are used as "feeding roosts" to consume fruits removed in the neighboring vegetation. The Stenodermatinae bat *Ectophylla* is also described in Central America for using tents both for diurnal roosting and for feeding activity (Brooke 1990). Nightly fruit consumption by bats generally takes a long time (pulp and/or juice extraction), and this exposes them to the risks of predation. The family Phyllostomidae, to which belong all tropical American tent-using bats (Stenodermatinae, Carolliinae), also comprises small insectivorous (Phyllostomatinae) and nectar-

ivorous (Glossophaginae) bats, but these have not been observed using tents. In Asia, the only known tent users are two small frugivorous Pteropidae species and an insectivorous Vespertilionid. The choice of feeding roosts is particularly important (Morrison 1978, 1980; Charles-Dominique 1991), and could constitute a sufficient selective pressure to lead some small frugivorous bat species towards tent-making (or tent-using) for fruit consumption. This feeding function, compatible with the diurnal roosting function, could be the main selective pressure leading to the evolution of tent-making or tent-using behavior.

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