Journal of Tropical Ecology (1996) 12:121–137. With 5 figures
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Tents and harems: apparent defence of foliage roosts by tent-making bats

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ABSTRACT. Palmate umbrella tents used by tent-making bats in Trinidad, West Indies, were observed in three species of Neotropical palms, *Sabal mauritiiformis*, *Coccothrinax barbadensis* and *Mauritia flexuosa*. Tents were most common in palm leaves that have supporting petioles angled at 50–70° above the horizontal. The shape and volume of tents is influenced mostly by leaf morphology (leaf width and leaflet length) and age of the tent. Tent-crowns varied from being heart-shaped in *S. mauritiiformis*, oval or round in *C. barbadensis* and spade-shaped in *M. flexuosa*. Leaves in which tents were constructed were most often beneath overhanging vegetation, and were generally free of vegetation below, allowing bats to enter and depart from tents without being impeded by the clutter of adjacent vegetation.

Singles and small apparent harem groups of two bat species, *Artibeus jamaicensis* and *Uroderma bilobatum*, were captured and observed in tents made from the leaves of *S. mauritiiformis* and *C. barbadensis*. No bats were observed in tents constructed in leaves of *M. flexuosa*. The apparent harem social organization in these and other tent-making bat species suggests that leaves modified into tents may provide critical and defendable resources that promote the evolution of polygyny. This hypothesis is based on the observed patchy distribution of suitable palm trees, the inappropriateness of many palm leaves as potential tents and the resultant architecture provided by palmate umbrella tents. We suggest that tent-making is an adult male behaviour.

KEY WORDS: *Artibeus jamaicensis*, bats, Chiroptera, Neotropics, Phyllostomidae, resource defence, tent architecture, tent-making behaviour, *Uroderma bilobatum*.

INTRODUCTION

At least 14 species of Neotropical bats and three species of palaeotropical bats have been attributed to tent-making habits (e.g. Charles-Dominique 1993, Kunz 1982, Rickart *et al.* 1989, Timm 1987). Although nearly 50 years have elapsed since so-called 'tents' were first reported, no bats have been observed in the act of tent-making. However, there is strong circumstantial evidence that the cuts in leaves that result in the tent-like enclosure are not the consequence of insect activity, and that tents are made by bats (Barbour 1932, Timm & Clauson 1990). Reports of tents being completed over a period of several days by a resident species or group (Barbour 1932, Brooke 1990, Timm & Clauson 1990, Timm & Lewis 1991) provides the best evidence to date concerning the identity of the tent-makers.

There is growing evidence that foliage tents are constructed and used by several bat species having polygynous mating systems. These include *Uroderma*

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bilobatum[1] (Timm & Clauson 1990, Timm & Lewis 1991), *Vampyressa nymphaea* (Brooke 1987), *Ectophylla alba* (Brooke 1990) and *Artibeus jamaicensis* (the present study). Several other species of bats that make tents may also have polygynous mating systems (e.g. Koepcke 1984, Timm 1987). The distribution and potential for defending critical resources can strongly influence animal mating systems (Bradbury & Vehrencamp 1977, Emlen & Oring 1977). The question arises as to whether foliage tents provide critical and defendable resources that enhance the potential for polygyny in tent-making bats.

In describing the harem mating system in the Jamaican fruit bat, *Artibeus jamaicensis*, Morrison (1979) asserted that successful harem defence was possible because males could defend the tree hollows, in which females roosted, from intrusions by other males. Morrison postulated that costs to males of defending less confined roosts such as caves and foliage might be prohibitive. The evidence that several species of foliage-roosting bats form harems leads us to question Morrison's (1979) suggestion that foliage roosts are neither limiting nor defendable.

Observations of *A. jamaicensis* also suggest that foliage roosting is more common in this species than once thought. Buchanan (1969) found *A. jamaicensis* roosting under unidentified leaves, and Goodwin & Greenhall (1961) extended this observation by reporting groups of 'mixed-sex colonies' up to 25 individuals roosting under palm leaves and in the foliage of mango and bread fruit trees. Jimbo & Schwassmann (1967), Morrison (1978, 1979) and Tuttle (1976) have either reported solitary bats and/or small groups of *A. jamaicensis* roosting beneath unaltered leaves of unidentified plants. Foster & Timm (1976) reported two males and several others that escaped capture, roosting under cut leaflets in a large pinnately leafed palm (*Scheelea rostrata*).[2]

Observations on the yellow-eared bat, *Uroderma bilobatum*, indicate that this species roosts almost exclusively in foliage, usually beneath large leaves which have been modified into tents (Timm 1987, Timm & Lewis 1991). Strong circumstantial evidence suggests that many roosting groups of *U. bilobatum* are harems. Barbour (1932) reported roosting groups, ranging from 2 to 59 individuals, beneath leaves of the palm *Prichardia pacifica*. Bloedel (1955) found females and nursing young beneath unidentified 'palm-leaf tents', and Goodwin & Greenhall (1961) found small clusters of 10 or more individuals roosting beneath leaves of certain palm trees, especially *Sabal mauritiiformis* (= *glaucescens*). Jones (1964) collected four females roosting beneath a 'tent' formed in a palm frond, and Dickerman *et al.* (1981) reported that *U. bilobatum* was frequently found in 'palm-leaf tents' occupied by one to seven individuals. Timm & Clauson (1990) noted that tent colonies typically ranged from 5 to 15 individuals, and consisted of one breeding male and females with their young. Reports of foliage roosts used by *U. bilobatum* include tents constructed in five

[1] Taxonomic nomenclature of bat species in this paper follows Koopman (1993).
[2] Taxonomic nomenclature of palms in this paper follows Uhl & Dransfield (1987).

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species of palms, including *Prichardia pacifica*, *Cocos nucifera*, *Livistonia chinensis*, *Sabal mauritiiformis* and *Scheelea rostrata*, and in one member of the banana family, *Musa* sp. (Timm 1987).

Here we report additional evidence that singles and harem groups of *A. jamaicensis* and *U. bilobatum* roost in foliage tents. We also describe characteristics and qualities of these roosts. We suggest that when foliage roosts are modified into tents, they provide both a critical and a defendable resource. Although foliage appears to be a ubiquitous and potentially unlimited resource available for roosting bats, we argue that not all foliage can be suitably modified into tents.

METHODS

Study sites

This study was conducted in Trinidad, West Indies, a small island (approximately 4540 km^2) that lies 12 km off the north-east coast of Venezuela. Trinidad has three mountain ranges extending along an east–west axis; the Northern Range which reaches a maximum elevation of 980 m, and the Central and Southern ranges each of which are successively lower. An alluvial plain dominates the landscape between the Northern and Central ranges (Beard 1946). Three study sites were selected following intensive searches for evidence of palm tents and tent-roosting bats. Two sites were located on the east coast (both near North Manzanilla) and one was in the Palm Marsh forest on the Aripo Savanna.

Depot Trace. This eastern coastal site is dominated by a relatively mature stand of the carat palm, *Sabal mauritiiformis*, where some individuals grow to heights of 10–15 m or more. Several smaller (immature) individuals were most commonly used for tent construction at this site. Coconut palms (*Cocos nucifera*) dominated the adjacent, cultivated lowland areas. The landscape is hilly and the clay and sandy soil is well drained at the highest elevations (5–10 m above sea level). In the lowland depressions the soil is often saturated, especially during the rainy season.

Coastal Upland. This eastern, dry, coastal, upland site is dominated by a small, mixed stand of palms, consisting mostly of small and intermediate-size individuals of *Cocos nucifera* and *Coccothrinax barbadensis*. Understorey vegetation included scattered stands of *Heliconia* sp. and immature forms of *Cocos nucifera*. It was the only site that we examined where tents were observed in *Coccothrinax barbadensis*, and only three individual trees were consistently used by bats for tent-making.

Palm Marsh. The Palm Marsh is located on the dissected alluvial terraces of the northern plain (Beard 1946) and is part of the Aripo Savanna Scientific Reserve.

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This distinct community, described by Beard (1946) as a *Mauritia–Chrysobalanus* association, borders the true savanna and merges with the adjacent Marsh Forest. The Palm Marsh also forms small islands lying within the sedge savanna. In contrast to the relatively dry coastal areas, the Palm Marsh has a seasonal wet climate.

Palms used in tent construction

The carat palm, *Sabal mauritiiformis*, is a widespread species distributed throughout coastal South America (Bailey 1947). In Trinidad it also occurs in coastal areas where it often dominates second growth forest. This palm is characteristic of dry, clay soils in evergreen and semi-evergreen seasonal forests (Beard 1946). Typically, it has 20 or more spreading, deeply divided leaves with drooping leaflets. Leaflets are 5–7 cm at the base and reach lengths of 1 m or more. The leaves are bright green above and blue-green below (Bailey 1947, Beard 1946).

The fan palm, *Coccothrinax barbadensis*, is indigenous to the Windward and Leeward Islands of the Lesser Antilles (Read 1979, 1986). Throughout its range it occurs mostly in littoral woodland and scrub woodlands, and grows mostly on limestone soils from sea level to 200 m. In Trinidad, *C. barbadensis* prefers well-drained soils, cliffs and windswept slopes, which face the sea in areas of low rainfall (Beard 1946). It is a small to medium-size palm, ranging in height from 2 to 5 m. This palm typically has 12–15 leaves (Read 1979), each of which are 1 m or more broad and are usually but not always circular in outline. Leaves have 50–70 segments, each ranging from 2 to 4.5 cm in width (at the widest point) and 25–45 cm long. The upper surface is glossy green and the lower surface has a silvery texture.

The moriche palm, *Mauritia flexuosa*, is indigenous to Trinidad, where individuals may grow up to 30 m in height (Bailey 1947). It is a widespread, economically important species throughout much of South America. In Trinidad it most commonly grows in clumps in the Aripo Savanna, where it is the principal vegetation in swampy areas (Beard 1946). The bole is straight and cylindrical, and at maturity there are 12–20 large leaves with long prominent petioles, each with deeply divided blades having narrow leaflets. Leaflets range from 1 to 2 m long and they are 4–5 cm or more broad near the middle, tapering to a long point.

Observations of tents and bats

We regularly searched for bats and tents in palms and censused palm tents at Depot Trace and the Coastal Upland sites from April to August 1984, and during January of 1985 and 1987. We made less frequent searches at the Palm Marsh site because of the highly saturated soil and dense, entangled, understorey vegetation, which made it difficult to approach tents without disturbing roosting bats.

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When tents were observed we attempted to approach them without disturbing or flushing roosting bats. However, on several occasions we inadvertently flushed bats as we approached occupied tents, especially on those occasions when tents were low and near the ground and we could not see the roosting bats until we were directly beneath the tent. Initially, we tried to capture roosting bats using a large 1.5 m diameter hoop-net or by using a 2 m length of mist net stretched between two hand-held poles. These methods proved cumbersome in dense understorey vegetation, and were abandoned. Successful captures generally were made using a 0.5 m diameter insect net, fitted with an extendable handle, although this method too was not always satisfactory.

Captured bats were examined for sex, age and reproductive condition (Anthony 1988, Racey 1988). Each was marked with a numbered, plastic, coloured wing band (A. C. Hughes), measured for forearm length and weighed to the nearest gm. Except for voucher specimens collected to confirm species identifications, each captured bat was released at the site of capture. Bats that were not captured, but could be observed in their roosts, were tentatively identified with the aid of binoculars, based on their general size, pelage colour and distinct markings. These identifications were later confirmed when possible from photographs. From observations alone we could not distinguish sexes of roosting bats, because there are no sexually distinctive markings or obvious sexual dimorphisms.

Whether or not bats were present, all plants with tents were marked with numbered, plastic tags for later identification and for assessing tent-leaf deterioration and mortality. At the end of our study (January 1987) we measured and recorded tent heights in *Sabal mauritiiformis*, the number and position of leaves with tents, tent condition and the angles of petioles of leaves which had tents. We subsequently cut down several selected tents of all three palm species to record leaf dimensions and other tent characteristics (e.g. size of tent-crown, length of cut leaflets, size of roost area and the number of cut veins and plications). We measured the heights above the ground of tents that were not cut down, using a surveying staff or an optical range finder. Two tents of each species were preserved as voucher specimens and deposited in the Boston University Herbarium. Sketches and photographs were made of tent-roosts in the field and composite drawings of leaf forms and tent architecture were made from photographs and voucher specimens (Figures 1–3).

RESULTS

Tent characteristics

Seventeen tents from *Sabal mauritiiformis* were measured for roost dimensions and examined for other characteristics. Tents in *S. mauritiiformis* apparently are formed when bats chew the veins and plications of the leaves until the veins and supporting tissue weaken, causing the area of the leaf distal to the cut to droop downward (Figure 1A–B). The overall configuration of the cuts varied

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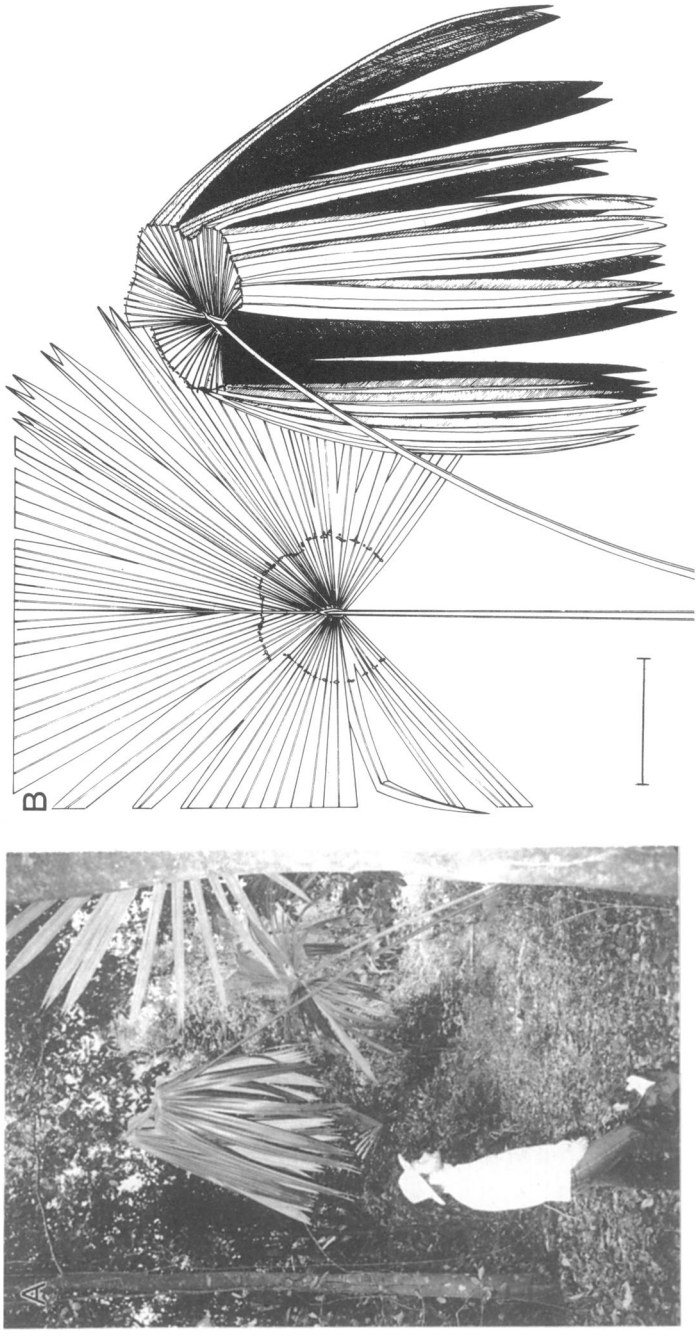


Figure 1. A. Photograph of a palmate umbrella tent constructed in a *Sabal mauritiiformis* leaf that was occupied by a small harem group of *Artibeus jamaicensis*. B. Illustration of a palmate umbrella tent constructed in a leaf of a *Sabal* palm showing the shape and dimensions of the cut area (crown), and the position of the cut leaflets. Scale of drawing = 40 cm.

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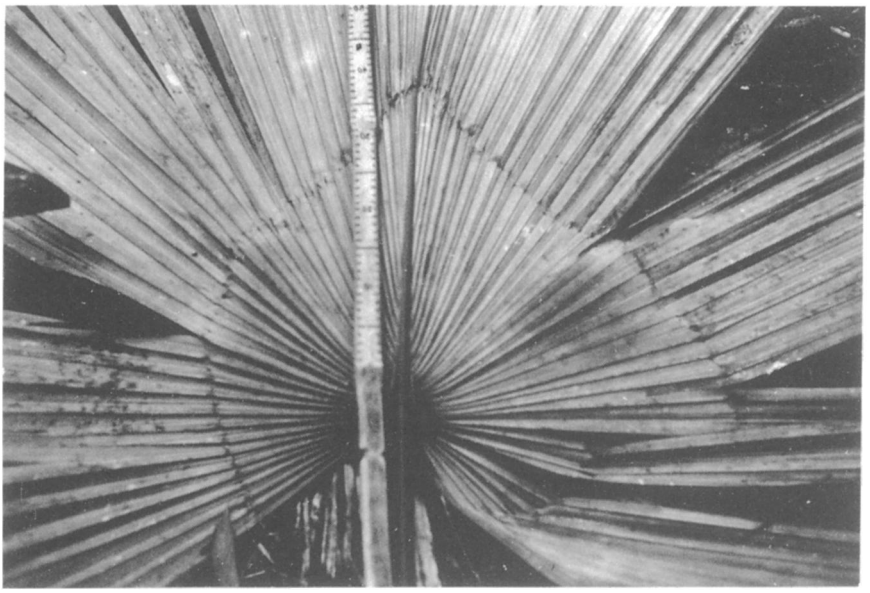


Figure 2. Photograph of the underside of a modified *Sabal* leaf showing the shape and dimensions of the crown and the shape and position of a typical roosting area in the tent. The roosting area on the tent-crown can be seen as the stained, darkened area to the right of centre near the cut. Scale in decimetres.

considerably, but they were generally heart-shaped (Figure 4A). Several variations on this pattern were observed, including partially cut leaves and two tents with partially chewed parallel, elliptical cuts. The number of veins chewed and the extent of chewing on the veins and plications varied considerably. The number of chewed veins ranged from 24 to 88 ($\bar{X} \pm SD = 60 \pm 20.8$; $N = 17$). The fewest number of chewed veins were recorded from partially completed tents, whereas the largest number were observed in completed tents. The ratio of chewed to unaltered veins was 1:1.3 for all tents that we measured. In addition to the chewed veins and plications, completed tents also had a completely or partially severed rachis. The cross-section of the rachis at the severance point ranged from 5 to 10 mm ($\bar{X} \pm SD = 7 \pm 2.1$) and probably was the most difficult part of the leaf for bats to cut. The crown width of *S. mauritiiformis* tents varied from 25 to 80 cm ($\bar{X} \pm SD = 47 \pm 15.8$) and the length of the severed and collapsed leaflets ranged from 85 to 150 cm ($\bar{X} \pm SD = 122 \pm 21$).

Tents in *S. mauritiiformis* ranged in shape from conical to cylinder-like, depending upon the position of the leaf on the tree, the number of veins cut and the age of the tent. Freshly cut tents generally assumed the shape of a frustum, in which the opening below was wider than the tent-crown. Older tents usually assumed a cylindrical configuration when the leaflets drooped perpendicular to the tent-crown, creating an opening that was about the same diameter. When some of the veins and plications were left uncut, the tent assumed an irregular shape and usually showed no apparent signs of occupancy.

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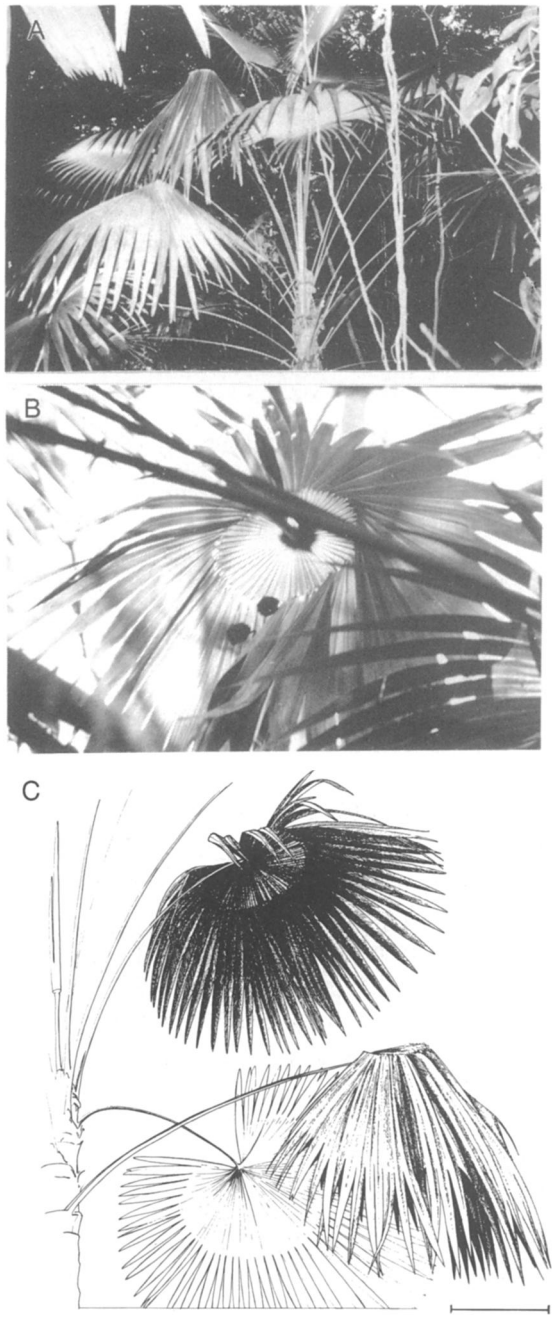


Figure 3. A. Photograph of a young *Coccothrinax barbadensis* tree showing a single palmate umbrella tent (left of centre) and several uncut leaves. B. Underside of a tent in a *Coccothrinax* leaf showing the shape of the tent-crown and the roosting position of two *Artibeus jamaicensis*. C. Illustration of two palmate umbrella tents constructed in leaves of *C. barbadensis*, showing the typical angle of the rachis, the shape and dimensions of the tent-crown, and the position of the leaflets in a tent that was occupied by a small group of *A. jamaicensis*. Scale of drawing = 30 cm.

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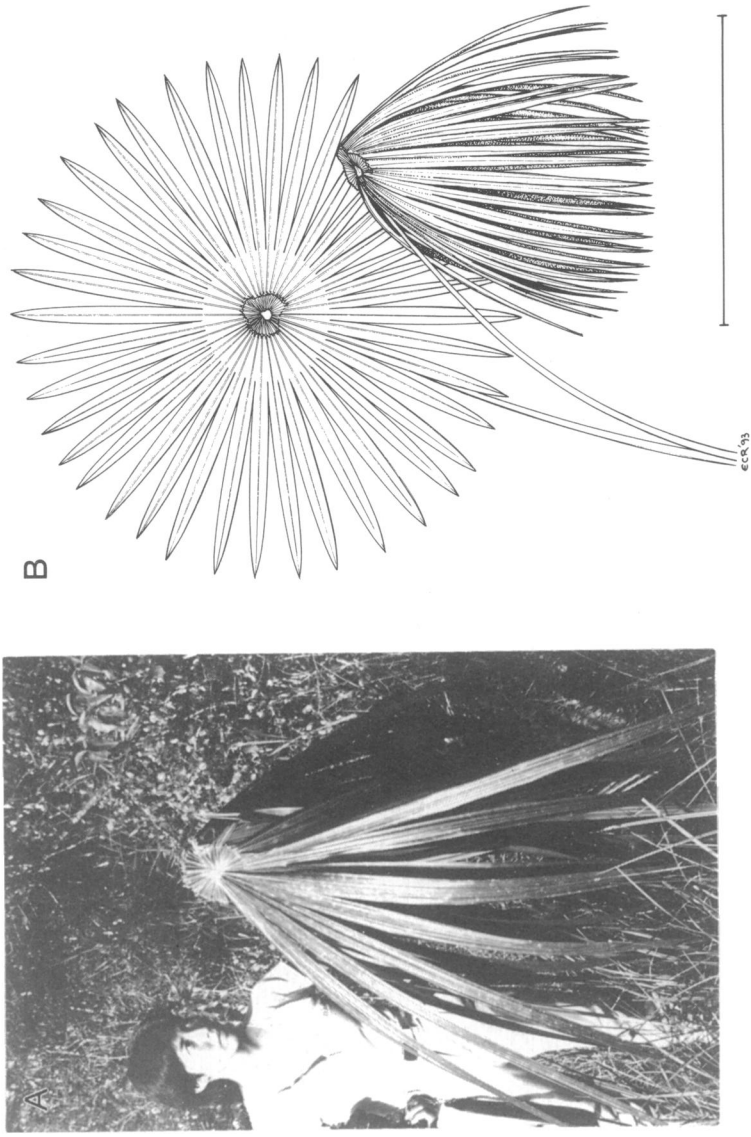


Figure 4. A. Photograph of palmate umbrella tent constructed in a leaf of a *Mauritia flexuosa* palm showing the diameter and shape of the tent-crown, and general shape and relative size of the tent. B. Illustration of a palmate umbrella tent constructed in a *Mauritia flexuosa* palm, showing size of cut area relative to size of leaf. Scale of drawing = 1.5 m.

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As tents aged and became damaged by wind and weather the partially chewed veins and leaf tissue provided less support for the collapsed, distal parts of the leaf and leaflets. Portions of aged and deteriorated leaves were easily broken off by the action of wind. When large segments of these tents sloughed off, these tents were not used by bats.

The space beneath an *S. mauritiiformis* tent provided roosting places for bats and a sufficient area to enter and leave the tent while on the wing. Often small openings created by partially cut and uncut leaflets, and along the area adjacent to the petiole, provided alternate exit routes through which bats sometimes crawled to escape our capture efforts. Normally, however, bats dropped from their roosting position along the crown of the tent and flew through the opening below when they escaped, and during nightly departures. During day-time observations, we saw little evidence that bats changed roosting position by crawling around in the tents. Judging from the presence of claw marks, however, it appears that bats periodically crawl on the under surface of tents. Claw marks and tooth marks also were observed on the upper (abaxial) surface of leaves. We assume that these claw marks were made when bats initially chewed veins at the time of tent construction. Because of the position of these veins on the upper surface of palm leaves and the inverted position of the plications, we believe that the veins are chewed by bats from the upper surface and the plications are chewed from below.

Judging from the size and position of stained areas on the under surface of palm leaves, it appears that bats roost mostly near the crown of the tent, usually hanging from or adjacent to the chewed areas in one or two preferred areas within the tent. These stained areas generally were oval in shape, averaging 10.2×20.4 mm. In addition to these stains, the silvery texture (leaf scales), characteristic of the under surface of leaves in *S. mauritiiformis* and *Coccothrinax barbadensis*, appeared to be worn off by the physical contact of roosting bats. Claw marks were most conspicuous on the adjacent leaf tissue forming the crown of tents, whereas faecal and urine stains were most commonly observed on the drooping parts of the blade and leaflets.

Most of the palms in which we observed or captured bats were less than 4 m in height and were located in the forest understorey. We did not attempt to measure the size of tents in *S. mauritiiformis* that exceeded 6 m in height. Immature carat palms typically had six to nine leaves of which two or three were commonly modified into tents. The height of the 17 tents that we measured ranged from 1.8 to 4.15 m ($\bar{X} \pm SD = 3.5 \pm 0.5$). The oldest tents were usually located on the outermost petioles on a given palm tree. Many of the partially cut distal segments on these older tents had dried and/or sloughed off. In some instances, freshly cut leaves appeared to be unsuitable as tents, especially if adjacent petioles and leaves, with or without tents, had collapsed or grew over them. Many freshly cut tents were still in good condition after eight months. None, however, appeared to be in a condition suitable for roosting after one year.

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Bats were found most frequently in tents that provided open access below, allowing them to enter and depart unimpeded by adjacent vegetation, and in tents that were protected by overhanging leaves from the same or near-by trees. Leaves of *S. mauritiiformis* that were most commonly modified into tents had petiole angles ranging from 50° to 70° from the horizontal. These leaves were usually intermediate in age and were more likely to remain open below as the distal parts of the leaves collapsed downward. Tents that were constructed from leaves with petioles forming angles greater than 70° usually were unsuitable, owing to the position of the collapsed leaf segments and the position of the petiole in the centre of the tent. Tents constructed in leaves where the petiole angle was less than 50° usually were older and had collapsed onto surrounding vegetation, making it difficult for bats to enter and leave the tent while on the wing.

Among the seven tents that we observed in *Coccothrinax barbadensis* (Figure 2A-B), including the two that we cut down and measured, each was similar in shape to those observed in *S. mauritiiformis*. The leaves in *C. barbadensis* generally were smaller, and the crown was smaller and more rounded (Figure 4B) than in *S. mauritiiformis*. When compared with the heart-shaped crowns of tents in *S. mauritiiformis*, the cut areas in *C. barbadensis* leaves were more uniform and the distal portions of the blade and leaflets drooped less severely. In two tents that we measured in *C. barbadensis*, one crown was 20 cm in diameter, whereas the other was 10 cm across. The length of the distal segment of the blade and leaflets averaged 80 cm in both specimens. Approximately 60 veins and plications had been either severed or partially chewed in these two tents. All the veins and plications had been partially severed in one tent, whereas only about half the veins and plications had been so modified in the other. The tents we measured were substantially smaller than two other tents observed at heights >6 m above the ground. Based on the size of bats occupying one of these tents (Figure 2B), we judged the diameter of the tent-crown to be approximately 150 cm.

We observed five complete or partially completed tents in *Mauritia flexuosa*. Three of these tents were in leaves estimated to be at least 10 m above the ground and were exceptionally large (>3 m diameter). Tents that we found in leaves less than 5 m above the ground were cut down, measured and photographed (Figure 3). The enormous overall size of its mature leaves, the relatively small blade area, the deeply dissected, long narrow leaflets and the relatively thick rachis are among the most striking features of *M. flexuosa*. The shapes of tent-crowns were generally pear- or spade-shaped. Seldom were all of the veins severed or chewed sufficiently to cause all the distal segments of a leaf to collapse; the unmodified veins and plications nearest to the petiole often left the area nearest to the petiole relatively open. Although the mid-vein or rachis of *M. flexuosa* ranged from 1.0 to 1.5 cm in cross-section, and appeared to be the most difficult part of a leaf for bats to sever, it was invariably severed on all tents that we observed. Relative to the overall size of the leaf, the tent-crown was relatively small. The overall shape of tents in *M. flexuosa* was similar to

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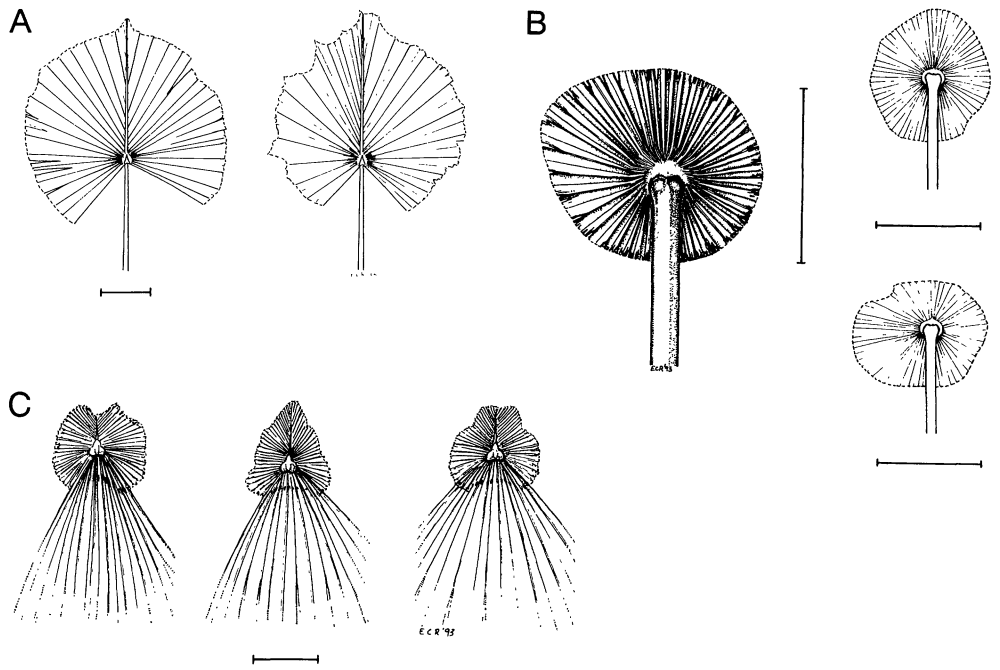


Figure 5. Variation in the shape of tent-crowns made by tent-making bats in three species of palms: A. heart-shaped crowns in *Sabal mauritiiformis*, scale = 10 cm; B. oval-shaped crowns in *Coccothrinax barbadensis*, scales = 30 cm and 20 cm, respectively; and C. spade-shaped crowns in *Mauritia flexuosa*. Scale = 10 cm. Tent-crowns in palmate palms are formed when bats partially chew the veins and plications of leaves (see text).

those observed in *S. mauritiiformis* and *C. barbadensis*, except that the widely spaced leaflets, relatively small crown and open end near the petiole (Figure 5A–C) usually created a more exposed and airy interior.

Tent-roosting bats

We captured and observed two species of bats, *Artibeus jamaicensis* and *Uroderma bilobatum*, roosting in tents constructed in *Sabal mauritiiformis* and *Coccothrinax barbadensis* (Table 1). No bats were observed roosting in tents constructed in leaves of *Mauritia flexuosa*. Although we captured several solitary *U. bilobatum* occupying tents, we were unsuccessful in capturing complete roosting groups. Several roosting groups were either flushed from tents as we approached them or several individuals escaped while we tried to capture or photograph them. Roosting groups of *U. bilobatum* ranged from four to six individuals. Singles and groups were observed or captured in tents in *S. mauritiiformis* ranging in heights from 2 to 8 m above the ground.

We successfully captured two complete roosting groups and five solitary *A. jamaicensis* roosting in tents constructed in *S. mauritiiformis* and *C. barbadensis*. Each group consisted of one mature male and two adult females. Only one other roosting group of *A. jamaicensis* was observed. Solitary bats included both

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Table 1. Sex and group composition of *Artibeus jamaicensis* and *Uroderma bilobatum* observed or captured while roosting in palmate umbrella tents in Trinidad. Most of the bats reported in the 'observed' categories escaped during our attempts to capture them. The identity of observed bats was confirmed visually in the field or by examining photographs.

Species	No. groups[1]	No. singles[1]
Artibeus jamaicensis		
Observed	3	4
Captured	2[2]	2[3]
Uroderma bilobatum		
Observed	4	10
Captured	3[4]	5[5]

[1] Some groups and singles were observed repeatedly in the same or near-by tents over the course of our study and some that were captured may have been included in the 'observed' categories.
[2] Group composition consisted of one adult male and one or three females. None of the females had pups.
[3] All were males.
[4] Two groups consisted of one male and three or six females. The other group consisted of four females. None of the females had pups but some were pregnant.
[5] All were females or young of the year.

males and non-reproductive females. One of the tents that we cut down and examined in detail had been recently modified, showed little evidence of prolonged use and was occupied by a single male *A. jamaicensis*.

Uroderma bilobatum was the most abundant tent-roosting bat at Depot Trace. We observed and/or flushed at least four separate roosting groups and at least nine singles. However, since we were unable to capture and mark most of these bats, we could not determine the size of the local population or establish whether some of the solitary bats that we observed were the same or different individuals that we later captured or observed in other tents. Only one small group consisting of two *U. bilobatum* was observed at the Coastal Upland site.

Tent-roosting bats appear to make use of preferred tents although they apparently are familiar with and used alternate tents. Two individuals of *A. jamaicensis* that we observed roosting in one of the tents shown in Figure 2A, regularly occupied this tent for nearly nine months (April to January). Singles and groups of both bat species that we disturbed during our capture attempts invariably flew to near-by tents. Similarly, they would often take flight if we unintentionally disturbed the near-by vegetation as we approached an occupied tent. Groups usually returned to their tent of origin within the same or following day. By contrast, solitary bats showed less fidelity and more often than not settled and remained in another near-by tent.

We never observed bats in the act of tent-making. Based upon our day-time observations of *Uroderma bilobatum* and *Artibeus jamaicensis* in tents, most individuals appeared to be alert but relatively inactive during this period. We observed no bats occupying tents at night, but we suspect that tents are constructed during this period. On more than one occasion we observed tents that were occupied alternately by individuals and groups of both species. On one occasion we observed two *U. bilobatum* occupying a tent for several weeks in an

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S. mauritiiformis leaf that was later occupied by a solitary *A. jamaicensis*. Because we captured this bat as a voucher specimen, we could not determine how long this single bat may have used this tent.

DISCUSSION

Tent architecture

Umbrella tents have been described in several species of palmate palms and a cyclanth. These include tents constructed in the palms *Prichardia pacifica* and *Livistonia chinensis* by *Uroderma bilobatum* (Barbour 1932), *Sabal mauritiiformis* by *Uroderma bilobatum* (Goodwin & Greenhall 1961), *Corypha* sp. by *Cynopterus sphinx* (Goodwin 1979), *Livistonia rotundifolia* by *Scotophilus kuhlii* (Rickart *et al.* 1989), *Sabal mauritiiformis* and *Coccothrinax barbadensis* by *Uroderma bilobatum* or *Artibeus jamaicensis* (this study) and in the cyclanth *Carludovica palmata* by *Artibeus watsoni* (Timm 1987). In each case the basic pattern of the tent is the same – bats alter the veins and plications in more or less similar ways. The shapes of tent-crowns are similar among species having different evolutionary histories and separate geographic distributions. These include one member of the family Pteropodidae (Goodwin 1979), three species of the family Phyllostomidae (subfamily Stenoderminae; Goodwin & Greenhall 1961, Timm 1987, present study) and one species belonging to the family Vespertilionidae (Rickart *et al.* 1989). These observations support the interpretation that similarity in tent architecture is more a reflection of leaf form than of convergence in behaviour by members of distantly related taxa. We believe that the type of cuts made in palmate palms, and the resultant tent architecture, is influenced more by the general shape of the leaf than by behavioural characteristics of the bat species assumed to be responsible for its construction.

Although Barbour (1932) suggested that the initial bites in the construction of tents are made when bats hover, our observations of tooth marks and claw marks on both surfaces of palm leaves suggest that bats most likely modify leaves by chewing veins while crawling upon the upper surface, and chew the plications from below. Given the rigid and highly fibrous composition of the palm veins and rachis, it seems unlikely that these structures could be successfully chewed while bats hover. The number of leaf veins that must be chewed in a palmate leaf can range up to 80 in the large leaves of *Prichardia* (Barbour 1932), *S. mauritiiformis* and *Coccothrinax* (this study). Based on the observations of Barbour (1932), it may take two or three nights for bats to complete a palmate umbrella tent.

Tents and harems

Our observations of tents and tent-roosting bats support the hypothesis that when leaves are modified into tents, the resultant roosts serve as both critical and defendable resources. The size and shape of the roosting space provided by umbrella tents are similar to those provided by solution cavities in caves,

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which are defended by males or at least two polygynous species, *Phyllostomus hastatus* (McCracken & Bradbury 1981) and *Artibeus jamaicensis* (Kunz *et al.* 1983). Thus, in addition to hollow trees (Morrison 1978, 1979; Morrison & Morrison 1981) and cave solution cavities (Kunz *et al.* 1983, McCracken & Bradbury 1981), palmate umbrella tents may provide the conditions necessary for their defence by males.

Because of the ephemeral nature of leaf-tents, one could expect tent-making bats to change roost sites and engage in tent-making rather frequently (Barbour 1932, Brooke 1990, Koepcke 1984, Timm & Clauson 1990, Timm & Lewis 1991). Tents that we marked in several *Sabal mauritiiformis* trees provided suitable conditions for roosting for at least nine months, and some tents in *S. mauritiiformis* and *Coccothrinax barbadensis* showed little sign of deterioration even after one year. Notwithstanding, it remains to be determined how many tents are actually used by a single bat or harem group on a regular basis, and how often new tents are constructed. It appears that solitary bats and roosting groups are familiar with and use more than a single tent in a particular area.

Our observations of several solitary males in tents, the apparent variance in tent quality and the occurrence of harem groups roosting in near-by tents, leads us to suspect that males construct and defend tents that are then used by groups of females. Studies are needed to test the hypothesis that males do, in fact, make and defend tents and that certain females consistently associate with a particular male. The probability of observing bats in the act of tent-making could be enhanced by experimentally removing or preventing access to all tents in a particular area. Such an experiment would also make it possible to establish whether roosting groups require more than one tent. Simultaneous estimates of field metabolic rates (Kunz & Nagy 1988) among solitary males and those associated with female groups would allow assessment of the cost/benefit relationships of tent-making and defence of harems.

An alternative to the hypothesis that males construct tents is that several members of a roosting group share the responsibility of tent construction. This could occur if female tent-making bats form social groups independent of males, as has been documented for *P. hastatus* (McCracken & Bradbury 1981). We have no evidence to support or refute this notion.

Our observations and those of Timm (1987), Timm & Clauson (1990) and Timm & Lewis (1991), where different bat species use the same tent at different times, indicate that tent-making bats may sometimes roost in tents made by other bats. This raises the question of whether bats usurp and perhaps defend tents that they do not construct. Considering the number of tents that are unoccupied in a given area, there is considerable potential for usurping of tents by individuals of the same species and different species. The possibility exists for a mixed strategy among tent-making bats where some individuals or species build tents and other individuals or species usurp them.

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In future studies on tent-making bats it will be important to establish which individuals and species are involved in tent construction, whether both sexes or all members of a roosting group participate (i.e. how costs are distributed) and, if cooperation is involved, whether the costs are repaid so that individuals that actually construct tents realize net fitness benefits. Finally, to evaluate fully the mechanisms that have been selected for tent-making, it will be necessary to establish the membership stability of roosting groups and to determine whether bats that construct tents and/or share roosts are genetically related.

Generally, tents made in palms with wide blades and long leaflets (*S. mauritiaeformis*) have larger crowns and larger volumes than tents made in palms with narrow blades and long, separated leaflets as in *M. flexuosa*. The most commonly used tents were generally free of vegetation below, allowing bats to enter and depart on the wing without being impeded by adjacent vegetation.

Singles and small apparent harem groups (2–6 individuals) of *Artibeus jamaicensis* and *Uroderma bilobatum* were captured and/or observed in tents of *S. mauritiiformis* and *C. barbadensis*. Although no bats were observed in the act of tent-making, we suggest that tent-making is an adult male behaviour and that tents provide resources that promote the apparently polygynous mating systems described for these and other tent-making bat species.

ACKNOWLEDGEMENTS

We thank the National Geographic Society for funding this study. We also thank Boston University (Office of the Provost), the Organization of American States and the American Philosophical Society for financial support. We thank Hugh Britten, Al Kurta, Simon Robson, Marty Fujita and Anne Brooke for field assistance. We also are grateful to Jake Kenny who suggested potential study sites, and Edward Rooks who made drawings of plants and tents. Pierre Charles-Dominique, D. W. Morrison and Robert M. Timm made helpful suggestions on an earlier version of this manuscript. We thank Robert Read of the Smithsonian Institution for identifying voucher specimens of palm species. Lastly, we thank Ian Lambie, Rita Iton, Edward Rooks and Francis Moran of the Asa Wright Nature Centre for their support and assistance during our stays in Trinidad. Carol W. James and Beesham Ramdial (Trinidad and Tobago, Department of Forestry and Wildlife) were instrumental in processing, collecting and export permits.

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Accepted 26 January 1995

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