

Chapter 1

Roosting Ecology of Bats

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1. INTRODUCTION

Bats spend over half their lives subjected to the selective pressures of their roost environment; thus it is not surprising that the conditions and events associated with roosting have played a prominent role in their ecology and evolution. Roosts provide sites for mating, hibernation, and rearing young; they promote social interactions and the digestion of food; and they offer protection from adverse weather and predators. Conditions that balance natality and mortality and enhance survivorship are intimately linked to roost characteristics and are paramount to the success of a species. The roosting ecology of bats can be viewed as a complex interaction of physiological, behavioral, and morphological adaptations and demographic response. The roosting habits of bats may be influenced by roost abundance and availability, risks of predation, the distribution and abundance of food resources, social organization, and an energy economy imposed by body size and the physical environment. For many bats the availability and physical capacity of roosts can set limits on the number and dispersion of roosting bats, and this in turn can influence the type of social organization and foraging strategy employed. For example, some bats as refuging animals (see Hamilton and Watt, 1970) may benefit from improved metabolic economy and information transfer but may be subjected to the added costs associated with increased commuting time, competition for food, and risks of predation.

The purpose of this review is to examine the diversity of roosting adaptations of bats and to consider how they are influenced by opposing selective pressures. I have intentionally avoided the use of a rigid classification of roost types (for a review of roost classifications see Gaisler, 1979); rather I have emphasized adaptations to day- and night-roosting behavior and ecology during

the nonhibernating period to achieve an integrated view of the relationships between roosting habits, foraging strategies, energy economy, and social organization. A thorough discussion of the physiological aspects of roosting, including hibernation, has been reviewed elsewhere (Chapter 4). The importance of roosts in the evolution of social behavior was emphasized by Bradbury (1977a).

Generalizations about the roosting ecology of bats are difficult to formulate, because the selective pressures on different species are varied and diverse. The factors affecting bats that roost in protected shelters should differ markedly from those affecting bats that roost externally. Sheltered roosts offer the advantage of relative permanency, microclimate stability, reduced risks of predation, and protection from sunlight and adverse weather. External roosts offer the advantages of being ubiquitous and abundant, yet many are temporary (e.g., foliage) and subject to environmental extremes. The relative number of species using external shelters generally decreases with distance away from the equator, and there is a general tendency for bats that roost in caves and man-made structures to be highly gregarious (Gaisler, 1979).

The associations of bats and roosts range from being obligatory to opportunistic. Some species have become highly dependent on certain types of roosts owing to their morphological and physiological specialization. For example, the highly developed adhesive disks on the feet and wrists of *Thyroptera tricolor* restricts this bat to roosting on the smooth inner surfaces of unfurled leaves (Findley and Wilson, 1974). Opportunistic species typically have generalized roosting habits and wider geographic distributions. An example of such a species is the Neotropical bat *Artibeus jamaicensis*. In regions where caves are present, this bat seeks daytime shelter in small recesses and cavities within caves (Goodwin, 1970). Where caves are absent, for example, on Barro Colorado Island in the Panama Canal Zone, this bat typically seeks shelter in tree cavities and foliage. A polygynous mating system is promoted by the defense of these limited roost resources (tree cavities) by males (Morrison, 1979); but to what extent this type of social organization is influenced by the kind and abundance of roosts in other situations remains to be determined for this and other species.

The evolution of wings and flight have permitted bats to exploit roost environments (and food resources) virtually unavailable to most other vertebrates. The evolution of echolocation was undoubtedly a principle determinant leading to the divergence of roosting (and feeding) habits. Largely because of their ability to echolocate, the Microchiroptera have successfully exploited a variety of internal shelters (e.g., caves, rock crevices, tree cavities, and man-made structures). The Megachiroptera have successfully adapted to a variety of external roosts, but they have been virtually excluded from most internal shelters because of their inability to echolocate. Only members of the megachiropteran genus *Rousettus* have independently acquired an ability to echolocate, which

they share with the microchiropterans, echolocating oil birds (*Steatornis*), and swiftlets (*Collocalia*).

What one ultimately observes in the roosting ecology of a species is tempered by constraints imposed by phylogenetic inertia (see Wilson, 1975), and a compromise of opposing selective pressures derived from roost and nonroost origins. Behavioral, physiological, and morphological characteristics of bats commonly regarded as adaptations for roosting, such as dorsoventral flattening, suction pads and disks on feet and wrists, cryptic markings and postures, clustering, torpor, synchronous nightly departures, and so forth should be regarded as compromises imposed by the manner of flight, body size, predator pressure, energy economy, and the physical environment.

2. DAY ROOSTS

2.1. Adaptations for Roosting

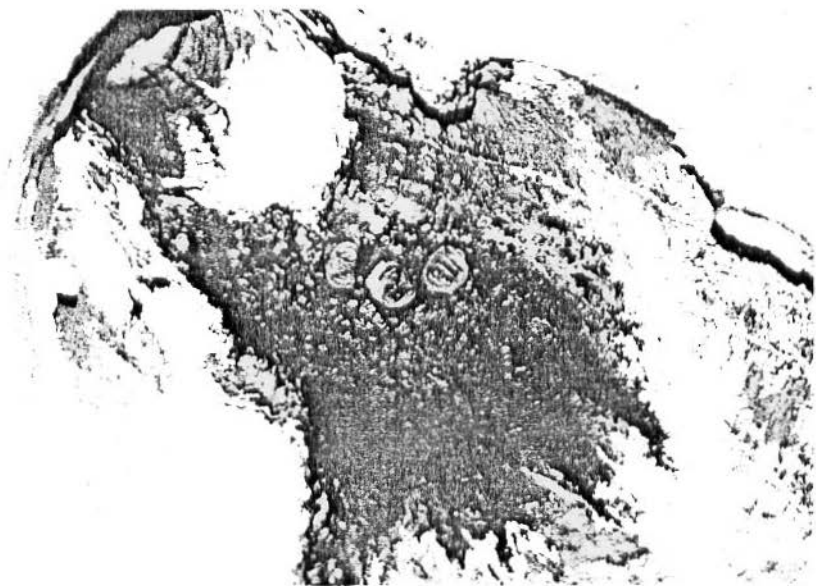
2.1.1. Cave-Dwelling Bats

Bats are the only group of vertebrates that have successfully exploited caves for permanent shelter. Most families and genera of bats include species that regularly or occasionally seek refuge in caves. We know little about the conditions that may have led to the use of caves as roosts, although Jepsen (1970) suggested that bat ancestors may have become cave dwellers to escape predators and to conserve moisture and energy between periods of high activity. Caves typically last for long periods of time and, consequently, many have become traditional locations for resident populations; however, they have the disadvantage of being uncommon in many areas and located at considerable distances from suitable foraging areas (Bradbury, 1977a).

Caves serve as roost sites for solitary bats and groups ranging up to the largest known mammalian aggregations. In the southwestern United States single caves in summer may house up to 20 million individual *Tadarida brasiliensis* (Davis *et al.*, 1962). In tropical Africa the numbers of *Hipposideros caffer* may approach 500,000 (Brosset, 1966), and in Australia maternity colonies of *Miniopterus schreibersii* may number up to 200,000 (Dwyer and Hamilton-Smith, 1965). Many caves provide shelter for more than one species; the combined population of four species of mormoopid bats occupying a cave in Mexico may reach 800,000 individuals (Bateman and Vaughan, 1974). Benefits derived from such large numbers in a single cave must be balanced against the increased costs of intraspecific competition for food, misdirected social behavior, and the increased incidence of parasites and disease.



A



B

FIGURE 1. (A) Small cluster of *Myotis grisescens* occupying a cave ceiling cavity, where trapped metabolic heat enhances an individual's energy economy in an otherwise cool cave. (Photo by M. D. Tuttle.) (B) Small harem group of *Artibeus jamaicensis* occupying a solution cavity in a cave ceiling. The darkly stained area indicates that this site has had prolonged use. This and other cavities promote population substructuring and facilitate the defense of these roosts by harem males. (Photo by C. D. Burnett.) For a similar example see Fig. 4C in Chapter 8.

The distribution of cave-dwelling bats varies geographically with the distribution of caves and their physical dimensions, topography, and microclimate (Brosset, 1966; Tuttle and Stevenson, 1978). Many areas with caves are unsuitable for bat roosts. Caves with cold, descending chambers are not occupied in summer and seldom in winter, and many cold caves in temperate regions are unsuitable for bats during maternity periods. For example, only 2.4% of the 1635 known caves in Alabama are used by *Myotis grisescens* in summer, and even fewer (0.1%) are used in winter (Tuttle, 1979). In tropical regions cave environments are typically more stable, and they are more uniformly inhabited than in temperate regions (Brosset, 1966).

Caves that offer a wide thermal range combined with structural and elevational complexity provide the greatest diversity of roosting sites (Tuttle and Stevenson, 1978). In tropical regions bats are often distributed internally along gradients of light intensity (Brosset, 1966). Many caves have large, spacious chambers that provide roost sites for large aggregations. The presence of crevices and cavities in cave ceilings and walls can have an important influence on the ecology and social behavior of bats (Fig. 1). They provide roosting sites for a variety of bats (Dalquest and Walton, 1970), they facilitate group substructuring and the defense of roosts or female groups against incursions of conspecifics (Bradbury, 1977a; McCracken and Bradbury, 1981), and they serve as heat traps that enhance metabolic economy (Dwyer and Hamilton-Smith, 1965; Tuttle, 1975; Humphrey, 1975).

2.1.2. Crevice-Dwelling Bats

Rock crevices and narrow spaces beneath exfoliating bark of tree trunks and branches provide a variety of abundant and ubiquitous roost sites for bats. Rock crevices provide relatively permanent roost sites, but spaces beneath loose bark are temporary and thermally more variable and often require bats to make frequent relocations. Crevice dwelling appears to be a prevalent feature of molossid and vespertilionids in arid and semiarid regions (Brosset, 1962d; Brosset, 1966; Barbour and Davis, 1969). Little is known about the roosting ecology of crevice-dwelling bats, because they are difficult to find and often located in inaccessible places.

Crevice-dwelling bats have been most extensively studied in the arid regions of the western United States. Vaughan (1959) found that *Eumops perotis* prefers crevices in vertical or near-vertical cliffs, situated in deep slopes. Roosts characteristically have moderately large openings that can be entered from below. Six is the typical number of bats seeking shelter in these crevices. Occupied crevices are at least twice as wide as a bat's body and the entrances are horizontal and face downward. Vaughan (1959) suggested that the choice of these roost

sites may be determined by the bats' need for space and to allow access to roosts from below.

Vertical and horizontal crevices, narrow fissures, and spherical chambers in rock cliffs are common roost sites of *Antrozous pallidus* (Vaughan and O'Shea, 1976). Typically, this bat prefers spacious crevices that permit internal movements and allow departures and returns to occur with outstretched wings. In summer deep, horizontal crevices are preferred, where cliffs serve as massive heat sinks. In spring and autumn bats roosting in vertical crevices are responsive to changes in ambient temperature. Temperatures in these crevices are low and bats remain torpid much of the day. Bats passively arouse as crevices become heated in late afternoon, further minimizing daily energy expenditure.

In the badlands of South Dakota singles and small maternity groups of *Myotis leibii* select small, dry, shallow roosts in horizontal and vertical crevices formed in siltstone boulders and sediment formed from a mixture of clay and volcanic ash (Tuttle and Heaney, 1974). Crevices are seldom more than 2.5 cm wide, ranging in depth from 2.5 to 20.5 cm. Temperatures in these crevices are uniformly high (26–33°C), averaging 4–5°C lower than outside ambient temperatures. The shallowest roost crevices are located in positions that receive the least amount of direct daily sunlight.

Vertical crevices in steep canyon walls are the most common roost sites of *Pipistrellus hesperus* (Hayward and Cross, 1979). These crevices are typically narrow, approximately 2.5 cm wide, and range in depth from approximately 25 cm to 1 m. Roost temperatures remain considerably below ambient temperatures, as the rock substrate has a buffering effect. This bat is usually solitary, but it occasionally forms small groups whose individuals roost near the openings of crevices, where they can retreat deeper to avoid temperature extremes.

Crevices beneath loose and exfoliating bark of trees provide shelter for small maternity colonies of *Myotis sodalis* (Humphrey *et al.*, 1977). These small groups seek refuge in patches and interconnecting spaces beneath the bark of bitternut and shagbark hickory trees. Spaces beneath loose bark of bitternut hickory trees are apparently preferred in spring and summer, as they are more effective in trapping solar heat and in providing large spaces for rearing young. Areas beneath the exfoliating bark of living shagbark are thermally more stable during cold periods in spring and autumn and thus provide effective alternate roosts at these times.

2.1.3. Use of Tree Cavities

Cavities in the trunks and branches of dead and living trees offer favored shelter for many bats, especially in tropical regions. Such sites are formed from scars on branches and large cavities derived from the rotted interior of old trees. Tree cavities offer protection against fluctuations in ambient temperature and

humidity (Verschuren, 1957; Maeda, 1974; Bradbury, 1977a; Morrison, 1979), and, as with hole-nesting birds (see Lack, 1968), they provide protection against predators and adverse weather. A disadvantage of tree cavities is that they offer limited roosting space for colonial species and they eventually rot and fall, requiring the periodic relocation of inhabitants (Bradbury, 1977a).

There are numerous reports of both Old and New World bats occupying tree cavities (Ryberg, 1947; Verschuren, 1957, 1966; Goodwin and Greenhall, 1961; Ognev, 1962; Hall and Dalquest, 1963; Kingdon, 1974; Tuttle, 1976b; Lekagul and McNeely, 1977), but few studies have considered the ecological aspects of these roost sites. In the Old World tropics tree cavities are most commonly used by members of the Nycteridae, Rhinolophidae, Hipposideridae (Brosset, 1966; Rosevear, 1965; Kingdon, 1974). In equatorial Africa small groups of *Nycteris arge*, *N. grandis*, *N. major*, and *N. nana* typically prefer trees with entrances located near the base (Rosevear, 1965; Kingdon, 1974). A similar preference is shown by the Neotropical phyllostomids *Trachops cirrhosus* and *Carollia perspicillata* (Fig. 2A). In Kenya the megadermatid *Cardioderma cor* forms groups of up to 80 individuals in hollow baobab trees (Fig. 2B), where roost cavities range from 2.2 to 4 m in height and are 1.8 to 3 m wide, each with a single entrance averaging 25 cm in width and 40 cm in height (Vaughan, 1976).

In the Neotropics tree cavities are used predominantly by phyllostomids, of which 15 genera, representing 28 species, are known to regularly or occasionally use such cavities as day roosts (Tuttle, 1976b). Tree cavities are also used by some molossids, vespertilionids (Walker, 1975), and *Noctilio leporinus* (Goodwin and Greenhall, 1961). The most intensive study of tree-roosting habits of a Neotropical bat was by Morrison (1979), who found that harem groups of *Artibeus jamaicensis* gain access to tree cavities through single openings, approximately 6 cm wide (Fig. 2C). Entry holes ranged in height from 2 to 15 m above the ground, and cavities typically consisted of long cylinders, 12–25 cm in internal diameter, extending 1.5–2 m above the entrance hole.

Tree cavities also provide favored roost sites for several species of Palearctic bats, where individuals typically hang from the upper parts of these cavities (Ryberg, 1947). In Japan Maeda (1974) found that *Nyctalus lasiopterus* occupied tree cavities, the largest of which were used as maternity roosts housing up to 40 individuals; the smallest cavities were used by males. Tree cavities were chosen for the position and shape of the tree and the height of the entrance above the ground. In the Soviet Union at least ten vespertilionid species roost in tree cavities, where two or more species may roost together (Ognev, 1962). *Myotis bechsteini* and *Pipistrellus nathusii* each form pure colonies in tree cavities, but these bats may form mixed colonies in man-made structures. In Finland *M. mystacinus* prefers tree cavities to buildings, and although *M. daubentoni* occasionally roosts in tree cavities, it shows a preference for buildings. In one of the most extensive studies on tree-roosting bats Gaisler *et al.* (1979) examined the

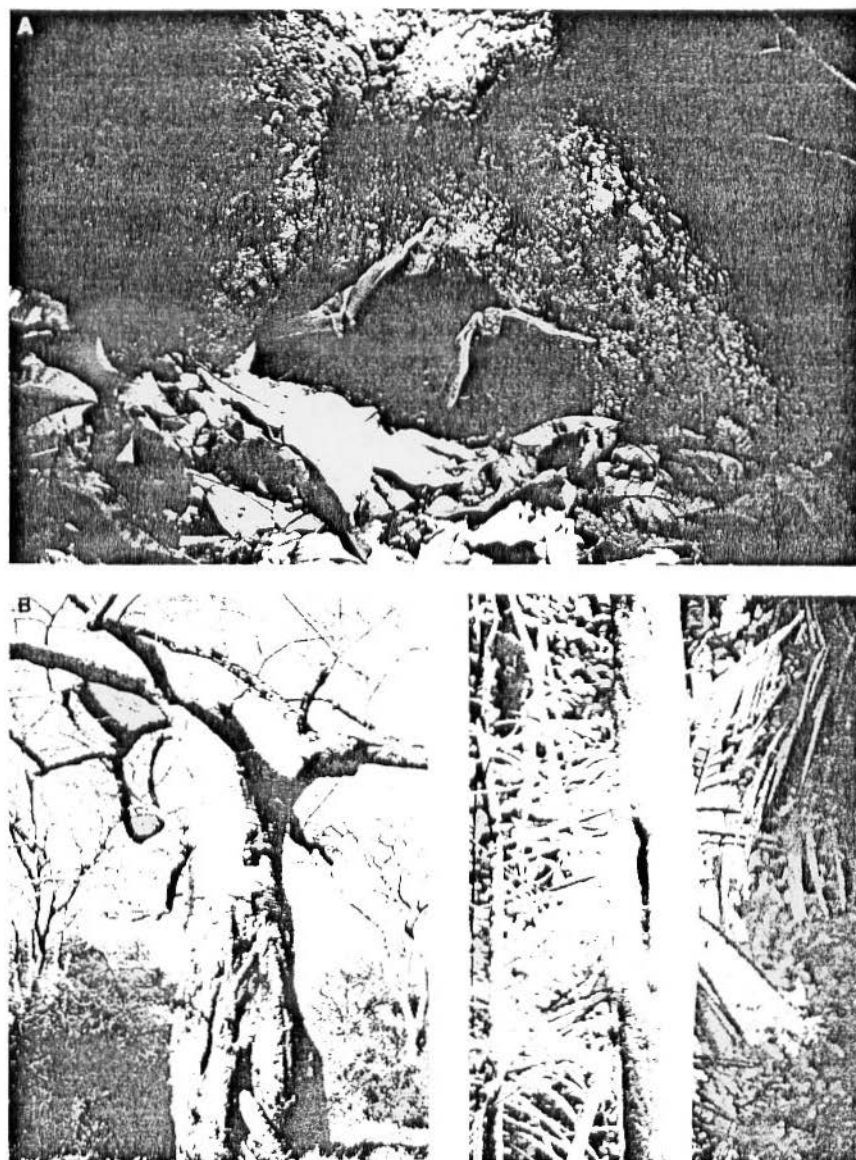


FIGURE 2. (A) A *Trachops circhiosus* entering (left) and a *Carollia perspicillata* departing (right) from a tree cavity through an opening located at the base of a tree. (Photo by M. D. Tuttle. Courtesy of the National Geographic Society.) (B) Cavities in baobab trees (*Adansonia digitata*) are preferred day-roosting sites of *Cardioderma cor*. (Photo by T. A. Vaughan. With permission from the American Society of Mammalogists.) (C) Tree cavity used by a small harem group of *Artibeus jamaicensis*. (Photo by D. W. Morrison.)

roosting habits of *N. noctula* in central Europe and found that 72.8% of these bats were found in tree cavities (21.8% occurred in buildings and 5.4% in man-made roost boxes and beneath loose bark). From March through October this bat forms maternity groups ranging from 3 to 54 individuals. Roost cavities in trees near the edge of wooded areas, in lowland and sloping regions, are preferred, including 13 different tree species distributed proportionately among the species occurring in the region. The principle criteria for roost selection were that trees had a high trunk below the crown and free (flight) space in front of the entrance. Roost entrances ranged in height from 1 to 16 m above the ground, but most bats occupied cavities at a height of 1.4 m.

That hollow trees are prevalent in nutrient-poor soils in tropical regions prompted Janzen (1976) to postulate that rotted hollow cores may be an adaptive trait selected as a mechanism for nitrogen and mineral trapping resulting from the accumulation of animal feces and subsequent microbial metabolism. If this hypothesis is correct, tree-roosting bats that deposit large quantities of nitrogen-rich guano (see Hutchinson, 1950) may play an important nutrient role in forest ecosystems.

2.1.4. Foliage- and Other External-Roosting Bats

A fundamental similarity among foliage-roosting bats is that their roost sites are temporary. As leaves die or unfurl they no longer provide suitable roosts. Foliage roosts often promote nomadic populations and low roost fidelity and provide minimal protection from variations in temperature and humidity (Bradbury, 1977a). Most foliage-roosting bats are solitary or form small groups, and, with few exceptions, they are distributed in tropical regions. Large aggregations of foliage-roosting bats are known only among the largest megachiropterans. Several foliage-roosting bats have a highly specialized morphology and behavior that limits their roosting habits to certain types of plants (see Section 2.1.5), some modify leaves into tentlike structures (see Section 2.1.6), and still others rely on some form of crypsis.

Many bats that roost externally on branches, tree trunks, and in foliage have bold, contrasting marks, bright colors, spotted patterns, reticulate wing venation, or assume distinct postures and dispersion patterns that defy visual detection. Such cryptic patterns and behaviors are prevalent among the Pteropodidae, Emballonuridae, Phyllostomidae, and Vespertilionidae and presumably confer some degree of protection from visually oriented predators.

The concealment of many foliage-roosting megachiropterans is enhanced by mottled and broken color patterns and sometimes by motionless postures. In some pteropodids hues of yellow, orange, and red resemble fruits and dry leaves, and contrasting lighter colors around the head and neck suggest a type of counter-shading (Dobson, 1877; Novick, 1977). The motionless postures often seen in



FIGURE 3. Mother and two young *Lasius cinereus* hanging from a spruce tree. (Photo by M. D. Tuttle. Courtesy of the National Geographic Society.)

Pteropus poliocephalus (Nelson, 1965a), *Epomops franqueti* (Jones, 1972), *Lavia frons* (Kingdon, 1974), and *Nyctimene major* (Walker, 1975), engulfed in folded wings, gives the appearance of dead leaves.

Contrasting patches and varying numbers and intensities of facial and dorsal stripes enhance crypsis in several vespertilionids, emballonurids, and phyllostomids. Among Old World vespertilionids cryptic markings are pronounced in *Myotis formosus*, *Murina aurata*, and in the so-called "painted bats" of the genus *Kerivoula*, many of which have long and woolly pelage, ranging in color from yellow to bright orange and scarlet (Dobson, 1877; Allen, 1939; Wallin, 1969; Walker, 1975). Some of the *Kerivoula* have a grizzled, frosted appearance, with long fingers that contrast against dark wing membranes and which apparently resemble tufts of moss (Walker, 1975). Members of the genus *Glauconycteris* have reticulate markings that resemble leaf venation and bold, contrasting marks on the pelage that suggest disruptive patterns (Rosevear, 1965; Walker, 1975; Novick, 1977). A white dorsal stripe and patches of white on the head and shoulders of the vespertilionid *Scotomanes ornatus* contrasts with an otherwise brownish pelage (Walker, 1975; Lekagul and McNeely, 1977). Cryptic colors and markings are also evident among New World bats of the genus *Lasiurus* which either roost singly or in small groups in foliage, in vines (Constantine, 1966), and in clumps of Spanish moss (Constantine, 1958a). The frosted, grizzled appearance of *L. cinereus* (Fig. 3) may offer protection from visually oriented predators.

Two distinct parallel white dorsal lines and the motionless roosting posture of *Saccopteryx bilineata* may confer protection from predators, as this emballonurid roosts on exposed buttresses and the trunks of trees (Bradbury and Emmons, 1974). Similarly, the brownish, grizzled, yellow-gray color and white, wavy dorsal lines of *Rhynchonycteris naso* resemble lichen when contrasted against the background of tree bark, on which it frequently roosts (Goodwin and Greenhall, 1961; Bradbury and Emmons, 1974). Distinct white facial and dorsal stripes of several phyllostomids, including the tent-making *Artibeus* and *Uroderma*, and members of the genera *Chiroderma*, *Enchisthenes*, *Vampyroides*, *Vampyrops*, and *Vampyressa* may confer protection from predators. Because many of these bats roost in foliage having either lobed or pinnate leaves (Davis, 1944; Goodwin and Greenhall, 1961; Jimbo and Schwassmann, 1967; Morrison, 1978a, 1980), facial stripes and dorsal markings may complement the disruptive patterns formed by individual leaflets (Foster and Timm, 1976).

Some foliage-roosting bats seek shelter where they are inconspicuous from the ground and nearby branches or roost high in the tree canopy, which reduces their vulnerability to predation or disturbance. Large groups of *Artibeus lituratus* and *Vampyroides caraccioli* commonly roost high in the tree canopy, where they may be conspicuous from the ground, but those that seek lower sites roost in smaller groups well concealed in understory foliage and vine-entangled sub-

canopy trees (Morrison, 1980). The North American tree-roosting bats *Lasiurus borealis*, *L. cinereus*, *L. intermedius*, and *L. seminolis*, commonly select roosts that are visible only from below, lack branches from which predators might detect and attack them, and are located over ground cover that minimizes reflected sunlight (Constantine, 1958a, 1966). Constantine (1966) found that the roosts of young and adult female *L. borealis* and *L. cinereus* were located higher in the tree canopy than were solitary males, and he suggested that this behavior may reduce their conspicuousness to predators and provide young bats with greater opportunities to initiate successful flights.

The roosts of most megachiropterans vary from being located in dense foliage in the darkest parts of trees (Ayensu, 1974) to open, conspicuous areas. For example, *Micropteropus pusillus* is often associated with dense foliage, *Epomops franqueti* hangs from small branches near clusters of leaves, and *Eidolon helvum* commonly roosts on sturdy but leafless branches near the trunks of large trees (Jones, 1972). Nelson (1965a) noted that *Pteropus poliocephalus* usually hangs from lower, shaded branches but moves to higher, more open areas of the tree canopy following disturbance. The roosts of *P. vampyrus* may be conspicuous, but they are often located in mangrove swamps, where they are inaccessible to intruders (Goodwin, 1979). Differences in the roosting positions of megachiropterans may be influenced by body size, the degree of crypticis, and flight ability. For example, the large megachiropteran *Hypsignathus monstrosus* roosts on exposed branches, high in forest trees, beneath the dense umbrella canopy, and where there is sufficient flight space between the roost and the understory vegetation (Bradbury, 1977b).

2.1.5. Morphological Specialization

Morphological changes associated with the evolution of flight have had a profound affect on the roosting habits and locomotion of bats (Vaughan, 1970a). For example, the hind limbs of most bats extend dorsolaterally, as if they had been rotated 90° from the position typical of terrestrial mammals. In some families, including the phyllostomids and natalids, this rotation may reach 180°, where it severely restricts quadrupedal locomotion. Vaughan (1970a) recognized three types of morphological modifications of the pelvic and hind limb structures that are related to different roosting habits and terrestrial locomotion in bats. The majority of bats, including most or all of the Emballonuridae, Nycteridae, Natalidae, and Vespertilionidae, have generalized roosting habits. These bats may hang from ceilings in contact clusters, cling to vertical surfaces, or roost in crevices or small holes. Another group, typified by the phyllostomid genera *Choeronycteris*, *Glossophaga*, *Macrotus*, extend their hind limbs to the rear and only their feet are in contact with the roost substrate. These bats usually assume a pendent posture and hang separate from each other, often suspended by one foot.

Bats that hang pendent commonly have large pectoral muscles, short bodies, and deep chests (Vaughan, 1959). Howell and Pylka (1977) suggested that selection for pendent roosting habits may have facilitated flight takeoff, reduced thermal disadvantages that accompanied conduction to a cool substrate (in caves), and lessened accessibility to predators. Roosting pteropodids typically assume a pendent posture and use their feet and wings for crawling. *Pteropus* and *Eidolon* are apparently incapable of crawling on horizontal surfaces (Lawrence and Novick, 1963), but they are agile with both wings and feet when crawling among branches in trees (Nelson, 1965a; Wickler and Seibt, 1976). Other pteropodids such as *Dobsonia peroni* and *Notopteris macdonaldi* are able to exploit shallow, dimly lit caves because of a unique insertion of the wing membrane that allows them to climb vertically and reach cave ceilings (Goodwin, 1979). A third group that includes the molossids often has modified pelvic and pectoral girdles as adaptations for roosting in crevices. Many of these bats have an extraordinary ability to crawl, but some require special roosts that permit vertical drops before taking flight, as in *Otomops wroughtoni* (Brosset, 1962c) and *Eumops perotis* (Vaughan, 1959).

In addition to the selective pressures imposed by echolocation and food habits (Chapter 6), roosting habits have had a marked influence on the evolution of skull shape. Bats that roost by hanging pendent in noncrevice shelters typically have well-rounded skulls (Vaughan, 1970a). Crevice-roosting bats, including molossids and some vespertilionids, show a marked dorsoventral flattening of the skull. Extreme flattening of the skull can be seen in the crevice-roosting molossids *Platymops setiger*, *P. petrophilus*, and *Neoplatymops mattogrossensis* (Peterson, 1965). Most small bats that seek shelter in crevices show little cranial modification for roosting (Vaughan, 1970a), but there are exceptions. For example, the small vespertilionid *Mimetellus moloneyi* has a strongly flattened skull (Kingdon, 1974; Walker, 1975); similarly, the crania of *Tylonycteris pachypus* and *T. robustula* are strongly flattened, allowing entry through narrow slits to the internode cavities of bamboo culm (Medway and Marshall, 1970, 1972).

Other morphological modifications for roosting include thickened pads or adhesive disks on the thumbs and feet (Table I). The greatest degree of specialization has occurred in the Thyropteridae and Myzopodidae, each having well-developed adhesive disks on the fore and hind limbs. Among the vespertilionids 6 genera and at least 11 species have pads on their thumbs and/or feet. Many if not most of these bats are probably specialized for roosting on the moist surfaces of leaves or within the internode cavities of bamboo.

The highly developed adhesive disks of the Neotropical *Thyroptera discifera* and *T. tricolor* (Fig. 4A) may limit these bats to certain types of roosts. Findley and Wilson (1974) found that *T. tricolor* roosts exclusively in unfurled leaves of *Heliconia* and similar plants in Costa Rica (Fig. 5), and they suggested that its numbers and distribution may be limited by competition for available

roost sites. *T. tricolor* apparently prefers the shelter of unfurled leaves in forests, forest clearings, and occasionally along roads and trails, where leaves are shaded for part of the day. This bat roosts singly or in small groups, where individuals arrange themselves in a head-up posture within the leaf. Virtually nothing is known of the roosting habits of *T. discifera*, but, judging from the similarity of

TABLE I
Bats Having Modified Thumb and Foot Pads or Disks

Family	Species	Region	References
Thyropteridae	<i>Thyroptera discifera</i> ^a	Neotropical	Walker, 1975
	<i>T. tricolor</i> ^a	Neotropical	Dobson, 1876; Goodwin and Greenhall, 1961; Wimsatt and Villa-R., 1970; Findley and Wilson, 1974; Walker, 1975
Myzopodidae	<i>Myzopoda aurita</i> ^a	Ethiopian	Walker, 1975; Schliemann and Mags, 1978
Vespertilionidae	<i>Eudiscopus</i> (= <i>Discopus</i>) <i>denticulus</i> ^b	Indo-Malayan	Osgood, 1932; Hill, 1969; Walker, 1975
	<i>Glischropus javanus</i>	Indo-Malayan	Tate, 1942; Hill, 1969
	<i>G. tylopus</i>	Indo-Malayan	Tate, 1942; Hill, 1969
	<i>Hesperoptenus blanfordi</i>	Indo-Malayan	Hill, 1969; Walker, 1975
	<i>H. tickelli</i> ^c	Indo-Malayan	Hill, 1969; Walker, 1975
	<i>Myotis bocagei</i>	African	Brosset, 1966, 1974, 1976; Walker, 1975
	<i>M. rosseti</i>	Indo-Malayan	Rosevear, 1965; Hill, 1969
	<i>Pipistrellus nanus</i>	African	Dobson, 1876; Verschuren, 1957; Rosevear, 1965; Brosset, 1966; Jones, 1971; Kingdon, 1974; Walker, 1975; LaVal and LaVal, 1977
	<i>P.</i> (= <i>Glischropus</i>) <i>tasmaniensis</i>	Australian	Walker, 1975
	<i>Tylonycteris pachypus</i>	Indo-Malayan	Dobson, 1876; Medway and Marshall, 1970, 1972; Walker, 1975
	<i>T. robustula</i>	Indo-Malayan	Dobson, 1876; Medway and Marshall, 1970, 1972; Walker, 1975

^aSpecialized disks.

^bPads only on hind feet (Walker, 1975).

^cFriction pads only on thumbs (Walker, 1975), but according to Hill (1969) pads are absent.

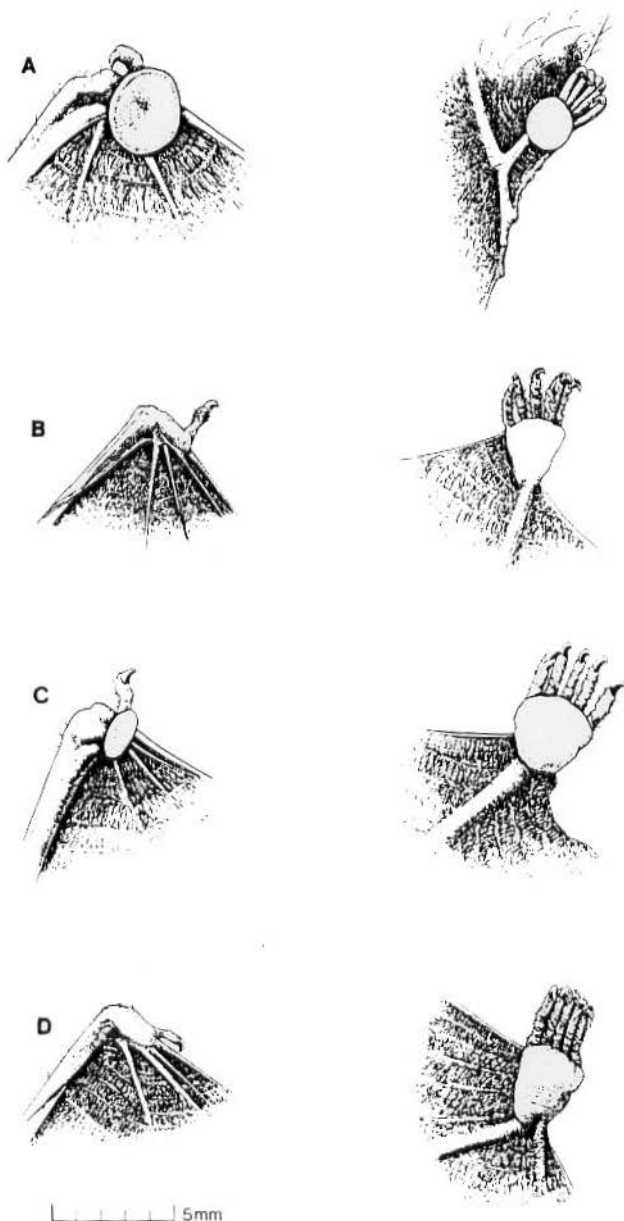


FIGURE 4. Morphological specialization of wrists and feet of (A) *Thyroptera tricolor* (MCZ 28142), (B) *Pipistrellus nanus* (MCZ 14840), (C) *Tylonycteris pachypus* (MCZ 47612), and (D) *Glischropus tylopus* (MCZ 33117). (Drawings prepared by P. Esty from specimens preserved in alcohol.)



FIGURE 5. (A) Unfurled banana leaf used as a day roost by *Thyroptera tricolor*. (Photo by M. D. Tuttle.) (B) Two *Thyroptera tricolor* clinging to the inner, moist surface near the opening of an unfurled leaf used as a roost. (Photo by M. D. Tuttle. Courtesy of the National Geographic Society.)

its foot and wrist disks, its roosting habits are probably similar to those of *T. tricolor*. The disk-winged bat *Myzopoda aurita*, endemic to Madagascar, sometimes roosts in the leaves of traveler's palm (*Ravenala*) (R. Peterson, in Findley and Wilson, 1974), but not much more is known of its roosting habits.

Among vespertilionids, foot- and thumb pads or wrist callosities are moderately to well developed, but the roosting habits of most species are little known. In northeastern Gabon *Myotis bocagei* regularly roosts singly or in small harem groups in unfurled banana leaves (Brosset, 1966, 1974, 1976). This bat is apparently restricted to riparian habitats and typically roosts within 5–50 m from a river. Sanborn (1949) found this bat roosting in the flower stalks of water arum. In villages where banana plants are cultivated this bat may have a continuous and localized source of unfurled leaves, and small groups may remain resident for several years at these sites (Brosset, 1976). A similar development of fleshy wrist pads and footpads (Fig. 4B) and roosting habits have been reported for *Pipistrellus nanus* (Verschuren, 1957; Rosevear, 1965; Brosset, 1966; Kingdon, 1974). LaVal and LaVal (1977) found that only 20.9% of 565 suitably unfurled leaves were occupied; the highest occupancy rate occurred when females and young roosted together (group size ranged from 2 to 6). LaVal and LaVal (1977) suggested that before the introduction of bananas to Natal, the indigenous *Strelitzia nicolai* may have been the preferred roost of *P. nanus*. In Kenya, where there are no musaceous plants, *P. nanus* commonly roosts between the leaflets of

palms growing along rivers and in buildings constructed of palm thatch, where males and females occur in small harem groups (O'Shea, 1980). It seems likely that harem groups of *P. nanus* should also occur in unfurled banana leaves, as in *M. bocagei*, but the census data from LaVal and LaVal (1977) are not compelling.

The fleshy pads on the feet and thumbs of *Tylonycteris pachypus* and *T. robustula* (Fig. 4C) apparently assist the claws in gripping the smooth surface within the internodal cavities of bamboo (Medway and Marshall, 1970, 1972). Access to these cavities is provided by a narrow, slitlike opening (Fig. 6), formed originally by the pupation chamber and emergence hole of a chrysomelid beetle. Internode cavities that are preferred as roosts vary in height from 1 to 10 m above the ground and typically have entrance holes located in the lower half of the cavity. The lower limit of the hole width is determined by body size, with the holes used by *T. robustula* being significantly larger than those used by *T. pachypus*. Both species may use the same roost sites, but usually on separate occasions (Medway and Marshall, 1970). Females of both species outnumber males by approximately 2:1, and females tend to be gregarious at all ages; adult males tend to roost singly or with other females in small harem groups (Medway, 1971; Bradbury, 1977a). Other bats known to roost in the interior of bamboo culm include *Glischropus tylopus* and *Pipistrellus mimus*, but specialized pads are known only for *G. tylopus* (Fig. 4D).

Short, stout legs, hairs on the inner and outer margins (Rosevear, 1965), short interfemoral membranes with hairs on the tail, which may have a tactile function (Lang and Chapin, 1917), appear to be adaptations for crevice roosting in some molossids and a mystacinid. The short, erect, velvetlike pelage, highly modified claws for digging, and the unique wing-folding behavior of *Mysticina tuberculata* appear to be extreme specializations for crevice dwelling (Daniel, 1979).

Bats that use external roosts, including *Murina aurata*, *Myotis formosus* (Wallin, 1969), *Lavia frons* (Wickler and Uhrig, 1969), *Lasiurus borealis*, and *L. cinereus* (Shump and Shump, 1980), typically have thick, long, woolly pelage and probably benefit from increased insulation. Rosevear (1965) suggested that the pelage of *Lavia frons* may be as important in maintaining body temperature as it is in reducing the effects of direct exposure to sunlight (Wickler and Uhrig, 1969; Jones, 1972).

The importance of well-developed vision for predator surveillance is highlighted by the degree of eye development, especially among externally roosting pteropodids, phyllostomids (Suthers, 1970, 1978), and emballonurids (Suthers, 1970; Bradbury and Emmons, 1974). Some phyllostomids, including *Artibeus hirsutus*, *A. jamaicensis*, *A. lituratus*, *A. phaeotis*, *A. toltecus*, *Centurio senex*, *Chiroderma salvini*, and *Sturnira lilium*, have a transparent dactylopatagium minus, which allows them to observe movements in the vicinity of the roost,

even though their wings may be folded over their faces when at rest (Vaughan, 1970b). *Centurio senex* sometimes covers its face with a partially translucent and hairless chinfold, which apparently allows it to see when this structure is stretched over its face (Goodwin and Greenhall, 1961).

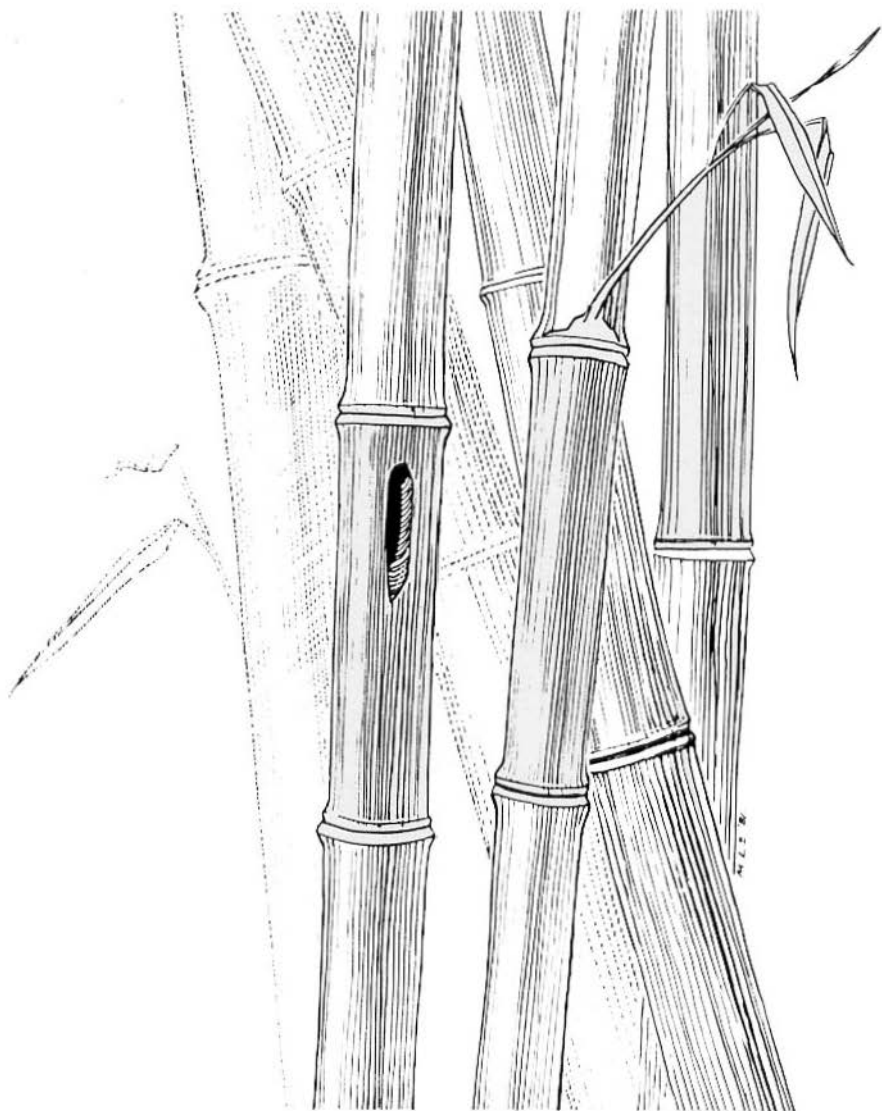


FIGURE 6. Giant bamboo culm used as roosts by *Tylonycteris pachypus* and *T. robustula*. Bats gain entry and exit to an internodal cavity via a slit formed from a pupation chamber of a crysmelid beetle. (Drawn from a photo in Medway and Marshall, 1970.)

TABLE II
Tent-Making Bats and Plants Used in the Construction of Tents

Bats		Plants		References
Family	Species	Family	Species	
Pteropodidae	<i>Cynopterus sphinx</i>	Palmaceae	<i>Corypha</i> sp.	Goodwin, 1979
Phyllostomidae	<i>Ectophylla alba</i>	Musaceae	<i>Heliconia imbricata</i>	Timm and Mortimer, 1976
			<i>H. latspatha</i>	Timm and Mortimer, 1976
			<i>H. pogonantha</i>	Timm and Mortimer, 1976
			<i>H. tortuosa</i>	Timm and Mortimer, 1976
			<i>H.</i> sp.	Timm and Mortimer, 1976
	<i>Artibeus cinereus</i>	Palmaceae ^a	Unspecified	Goodwin and Greenhall, 1961
	<i>A. jamaicensis</i>		<i>Scheelea rostrata</i>	Foster and Timm, 1976
	<i>A. watsoni</i>		<i>Geonoma cuneata</i> (= <i>ducurensis</i>)	Chapman, 1932; Ingles, 1953
			<i>G. ovicarpa</i> (= <i>hinervia</i>)	Chapman, 1932; Ingles, 1953
	<i>Uroderma hilobatum</i>		<i>Coccoloba macleodii</i>	Barbour, 1932; Goodwin and Greenhall, 1961
			<i>Levinsia chinensis</i>	Barbour, 1932
			<i>Pritchardia pacifica</i>	Barbour, 1932
			<i>Sabal mauritiformis</i> (= <i>glaucescens</i>)	Barbour, 1932; Goodwin and Greenhall, 1961
	Unspecified		<i>Asterogyne martiniana</i>	Foster and Timm, 1976
			<i>Bactris wendlandiana</i>	Foster and Timm, 1976
			<i>Geonoma congesta</i>	Foster and Timm, 1976

^aTaxonomic designation of the American Palmaceae follows Glassman (1972).

2.1.6. Bats That Modify Their Roost Environment

The ultimate adaptation of a species occurs when it manipulates the physical environment to its advantage. At a primitive level colonial bats may inadvertently alter their physical environment by depositing feces and urine or increasing the temperature of the roost as a by-product of metabolism, but the ultimate in roost modification occurs when changes result from self-directed behavior. Such is the case among the "tent-making" pteropodids and phyllostomids (Table II) and a "burrowing" mystacinid.

Five species of phyllostomids and one pteropodid modify the leaves of at least five species of *Heliconia* (Musaceae) and nine species of palm (Palmaceae) for use as roosts. The phyllostomid *Ectophylla alba* typically constructs tents from *Heliconia* (Timm and Mortimer, 1976), but other phyllostomids either use

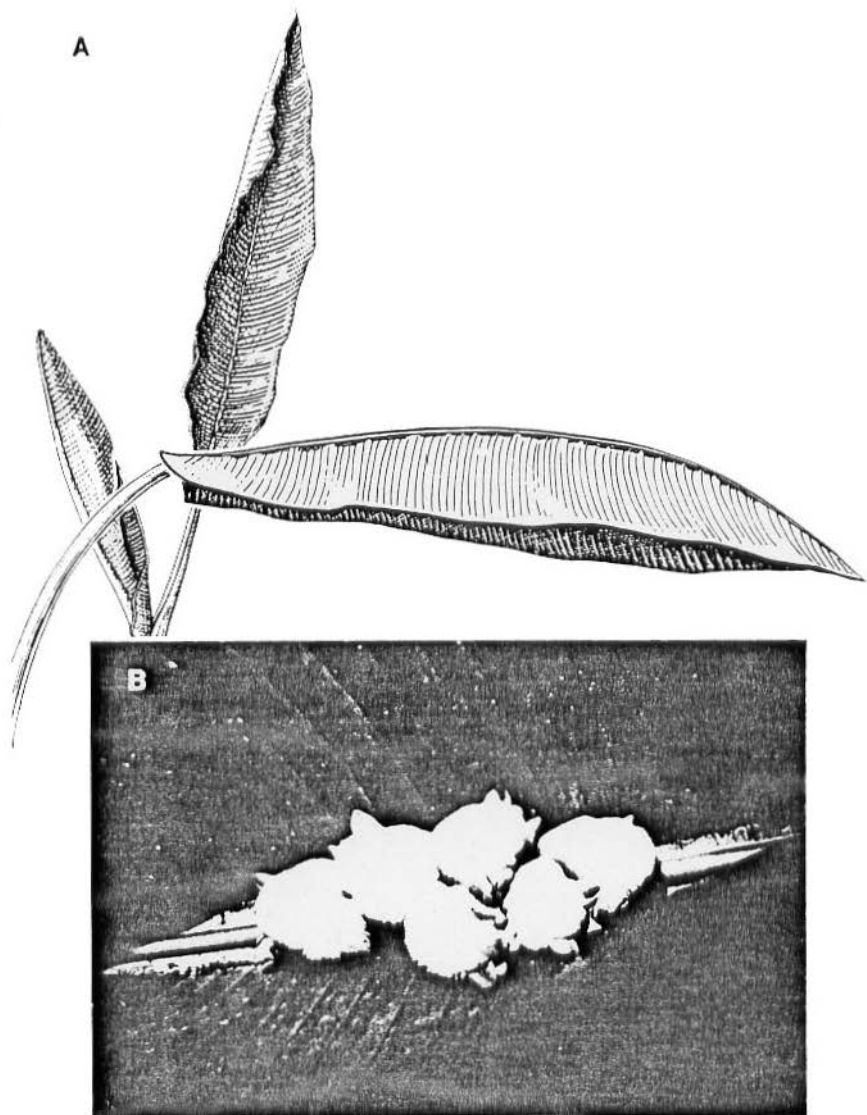


FIGURE 7. (A) Tent roost of *Ectophylla alba* constructed from a *Heliconia* leaf. (B) Group of *E. alba* hanging from the underside of a *Heliconia* tent. Note the chewed areas on either side of the midrib. (Photo by R. M. Timm. With permission from the Ecological Society of America.)

broadleaf or pinnate palms for tent making (Chapman, 1932; Barbour, 1932; Allen, 1939; Goodwin, 1946; Ingles, 1953; Goodwin and Greenhall, 1961; Timm and Mortimer, 1976; Foster and Timm, 1976). *Ectophylla alba* modifies leaves of *Heliconia* by chewing veins that extend perpendicular to the midrib, causing the sides of the leaf to droop (Fig. 7A). The veins are only partially chewed, leaving interconnected tissue that provide some support for the length of the leaf. Most of the support for the tent comes from the uncut basal and distal parts of the leaf. These bats hang singly or in small groups (2-6) from small claw holes near the center of the leaf (Fig. 7B). *Ectophylla alba* appears to be opportunistic in its selection of leaves, choosing them for making tents from several species of *Heliconia* in proportion to their occurrence in the forest. A preference, however, is shown for leaves that grow horizontally, thus providing maximum protection from sunlight, rain, and predators (Timm and Mortimer, 1976).

Uroderma bilobatum constructs tents from large, stiff palm fronds of *Prichardia pacifica* by biting the ridges of plications on the underside of the leaf until it weakens and droops downward (Fig. 8). This bat roosts singly or in small groups (2-59), often hanging from the cut portion of the leaf. Eventually the distal part of the leaf dries and sloughs off and a new leaf has to be cut (Barbour, 1932). Tents constructed by *Artibeus watsoni* from broadleaf palms are typically formed when this bat makes J-shaped cuts beginning near the distal end of the blade along the rachis and curving back to the base of the blade and out to each side (Fig. 9A). Variations on this pattern exist (Fig. 9B), but whether these reflect differences in plant species or in tent-making behavior is unknown. Pinnate palms are modified into tents when *A. jamaicensis* chews the midrib of leaflets, removing pieces of tissue and leaving small holes (Foster and Timm, 1976). This causes the terminal parts of leaflets to fold perpendicularly to the plane of the rachis, forming a lanceolate tent (Fig. 9C).

The use of broadleaf palms for tent construction appears to be the most common. Foster and Timm (1976) found that nearly two-thirds of the tents observed in Costa Rica were constructed from fronds of the simple bilobed *Asterogyne martiana*. Although broadleaf palms may offer greater protection from rain and sunlight, pinnate leaves may enhance crypticity, if contrasting, white facial and dorsal stripes complement the disruptive pattern of leaflets (Foster and Timm, 1976).

The pteropodid *Cynopterus sphinx* constructs tents from large pinnate fronds of the *Corypha* palm by chewing veins of the leaflets, creating "a characteristic flask-shaped pattern within the blade," which causes the collapse of distal leaflets to form the sides of the tent (Goodwin, 1979). Solitary bats and small groups cling with their toes to the veins of the "roof," hanging against the sides of the shelter where they apparently are less conspicuous from below. The only other pteropodid known to modify plants for shelter is *Cynopterus brachyotis*, which sometimes bites off the center seed string of the *Kitul* palm, leaving a hollow in which to roost (Phillips, 1924).

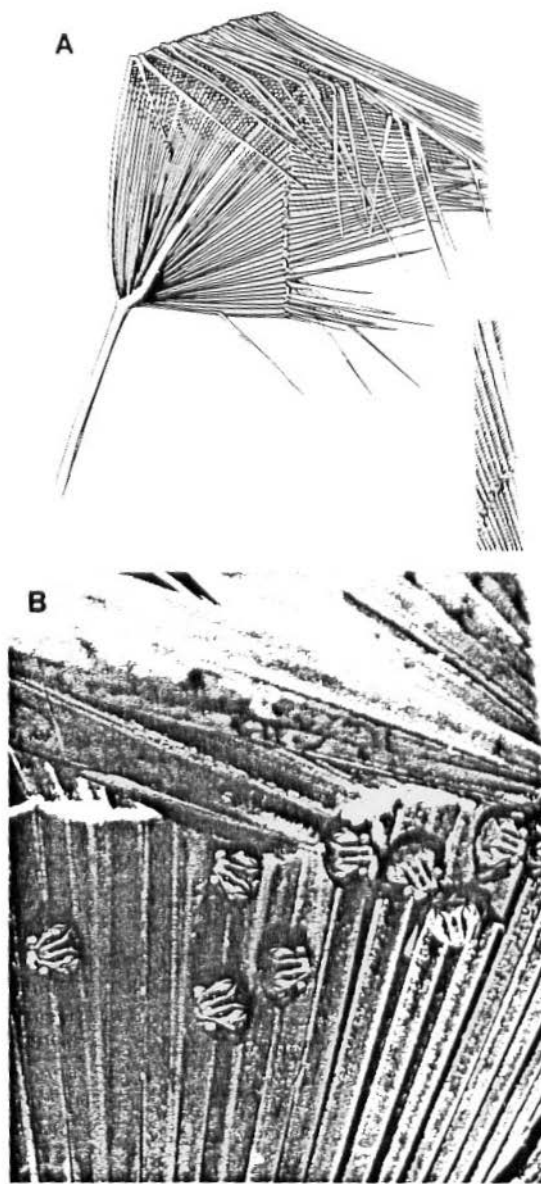


FIGURE 8. (A) Typical tent roost of *Uroderma bilobatum* on a frond. The inset illustrates the manner in which the plications of a photo in Barbour, 1932. (B) Group of *Uroderma bilobatum*. (Photo by I. F. Greenbaum.)

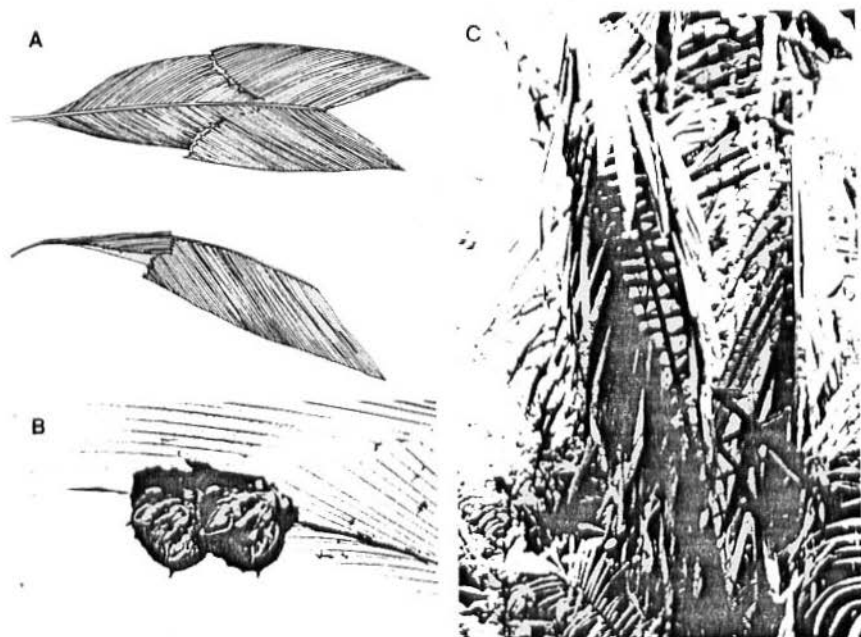


FIGURE 9. (A) Palmate palm frond modified into a tent by *Artibeus watsoni*. (B) Two *A. watsoni* hanging from underside of tent. (Photo by M. D. Tuttle.) (C) Tent roost in a pinnate palm, *Scheelea rostrata*, constructed by *A. jamaicensis*. (Photo courtesy of R. M. Timm. With permission from the Association of Tropical Biology.)

Future studies on the ecology of tent-making bats should attempt to determine how much time and how many bats are involved in tent construction. The relative cost appears to be high, considering the number of veins that are severed and the temporary nature of these roosts. Judging from the observations of Barbour (1932), new tents from *Prichardia* fronds are constructed by small groups of *Uroderma bilobatum*; single bats are apparently unable to complete a tent in one night. The number of bites required to sever the veins of a frond may range from as few as 44, in tents formed from the simple bilobed leaves of *Asterogyne*, to as many as 80, in the large palmate leaves of *Prichardia* (Foster and Timm, 1976). These observations suggest that tent making typically involves the cooperation of several bats, but how many individuals are involved and whether both sexes participate remains to be clarified. Although solitary males and groups of female *Uroderma* with their young have been observed in tents (Barbour, 1932), no bats have been observed in the act of tent making. At what age tent making begins and whether it is an innate or learned behavior is unknown. The fact that *Ectophylla alba* constructs tents from plant species having similar leaf forms suggests that at least for this species some specificity

exists. There is some latitude in the use of different leaf forms for tent construction among other tent-making species. Barbour (1932) and Foster and Timm (1976) suggest that the initial bites used in tent construction are probably made while bats hover, but direct observations are needed to verify this suggestion and to confirm whether additional bites are made by bats when crawling on or hanging from the leaf.

Because tent roosts constructed from leaves are by nature ephemeral, bats no doubt regularly engage in tent making. Timm and Mortimer (1976) suggested that each colony of *E. alba* may use a series of tents, since they seldom observed bats using the same tent for more than two consecutive days. Similarly, Barbour (1932) observed considerable turnover in the use of tent-roosts by *Uroderma bilobatum*. If a high roost turnover occurs, it would be interesting to determine whether there is any consistent group fidelity and whether bats that share a tent-roost are genetically related.

A unique form of roost construction has been reported for *Mysticina tuberculata*, a monotypic species endemic to New Zealand (Daniel, 1979). This bat uses its teeth and claws to excavate cavities and tunnels in the wood of fallen kauri (*Agathis australis*) trees, where individuals form dense clusters in the largest cavities and rest "head-to-tail like peas in a pod" in adjoining tunnels. The heat generated in these wet tunnels and cavities by a colony of 150–200 bats can result in temperatures of 39°C and a humidity of 100%. Daniel (1979) suggested that this "rodent-like" behavior may have evolved in response to a lack of predators and competition from other mammals.

The mere presence of active bats in sheltered roosts can have a profound affect on the roost environment. The accumulation of bat guano, with its relatively high water-holding capacity, can raise the humidity of roosts, (Verschuren, 1957) as can the accumulation of urine on wooden beams in buildings (Kunz, 1973b). Heat produced as a by-product of metabolism and trapped in crevices and cavities can markedly raise the temperature of a roost during periods of occupancy (Dwyer and Harris, 1972; Voûte, 1972; Kunz, 1974), as well as over longer periods (Henshaw, 1960; Herreid, 1963; Dwyer and Hamilton-Smith, 1965; Tuttle, 1975). Daily and seasonal temperature increments will vary according to the number of bats present, their level of activity, the size and configuration of the roost, and the radiative and conductive properties of the roost substrate. Some bats have successfully exploited otherwise cool caves by selecting sites that facilitate the entrapment of metabolic heat. The importance of selecting roost sites that enhance the energy economy of bats has been thoroughly treated by Dwyer and Hamilton-Smith (1965), Dwyer (1971), Humphrey (1975), and Tuttle (1975). The prolonged use of caves by large numbers of bats can lead to the erosion of ceilings (Dwyer and Hamilton-Smith, 1965; Tuttle, 1975), which may improve the gripping quality of the substrate as well as enhance the entrapment of metabolic heat (Tuttle, 1975). Cavities in trees and

buildings may be altered by the scratching action of bats, and this too may improve the gripping quality of the roost substrate (Ryberg, 1947).

The use of a roost by bats for extended periods may lead to temporary and sometimes inalterable changes in the roost environment. If modifications are severe, this may explain why some roosts become temporarily or permanently abandoned. The accumulation of nitrogenous wastes and feces may create high concentrations of ammonia in some caves (Constantine, 1958b, 1967; Mitchell, 1964; Dwyer and Hamilton-Smith, 1965; Brosset, 1966) and cause physiological stress on its inhabitants or alter species composition. As the concentration of atmospheric ammonia increases in caves, species diversity tends to decrease (Studier, 1966). For example, in Mexico and the southwestern United States *Tadarida brasiliensis* is the only bat remaining when atmospheric ammonia concentrations reach a maximum. The accumulation of guano in tree cavities and similar shelters in buildings may reduce the amount of roosting space (Ryberg, 1947; Medway and Marshall, 1970); similarly, the incrustation of crystallized urea on roost substrates, especially in buildings (Ryberg, 1947) may limit accessibility to preferred roost sites. Odors produced by decomposing guano and urine (Davis, 1944; Hall and Dalquest, 1963; Goodwin, 1970; Constantine, 1967) may attract various predators. The prolonged use of trees by fruit-eating megachiropterans may lead to severe damage and sometimes death of the roost tree due to the accumulation of urine and feces (Ayensu, 1974) and partial or complete defoliation (Nelson, 1965a; Okon, 1974).

2.1.7. Mixed-Species Associations

During nonbreeding periods interspecific associations appear to occur regularly among bats that use internal shelters (e.g., Verschuren, 1957; Goodwin and Greenhall, 1961; Rosevear, 1965; Brosset, 1966, 1974; Villa-R., 1966; Barbour and Davis, 1969; Wallin, 1969; Medway, 1969; Dalquest and Walton, 1970; Kingdon, 1974; Fenton and Kunz, 1977; Bradbury, 1977a; Lekagul and McNeely, 1977). Most of these associations appear to be casual, perhaps resulting from limited numbers of suitable roost sites or from the convergence in requirements for temperature, moisture, and darkness. Most species appear to use separate shelters during the maternity period, although exceptions include species that roost in different parts of the same shelter.

Bats may benefit energetically by roosting in direct contact with other species or in close proximity to large active aggregations, where benefits are derived from an increase in roost temperature. Both situations prevail in Cuban caves, where *Brachyphylla nana* and *Erophylla sezekorni* roost among large aggregations of *Phyllonycteris poeyi*, and where *Mormoops blainvilli* and *Pteronotus* spp. roost separately but in the same parts of the cave as *Phyllonycteris poeyi* (Silva-Taboada and Pine, 1969). Similarly, the roost associations in

Jamaican caves between *Pteronotus parnellii* and *Monophyllus redmani* and *Natalus major* and *N. micropus* may benefit energetically from a mutually warmed environment (Goodwin, 1970). While these and many other roost associations may be casual, the possibility exists that some have or will become obligate.

Evidence in support of the latter suggestion is based on observations by Dwyer (1968), who found maternity colonies of *Miniopterus australis* occupying cool caves at the southern limit of its distribution in New South Wales (Australia), where this bat is invariably associated with large aggregations of *Miniopterus schreibersii*. In other parts of Australia where caves are intrinsically warmer, these two species do not regularly roost together. Similarly, Tuttle (1976a) suggested that the reproductive success of small maternity colonies of *Myotis grisescens* in Florida caves may be augmented when this bat forms colonies with *Myotis austroriparius*. Bearing on this argument are the findings of Tuttle (1975, 1976c) that postnatal growth rates and postflight survival of *Myotis grisescens* can be severely reduced if colony sizes are too small to sufficiently increase the cave temperature. Whether the success or failure of other species populations can be explained on the basis of interspecific associations invites further study. Notwithstanding improved energy economy, another potential benefit that may be derived from interspecific roost associations is reduced predation, resulting either from improved predator surveillance or benefits derived from the so-called "selfish herd" effect (see Hamilton, 1971). Potential disadvantages of interspecific associations may result from misdirected social behavior (Bradbury, 1977a), competition for roost space, increased conspicuousness to predators, and an increased incidence of parasites and disease (see Constantine, 1970).

2.1.8. Synanthropy: A Paradox of Human Influence

Many bats have successfully adapted to a variety of man-made structures for roosts. The exploitation of these structures as substitutes for caves, tree cavities, and other natural roosts supports the view that most bats are highly adaptable and opportunistic in roost selection. Tombs, crypts, ancient ruins, wells, cellars, mine tunnels, storm sewers, basements, and other structures of stone and brick are regularly used by "cave-dwelling" species. The interiors of walls, attics, and the hollow floor spaces of human dwellings, church lofts, barns, schools, and other such structures have commonly become substitutes for natural tree cavities. Buildings, especially of European-style architecture, offer a rich variety of internal roosting places for bats, often more diverse than in their original habitat (Ryberg, 1947; Gaisler, 1963b; Voûte, 1972). Crevices under tile and corrugated metal roofs, expansion joints, and spaces beneath wood shingles and shutters provide alternatives to natural roosts such as rock crevices and exfoliating tree bark. Bridges may also provide suitable roosting places (Davis and Cockrum, 1963; Villa-R, 1966), especially in older-style structures with wood supports,

stone bridges with open ends having cavelike chambers, and wooden railway bridges. Coincident with modern road and highway improvements, many of these sites have given way to bridge designs of steel and concrete, which are generally unsuitable for bat roosts.

The exploitation of man-made structures as substitutes for natural roosts (Ryberg, 1947; Gaisler, 1963a, 1963b; Brosset, 1966; Villa-R, 1966; Barbour and Davis, 1969; Wallin, 1969; Fenton, 1970; Sluiter *et al.*, 1971; Gaisler *et al.*, 1979) offers compelling evidence that bats quickly take advantage of newly available structures. Within historical times a variety of species have become predominantly linked to buildings, especially during maternity periods. In northern Europe these include *Rhinolophus hipposideros* (Gaisler, 1963a, 1963b); *Myotis mystacinus* (Nyholm, 1965); *Eptesicus nilsoni*, *Pipistrellus pipistrellus*, *Plecotus auritus*, and *Plecotus austriacus* (Wallin, 1969; Horáček, 1975). In India *Taphozous melanopogon*, *Taphozous perforatus*, and *Megaderma lyra* almost exclusively roost in man-made structures (Brosset, 1962a, 1962c), as does *Tadarida pumila* in parts of Africa (Kingdon, 1974). *Molossus molossus* is the most prevalent house bat in Trinidad (Greenhall and Stell, 1960) and perhaps in the Neotropics. In Panama *Myotis nigricans* is almost invariably found in buildings (Wilson, 1971), and in Paraguay *Myotis nigricans* and *Myotis albescens* are both strongly dependent on roosts in buildings constructed within the last century (Myers, 1977). In North America *Eptesicus fuscus*, *Myotis lucifugus*, and *Myotis yumanensis* have so completely adapted to man-made structures during maternity periods that there are few records from natural roosts (Barbour and Davis, 1969).

The association of bats with man-made structures appears to vary geographically. *Rhinolophus hipposideros* in northern Europe almost always uses buildings in summer; but in southern Europe, where caves are more abundant, this bat is less dependent on human dwellings (Gaisler, 1963b). Gaisler found no direct evidence that the use of buildings has enabled *R. hipposideros* to extend its distribution, but Fenton (1970) suggested that the use of buildings by *Myotis lucifugus* in Canada may have allowed this bat to extend its distribution to otherwise uninhabitable regions. Similarly, *M. velifer* and *Tadarida brasiliensis* both have expanded recent distributions beyond the limit of caves in North America by using man-made structures for maternity roosts (Kunz, 1973b, 1974; Kunz *et al.*, 1980). Davis *et al.* (1962) suggested that the use of buildings by *T. brasiliensis* in Texas allowed populations to increase by as much as 15% above the number before modern building construction. Wilson (1971) suggested that the availability of buildings in Panama may have allowed *M. nigricans* to expand its former distribution and increase in local abundance.

Introduced and cultivated plant species provide suitable roost sites for many foliage-roosting species. Clumped stands of bamboo (*Gigantochloa scortechnii*) maintained in forest reserves in Malaysia provide an abundance of potential roost sites for *Tylosycteris pachypus* and *T. robustula* (Medway and Marshall, 1972).

Similarly, the occurrence of *Myotis frater* in Japan may be due solely to the conservation of bamboo (Wallin, 1969). The introduction and cultivation of banana plants in parts of Africa provides a continuous roost resource for *Pipistrellus nanus* (LaVal and LaVal, 1977) and *M. bocagei* (Brosset, 1976). The introduction and establishment of the neem tree in West Africa at the turn of the last century has provided a favorite roost (and food resource) for *Epomophorus gambianus* (Ayensu, 1974) and other fruit-eating megachiropterans. In the Neotropics *Uroderma bilobatum* has successfully adapted its tent-making habits to an introduced palm, *Prichardia pacifica* (Barbour, 1932).

Although building construction, mining operations, and the introduction of various plant species have undeniably led to the increased numbers of some species, other activities of man have been detrimental to the roosting (and feeding) habits of bats (Stebbing, 1980). Extensive deforestation and forest management have had marked impacts on available roosting sites, especially in tropical regions, where tree-roosting species predominate. The effects of continued deforestation will ultimately force many species into small patches, and forest management will most certainly deprive others of the use of tree cavities. One can expect that as the availability and composition of roost resources change, bat faunas will invariably be altered. Species with less specialized roosting habits (e.g., *Carollia perspicillata* and *Artibeus jamaicensis*) are more likely to sustain marked changes in roost availability. However, because the roost and food resources of most species are intimately linked, the reduction or elimination of only one of these resources will have a severe impact on the continued success of many species.

Increased efforts have been made to promote the extermination of bats that roost in man-made structures. A growing interest in building restoration and home energy conservation, especially in temperate regions, has led to the elimination of many roosts located in such structures (Greenhall, 1982). The use of chemicals as wood preservatives, treatment against wood-boring insects, and the treatment of roost sites with toxic chemical repellents and pesticides has inadvertently altered roost sites and reduced or eliminated populations of several species (Braaksma, 1980).

The inevitable consequences of forest management, building restoration, deforestation, the increased recreational use of caves, and vandalism has doubtless led to a reduction in the numbers and diversity of roost sites and bats in many regions. Efforts to stem the loss of valuable roosts have been made during the past two decades, especially in Europe (e.g., Daan, 1980) and more recently in North America, to provide protection to bats by encouraging the construction of artificial roosts (Stebbing, 1974; LaVal and LaVal, 1980; Greenhall, 1982) (See Fig. 10) and the use of well-planned cave gating (Tuttle, 1977) to offset the destruction and disturbance of natural roosts and the eviction of bats from man-made structures. Placing caves in land trusts and their purchase by Federal, state,

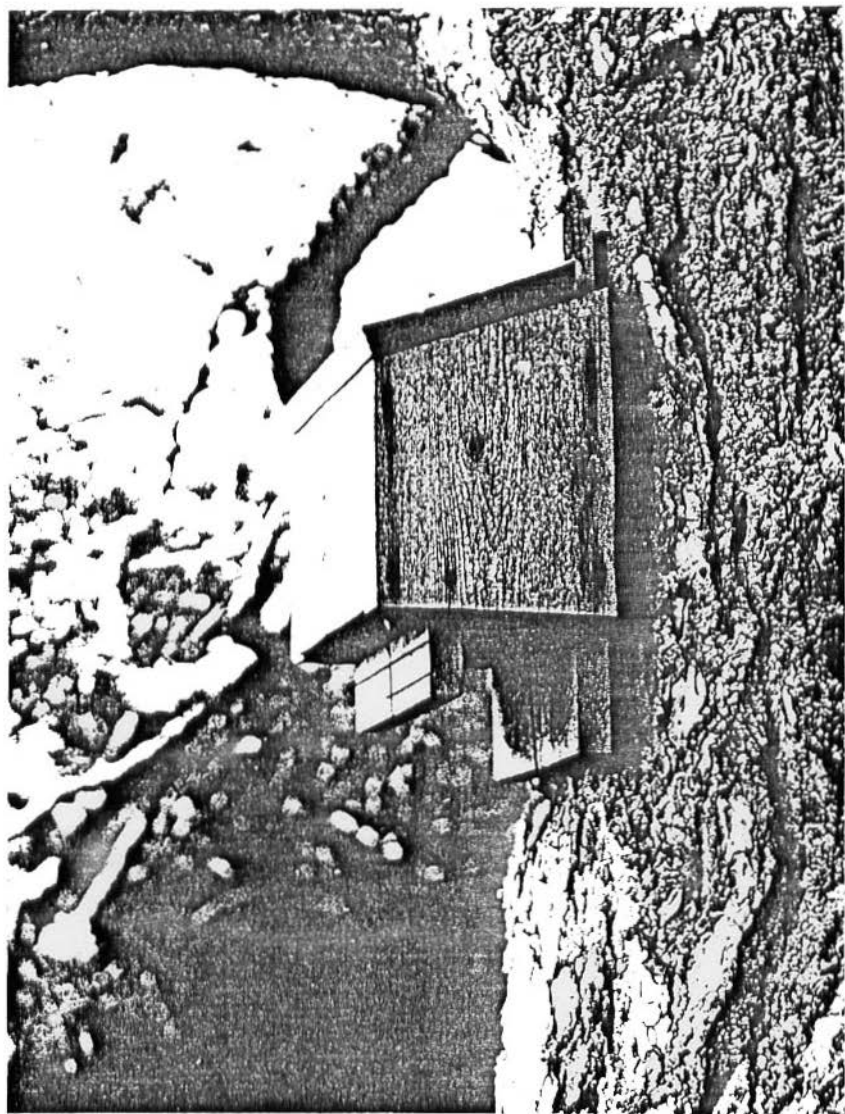


FIGURE 10. Roost box used to encourage bats that otherwise may have used tree cavities. (Photo by S. C. Bisserrôt.)

and local governments and private organizations have helped to restore and protect many valuable roosts, but additional efforts are needed to insure that other roost resources are equally protected.

2.2. Roost Activities and Time Budgets

2.2.1. Return Behavior and Roost Selection

Bats use a combination of spatial familiarity and acoustic and visual cues to locate roosts (Davis, 1966; Griffin, 1970; Williams and Williams, 1970; Findley and Wilson, 1974; Fenton and Kunz, 1977). Daily return behavior involves considerable ritualized behavior once bats have reached the vicinity of a roost, which often includes a generalized reconnaissance of the site and several landing trials before entry. Return rituals have been described for several species, including *Antrozous pallidus* (Vaughan and O'Shea, 1976), *Myotis dasycneme* (Voûte *et al.*, 1974), *M. nattereri* (Laufens, 1973), *Pipistrellus hesperus* (Cross, 1965; Hayward and Cross, 1979), *P. nanus* (O'Shea, 1980), *P. pipistrellus* (Stebbings, 1968; Swift, 1980), *Tadarida macrotis* (Vaughan, 1959), *Thyroptera tricolor* (Findley and Wilson, 1974), *Tylonycteris pachypus*, and *Tylonycteris robustula* (Medway and Marshall, 1972). Voûte *et al.* (1974) suggested that the prolonged return ritual of *M. dasycneme* may be necessary for establishing contacts with conspecifics. Audible "directive calls" emitted by individual *Antrozous pallidus*, as they congregate in the vicinity of their day roost, may provide a focal point to which other bats are attracted (Vaughan and O'Shea, 1976). After one or more bats enter a roost crevice, these bats answer the directives of flying bats, which subsequently leads to the entry of others. The preentry rituals of *Tylonycteris pachypus* and *T. robustula* apparently promote the establishment of day-roosting groups (Medway and Marshall, 1972).

2.2.2. Communication and Social Interactions

Vision probably plays an important communicative role in bats that use external roosts. For bats that seek roosts in the darkness or in the dimly lit interior of a protected shelter, the perception of light may function mostly as a Zeitgeber for synchronizing endogenous rhythms (see Chapter 5). For most bats sensory communication occurs predominately in the acoustic and olfactory modes. The variety of integumentary and facial glands (Quay, 1970) and the increasingly recognized vocal repertoire of bats (Nelson, 1964; Gould, 1971, 1977; Brown, 1976; Fenton *et al.*, 1977c; Barclay *et al.*, 1979; Porter, 1979a, 1979b; Brown and Grinnell, 1980) emphasize the importance of acoustic and olfactory communication during the roosting period.

Scent glands are most notably located on the head, chest, wings, and in the anal region (Quay, 1970), but little is known of how they are used in a social context. Group odors produced from guano and urine deposition may be important in promoting contact between individuals, but much remains to be learned of the olfactory ability of bats (Bhatnagar, 1975). Vaughan and O'Shea (1976) suggested that part of the return ritual of *Anirozous pallidus* may function primarily to confirm their own scent or that of roost mates. Bats that engage in contact clustering invariably exchange individual odors, which may combine to produce group odors; however, individual recognition probably prevails in most species (e.g., Nelson, 1964; Brown, 1976; Kolb, 1977). Hovering behavior observed in some emballonurids appears to involve scent communication from glandular sacs located on the wings (Bradbury and Emmons, 1974; Bradbury, 1977a). Individual and group spacing patterns seen in pteropodids (Nelson, 1965a), rhinolophids (Ransome, 1978), and emballonurids (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976; Bradbury, 1977a) may involve substrate or conspecific marking. Olfaction also appears to be important in mother-infant recognition in several species, including *Pteropus poliocephalus* (Nelson, 1964, 1965a), *Rousettus aegyptiacus* (Kulzer, 1958, 1961), *A. pallidus* (Brown, 1976), *Myotis myotis* (Krátky, 1971; Kolb, 1977), and *Nycticeius humeralis* (Watkins and Shump, 1981).

Many bats rely strongly on acoustic signals in the day roost. Vocalizations may include audible or ultrasonic components given in response to agonistic encounters with conspecifics (Nelson, 1964, 1965a; Bradbury and Emmons, 1974; Porter, 1979a, 1979b) or the approach of intruders (Verschuren, 1957; Nelson, 1965a), or they may serve as spacing- (Nelson, 1964, 1965a; Brown, 1976; Porter, 1979a, 1979b) or contact-promoting signals (Vaughan and O'Shea, 1976; Kolb, 1977; Porter, 1979a, 1979b). Acoustic recognition between mothers and infants has been reported for several species, including *Plecotus townsendii* (Pearson *et al.*, 1952), *Tadarida condylura* (Kulzer, 1962), *Pteropus poliocephalus* (Nelson, 1964, 1965a), *Nycticeius humeralis* (Jones, 1967; Watkins and Shump, 1981), *Eptesicus fuscus* (Davis *et al.*, 1968; Gould, 1971), *Myotis lucifugus* (Gould, 1971), *Desmodus rotundus* (Schmidt, 1972; Gould, 1977), *Myotis myotis* (Kolb, 1977), *Macrotus californicus*, *Carollia perspicillata*, *Leptonycteris sanborni* (Gould, 1977), and *Myotis velifer* (Brown and Grinnell, 1980), and these appear to promote contact between individuals beyond the effective range of olfaction.

Whether or not bats vocalize during the roosting period depends on the prevailing environmental conditions, the number of bats present, and the type of social organization. The molossid bat *Otomops wroughtoni* either roosts singly or in small groups and remains silent and motionless during the day (Brosset, 1962c). By contrast, gregarious species such as *Miniopterus schreibersii*

(Brosset, 1962c; Dwyer, 1964), *Tadarida brasiliensis* (Davis *et al.*, 1962; Constantine, 1967), *T. condylura*, *T. midas*, *Eidolon helvum* (Rosevear, 1965; Okon, 1974), *Rousettus leschenaulti*, *Pteropus giganteus* (Brosset, 1962a), and *Dobsonia muluccensis* (Dwyer, 1975), often betray their presence at a roost by constant chatter. On hot days *Myotis myotis* responds with an increased frequency of audible vocalizations and restlessness (DeCoursey and DeCoursey, 1964). Similarly, *Antrozous pallidus* emits irritation buzzes and squabble notes on hot days, which may promote individual spacing (Vaughan and O'Shea, 1976). The frequent audible vocalizations of *Myotis lucifugus* on cool days appear to be associated with attempts by individuals to gain or protect central positions within clusters (Barclay *et al.*, 1979; Burnett and August, 1981).

2.2.3. Time-Activity Budgets

While it may be relatively simple to quantify the amount of time that bats spend in their day roost (because times of entry and departure and periods of occupancy can be recorded or observed directly), placing individual behavior in a temporal context and establishing the appropriate environmental conditions during the roosting period are more problematical. Because most roosting bats are sensitive to human disturbance, prolonged observations are certain to disrupt normal roosting behavior unless experiments are designed to minimize or reduce disturbance. Direct observations making use of ambient light or supplemented with infrared light and night-viewing devices (see Burnett and August, 1981) hold the greatest promise for observing the undisturbed behavior of bats in roosts. Tape recordings of audible sounds (Ransome, 1978) may prove helpful under some situations. If direct observations are made under conditions of ambient light, they should be designed to prevent bats from seeing the observer.

The period immediately following the return of gregarious species is predominated by cluster formation and settling (McCann, 1934; Kulzer, 1961; Dwyer, 1964; Burnett and August, 1981). Among territorial species conflict for roost positions, as observed in *Pteropus poliocephalus* (Nelson, 1965a), *P. giganteus* (Neuweiler, 1969), and *Saccopteryx bilineata* (Bradbury and Emmons, 1974) may involve periods of intense conflict between males and the relocation of displaced individuals. Within an hour or two following returns, a lull in activity becomes evident.

The day-roost period may occasionally be interrupted by bouts of spontaneous activity, including self-grooming (Nelson, 1965a; Bradbury and Emmons, 1974; Wickler and Seibt, 1976; Burnett and August, 1981), allogrooming (Bradbury, 1977a), copulation (McCracken and Bradbury, 1981), and flight. Burnett and August (1981) directly quantified the day-roosting activity of bats in a maternity roost of *Myotis lucifugus*, based on observations of individual focal groups, using a night-viewing device (Fig. 11). Their analysis of five behavioral

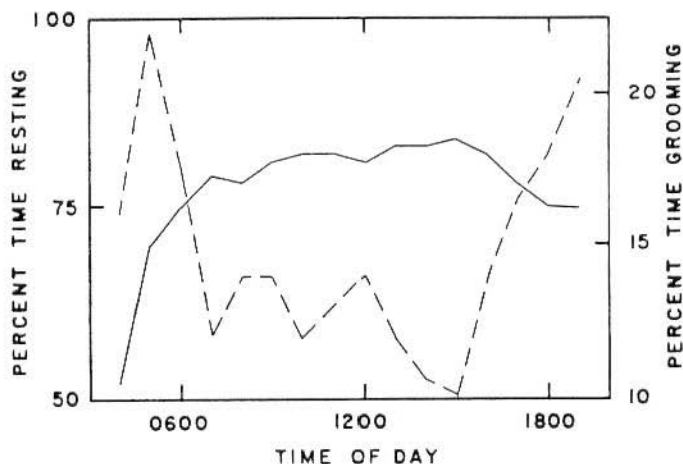


FIGURE 11. Time budget of day-roosting *Myotis lucifugus* showing the percentage of time spent resting (solid line) and that spent grooming (broken line), averaged over a 13-week period. (From Burnett and August, 1981. With permission from the American Society of Mammalogists.)

categories (resting, active, grooming, moving, and flight) indicate that the day-roosting period was predominated by rest (79%). Grooming occurred primarily following the return from feeding and again before the onset of nightly departure. Although grooming accounted for a relatively small percentage (14%) of the day-roosting time budget, it represented more than half of the energy expended during the same period.

Short daytime flights occur most commonly among externally roosting bats, most notably pteropodids (Verschuren, 1957; Rosevear, 1965; Nelson, 1965a; Ayensu, 1974; Kingdon, 1974; Goodwin, 1979) and emballonurids (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976). At certain times bats that roost in protected shelters engage in flight during the day. Daytime flights may involve changes in roost position in response to intruders (Verschuren, 1957; Nelson, 1965a; Constantine, 1967), retreat from sunlight (Ayensu, 1974), practice flights by young bats (Davis and Hitchcock, 1965; Kunz, 1973b, 1974), and occasional feeding flights beneath the tree canopy (Bradbury and Emmons, 1974). Burnett and August (1981) found that spontaneous daytime flights of bats in a maternity roost of *Myotis lucifugus* accounted for less than 1% of the total activity budget.

The timing and rate of defecation is determined by the type of food eaten, the recency of food consumption, and the rate of digestion. Defecation occurs most commonly in the first few hours following the return of bats to the roost (Kunz, 1974; Wickler and Seibt, 1976; Bradbury, 1977b; Ransome, 1978; Ramage, 1979). Ransome (1978) and Ramage (1979), respectively, reported

that the peaks of defecation for *Rhinolophus ferrumequinum* and *Myotis lucifugus* occurred within the first 2–3 hr following return to the roost, followed by a lull in mid- to late afternoon and a slight increase shortly before nightly departure. Generally the high rate of defecation in early morning reflects the rapid digestion and food-passage time following the most recent feeding (see Klite, 1965; Nelson, 1965b; Buchler, 1975). The timing and rate of urination closely parallels the pattern of defecation in *R. ferrumequinum* (Ransome, 1978). Seasonal differences in daily timing and rates of defecation and urination will be strongly influenced by energy considerations, water balance, reproductive state, age, physiological condition, and the level of activity (Kunz, 1974; Buchler, 1975; Ransome, 1978).

The timing of some roost activities may be influenced as much by the environment as it is by endogenous factors. Bats that roost in buildings and rock crevices that are subjected to the radiant heat of the sun (directly or indirectly) commonly engage in movements in mid-day to avoid heat stress (Gaisler, 1963a; Licht and Leitner, 1967; Wilson, 1971; O'Farrell and Studier, 1973; Kunz, 1974; Vaughan and O'Shea, 1976). Many bats seek roosts that promote torpor on cool days (and some appear to select roost sites that promote torpor until midday) and facilitate passive arousals from solar heating in the late afternoon (Vaughan and O'Shea, 1976; O'Shea, 1980).

Preemergence behavior may begin as early as two hours before emergence and may include intensive grooming (Neuweiler, 1969; Burnett and August, 1981), increased locomotor activity (Twente, 1955; Dwyer, 1964; Jimbo and Schwassmann, 1967; Wilson, 1971; Voûte, 1972; Voûte *et al.*, 1974; Kunz, 1974; Gaur, 1980), and heightened vocal activity. Marimuthu *et al.* (1978) suggested that the increased vocal activity of *Hipposideros speoris* prior to emergence may be a form of social entrainment.

Because many roost activities, including metabolism, can be affected by the thermal environment of the roost, an analysis of time-activity budgets requires a thorough knowledge of the environmental conditions during the roosting period. Presently there are no published studies where the complexities of the roost environment have been thoroughly examined. In most studies little more than daily, weekly, or monthly averages or extreme temperatures have been reported, and little consideration has been given to where the temperatures are recorded relative to the location of bats within a roost or to the extent of spatial variability of temperatures within a roost. Notable exceptions include studies where hourly or continuous temperatures have been recorded in both occupied and unoccupied roosts (Licht and Leitner, 1967; Dwyer and Harris, 1972; Voûte, 1972; Kunz, 1973b, 1974, 1980; Vaughan and O'Shea, 1976; Humphrey *et al.*, 1977; Burnett and August, 1981). Use of these data, however, is problematical when estimating temperature-dependent metabolic rates (e.g., Studier and O'Farrell, 1976). For example, Burnett and August (1981) found that the estimated energy costs of

day roosting in *Myotis lucifugus* was two times greater when they used temperatures of cooler, unoccupied roosts as compared to warmer temperatures of occupied roosts.

Temperatures recorded in crevices and cavities occupied by active bats are typically warmer than unoccupied sites owing to the entrapment of metabolic heat and sometimes because the body surface of bats may be in direct contact with temperature probes (e.g., Voûte, 1972; Kunz, 1974, 1980). Which of these conditions (occupied or unoccupied) more appropriately represents the thermal environment of roosting bats? For clustered bats the answer depends on the position of a bat within the cluster. When bats are densely packed, the body surfaces of centrally located bats are almost entirely subjected to temperatures equivalent to the surface temperatures of adjacent bats. Those roosting on the periphery of a cluster will be subjected to a thermal environment intermediate between conditions in the center of a cluster and that experienced by nearby solitary bats, which in the latter case would be comparable to temperatures in "unoccupied" roosts. Bats roosting on the periphery of clusters in open areas will normally experience cooler temperatures than do peripherally roosting bats confined to crevices. As Burnett and August (1981) found, bats on the periphery of open clusters showed higher levels of activity than those in central positions, probably because of the exposure to cooler temperatures. Future studies that address daily activity budgets should consider quantifying the hemispheric thermal environment of both solitary and clustered bats, using a combination of modeling and empirically derived measures of heat flux via radiation, convection, conduction, and evaporation (see Bakken, 1976).

2.3. Roost Fidelity

Factors affecting roost fidelity include the relative abundance and permanency of roost sites, the proximity and stability of food resources, response to predator pressure, and human disturbance. Roost fidelity may change seasonally, and it can be affected by reproductive condition, sex, age, and social organization (Verschuren, 1957; Humphrey, 1975; Bradbury, 1977a). Bats show little loyalty to foliage roosts that are abundant and temporary, but they typically show a strong attachment to permanent sites such as caves, tree hollows, and man-made structures. Roost fidelity appears to be highest during the maternity period (Humphrey, 1975; Tuttle, 1976a). In temperate regions bats show a high degree of fidelity to hibernacula but lesser degrees of loyalty to transient roosts and swarming sites (LaVal and LaVal, 1980). Although many bats appear to be loyal to certain preferred roosts, there is a growing recognition that most bats establish and maintain familiarity with one or more alternate roosts. Tuttle (1976a) suggested that reports of apparent disloyalty probably result from insufficient knowledge of a species' normal movement patterns.

Fidelity to a home area rather than to a specific roost appears to be a common characteristic among foliage-roosting bats. The foliage-roosting *Artibeus lituratus* and *Vampyroides caraccioli* seldom use the same roost for more than two consecutive days (Morrison, 1980). *Ectophylla alba* uses freshly cut *Heliconia* leaves for up to two days before moving to other sites (Timm and Mortimer, 1976). Similarly, the tent-making pteropodid *Cynopterus sphynx* makes frequent movements to other foliage roosts (Goodwin, 1979). Findley and Wilson (1974) reported that *Thyroptera tricolor* remained up to 24 hr in unfurled *Heliconia* leaves, and the comparable stage of banana leaves becomes unsuitable as roosts for *Myotis bocagei* and *Pipistrellus nanus* after one or two days (Brosset, 1974; LaVal and LaVal, 1977).

The relationship between roost permanency, roost fidelity, and social organization is complex. For example, *Artibeus jamaicensis* may use a variety of day roosts, including foliage, hollow trees, and caves (Goodwin and Greenhall, 1961; Jimbo and Schwassmann, 1967; Goodwin, 1970; Foster and Timm, 1976; Morrison, 1978a, 1979). Individuals that use foliage roosts seldom remain at one roost for more than a few days (Foster and Timm, 1976; Morrison, 1979), and commuting distances to feeding trees are relatively short (Morrison, 1978a). Commuting distance is nearly two times greater for harem males and females that roost in hollow trees as it is for males that roost in foliage (Morrison, 1978a). For female groups and their harem males, fidelity to a particular tree hollow is higher than it is for bachelor males in foliage roosts. Morrison (1979) suggested that the availability and defensibility of suitable tree holes by the male *A. jamaicensis* probably facilitates strong roost fidelity and harem maintenance. In other areas where foliage roosts and caves are predominantly used as day roosts, the defense of roosts by males may be prohibitive (Morrison, 1979). Porter (1979a) reported male defense of harem groups in the cave-dwelling *Carollia perspicillata*, whose harems were maintained in close proximity to other groups. Similarly, in other species, such as *Myotis adversus* (Dwyer, 1970), *Tylonycteris pachypus*, *T. robustula* (Medway and Marshall, 1972), and *Pipistrellus nanus* (O'Shea, 1980), the high degree of roost fidelity of harem males reflects the defense of roost sites from intrusion by other males.

For some species the relative proximity and stability of food resources appear to have a bearing on roost fidelity. *Desmodus rotundus* may use several roosts when prey populations are widely scattered (Wimsatt, 1969; Turner, 1975), but when prey populations are stable and located near roost sites, fidelity to a single roost appears to be high (Young, 1971). Among temperate insectivorous species fidelity to day roosts is commonly low following the breakup of maternity roosts in late summer and early autumn, and this may, among other factors, be prompted by reduced insect abundance (e.g., Gaisler, 1963a; Stebbings, 1968; Laufens, 1973; Kunz, 1974; Ransome, 1978).

Some bats are likely to change roosts frequently if they are subject to severe predator pressures. Bradbury and Emmons (1974) suggested that frequent changes in roost sites by small groups of *Saccopteryx leptura* may reduce detection by predators. By contrast, its congener *S. bilineata* shows a high degree of roost fidelity, because it relies more on crypsis and on the ability to seek shelter in dark buttress cavities of trees. Similarly, the frequent movements of the male *Artibeus jamaicensis*, *A. lituratus*, *Vampyroides caraccioli* (Morrison, 1978a, 1979, 1980), and other foliage-roosting bats may reduce their vulnerability to predators.

Apparent disloyalty to roost sites may be due as much to human disturbance as it is to other factors (see Nyholm, 1965; Stebbings, 1968; Humphrey and Kunz, 1976; LaVal and LaVal, 1980). When bats are disturbed, they often abandon traditional roosts and take up residence at one or more alternate roosts (Pearson *et al.*, 1952; Sluiter and van Heerdt, 1966; Tuttle, 1976a).

3. NIGHT ROOSTS

Night roosts include places used to ingest food transported from nearby feeding areas, resting places for bats following one or more feeding bouts, feeding perches used by sit-and-wait predators, and calling roosts as part of leks. They may promote digestion and energy conservation, offer retreat from predators, serve as centers for information transfer about the location of food patches, and facilitate social interactions.

Factors governing the selection of night roosts vary widely among species, but roost availability, darkness, shelter from wind, proximity to feeding areas, and reduced risks of predation probably are most important. Bats are opportunistic in their choice of night roosts, but the overriding factor seems to be that they are located in the vicinity of feeding areas so that costly commutes to day roosts can be avoided and risks of predation minimized. Night roosts occur in a variety of places, including areas beneath bridges (Krutzsch, 1955a; Dalquest, 1957; Davis and Cockrum, 1963; Hirshfeld *et al.*, 1977), on rock surfaces (Dalquest, 1947; Nyholm, 1965; Howell, 1979), in rock crevices (Cross, 1965; Hayward and Cross, 1979; Hirshfeld *et al.*, 1977), in caves and mine tunnels (Sanborn and Nicholson, 1950; Dalquest, 1947; Vaughan, 1959; Davis *et al.*, 1968; Kunz, 1974; O'Shea and Vaughan, 1977), in abandoned and occupied buildings (Dalquest, 1947; Krutzsch, 1954; Schowalter *et al.*, 1979; Anthony *et al.*, 1981), in porches, breezeways, and garages (Dalquest, 1947; Vaughan, 1959; Barbour and Davis, 1969), in barns (Orr, 1954; Hoffmeister and Goodpaster, 1954; Kunz, 1974; Anthony *et al.*, 1981), park shelters (Kunz, 1973a), thatch houses (Hall and Dalquest, 1963; O'Shea, 1980), on the walls of buildings (Brosset, 1962b;

Fenton *et al.*, 1977a), on branches in small trees and shrubs (Dalquest, 1947; Nyholm, 1965; Hirshfeld *et al.*, 1977), and on desert plants (Howell, 1979).

3.1. Resting Places

Bats invariably use flight in pursuit of "prey," and most species have evolved nightly activity patterns to minimize the amount of time spent in flight. The timing and duration of nightly "rest" periods vary with species, according to the length of the night, their reproductive condition, prey availability, prevailing temperature, feeding success, food-passage time, and social interactions. One and occasionally two prolonged night-roosting periods are known for some insectivorous species and two nectarivorous bats. Typically, insectivorous bats enter night roosts after an initial feeding period (Krutzsch, 1954; Kunz, 1973a, 1974; Anthony and Kunz, 1977; O'Shea and Vaughan, 1977; Funakoshi and Uchida, 1978; Anthony *et al.*, 1981), often departing to feed or drink one or more times before eventually returning to their day roost. Nectarivorous bats may rest for short intervals (≈ 20 min) in feeding areas and later retreat to protected shelters for prolonged night roosting (Howell, 1979).

Other bats roost for short intervals during the night to consume prey that they have captured in flight or on the ground, only later to engage in an extended rest period. This behavior seems most common among insectivorous species that take relatively large prey. Vaughan (1959) interpreted the intermittent night traffic of *Macrotus californicus* in and out of day roosts as evidence that individuals feeding near the day roost were transporting prey to eat. The intermittent returns and departures of *Antrozous pallidus* at night roosts (Beck and Rudd, 1960; Orr, 1954; O'Shea and Vaughan, 1977) commonly involves the transport of large insects and other arthropod prey. Similar behavior has been reported for *Eptesicus fuscus* (Krutzsch, 1946). In the most northern latitudes, where summer nights are short, bats appear to forgo an extended night-roosting period. In Finland *Myotis mystacinus* and *Myotis daubentoni* each have a single feeding period interrupted by short rest stops (Nyholm, 1965). Similarly, in Sweden *Eptesicus nilssoni* has only one feeding period, interrupted by intermittent rests (Ryberg, 1947), but in Germany this bat has two feeding periods interrupted by a longer night-roosting period (Eisentraut, 1951).

Solitary bats and those that form small colonies typically return to their day roost at night, whereas species that form large aggregations seldom return to their day roost before dawn. For example, at places where *Tadarida brasiliensis* forms small daytime colonies in buildings (Krutzsch, 1955a; Davis *et al.*, 1962) and under bridges (Krutzsch, 1955a; Davis and Cockrum, 1963; Hirshfeld *et al.*, 1977) many, if not most, individuals return to these sites at night. By contrast, few individuals from large colonies return before sunrise (Davis *et al.*, 1962). Thus increased time associated with long-distance commuting in some species

(Williams *et al.*, 1973; Bateman and Vaughan, 1974) may promote the use of night roosts located in proximity to feeding areas.

Several factors interact to influence patterns of night-roost use, and this is especially apparent during the maternity period. Maternity roosts are commonly used as night roosts by lactating females and newly volant young, including *Myotis dasycneme* (Voûte *et al.*, 1974), *M. grisescens* (Tuttle, 1975; LaVal and LaVal, 1980), *M. nattereri* (Laufens, 1973), *M. lucifugus* (Anthony and Kunz, 1977; Anthony *et al.*, 1981), *M. myotis* (Krátky, 1971), *M. velifer* (Kunz, 1973b, 1974), *Antrozous pallidus* (Beck and Rudd, 1960; O'Shea and Vaughan, 1977), *Pipistrellus javanicus* (= *abramus*) (Funakoshi and Uchida, 1978), *P. pipistrellus* (Swift, 1980), and *Rhinolophus ferrumequinum* (Ransome, 1973, 1978). Early returns to maternity roosts at night by terminally pregnant and lactating females may reflect a lower feeding efficiency (during pregnancy) and a need to suckle young (during lactation). Early returns of newly volant young bats to maternity roosts at night probably can be explained by their inefficient foraging and a continued need to nurse when they are first learning to fly (Kunz, 1974).

The selection of some types of night roosts and the duration of occupancy may be influenced directly or indirectly by lunar periodicity. Some desert bats apparently use more protected shelters during brighter lunar periods than during darker ones (Hirshfeld *et al.*, 1977). Fenton *et al.* (1977a) noted that at least three species of insectivorous bats in Africa forego a second feeding period and undergo a prolonged night-roosting period during bright moonlight, in an area where bat hawks feed on bats (Fenton *et al.*, 1977b). The significance of this and similar behavior, termed "lunar phobia" may represent a response to increased risks of predation (Fenton *et al.*, 1977b; Morrison, 1978b, 1980; Chapter 5), but it does not account for the reduced activity of bats during bright moonlight when they are not exposed to severe predation pressure. Anthony *et al.* (1981) found that the early entry of *Myotis lucifugus* into night roosts on bright moonlit nights could best be explained as a response to low insect abundance. In Africa Fenton *et al.* (1977a) also observed reduced insect activity on nights with bright moonlight, but noted that some bats fed more often beneath the tree canopy and less in open areas, suggesting that some insects may fly preferentially in areas sheltered by moonlight.

The most thorough study of night-roosting ecology and behavior has been on *Myotis lucifugus* (Anthony *et al.*, 1981). The amount of time that night roosts, separate from maternity roosts, are occupied by this bat is closely associated with reproduction and prey abundance. The use of night roosts by *M. lucifugus* appears to promote digestion and provides conditions that minimize energy expenditure when efficient foraging is prohibited during cool periods and when insect abundance is low. At these times *M. lucifugus* retreats to small cavities (Fig. 12), where individuals typically form tight clusters, and otherwise remain

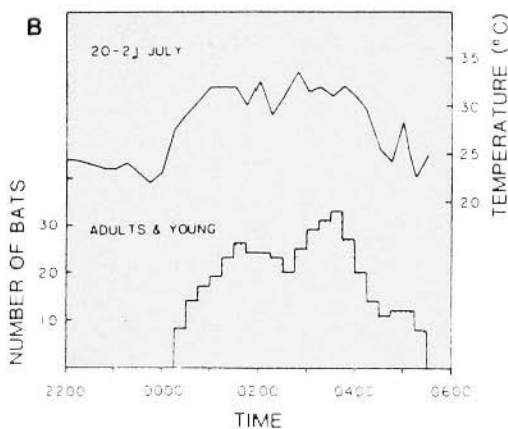
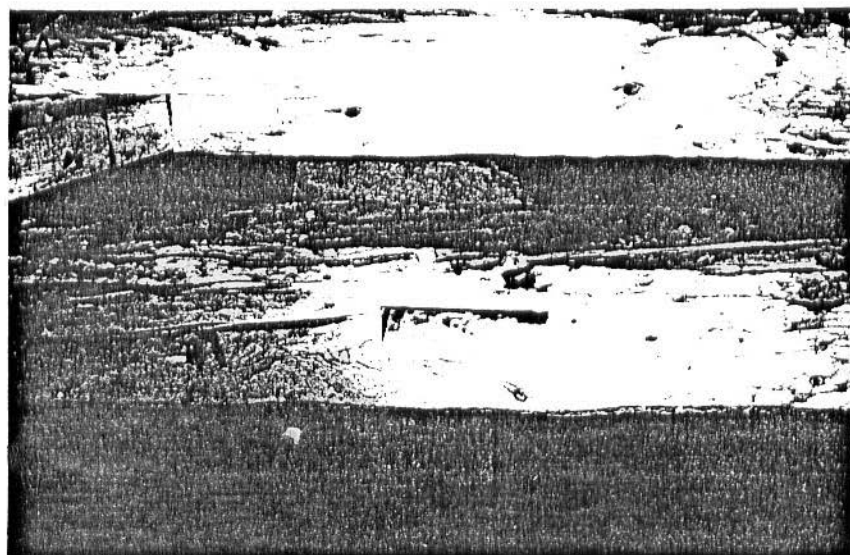


FIGURE 12. (A) A mortice cavity used by individuals and small groups of *Myotis lucifugus* for night roosting. (Photo by T. H. Kunz.) (B) Temperature profile in a mortice cavity denoting the period of night-roost occupancy and the number of bats present contributing to the temperature increase. (Modified from Anthony *et al.* 1981.)

alert. During pregnancy these separate night roosts are used extensively and bats usually remain throughout a continuous night-roosting period. During lactation separate night roosts are used intermittently, mostly by nonreproductive females at maternity colonies, and individual turnover is high. In late summer, when young are weaned, the number of bats using separate night roosts increases and a single period of occupancy prevails with only moderate individual turnover.

Some bats may enter torpor in night roosts to promote energy economy. For example, *Antrozous pallidus* enters nightly torpor during cool months (O'Shea and Vaughan, 1977) as does *Pipistrellus nanus* in the dry season, when the density of insect prey is low (O'Shea, 1980), but at other times they remain active.

We know little about the social interactions of bats in night roosts and how they may influence times of occupancy, roost composition, and how social interactions in night roosts may affect the social organization of bats in day roosts or during feeding periods. Males of *Pipistrellus nanus* occupy day roosts at night for extended periods during the mating season, defending these roosts from other males and advertising their locations to females (O'Shea, 1980). In species that defend roosts against incursions of conspecifics during the day but not at night, this situation could lead to paternity leaks at night roosts and negate the benefits derived from the vigorous defense of day roosts (Porter, 1979a). Start and Marshall (1976) suggested that the primary role of communal roosting and group foraging in the flower-visiting bat *Eonycteris spelaea* may be to function as a center for information transfer (see Ward and Zahavi, 1973) on the location of widely scattered food sources. Similarly, the periodic night-roosting behavior of *Leptonycteris sanborni* may facilitate information transfer and provide optimum conditions for promoting energy economy, the digestion of food, grooming, and pollen consumption (Howell, 1979). The use of night roosts by *Myotis lucifugus* has no apparent social function (Barclay *et al.*, 1979).

3.2. Feeding Perches

Several members of the Megadermatidae, Nycteridae, and Hipposideridae are sit-and-wait predators that closely integrate night roosting with feeding. Feeding perches are commonly established within a few meters of day roosts and are usually conspicuous owing to the accumulation of culled remains of prey (e.g., Verschuren, 1957; Rosevear, 1965). These bats may hang from feeding perches from one to several hours, acoustically and sometimes visually scanning the immediate environment for prey (Vaughan, 1976, 1977). They make short feeding sallies (<10 sec), returning to a perch, where the hard parts are culled and the palatable parts consumed. The amount of time these bats typically spend in feeding perches exceeds the time spent in flight. *Cardioderma cor* may spend over 95% of its time on feeding perches, allocating the remainder to short flights to nearby perches and in the pursuit of prey (Vaughan, 1976). The amount of time *Hipposideros commersoni* spends in its feeding perch exceeds the time spent flying by a factor of 4.5 to 1 (Vaughan, 1977).

Similar, although less-detailed observations have been made on *Megaderma lyra* and *Megaderma spasma*, both species hunt near their day roost, to which they usually retreat at night to consume their prey (Brosset, 1962b). *Nycteris thebaica* forages in the vicinity of its day roost, feeding in open areas, but

consumes its prey in separate feeding roosts (Rosevear, 1965). *Macroderma gigas* usually eats its prey at the place of capture, but it also provisions its young by taking food to the day roost (Douglas, 1967), as does *Vampyrus spectrum* (Vehrencamp *et al.*, 1977).

Whether these bats return to their day roosts at night or use separate feeding perches probably reflects compromises involving risks of predation, commuting costs, and the size of their prey. Solitary sit-and-wait predators are likely to be at risk from predation if and when they consume prey in exposed areas, but this risk should be balanced against the additional costs and risks of predation while commuting and transporting extra baggage to a safer roost.

3.3. Feeding Roosts

Bats that eat fruit, flowers, nectar, pollen, and leaves are almost without exception restricted to the Megachiroptera, the New World Phyllostomidae (Chapter 8), and to the Mystacinidae (Daniels, 1979). Phyllostomids typically transport fruit from fruiting trees to separate feeding roosts, where all or parts of the food items are eaten. By contrast, fruit-eating megachiropterans more commonly consume fruit at fruiting trees.

3.3.1. Fruit-Eating Microchiroptera

Among New World fruit-eating bats, *Carollia perspicillata* (Heithaus and Fleming, 1978), *Artibeus jamaicensis* (Jimbo and Schwassmann, 1967; Morrison, 1978a, 1978b), *A. lituratus*, and *Vampyroides caraccioli* (Morrison, 1980) are best known for their use of separate feeding roosts. Predator pressure appears to be the leading selective factor promoting the use of these roosts (Fenton and Fleming, 1976; Fenton *et al.*, 1977b; Heithaus and Fleming, 1978; Morrison, 1978a, 1978b, 1980; Howe, 1979). However, the use of certain trees as feeding roosts may represent a compromise between decreased detection by predators, costs associated with traveling greater distances (Morrison, 1978a, 1980), and selection for efficient seed dispersal (Chapter 9). Preferred feeding roosts are often located in trees with a densely leaved crown, downwind from parent trees, and over moist areas (Janzen *et al.*, 1976). *Carollia perspicillata* typically selects feeding roosts within 30–40 m of a fruiting tree, usually in dense foliage, and less than 4 m above the ground (Heithaus and Fleming, 1978). Up to 40–50 trips are made each night between a fruiting tree and feeding roost. If a fruit is too large to transport, it may be eaten in the fruiting tree (Goodwin and Greenhall, 1961).

The feeding roosts of *Artibeus jamaicensis* are often located on the underside of small palms, located at distances ranging from 25 to 400 m from fruiting trees (Jimbo and Schwassmann, 1967; Morrison, 1978a). Caves used as day

roosts may also be used as feeding roosts (Goodwin, 1970; Gardner, 1977). *Artibeus jamaicensis* typically makes 10–15 round trips per night between fruiting trees and feeding roosts, spending over 80% of the night in its roost. How much of this time is allocated to actual feeding and how much to other activities remains to be determined. The amount of time spent in feeding roosts is modified on bright, moonlit nights, when bats suspend feeding and return early to their day roost. On dark nights *A. jamaicensis* spends less time occupying feeding roosts and more time searching for newly ripened fruit trees (Morrison, 1978a, 1978b). Similar although less-detailed observations have been reported for *A. lituratus* and *Vampyroides caraccioli*, both of which fly directly to fruiting trees upon departure from their day roost (Morrison, 1980). Both species may visit two or three trees in the course of a night at distances ranging from 150 to 2300 m from a day roost. These bats transport fruit to feeding roosts located less than 100 m from fruiting trees, but their nightly activity does not appear to be influenced by moonlight.

3.3.2. Fruit-Eating Megachiroptera

While New World fruit-eating bats use separate feeding roosts, most fruit-eating megachiropterans spend the night in the same trees in which they feed. What may account for this difference lies in their contrasting modes of orientation and navigation; phyllostomids rely mostly on echolocation, whereas megachiropterans depend principally on vision (Novick, 1977). Although pteropodids commonly feed in the dark, they apparently require subdued light (including moonlight) for navigation (Gould, 1978) and thus are likely to minimize flight at night. *Rousettus* is capable of echolocating, but apparently it cannot carry food in its mouth while doing so, thus accounting for its feeding and night-roosting activities in the same tree (Lekagul and McNeely, 1977). Low risks of predation may also explain why some megachiropterans night roost and feed in the same trees (Fenton *et al.*, 1977b).

3.4. Calling Roosts

Nocturnal calling roosts are common among male epomophorine bats in Africa, including *Hypsiphatius*, *Epomops*, *Micropteropus*, and *Epomophorus* (Brosset, 1966; Kingdon, 1974; Wickler and Seibt, 1976; Bradbury, 1977a, 1977b). One of the most thoroughly studied of these is *H. monstrosus* (Bradbury, 1977b). Upon leaving its day roost, males assemble in calling aggregations known as leks, usually located in riparian forests along streams and rivers. Individual calling roosts are typically 10 m apart and often located in unusually rich food patches, yet there is no evidence that males defend these resources. Most of the time at calling roosts is allocated to overt displays, attacks on other

males, loud calling, and grooming. The calling frequency varies during the night, with an early calling session devoted to mate attraction and copulation; a morning session apparently involves territorial establishment.

The calling roosts of the male *Epomophorus wahlbergi* are similar to *Hypsignathus monstrosus*, as described by Wickler and Seibt (1976). Soon after leaving day roosts, male *Epomophorus wahlbergi* fly to nearby trees, where they hang from small branches approximately 2–3 m above the ground. After a period of calling and physical display individuals shift their calling perches to other trees. Similar calling roosts are formed by *Epomops franqueti* (Bradbury, 1977a). At night males establish calling roosts that are usually widely dispersed, located at distances of 100 m or more. Males may have several calling roosts to which they move at regular intervals during the night and steady calling may continue for hours.

Little is known of individual time budgets for these bats. For example, it would be interesting to determine what compromises are made by males between time spent calling and time allocated to foraging. Bradbury (1977b) suggests that the need for foraging time may prohibit most male *Hypsignathus monstrosus* from using both calling sessions in the same night. After departing from calling roosts, most male *Hypsignathus* forage until dawn and then fly directly to day roosts, although some apparently return to the calling assemblage a second time. It would be interesting to know whether the few individuals that return to a calling assemblage a second time in the same night contribute to most of the matings.

4. SUMMARY

The roosting ecology of bats can be viewed as a compromise of opposing selective pressures derived from roost and nonroost origins. The availability of roosts, roost dimensions, energetic considerations, and risks of predation are major determinants of roost use. Roosting habits may vary seasonally, according to sex, reproductive condition, social organization, and food habits. The type of roost, the number of occupants, roost associates, and roost activities are influenced by the manner of flight, the mode of orientation, the dispersion and abundance of food resources, predation risks, social interactions, and energy economy imposed by body size and the physical environment.

Bats have successfully exploited a variety of shelters, including caves, rock and tree crevices, foliage roosts, tree cavities, and man-made structures. Some caves provide spacious chambers that support the largest known mammalian aggregations. Cave topography and structure may enhance the energy economy of roosting bats by the entrapment of metabolic heat and promote population substructuring and the evolution of diverse social systems. Although caves and

tree cavities provide protection against most predators and buffers against fluctuations in temperature and adverse weather, tree cavities offer limited space for large aggregations and some caves are unsuitable as roosts, especially when located at considerable distances from profitable feeding areas and when they are too cold or too warm to promote efficient thermoregulation. Some bats have evolved specialized roosting postures, pelage characteristics, and body shapes to accommodate crevice-dwelling habits.

Foliage roosts offer the advantage of being ubiquitous and abundant, but they are relatively temporary and thus require bats to make frequent relocations. Most foliage-roosting bats are solitary or form small groups, and they are mostly distributed in tropical regions. Large aggregations of foliage-roosting bats are exclusively restricted to the Megachiroptera, because most are precluded from using internal shelters owing to their inability to echolocate. Foliage-roosting bats include forms with highly specialized foot pads and wrist pads for roosting on the moist surfaces of leaves, some modify leaves into tentlike structures, and others rely on crypsis. Crypsis may be enhanced by pelage colors that resemble ripe fruits and dead leaves, by countershading, disruptive markings, reticulate wing venation, and motionless postures.

Factors promoting high roost fidelity include roost permanency, morphological specialization, proximity to food resources, the stability of food resources, low risks of predation, microclimatic stability, and complex social organization. As a rule, bats show the highest fidelity toward roosts in tropical caves and the lowest toward foliage roosts. Roost fidelity is highest among females during the maternity period and lowest among solitary males.

The use of man-made structures as substitutes for natural roosts provides convincing evidence that many bats are highly opportunistic in their roost selection. Some bats have become so dependent on man-made structures that there are few recent records from natural shelters; others have extended their former distributions into otherwise uninhabited regions. The introduction and cultivation of certain plant species have increased the availability of roost (and food) resources for some bats. Paradoxically, the adverse consequences of deforestation, forest management, building restoration, the increased recreational and commercial use of caves, and vandalism has led to a decrease in the number and diversity of roosts and bats in some regions.

The daytime activity of bats can be characterized as a period of rest interrupted by periods of spontaneous and rhythmical activity. Bats are most active in their day roost following their return from feeding. This is followed by a lull in activity in midday, with an increase in activity occurring shortly before nightly departure. The amount of time that bats allocate to day-roost activities is influenced by the type of roost, its microclimate, the risks of predation, and the kinds of social interactions among roost mates. In contrast to bats that roost in protected shelters, bats that roost in exposed situations appear to allocate a greater

proportion of their time to predator surveillance. Species that form large aggregations are generally more active than solitary bats and those roosting in small groups.

Night roosts may be used by bats to consume food that has been transported from nearby feeding areas, and they may serve as resting places following one or more feeding bouts, as feeding perches for sit-and-wait predators, and as calling and mating roosts for territorial species. The use of night roosts can promote the digestion of food, provide retreat from predators, and serve as centers for information transfer. Selection of night roosts in small protected areas may be important to the energy economy of bats, especially for those species living in cool, temperate environments. The use of night roosts and the duration of occupancy may be influenced by colony size, lunar periodicity, prey abundance, predator pressure, and ambient temperature. The selection of night roosts in or near foraging areas should be important in reducing the risks of predation and the time and energy costs associated with lengthy commutes to day roosts. Some fruit-eating bats may transport fruit to separate feeding roosts, whereas others feed and roost at night in the same trees. Differences between these two strategies may be influenced by differences in predation risks at fruit trees and by contrasting modes of orientation during flight.

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