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The World of Tent-making Bats
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by Thomas H. Kunz

When one thinks of tents and harems, the first image that comes to mind is the Arabian desert and the harems that for centuries have been kept by wealthy sultans. Certainly the last thing most people would think of is bats. But some bats do live in tents, albeit ones made of leaves; and, like a sultan with a harem, a single male bat and a group of females form the most common social structure in these tent roosts. By biting the veins of leaves, such bats cause a leaf to collapse downward, forming a partially enclosed tent-like space under which to roost.

Worldwide, only a few bats are known to construct their own roosts. Most rely on existing structures, natural or otherwise, or simply roost beneath tree bark or on branches, concealed in the foliage. Bats that modify leaves to create a roost have several characteristics in common. For one, their body size tends to be relatively small, allowing them to be supported and hidden by a single large leaf, as well as enabling them to navigate in the cluttered tropical forest environment where all tent roosts have thus far been found. Primarily what they have in common, however, appears to be the type of social structure they form. The group composition of bats that occupy tents strongly suggests that they are polygynous, or a type that forms harems, a common reproductive strategy among mammals.

In this type of social system, a single adult male bat lives and mates with a group of several adult females, typically five to 15 bats. The male rigorously defends his harem or tent against intruders and challengers. In some species of polygynous bats, harem males may retain their groups for as long as three years, while the females may stay together much longer, perhaps even for life. However, the stability of groups roosting in leaf tents, and how the group members are related to each other, are factors largely unknown.

Among bats found in tents, roosting groups remain together during the mating season for several weeks or months in one or more tents. At other times of the year bachelor males roost alone beneath tents, and females may form groups exclusively with their young in tent roosts. Not all bats that form harems are known to utilize tent roosts, though further study will likely reveal that additional species do. And by the same token, we cannot assume that all groups found in tents use them to raise their young.

Scientists first discovered the ability of some bats to construct their own roosts 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. 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. Chapman referred to these modified leaves as "tents," since they resembled and provided protection similar to the canvas tents made by humans. Since then, many other types of leaf roosts have been found and designated as tents regardless of whether they resemble them or not.

In the 1970s and early '80s, research conducted by several ecologists, most notably Robert Timm from the University of Kansas and Anne Brooke from Boston University, added greatly to our knowledge of the so-called tent-making bats. Most of their research was conducted in the lowland tropical forests of Costa Rica and

supplemented by observations in Peru and Ecuador. The collective research efforts of these scientists and others have, to date, identified 15 species of Latin American bats and three from India and Southeast Asia that roost in tents.

What is remarkable is that these bats come from two distantly related, but divergent, groups. Bats, which belong to the order Chiroptera, are further divided into two suborders. The Microchiroptera are found worldwide and comprise nearly 80 percent of the world's bat species. The Megachiroptera are found only in the Old World tropics and comprised of a single family--the Pteropodidae--or flying foxes. Thus far, among the "microbats," tent-making has been discovered only in leaf-nosed bats of the family Phyllostomidae, found throughout Latin America and the Caribbean. Of the three Old World tent-making bats, two are of the same genus (*Cynopterus*), and one, curiously, is a small insectivorous bat (*Scotophilus kuhlii*) that, while found roosting in leaf tents, may not actually construct them.

The plants that these bats modify include large and small understory palms, lianas (vines), bananas, philodendrons, small saplings, and several epiphytes. Leaf shapes and sizes vary considerably. Worldwide, they comprise some 80 species of vascular plants from 17 families.

Tents may have several advantages over traditional roosts like tree hollows or caves. In tropical forests, such roosts are often unavailable or uncommon. Bats in tents are, for the most part, concealed. Tents may also enable bats to be more easily alerted to approaching predators, such as snakes or primates, whose weight and activity is likely to disturb the surrounding foliage. Tents are often as high as 20 feet above ground, although about 12-13 feet is more typical, and some are even as low as three feet. Typically, tents are made beneath overhanging vegetation with few or no obstructions directly below, allowing bats to enter and depart without being impeded. Since tents usually provide a clear view from below, most roosting bats are alert to approaching predators and can quickly escape. (The advantage of alertness is obvious in the many unsuccessful attempts of researchers to capture bats roosting beneath a leaf!)

In addition, leaf tents provide shelter from rain and sunlight and offer ideal conditions for rearing young in warm, tropical climates. Harems in tents are also defendable against challenging bats; the shape of the roost space created under a leaf is similar to tree hollows and cavities in caves chosen by other polygynous bats.

Because of the ephemeral nature of leaf tents, one might expect tent-making bats to change roost sites and engage in tent making rather frequently. But in field research, marked tents provided suitable conditions for at least nine months, and in some cases showed little sign of deterioration even after one year. In the forest subcanopy, where tents are found, the effects of wind and rain storms are not felt as acutely as in the upper canopy. Observations that more than one species alternately uses the same tent suggest that all bats that roost in tents may not construct them and that some bats may, in fact, appropriate tents made by others. Considering the great number of tents that are unoccupied in a given area, there is abundant opportunity for usurping these roosts.

Tent-roosting bats appear to make use of preferred tents although they apparently are familiar with, and use, alternates. Within a small area of forest, there may be 15 or more tents, and at least two or three of the leaves on a single plant may have been modified. In field work that I conducted with Gary McCracken in Trinidad, we observed that single bats and groups invariably flew to nearby tents when we came too close or even if vegetation in the vicinity was disturbed.* Groups usually returned to the original tent within the same or following day, but solitary bats showed less fidelity and more often than not settled and remained in another nearby tent. All of our observations were made during the day, which appears to be the main time when tent-making bats use these roosts. Although they were largely inactive, they were always extremely alert. We observed no bats occupying tents at night, though we suspect that this is when tents are constructed.

Tent-making status has generally been conferred upon all bats found roosting in tents, but hardly anyone has actually observed them in the act of modifying a leaf. For the most part, the evidence has been highly circumstantial. Until recently, the closest that scientists had been to making such a discovery were observations that

new, partially constructed tents had appeared over several days, and that leaves of some occupied tents had undergone minor modifications overnight.

The single exception is the short-nosed fruit bat (*Cynopterus sphinx*), a small flying fox found in India and Southeast Asia. In a recent study, conducted in collaboration with J. Balasingh and John Koliraj from St. John's College in southern India, direct observations indicate that it is the harem male that constructs tents. For other species, however, it remains to be determined whether tents are made by a single male bat preparing a roost for its harem or whether several members of a roosting group cooperate in tent construction.

Despite the great variety of plants used by bats in tent construction, there are only a limited number of different leaf forms that can be altered by bats and function as roosts. The similar manner in which bats in both the New and Old World chew veins of leaves or stems, and the manner in which leaf segments collapse to form a particular style of tent, suggests that tent architecture may be largely a consequence of plant form. What drives these divergent groups to construct tents in the first place is another matter.

Thus far, eight basic architectural styles have been identified, and not all rely on a single leaf, some tents being formed from clusters of several leaves. Some are enclosed and concealing, others are more exposed and airy, and some are cylindrical, shaped like a cone or an inverted boat. Only three styles are known to occur in both the New and Old World, four are unique to Latin America, and one has been found only in India and Southeast Asia.

This one, called a "stem" tent, can hardly be described as a typical tent, as it is not made from leaves. Collaborating with Hari Bhat from the Institute of Virology in western India, we have found that male short-nosed fruit bats sever the central strings of immature flower and fruit clusters on kitul palms. As the flowers mature into fruits, the altered cluster forms a bell-shaped cavity in which other bats can eventually roost. Similarly, J. Balasingh, John Koliraj, and I have observed stem tents made by this same species in which a single male severed up to 300 stems in a cluster of dense vines, forming an inverted cavity surrounded by uncut stems and leaves. Such a tent may take a male several weeks to complete, after which he may be joined by up to 20 females.

Most tent-making bats may roost in, or construct, tents in several different types of plants, and appear to have a repertoire of creating various styles of tents. One species, *Uroderma bilobatum*, has been found in seven of the eight tent styles. Other bats, however, appear to construct only one type of tent. For example, Honduran white bats have been found only in "boat" tents. Such tents are common in Costa Rica where these bats are often found. Further study is needed to determine whether in fact most species are limited to constructing a particular style of tent, but use tents constructed by other species if they are available. For now, however, the Honduran white bat appears to be the exception.

Among the eight basic styles of tents, there is considerable variation. For example, at least three variations of apical tents (where the leaf collapses to form an apex) have been observed in the simple leaves of a philodendron. Furthermore, the number of veins bats chew and the extent to which they chew them also varies considerably, even from leaf to leaf on the same plant. They may engineer a roost where all of the veins are chewed, yet modify only about half of another leaf.

Interesting variations in tent style also can occur when more than one bat species modifies the same tent at different times. In one such example in Trinidad, Gary McCracken and I found that the leaf of a large epiphyte, *Anthurium jenmanii*, was alternately occupied by small harem groups of *Artibeus cinereus* and *Mesophylla macconnelli*. The large oblong leaf had been modified with a long cut parallel to the midrib, as is characteristic of boat tents. Superimposed on this tent style were two J-shaped cuts similar to those observed in "paradox" tents, where the leaf collapses perpendicular to the midrib instead of along it. Previous observations of the two bat species indicated that each species was associated with a particular method of modifying leaves, but which bat first constructed this roost is unknown.

Not all of the cuts that tent-making bats make may be for the purpose of creating the roost. When disturbed, bats

have sometimes been observed to escape through small openings created by partially cut and uncut leaflets along the stem. In other cases, cuts in some styles of tent appear to be nonfunctional with respect to tent architecture but may prove to be made strictly as places for the bats to gain a foothold.

How tent bats go about choosing a particular variety of leaf to modify is largely unknown. For instance, the moriche palm, native to Trinidad, has leaves that are extremely tough and fibrous, posing an intriguing question of why bats would engage in such a difficult task when other suitable leaves are available. Another Trinidadian plant, wild tannia (*Xanthosoma undipes*), has a foul smelling (and tasting) latex-like sap that is produced when the veins are severed, yet tents constructed from these leaves are relatively common.

Although the similarity in tent architecture observed in both the New and Old Worlds may be no more than a simple consequence of similarity in leaf form, observations that these distantly related groups of bats modify similar leaves in nearly identical ways suggests evolutionary convergence in tent-making behavior. The striking parallels in tent architecture, tent making, and tent roosting behavior among the two groups of bats certainly support such an interpretation.

Among the Mega- and Microchiroptera, similar selection pressures may have led to the evolution of tent-making behavior in some subcanopy, foliage-roosting bats. Since both the tent-making Old World megabats and New World microbats are all mostly frugivorous and relatively small, they are probably subjected to similar foraging and roosting constraints in the structurally similar tropical forests in which they live. By modifying understory leaves, individuals and small groups of these bats may be able to exploit locally available food sources more effectively than they otherwise could in areas where other preferred roosts are absent or uncommon.

Further studies of tent-making bats may help unravel some the mysteries about this unique behavior among bats. We still do not know how many species actually construct the tents (as opposed to those that may merely roost in them), and we do not know which individuals are involved in tent construction, whether it is only males or whether other members of a roosting group cooperate. Other discoveries yet to be made are how long it takes for a tent to be completed, how long it is occupied, and how many different tents a single group may utilize during a given period. Until some of these questions are answered, tent-making in bats will remain an fascinating but elusive behavior.

[footnote 1]
** One notable exception to this is the tiny Honduran white bat (Ectophylla alba). Field researchers in Costa Rica have reported that they take flight only if the main stem of their tent is disturbed. Their tents are generally low to the ground (about six feet), but as sunlight filters through the leaf, their white fur takes on a greenish cast, almost completely concealing them if they remain still.*

[bio]
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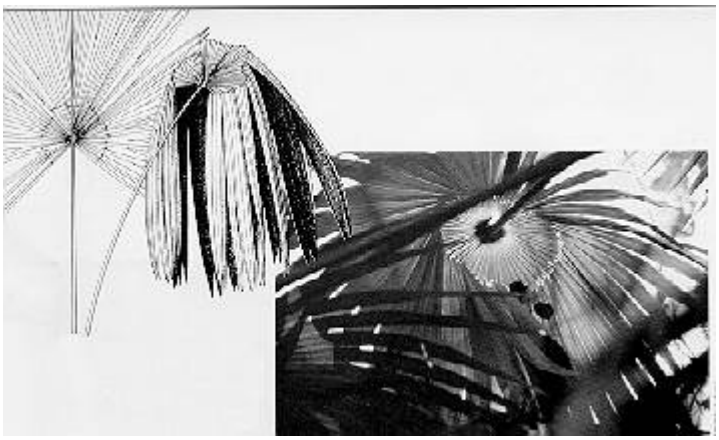
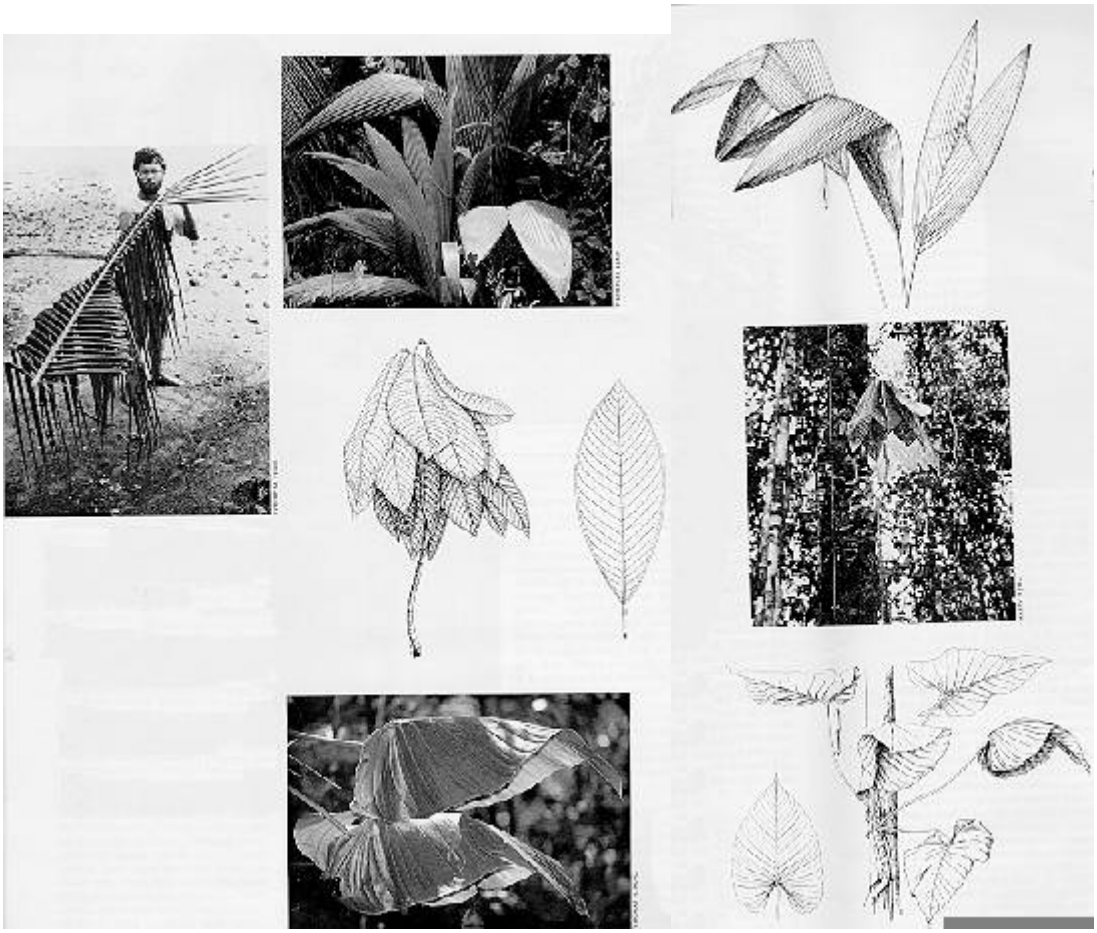
Shaped like an inverted boat, boat tents (above) are one of eight distinct styles constructed by the so-called tent-making bats. Unlike other such bats, Honduran white bats (opposite page) create only this style of tent, which is formed when they chew lateral veins along both sides of a leaf's midrib, causing the leaf to droop. The Heliconia leaf tent at the left is old and deteriorated, but the one on the right is newly made. This style is found only in Latin America.



Looking up, the author spotted two bats roosting beneath a palmate umbrella tent in Trinidad. In this tent style, bats partially chew the veins of large fan-like palms, forming a semi-circular pattern around which the leaf blades collapse. Palmate umbrella tents have been found in both the New and Old World.

Only one species, the short-nosed fruit bat, has been seen actually modifying a leaf. The bat hooks its thumbs through the leaflets of the palm (inset) and pulls itself up to bite along the midrib.



Most tent-making bats appear to have a repertoire of several different styles. Pinnate tents (above) have thus far

been found only in Costa Rica and Peru and only in palms with feather-like fronds. Bifid tents (above right) are much more common and have been seen in a variety of plants throughout the Caribbean and Central and South America. In this style, the lobes collapse, forming a triangular-shaped space where the bats roost. Conical tents (center) are found in both the New and Old World. In Indonesia, the author observed conical tents that were nearly identical to those he found in Costa Rica. Bats are well concealed in the collapsed, overlapping leaves in this style. Apical tents (below) have been observed in many different leaf types throughout Latin America and also in Indonesia.

Uroderma bilobatum, found throughout Latin America, has one of the most versatile tent-making repertoires. These bats have been found in seven of the eight tent architectural styles. The one shown here is a boat tent, occupied by a small group of mothers with their young.