Tents and Harems: Alteration of Leaves by Foliage-Roosting Bats

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When one thinks of "tents and harems," what often comes to mind is the Arabian desert and the harems that have for centuries been kept by wealthy sultans. Instead, this article is about bats, those which live beneath leaves that they modify and use as shelters. In Trinidad, and elsewhere throughout the New World tropics, several species of fruit-eating bats modify leaves of vines, epiphytes, and palms for their use as so-called "tents" (1-4). The group composition of bats that occupy these tents strongly suggests a harem type of social organization. Roosting groups often consist of a single male and several females (and their young), although others may roost alone or sometimes in all-female groups. Leaves modified into tents are thought to provide shelter from rain, predators, and sunlight, offering ideal conditions for rearing young.

In 1932, Thomas Barbour, a naturalist from Harvard University's Museum of Comparative Zoology, who had been conducting research in Panama, discovered that some bats modified plants by cutting the veins of palms and banana leaves (5). He noted that these cuts caused parts of the leaves to collapse downward forming a partially enclosed space under which the bats roosted. In the same year, Frank Chapman, a naturalist from the American Museum of Natural History who also had been working in Panama, reported observations similar to those of Barbour (6). Chapman referred to these modified leaves as tents, since they resembled and provided protection similar to man-made tents. In the intervening years, several American ecologists, most notably Robert Timm from the University of Kansas and Anne Brooke from Boston University, made several new discoveries on these so-called tent-making bats (7-10). Most of their research was conducted in the lowland tropical forests of Costa Rica, supplemented by observations made in Peru and Ecuador.

The collective research efforts of Timm, Brooke, and others have to date identified at least 15 species of bats that roost in tents constructed from the leaves of over 50 species of Neotropical plants. These plants include large and small understory palms, cyclanths, epiphytic lianes, bananas, small saplings, and epiphytes. Other reports of tents and tent-roosting bats include three species of bats from the Old World tropics (Timor, Philippines, India, and Indonesia) (2). Although these and other bats have been commonly referred to as tent-making bats, no one has actually observed or reported bats in the act of making a tent. The closest that scientists have come to making such a discovery are observations that new, partially constructed tents have appeared over several days, and that leaves of some occupied tents have undergone minor modifications overnight. As in all disciplines of science, however, repeated observation of the same or similar events does provide important supporting evidence on which to formulate hypotheses and predictions, and to draw reasonable inferences.

During certain times of the year, many of the so-called tent-making bats roost in small groups, consisting of one male and several females sometimes with their young. These groups are referred to as "harems" and may remain together for several weeks or months in the same or different tents. At other times of the year males may roost alone beneath such tents while females form groups exclusively with their young. Sometimes, more than one species may alternately use the same tent, which suggests that not all bats that roost in tents participate in their construction.

The earliest observations of tent-making bats in Trinidad were reported by two American zoologists, George Goodwin and Arthur Greenhall (11). who conducted extensive investigations on bats in Trinidad and Tobago, in association with Greenhall's research on paralytic rabies. They recorded that the yellow-eared bat, *Uroderma bilobatum*, roosted in small clusters of 10 or more individuals "on the underside of the fan-shaped leaves of certain palm trees," especially the carat palm, *Sabal mauritiaeformis*. The large, native palm is common in coastal areas of eastern Trinidad, where it may grow to heights up to 12-15 m. Goodwin and Greenhall noted that *Uroderma* constructed tents by making "a series of cuts across the pleated surface of a leaf, causing half of the leaf to bend at an angle to form a protected retreat."

Goodwin and Greenhall found three lactating females, four non-breeding males, and two non-gravid females of *U. bilobatum* under the fronds of a coconut palm tree. They suggested that Heller's broad-nosed bat, *Vampyrops helleri*, had similar habits to the yellow-eared bat, *Uroderma bilobatum*, although no mention was made of the type of tent that was made. Among other types of roost, Goodwin and Greenhall found two *U. bilobatum* roosting under the leaves of a carat palm, although they made no explicit reference to "tents". In their account on the habits of the pigmy fruit bat, *Artibeus cinereus*,

Table 1. Plants used by tent-roosting bats in Trinidad.

Plant Family	Plant Species	Bat Species	Localities[a]	Source
Araceae	*Philodendron fragrantissiumum*	*Artibeus cinereus*	1	Kunz et al. 1993
	Philodendron ornatum	*Artibeus cinereus*	1,4	Kunz et al. 1993
	Philodendron simsii	None observed	1,4	Kunz et al. 1993
	Philodendron fendleri	None observed	1	Kunz et al. 1993
	Xanthosoma undipes	*Artibeus cinereus*	2	Kunz et al. 1993
	Anthurium jenmanii	*Artibeus cinereus*	1	Kunz et al. 1993
		Mesophylla macconnellii	1	Kunz et al. 1993
Cecropiaceae	*Cecropia peltata*	*Uroderma bilobatum*	2	Buchanan, 1969
Heliconiaceae	*Heliconia* sp.	*Artibeus cinereus*	3	Kunz et al. 1993
Musaceae	*Musa* sp.	not determined	2	Buchanan, 1969
Palmae	*Sabal mauritiaeformis*	*Uroderma bilobatum*	7	Goodwin & Greenhall, 1961
		Uroderma bilobatum	3	Kunz et al. 1993
		Artibeus jamaicensis	3	Kunz et al. 1993
	Cocos nucifera	*Uroderma bilobatum*	7	Goodwin & Greenhall, 1961
		Artibeus cinereus	6	Kunz et al. 1993
	Manicaria saccifera	None observed	1	Kunz et al. 1993
	"palm"	*Artibeus cinereus*	7	Goodwin & Greenhall, 1961
	Mauritia flexuosa	None observed	5	Kunz et al. 1993
	Prestoea pubigera	None observed	4	Kunz et al. 1993
	Pritchardia thurstonii	None observed	3	Buchanan, 1969; Kunz et al. 1993
Polygonaceae	*Coccoloba latifolia*	*Artibeus cinereus*	1	Kunz et al. 1993

aLocalities: (1) Long Stretch Scientific Reserve, (2) Arima Valley, (3) North Manzanilla, (4) Morne Bleu, (5) Aripo Savanna, (6) Manzanilla-Mayaro, (7) Royal Botanical Garden.

Goodwin and Greenhall noted that this bat roosted in small colonies of a few individuals under the cut leaves of palm trees and on the underside of banana leaves. No mention was made of any particular palm species or whether the banana leaves had actually been cut. In 1962, Greenhall and Goodwin reported a small group of ten McConnell's yellow-eared bats (*Mesophylla macconnelli*) roosting under leaves of a large forest epiphyte, *Anthurium jenmanii*, although they made no reference to its use for tent construction (12).

A few years later, Marcus Buchanan (1969), a former resident director of Simla (the William Beebe Tropical Research Station), published a report entitled "Bats of the Arima Valley, Trinidad, W.I." (13), and noted that "medium-sized bats with white facial markings were flushed from cut and partially dried banana, *Cecropia*, or palm leaves." Although no bats apparently were captured, Buchanan suggested that they were probably *Uroderma bilobatum*, *Vampyrops helleri*, or *Artibeus cinereus*. In his account of *U. bilobatum* Buchanan stated that this bat roosts in tents made by cutting leaf-ribs causing leaf (sic) to fold, especially palm (*Sabal* sp.), *Cecropia*, and banana (*Musa* sp.). He suggested that *Vampyrops helleri* had habits similar to *U. bilobatum*, but occasionally roosted in hollow trees and buildings. Buchanan reported that the lesser Trinidadian fruit bat, *A. jamaicensis*, roosted under leaves, in hollow trees, and in caves, but he made no reference to its occupancy or construction of tents.

During the mid-1970's and early 1980's published reports by Robert Timm and his colleagues working in Costa Rica, and similar observations reported by other investigators, suggested that some of the so-called tent-making bats may form stable roosting groups. Intrigued by this idea, we sought support from the National Geographic Society, the Organization of American States, and our respective universities to begin an investigation on the roosting habits and social organization of tent-making bats in Trinidad. We began our field studies in the spring of 1984, after conducting a preliminary survey of potential habitats suggested to us by Professor Julian Kenny of the University of West Indies. Initially, we concentrated our efforts in the Marsh Forest and Palm Marsh habitats in the Aripo Savannas (Long Stretch) Scientific Reserve (14), and at two sites along the northeastern coast. Later, observations at these sites were supplemented by less frequent visits to a coastal site near Blanchisseuse, to Morne Bleu, and to two sites in the Arima Valley (St. Pat's and Simla). This report summarizes some of our findings on tent-making bats in Trinidad, spanning the period from March 1984 through April 1990 (Table 1). Most of our observations were made

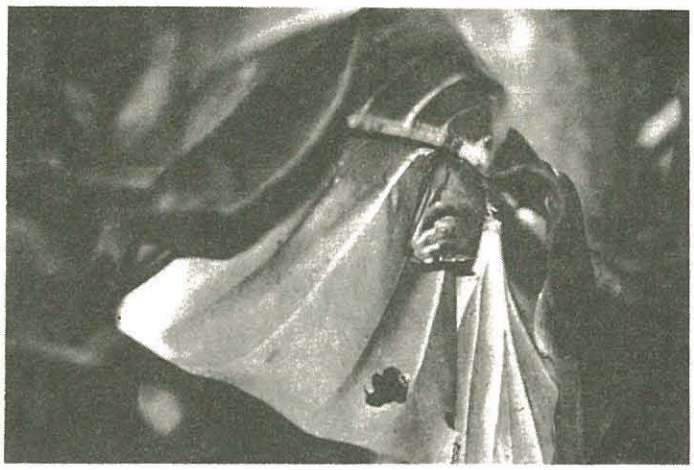

Figure 1. A solitary *Artibeus cinereus* in the Marsh Forest of the Aripo Savanna hanging from the mid-rib of a *Philodendron simsii* leaf that was modified into a simple apical tent.

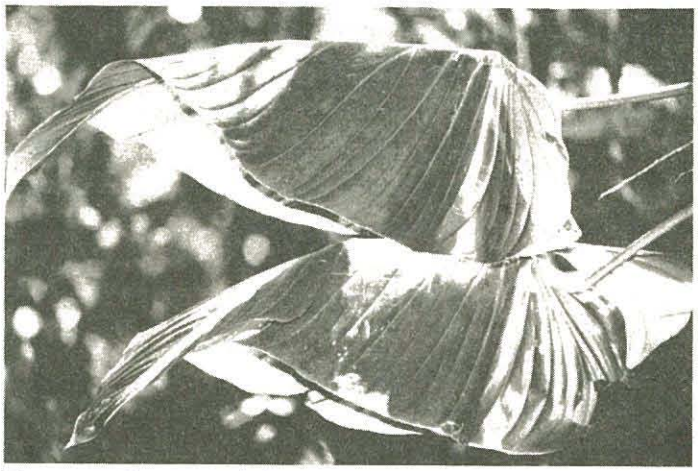

Figure 2. Two apical-shaped tents in *Philodendron ornatum* in the seasonal Palm Marsh of the Aripo Savanna Scientific Reserve used both by the pigmy fruit bat, *Artibeus cinereus* and McConnell's yellow-eared bat, *Mesophylla macconnelli*. Note that the basal veins are chewed, causing the lobes of the leaves to collapse.

from mid-March through mid-September 1984 January and April 1985, January and April 1987, and May 1990.

In 1984, while censusing the Marsh Forest and Palm Forest habitats of the Aripo Savanna for tent-roosting bats, we recorded tents constructed in the leaves of at least four species of epiphytic lianes (*Philodendron fragrantissimum*, *P. fendleri*, *P. ornatum*, *P. simsii*), one species of epiphyte (*Anthurium jenmanii*), and two species of palms (*Manicaria saccifera* and *Mauritia flexuosa*). We observed and /or captured (and released) individuals and small groups of three species of bats (*Artibeus cinereus*, *Uroderma bilobatum* and *Mesophylla macconnelli*) roosting in tents (Figure 1). Our observation in April of 1984 that *Mesophylla macconnelli* roosted in tents was consistent with a report published in that same year by Juliane Koepcke (15), a German ecologist who found small groups of M. *macconnelli* roosting beneath cut leaves of *Anthurium* sp. and a small, understory palm (*Geonoma* sp.) in the lowland rain forest of Peru.

In the Marsh Forest habitat we marked (using orange plastic tags) and recorded the location of each tent, the number of modified leaves on a particular plant, the height of tents above the ground, the size of the leaves, the number of chewed veins, the shape of each tent, and the relative vertical position of each tent in the understory. We also recorded ambient temperature and humidity from above and below tents to characterize roost microclimates. We recorded the presence or absence of bats, and censused the number of bats present (visually or by direct capture) in most occupied tents. On several occasions bats either escaped our capture efforts or flew from tents before we were close enough to capture them. Captured bats were marked on the forearm with small, plastic, numbered bands for later identification, weighed, measured, and released at the site of capture. Censusing bats in the Marsh Forest was especially difficult during the rainy season because of the noise created from the sloshing sounds of our wellingtons, as we waded nearly calf-deep in water-filled trails.

In upland habitats along the eastern coast, and in forest habitats that had little or no standing water, it was possible to approach and capture bats with more success. Overall, we captured nearly 100 tent-roosting bats, which accounts for about half of those we actually observed in tents. Sometimes we were able to capture only a few members of roosting groups, as some individuals eluded our attempts to capture them. On other occasions we either flushed bats prematurely as we approached a roost or they roosted too high to be captured with our hand nets.

In the Marsh Forest the heart-shaped leaves of *Philodendron* spp. were the ones most commonly used by bats for tent construction (Figure 2). Tents in *Philodendron* typically were constructed 2 or 3 m above the ground, where they were usually protected from direct sunlight during most of the day. Most leaves that had been modified into tents were oriented so that the space directly below the bats was usually free from branches and vines so as to allow the bats to fly in and out of a tent without being impeded by nearby vegetation. Typically, tents were made from *Philodendron* leaves when bats chewed several of the basal veins, and sometimes the mid-rib, approximately one-third of the way from the leaf tip. This caused the lateral lobes of the leaves to droop downward. If the mid-rib was chewed, the distal tip of the blade also drooped downward, forming a semi-enclosed, apically-shaped structure. There was some variation in how heart-shaped leaves were modified by bats; some tents were formed when each of the lateral veins were chewed, either at an angle or parallel to the midrib.

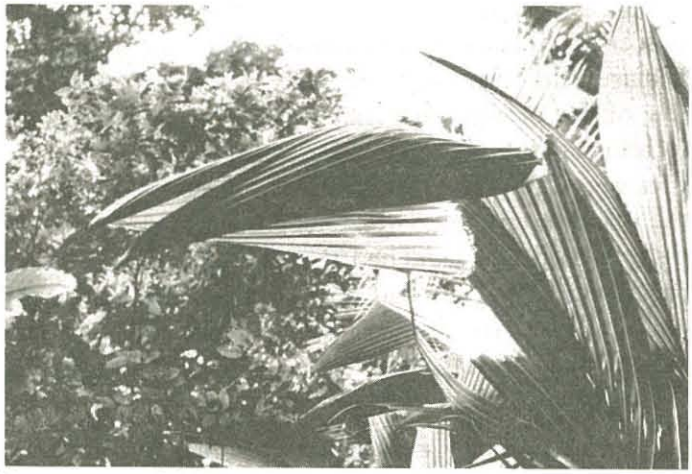

Figure 3. Bifid leaves of immature coconut palms (*Cocos nucifera*), along the Manzanilla-Mayaro coast that were modified into tents by the pigmy fruit bat, *Artibeus cinereus*.

The Palm Marsh in the Aripo Savanna was dominated by large stands of the palm *Maurita flexuosa*, interspersed by expanses of sedge savanna. Mature trees of this species often reach 30 m or more and, because of their height above the ground, we could not see bats roosting in these leaves. Although we observed umbrella-shaped tents in several of the large leaves of young understory *Mauritia* palms, we did not observe bats roosting in them. Tents made from leaves of these immature *Mauritia* trees often exceeded heights of 5 m above the ground, thus making it nearly impossible to capture roosting bats. The chewed areas in the crowns of these leaves were roughly spade-shaped. The long, distal segments of the leaf drooped downward at an angle, forming a rather airy umbrella-like enclosure. What is intriguing about bats that construct tents in these large palmate leaves is that they are able to chew and sever the very tough and fibrous rachis and veins. When the tents are made and how long it takes a bat to complete such a tent or whether several bats participate in their construction is unknown.

Along the north and east coastal regions of Trinidad we commonly observed tents and tent-roosting bats in the broad, bifid leaves of immature coconut palms (*Cocos nucifera*). Several of these tents were occupied by singles or small groups of *Artibeus cinereus*. Tents in young coconut palm leaves and other bifid-leaved palms are formed when two, roughly "J-shaped" cuts are made, one in each segment of the bifid blade (Figure 3). This causes the two lobes to collapse downward, forming a pyramid-shaped enclosure. Typically, tents constructed in young *Cocos* leaves ranged from 1 to 2.5 m above the ground. In the Marsh Forest of the Aripo Savanna, we observed a similar type of tent cut in the understory palm *Manicaria saccifera*, and these tents were at least two meters above the ground. Roosting groups of *Artibeus cinereus* ranged from 2 to 6 individuals, and usually consisted of a single adult male and one or more females (sometimes with their young).

Figure 4. Leaf of the palm *Sabal mauritiaeformis* that was modified into an umbrella tent (near North Manzanilla). Bats from Trinidad known to construct and occupy this type of tent include Peter's tent-making bat (*Uroderma bilobatum*) and the Lesser Trinidadian fruit bat (*Artibeus jamaicensis*).

In the relatively dry, upland areas on the northeast coast of Trinidad (near North Manzanilla), we observed numerous tents in the large palmate palm, *Sabal mauritiaeformis* (Figure 4). Several of these tents were occupied by small groups and singles of *Uroderma bilobatum* and *Artibeus jamaicensis*. The composition of these roosting groups, which consisted of several females (sometimes with young) and a single male, suggests a harem type of social organization. The umbrella-shaped tents in *Sabal* were made when bats created a roughly heart-shaped or circular shaped cut around the areas where the petiole is attached to the blade. The distal parts of the blade collapsed downward at an angle, as in *Mauritia flexuosa*, forming a semi-enclosed roosting space, resembling a partially opened umbrella. Because the leaves of *Sabal* are less deeply dissected, as compared to *Mauritia*, the resultant enclosure is darker and less exposed to wind, rain, and direct sunlight. Judging from the tooth marks on these and other palm leaves, it appears that the veins are chewed from above and the plications are chewed from below. We also observed similar types of tents constructed from leaves of the palmate palm, *Coccothrynax barbadensis*, some of which were occupied by singles and small roosting groups of *Uroderma bilobatum* and *Artibeus jamaicensis*. The shape of the cut and the resultant tent architecture were similar to those observed

Figure 5. Patch of wild tannia (*Xanthosoma undipes*) in the Arima Valley, that is used by the pigmy fruit bat (*Artibeus cinereus*) for tent-making. One of the authors (Kunz) can be seen trying to capture bats roosting beneath a tent. This type of tent is formed when bats chew the basal veins of simple heart-shaped leaves, causing the basal lobes of a leaf to droop downward.

in *Sabal mauritiaeformis*, except that the cut areas generally were rounded in shape.

In the moist, rocky ravines in the Arima Valley, we observed tents and tent-roosting bats in the large heart-shaped leaves of *Xanthosoma undipes* (Figure 5). This succulent plant commonly grows in shaded, moist areas in what appears to be several separate plants all connected by thick, ground-hugging rhizomes. Within a single patch we found upwards of 15 tents, sometimes with 3 to 4 leaves on a "single plant" having been modified into tents. These tents were similar to those we observed in *Philodendron* sp., in which several of the basal veins were chewed and the lobes of the leaves dropped downward. The leaves selected for tents in *Xanthosoma* ranged in height from 1 to 2 m above the ground. Typically, the bats chose large leaves that were oriented horizontally. Given the foul-smelling (and foul-tasting) latex-like sap that is produced when the veins of leaves from *Xanthosoma* are severed, it is unclear why bats select leaves of this plant for tent-making. The only bats that we either observed or captured in or near *Xanthosoma* tents were *Artibeus cinereus*.

In mid-April 1987 when we returned to Trinidad to continue our studies on the bats and tents that we had marked on previous visits, we learned to our utter dismay that two of our primary study sites (Marsh Forest and a coastal site near North Manzanilla) had suffered from extensive fire damage. When we first arrived at the Marsh Forest site, it was clear to us that few if any of the tents had survived the intense fire and heat that had swept through it only days before. Most of the large palms and understory trees that had supported the epiphytic lianes (*Philodendron* spp.) and a large epiphyte (*Anthurium*) had been burned extensively and were no longer standing. Among the few lianes and epiphytes that remained tenuously attached to the severely burned but standing host trees, all had suffered extensive heat and/or direct fire damage. Although they were badly scorched, we did find a few of the orange tags that we had used to mark the location of tents when we began our study. Intense ground fires were still burning in the Marsh Forest when we left the island three weeks later. Obviously, we were extremely disheartened and saddened that we could not continue the research that we had begun at this site three years earlier. The fire damage to the Marsh Forest and surrounding habitats was so severe that recovery to its former condition will most likely take decades.

The Marsh Forest was not the only site in Trinidad that suffered from extensive fire damage in 1987. This had been one of the driest years on record, and scattered fires damaged crops and razed valuable forest land, and destroyed many human dwellings, especially those in rural areas. Brush and forest fires throughout the Northern Range had done severe damage to primary forest habitats, including those on El Tucuche. One of our primary study sites in North Manzanilla also suffered extensive fire damage, where a primary stand of *Sabal mauritiaeformis* was almost completely destroyed. The heat from ground fires destroyed several of the large trees by deeply burning the roots, many of which had already been reduced to red-hot embers by the time of our arrival. It was obvious from the severely damaged leaves that most, if not all of the tents that were present at the time of the initial fire had been destroyed; presumably all of the bats had either abandoned the site or were killed from the intense heat.

In May 1990 we again returned to Trinidad and surveyed the two primary study sites that had sustained severe fire damage in 1987. It was immediately obvious that what we had judged to be extensive damage in 1987 was worsened by additional fires in 1988. Many of the large trees that were still standing in 1987, and that we assumed might survive, were totally destroyed in 1988. The deep, intense, slow burning ground fires in the hummocky Marsh Forest of the Aripo Savanna had caused such severe damage that short-term recovery seemed most unlikely.

Regrettably, what remained of the Marsh Forest in May of 1990 consisted of burned trunks of formerly enormous palms and the decaying litter left from fallen trees. Although the Marsh Forest was again becoming green from the growth of rapidly invading pioneer plants, the former character of the forest, including its unique flora and fauna, had been destroyed. It is clear that the destructive fires in 1987 and 1988 have radically changed a very significant part of the Trinidadian landscape. Many of the unique plants, animals, fungi, and microbes that

made up this forest community are today little more than a memory.

Belatedly, there is a hard lesson to be learned from all of this. Many, if not most of the habitats in tropical and other regions of this planet, harbour unique, fragile communities of interacting organisms, each of which is intimately linked to the soil that supports it. Inadvertent or intentional acts which lead to the burning of even the most seemingly simple habitats, adversely affect the survival of the natural communities of which bats are a part. Although wind-blown surface fires in many parts of the world play an important ecological role in maintaining the character of grassland, chaparral, and coniferous forest communities, the deep, slow burning fires that ravaged many parts of Trinidad in 1987 and 1988, especially the Marsh Forest, have caused a loss of biological diversity from which recovery will take decades, if not centuries.

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