A Roof over Their Feet

Tent-making bats of the New World tropics turn leaves into living quarters

by Robert M. Timm and Barbara L. Clauson



The first scientist to suggest that bats cut leaves to fashion roosting shelters was Thomas Barbour, a naturalist from Harvard who was working in Panama. In 1932 he reported observing a common species of leaf-nosed bat (since named Peters's tent-making bat) clinging to the underside of a palm frond that had curiously cut veins. Because larval insects also make patterned cuts in tender, developing leaves, much of Barbour's paper on the subject reads like an attempt to convince himself, as well as the reader, that bats, not insects, were responsible for the incisions. He concluded that bats were indeed modifying leaves but also found it "inconceivable that the habit should be a common one." Later in the same year, Frank Chapman, of the American Museum of Natural History, reported that a Thomas's fruit-eating bat cut the veins of a native palm to produce what he called a "tent." But little more on the phenomenon appeared in the scientific literature for the next forty-five years.

After reading these early reports, we began actively searching for roosting tents on our research expeditions to the tropical rain forests of Costa Rica, Ecuador, and Peru. These forests were so overwhelmingly lush that at first we found it difficult to focus on individual trees and shrubs. But gradually we were able to see, scattered among the foliage, some leaves that were atypically folded. After examining them carefully, we were confident that these leaves were not old, nor had they been damaged by insects or broken by fallen branches. Rather, the veins and midribs had been severed in a very deliberate and patterned way. Further searching revealed that bats were roosting under many of these folded leaves.

Leaves altered by bats provide good camouflage, and perhaps this is why leaf tents have long been overlooked. But once we knew what to look for, we could readily locate the tents; in a single day we often found dozens, of several different types, each occupied by a different species of bat. Unlike previous researchers, who were limited to netting bats on their nocturnal forays, we were able to capture bats unharmed during the day at these roosts.



Our study of hundreds of tents has helped us shed light on the behavior and ecology of the bats that make them.

To date, individuals of fourteen New World tropical species, all small- to medium-sized fruit eaters known as phyllostomids, or leaf-nosed bats, and two Old World species have been found to construct tents. Most of these species roost almost exclusively in tents. While we have not yet watched bats in the actual process of cutting leaves, we have been able to follow the building of a tent over several successive days, finding more cut leaflets each morning. Tent-making bats chew the veins that branch out from the leaf's midrib in such a way that the sides of the leaf droop but do not fall off. The tissues are not completely severed, and tough, fibrous strands hold the living leaf together. The resultant structure of rigid midrib and folded leaf sides is roughly pyramidal or tentlike. Hooking their feet into the midrib, veins, and rough spots on the underside of the leaf, hanging bats are well concealed from above and on both sides. When the drooping sides touch, the bats are also hidden from below.

Tents protect bats from predators, rain, wind, and intense tropical sunlight and are also shelters for the young. For newborn and young bats, the tent's protection may be critical. Like most species of bats, tent-making bats give birth to a single young at a time. In some species the mother carries the infant with her on her daily foraging rounds, but when it becomes too cumbersome, she leaves it, still flightless and vulnerable, in the tent unattended. Females of other species transport the young to an alternate roost while they forage and then retrieve it before returning to the tent to spend the daylight hours.

Bats of some species construct a number of tents, scattering them throughout a relatively restricted area of forest, and use one for several days before shifting to the next. When flushed from one of these roosts during the day, the bats often fly to another of their tents some distance away, although they sometimes circle and attempt to return to the same tent. Other species make and use only one leaf tent at a time, occupying it for two months or

more. Occasionally we find "cheaters," bats that are using a tent characteristic of another species. These opportunistic bats may usurp an occupied tent or simply use one they have found unoccupied.

The number of occupants in any one tent depends on the species and the season and may offer clues to the mating and social systems of different species. The tents of solitary species are small and simple and house either an individual or a female and her offspring. In monogamous species, mated pairs usually share the tent and may be accompanied by their single young. The large tents of polygynous, harem-forming species, such as Peters's tent-making bat, however, hold colonies that average from five to fifteen bats, and sometimes contain as many as fifty. Such roosts generally contain one breeding male and his entourage of females and young. A question that bears future investigation is whether a good tent in a prime location can help males of polygynous species attract mates and keep a harem.

Each species of bat forms from one to several characteristic types of tents. Many bats display a preference for certain kinds of plants and leaf shapes. Several species of Artibeus and Vampyressa bats select heart-shaped leaves from various related species of plants in the Araceae family and fashion a characteristic style of tent from each. Other species are generalists. Thomas's fruit-eating bats use a variety of differently shaped leaves, such as the palmate leaves of the Panama hat palm, elongate leaves of banana and bird of paradise plants, heart-shaped leaves of Anthurium. and forked leaves of small ground palms, as well as the compound leaves of coconut palms. But basic tent construction remains the same: the bats chew through the veins or leaflet midribs that support the sides of the leaf.

In the course of our investigations, we documented what must be a relatively recent shift to a new plant species and tent type for Peters's tent-making bats. Typically users of palm fronds, these bats make cuts that gradually converge toward the center of the leaf in an inverted \vee shape, causing the leaf to collapse downward. But we have also found this bat

roosting in leaves of the banana plant, a species introduced into the New World tropics within the last 450 years. The vein structure of banana leaves differs from that of the native palms that these bats usually select for tent construction. When the bats cut their V on banana leaves, the side veins do not fold; only the cut to the midrib that causes the tip to droop results in the formation of a tent. Although these tents form acceptable shelters, the bats "waste" considerable time and energy making unnecessary cuts. These bats seem to be "locked" into the style of cutting that works on native plants

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Mistakes in leaf choice are rare, and most attempts to fashion tents from unusual species of plants are quickly abandoned, perhaps because the leaf is dis-

tasteful or difficult to cut. Dieffenbachia. a plant that abounds on the forest floor, would appear to be ideal for tent construction because of the size, shape, and structure of its leaves. But of the several hundred tents we observed over the past fifteen years, just one-incomplete and unoccupied—was in a Dieffenbachia. The plant exudes a thick, milky, sticky, foulsmelling sap containing calcium oxalate crystals and cyanide-producing glycosides poisonous to most mammals. Ingestion of the sap causes intense pain and swelling in the mouth and throat in humans, typically making speech difficult, hence its common name, dumb cane. A first mouthful of noxious Dieffenbachia sap may deter a bat from using the plant's leaves as tents. The chemicals that probably evolved to protect the plant from herbivores appar-

ently discourage tent makers as well.

Bats routinely select fully emerged leaves for new tents, and we suspect that tents found in old or worn leaves have been in use for several weeks or even several months. The angle of the leaf is also important in protecting the bat from the elements and for concealment. Some species choose horizontal leaves, whereas others select those hanging at more acute angles. The angle that affords the greatest protection varies depending on the shapes of leaves and styles of tents.

Fashioning a tent is a time- and energyconsuming process for the bats, which are

very small in comparison to some of the leaves they use. We found Artibeus gnomus, for example, roosting under a Monstera leaf, whose half-inch-wide veins are broader than the bat's mouth; yet this leaf bore twenty-six cut veins. For other species, such as Peters's tent-making bat, which roosts under huge palm fronds

more than eighteen feet long, the job is even more daunting. As many as 150 leaflets need to be cut on a single frond.

Palms are notoriously tough, woody, fibrous, and spiny. Why do bats choose such leaves when tender, pliable species are available? Precisely for those same characteristics of strength and resilience. Many tent leaves are in serviceable condition after two months of use. Tough fibers hold leaves together and allow passage of nutrients even when chewed, whereas more delicate leaves decay rapidly or fall apart when cut. These same sturdy types of leaves are used by native peoples as roofing throughout the Neotropics.

As for spines and razor-sharp stems that the bats must contend with, the more the better. Bats tuck their tiny bodies between spines or use them as convenient toeholds, while prickly stalks discourage intruders such as snakes and biologists who try to investigate a tent.

Probably for the same reasons they make good bat roosts, tents are ideal sites for the paper nests of wasps. We found Polybia wasps, noted for their aggression, to be common in bat tents. The tents occupied by wasps are usually intact and seemingly occupiable by bats, with leaves in relatively good condition. However, we never observed bats roosting in a tent once wasps had made a nest there.

Most predators, particularly those relying on evesight, seem to be unaware that the folded tent is anything other than a dying leaf. In addition to concealment, tents provide bats with an early warning system; the stems they hang on are often thin and springy, and even slight shifts of the stem cause magnified movements of the leaf. If a predator locates the bats, its approach up the stem jars the leaf and alerts the bats, which immediately flush.

The list of predators active at the roosts of non-tent-making tropical bats is lengthy

A cluster of adult male and female Caribbean white bats share a daytime dormitory in a Heliconia leaf, right. The bats hook their claws into the incisions they have made along the leaf's midrib and nestle in the fold, below. Like other leaf-nosed species, these bats have elaborate snouts that help them to echolocate, but their bright white fur is a rarity.



and includes snakes, opossums, skunks, weasels, raccoons, domestic and wild cats, foxes, and even carnivorous bats such as the spectral or false vampire bat. Nonetheless, early in our study, we presumed that tent-making bats were almost immune from predation when roosting. We had read only a single report of predation, that of a tent-roosting bat caught by a snake in Trinidad. Later, however, while working in Costa Rica with Sue Boinski, then of the University of Texas at Austin, we found that Central American squirrel monkeys not only learn to recognize batmodified leaves but also seek them out. These intelligent omnivores eat both wasp larvae and bats. Adult males are the most successful at capturing prey from the tents. On locating a bat tent, the monkey approaches it stealthily from below, being careful not to disturb the roost leaf. It peers up into the tent to determine that it is indeed occupied by either bats or wasps, then climbs above the tent on a nearby plant. From this vantage, the monkey launches itself into the air and crashes down onto the tent, dislodging the occupants and snatching at falling and flying bats. Once on the ground the monkey searches for and consumes wasp larvae or any injured or young bats unable to fly. If adult stinging wasps are present, the monkey rolls away from the landing point. It then runs back to grab bits of the broken nest, which it carries a safe distance away before extracting larvae and pupae. Uninjured bats capable of flight are often able to escape the monkeys.

Double-toothed kites, birds of prey frequently found in association with monkeys, and in particular squirrel monkeys, are often seen perched on horizontal branches amid a foraging troop. The kites use the monkeys as "beaters" to drive out prey. Active monkeys disturb large insects such as katydids, cicadas, cockroaches, and grasshoppers, as well as small lizards and frogs. If these prey elude the monkeys, the kites swoop out and intercept the creatures. We have occasionally observed kites capturing adult bats flushed from their roosts by monkeys.

Rather than the rarity described by Thomas Barbour some fifty years ago, tent making is a common practice among small, fruit-eating bats of Central and South America. Finding the tents has given us a glimpse of the ecology of these Neotropical mammals, but long-term studies of marked bats and of possible variations among individuals, populations, and species will be essential in unraveling the role tent makers play in the complex communities of the tropical rain forest.

After a night of foraging, a female Thomas's fruit-eating bat and her single offspring, which is already able to fly, retreat to the safety of a leaf tent. Bats of this species construct tents by biting veins in a precise pattern in durable, waterproof foliage, such as this Panama hat palm leaf in Corcovado National Park in Costa Rica.

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