

Ecology of Cavity and Foliage Roosting Bats

Thomas H. Kunz and Linda F. Lumsden

Introduction

Bats occupy a wide variety of roosts in both natural and manmade structures. More than half of the approximately 1,100 species of living bats use plants exclusively or opportunistically as roosts. Others seek shelter in caves, rock crevices, mines, tombs, buildings, bridges, and other manmade structures. Some bats roost in cavities constructed by other animals, including bird nests and nests of ants and termites, whereas others roost in exposed places on branches and the trunks of trees. Thus, it is not surprising that the conditions and events associated with roosting have played a major role in the ecology and evolution of bats (Kunz 1982). Roosts are important sites for mating, hibernation, and rearing young. They often facilitate complex social interactions, offer protection from inclement weather, promote energy conservation, and minimize risks of predation.

Roosting habits of bats are influenced by the diversity and abundance of roosts, the distribution and abundance of food, and an energy economy influenced by body size and the physical environment. Roosting ecology is ultimately tempered by constraints of phylogenetic inertia and a compromise of opposing selective pressures derived from both roost and nonroost sources (Kunz 1982). Morphological, physiological, and behavioral characteristics of bats commonly regarded as adaptations for roosting include flattened skulls, suction pads and disks on feet and wrists, cryptic markings and postures, clustering, torpor, and synchronous nightly departures. These traits reflect compromises imposed by manner of flight, body size, predator pressure, energy economy, and variations in the physical environment (Kunz 1982).

Bats seek shelter in a wide variety of roost types, ranging along a continuum from ephemeral to permanent. At one extreme, roosting sites in caves, mines, and some rock crevices offer the advantages of relative permanency, thermal stability, and protection from climatic extremes but may be patchy in distribution. At the other extreme, spaces beneath exfoliating bark and foliage generally are ephemeral and more subject to environmental extremes but are more abundant and ubiquitous (Kunz 1982). Associations between bats and roosts range from being obligatory to opportunistic, with selection of a particular type of roost dependent on its availability (Kunz 1996).

We focus this review primarily on bats that seek shelter in tree cavities, in foliage, on exposed branches and boles of trees, natural cavities, or structures modified by bats. This emphasis is timely because forests have become increasingly threatened by anthropogenic factors (e.g., timber management, deforestation, and associated habitat alteration and loss). Knowledge of roost requirements is a prerequisite to understanding the impact of disturbance on bat populations and to providing focus to conservation efforts (Fenton and Rautenbach 1998; Pierson 1998). Bats that occupy habitats that are highly susceptible to disturbance and loss are of special concern to conservation biologists. Only in recent history have manmade structures, such as mines, bridges, and buildings, provided alternative habitats comparable to caves and tree cavities.

Types of Roosts

Tree Cavities

Tree cavities are important roost resources in both temperate and tropical regions (Barclay and Brigham 1996; Boonman 2000; Kunz 1982, 1996; Pierson 1998; Rosevear 1965; Sedgeley and O'Donnell 1999b; Simmons and Voss 1998; Tuttle 1976; Verschuren 1957, 1966; figs. 1.1 and 1.2). In North America, Europe, Asia, and Australia, tree cavities are used mostly by members of the Vespertilionidae. In Africa, they are used mostly by members of the Vespertilionidae and Hipposideridae. In the Neotropics, tree cavities are used primarily by members of the Phyllostomidae and Emballonuridae. Although cavity-roosting habits are most common among microchiropterans, they may be more common in some small megachiropterans than previously recognized (Bonaccorso 1998; Flannery 1995; Rainey 1998).

Within temperate regions, the proportions of species assemblages that use tree cavities vary geographically (Humphrey 1975). In western North America and Australia, where extensive areas of native forests remain, a relative high proportion of bat species roost in tree cavities (Barclay and Brigham 1996; Churchill 1998; Pierson 1998; fig. 1.1A). By contrast, in western Europe and eastern North America, where natural tree cavities have been depleted by extensive clearing of forests and misguided forest management practices, many cavity-roosting species now rely considerably on manmade structures such as buildings (Kunz and Reynolds, in press), bridges (Kunz 1982), and bat houses (Mayle 1990; Tuttle and Hensley 1993). In some areas, tree cavities provide suitable roosting habitats for bats on a year-round basis. At higher latitudes, tree cavities may be too cold during winter months, and thus bats must seek alternative roosts, usually in caves or other subterranean structures (Mayle 1990). In lowland tropical regions, where caves are absent, tree cavities provide one of the primary roosting habitats for bats. On Barro Colorado Island, Panama, tree cavities are commonly occupied by small harem groups of *Artibeus jamaicensis* (Morrison 1979; fig. 1.1B).

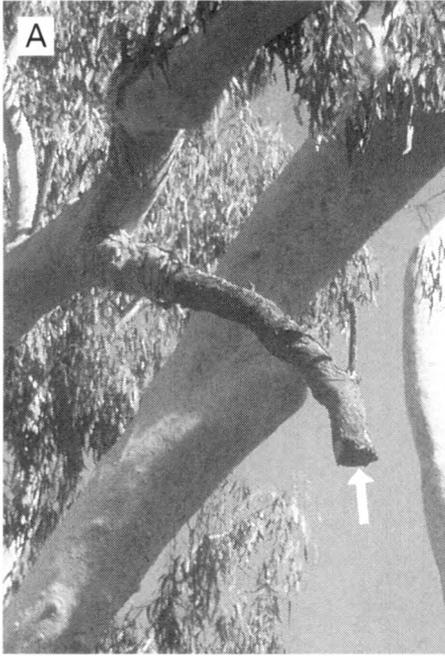


Figure 1.1. A, Small cavity in dead branch of a river red gum (*Eucalyptus camaldulensis*) in temperate southeastern Australia (photo by L. Lumsden); B, tree cavity used by a small harem group of *Artibeus jamaicensis* on Barro Colorado, Panama Canal Zone (photo by D. W. Morrison); C, a partially rotted basal cavity in a large, buttressed tree (*Pradosia cochlearia*) in a lowland tropical rainforest offers shelter to *Glossophaga soricina*, *Micronycteris megalotis*, and *Carollia perspicillata* in French Guiana (from Simmons and Voss 1998; photo by R. Voss); D, basal and bole cavities in a baobob tree (*Adansonia digitata*) used as day-roosting sites by *Cardioderma cor* in west Africa (photo by T. A. Vaughan). Arrows denote roost openings.



Figure 1.2. *A*, Partially rotted, fallen tree with a cavity used as a day roost by *Furipterus horrens* (from Simmons and Voss 1998; photo by R. Voss); *B*, underside of a broken tree trunk (arrow) used as a day roost by *Peropteryx macrotis*, *P. kappleri*, and *Cormura brevirostris* (from Simmons and Voss 1998; photo by R. Voss). Arrows denote roost areas.

Buttress cavities form semidarkened spaces on the exterior of lowland tropical trees (Kaufman 1988; Richards 1996; Whitmore 1998), and provide ideal roosting habitats for tropical bats (Simmons and Voss 1998; Tuttle 1976). In strangler figs, adjacent buttresses may fuse or anastomose to form deep, vertical cavities adjacent to the bole (fig. 1.1C). Such cavities and the spaces between adjacent buttresses are often used as day roosts by *Saccopteryx bilineata* (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976). Cavities that form in baobab trees (*Adansonia digitata*) are commonly used by *Cardioderma cor* (Vaughan 1976; fig. 1.1D) and several other microchiropteran species in Africa (Verschuren 1957).

Cavities may form in the boles, trunks, or branches of live and dead trees. In general, large dead trees (snags) remain standing for longer periods than do small trees, with snags in old-growth Douglas fir (*Pseudotsuga menziesii*) thought to take 250 yr after death to completely decompose (Cline et al. 1980). In many areas, these snags provide important roosting sites for bats (e.g., Brigham et al. 1997; Crampton and Barclay 1998; Lumsden et al. 2002b; Mattson et al. 1996; Ormsbee and McComb 1998; Zielinski and Gellman 1999).

In old-growth temperate and tropical forests, basal cavities sometimes form in the interior of living trees, when the heartwood is exposed to fire (Finney 1991). These basal cavities share some characteristics with caves, including stable temperatures and humidity, pronounced light gradients, protection from rain, relatively spacious internal flight space (Gellman and Zielinski 1996), and extended longevity, with some trees living up to 2,000 yr (Becking 1982). Because basal cavities may persist for a major portion of a tree's life, they are considered to be important resources for cavity-roosting bats (Gellman and Zielinski 1996). That hollow trees are prevalent in nutrient-poor soils, especially in tropical regions, led Janzen (1976) to suggest that rotted cavities may be selected as a mechanism to trap minerals and nitrogen from the accumulation of animal feces. If this hypothesis is correct, deposits of nitrogen-rich guano from bats may play an important role in forest dynamics (see Gellman and Zielinski 1996; Pierson 1998).

Cavity formation in trees results from a range of processes, including fungal infection, insect attack, excavation by termites and woodpeckers, lightning strikes, fire, and natural damage to branches (Bennett et al. 1994; Betts 1996; Gibbons 1994; Kalcounis and Brigham 1998; Mackowski 1984; Pierson 1998). The number and size of cavities vary with the diameter, age, and height of the tree, with larger and older trees having experienced longer periods of exposure to processes of cavity formation and development than smaller trees (Bennett et al. 1994; Lindenmayer et al. 1993; Sedgeley and O'Donnell 1999b). These relationships vary among species, with some trees forming cavities at earlier stages of growth than others (Bennett et al. 1994; Cline et al. 1980; Gibbons 1994; Raphael and Morrison 1987). In Australia and New Zealand, where no vertebrate species are known to excavate tree cavities, roosts used by

bats are more often found in older trees. Tree cavities that form due to physical forces or actions of invertebrates generally do not develop until trees are large and old, usually after 100 or more years (Mackowski 1984; Mawson and Long 1994).

When trees with cavities and buttresses die and fall, they may continue to provide roosting spaces for bats (fig. 1.2). In the tropics, cavities in fallen tree trunks are commonly used as roosts by members of the Emballonuridae (e.g., *Emballonura monticola*, *Cormura brevirostris*, *Peropteryx leucoptera*, *Saccopteryx bilineata* [Bernard 1999; Lekagul and McNeely 1977; Reid 1997; Tuttle 1970]) and Phyllostomidae (e.g., *Carollia perspicillata*, *Lonchophylla thomasi*, *Miconycteris hirsuta*, *M. megalotis*, *Mimon crenulatum*, *M. bennettii*, *Trachops cirrhosus* [LaVal 1977; Reid 1997; Simmons and Voss 1998; Tuttle 1970]). In Central America, fallen trees appear to be the primary roosting habitat for *Furipterus horrens* (Reid 1997), with up to 59 individuals recorded from a single roost (LaVal 1977).

Selection of Tree-Cavity Roosts

Knowledge of how bats use tree cavities has increased in recent years, largely due to the use of radiotelemetry. Early research on cavity-roosting bats concentrated mostly on relatively large species (e.g., Barclay et al. 1988; Fenton 1983), but with radio transmitters currently weighing less than 0.5 g, knowledge of small cavity-roosting species (<6 g), such as *Myotis californicus* (Brigham et al. 1997) and *Vespadelus pumilus* (Law and Anderson 2000) have markedly increased.

Several patterns have begun to emerge in the types of roosts used by cavity-roosting bats. Recent studies have focused on whether bats select particular roost attributes relative to their abundance (see references in table 1.1). To this end, roost and available habitat features have been measured and compared statistically. Because cavity-roosting bats generally do not modify their roost environment, they select roost sites from those that form from physical means, invertebrate activity, or facilitated by cavity excavators. In north temperate regions, several species of bats occupy abandoned woodpecker cavities (e.g., Betts 1996; Gaisler et al. 1979; Kalcounis and Brigham 1998; Pierson 1998; van Heerdt and Sluiter 1965), and in fact some species select these cavities in preference to those that form by physical or invertebrate action. For example, 85% of the 81 *Nyctalus noctula* roosts reported by Boonman (2000) in the Netherlands were observed in cavities excavated by woodpeckers. In these and similar situations, roost selection was strongly influenced by the preference of the original excavators for nesting sites and the decay characteristics of the tree (Kalcounis and Hecker 1996).

Selection pressures (in particular due to microclimate variables and predators) that govern the choice of tree and site characteristics should be similar regardless of the species of bat (Vonhof and Barclay 1996). Vonhof and Barclay

(1996) and Brigham et al. (1997) predicted that cavity-roosting bats should require a number of large dead trees, in specific stages of decay and that project above the canopy in relatively open areas (fig. 1.3).

To assess the generality of these predictions, we summarize results from 26 studies (table 1.1) that have statistically assessed selection of various roost tree and site attributes. Some species in these studies roosted both in tree cavities and beneath exfoliating bark, and these were not separated in the assessment of roost selection. Thus, we include information on tree cavities and spaces beneath exfoliating bark. Roosts located beneath exfoliating bark are treated in more detail below.

Selection of roosts can occur at a number of different levels (cavity, tree, stand, and landscape), and various studies have addressed one or more of these criteria. Most studies have assessed selection at the level of the tree and/or the stand, with fewer studies providing information on cavity selection and landscape characteristics.

Cavity size and shape may directly influence the number of bats present, their social structure, and roost microclimate (Kunz 1982). Several investigators have demonstrated differences in the types of openings used by bats to gain access to roosts (Lumsden et al. 2002b; Vonhof and Barclay 1996), but few studies have measured "available" cavities to assess whether bats actually select particular types of cavities. A notable exception is the study by Sedgely and O'Donnell (1999a) in New Zealand, who compared characteristics of 84 tree cavities used by *Chalinolobus tuberculatus* with 57 other available but unoccupied cavities. Roosts were predominantly formed in knotholes with medium-sized openings and had thick cavity walls with dry, medium-sized internal spaces. Roosts typically were high above the ground, and the areas that surrounded the openings were uncluttered by adjacent vegetation. Sedgely and O'Donnell (1999a) suggested that these characteristics facilitated easy access to the roost and provided good insulation. The microclimate (temperature and humidity) in available cavities was also compared, with roost cavities being the most stable, as well as having higher humidities and temperatures that continued well into the night (Sedgely 2001).

Cavity roosts may be selected by bats to increase their protection from predators and competitors. Predation on bats may occur within the roost or as they depart at dusk (Fenton et al. 1994; Speakman 1991). Bats that enter torpor on a daily (or extended) basis may not be sufficiently alert to escape from predators and, hence, need to select roosts that deny entry to predators. In temperate regions of Australia, predation by birds and arboreal animals, including goannas, pythons, and marsupial carnivores, may exert a strong selection pressure on bats to choose tree cavities with openings not much larger than their own body size (Tidemann and Flavel 1987). However, small openings to tree cavities may not be as important in areas that lack predators (e.g., in New Zealand [Sedgely and O'Donnell 1999a]) or in tropical regions, where some

Table 1.1. Selection of commonly measured habitat variables of roost sites used by temperate tree-roosting microchiropteran species (expanded from Sedgely and O'Donnell 1999b)

| Species | Country | Sex | No of Roosts | Type of Cavity | Variables Assessed for Selection | | | | | | | | | | References |
|-----------------------------------|-----------------|---------|--------------|----------------|----------------------------------|--------------|-------------|-----------------|--------|---------------------------------|-----------------------|-------------|-----------------|------------------------------------|------------|
| | | | | | Tree sp. | Dead/Decayed | Large Diam. | Tall Roost tree | % Bark | Low Canopy/Clutter around Roost | Aspect of Roost Entr. | Roost Stand | Other | | |
| <i>Chalinolobus gouldii</i> | Australia | M & F | 89 | H | ... | 0 | + | ... | ... | ... | 0 | + | ... | Lumsden et al. 2002a, 2002b | |
| <i>Chalinolobus tuberculatus</i> | New Zealand | M & F | 291 | H | + | + | + | ... | ... | + | 0 | + | 1, 5, 6, 8 | Sedgely and O'Donnell 1999a, 1999b | |
| <i>Eptesicus fuscus</i> | Canada | F (Mat) | 15 | H | + | + | + | ... | ... | ... | ... | ... | 3, 10 | Vonhof 1996 | |
| <i>Eptesicus fuscus</i> | Canada | F (Mat) | 27 | H | + | ... | ... | ... | ... | ... | + | ... | 7 | Kalcounis and Brigham 1998 | |
| <i>Falsistrellus tasmaniensis</i> | Australia | M | 8 | H | 0 | ... | + | ... | ... | ... | ... | + | ... | Herr 1998 | |
| <i>Lasionycteris noctivagans</i> | USA | M & F | 35 | H UB | ... | + | + | ... | ... | ... | + | + | 14 | Mattison et al. 1996 | |
| <i>Lasionycteris noctivagans</i> | Canada | F (Mat) | 12 | H UB | + | 0 | + | ... | ... | ... | ... | ... | 10, 12 | Vonhof 1996 | |
| <i>Lasionycteris noctivagans</i> | Canada | F | 36 | CR | + | ... | + | ... | ... | ... | ... | ... | ... | Barclay et al. 1988 | |
| <i>Lasionycteris noctivagans</i> | USA | F (Mat) | 17 | H | 0 | + | 0 | ... | ... | 0 | 0 | 0 | 2, 8, 9, 10, 11 | Betts 1998 | |
| <i>Lasionycteris noctivagans</i> | USA | M & F | 15 | ? | + | + | + | ... | ... | ... | ... | + | ... | Campbell et al. 1996 | |
| <i>Myotis californicus</i> | Canada | F (Mat) | 19 | UB H | + | + | + | ... | ... | 0 | 0 | + | 11, 12 | Brigham et al. 1997 | |
| <i>Myotis daubentonii</i> | The Netherlands | ... | 27 | H | + | ... | ... | ... | ... | ... | 0 | ... | 15 | Boonman 2000 | |
| <i>Myotis evotis</i> | Canada | M & F | 19 | UB | + | ... | + | ... | ... | 0 | + | + | 6 | Vonhof and Barclay 1997 | |
| <i>Myotis evotis</i> | USA | F | 73 | UB | + | + | 0 | + | + | + | 0 | + | 16 | Waldien et al. 2000 | |
| <i>Myotis septentrionalis</i> | USA | F (Mat) | 32 | UB H | + | 0 | 0 | ... | ... | ... | ... | ... | ... | Foster and Kurta 1999 | |
| <i>Myotis septentrionalis</i> | USA | F (Mat) | 47 | ? | ... | + | + | ... | ... | 0 | ... | + | ... | Sasse and Pekins 1996 | |
| <i>Myotis sodalis</i> | USA | F (Mat) | 23 | UB | + | ... | + | ... | ... | 0 | ... | ... | ... | Kurta et al. 1996 | |
| <i>Myotis sodalis</i> | USA | F (Mat) | 54 | ? | ... | + | 0 | ... | ... | 0 | + | ... | ... | Callahan et al. 1997 | |
| <i>Myotis volans</i> | USA | F (Mat) | 41 | ? | 0 | + | 0 | ... | ... | ... | ... | 0 | 9, 14 | Ormsbee and McComb 1998 | |

| | | | | | | | | | | | | |
|---|-----------------|---------|-----|-------|-----|-----|-----|-----|-----|-----|-------|-----------------------------|
| <i>Nyctalus noctula</i> | The Netherlands | ... | 81 | H | + | ... | ... | ... | 0 | ... | 6, 15 | Boomman 2000 |
| <i>Nyctophilus bifax</i> | Australia | F (Mat) | 52 | H UB* | ... | + | ... | ... | ... | ... | ... | Lunney et al. 1995 |
| <i>Nyctophilus geoffroyi</i> | Australia | M & F | 139 | H UB | ... | + | ... | ... | + | ... | ... | Lumsden et al. 2002a, 2002b |
| <i>Nyctophilus gouldi</i> | Australia | M & F | 38 | H UB | + | ... | ... | ... | ... | ... | ... | Lunney et al. 1988 |
| <i>Vespudelus darlingtoni</i> | Australia | M & F | 10 | H | + | ... | + | ... | ... | + | ... | Herr and Klomp 1999 |
| <i>Vespudelus pumilus</i> | Australia | M & F | 91 | H | + | + | ... | ... | ... | ... | ... | Law and Anderson 2000 |
| Species that were combined in analysis: | | | | | | | | | | | | |
| <i>Chalinobius morio</i> | Australia | M & F | 23 | H UB | 0 | + | ... | ... | ... | ... | ... | Taylor and Savva 1988 |
| <i>Nyctophilus geoffroyi</i> | | | | | | | | | | | | |
| <i>Vespudelus regulus</i> | | | | | | | | | | | | |
| <i>Vespudelus darlingtoni</i> | | | | | | | | | | | | |
| <i>Lasionycteris noctirogans</i> | Canada | F | 27 | H | + | + | 0 | + | ... | ... | 4, 6 | Crampton and Barclay 1998 |
| <i>Myotis lucifugus</i> | Canada | M & F | 21 | UB H | + | + | ... | + | 0 | ... | 13 | Vonhof and Barclay 1996 |
| <i>Lasionycteris noctirogans</i> | Canada | M & F | 21 | UB H | + | + | ... | + | 0 | ... | 13 | Vonhof and Barclay 1996 |
| <i>Eptesicus fuscus</i> | | | | | | | | | | | | |
| <i>Myotis evotis</i> | | | | | | | | | | | | |
| <i>Myotis volans</i> | | | | | | | | | | | | |
| <i>Myotis lucifugus</i> | Canada | F | 8 | H UB | 0 | ... | 0 | - | 0 | ... | 5 | Grindal 1999 |
| <i>Myotis septentrionalis</i> | USA | F (Mat) | 121 | UB H | ... | + | + | 0 | ... | ... | 16 | Rabe et al. 1998 |
| <i>Myotis evotis</i> | | | | | | | | | | | | |
| <i>Myotis occultus</i> | | | | | | | | | | | | |
| <i>Myotis thysanodes</i> | | | | | | | | | | | | |

(continued on next page)

Table 1.1. (continued)

| Species | Country | Sex | No Roosts | Type of Cavity | Variables Assessed for Selection | | | | | | | References | | |
|--|---------|-----|--------------|----------------------|----------------------------------|------------------|----------------|-----------------------|-----------|---|--------------------------------|------------|----------------|-------|
| | | | | | Tree sp. | Dead/ Decayed | Large Diam. | Tall Roost tree | % Bark | Low Canopy Cover/ Clutter around Roost | Aspect of Roost Entr. | | Roost Stand | Other |
| <i>Myotis volans</i> | | | | | | | | | | | | | | |
| <i>Eptesicus fuscus</i> | | | | | | | | | | | | | | |
| <i>Antrozous pallidus</i> | | | | | | | | | | | | | | |
| <i>Myotis auricularis</i> | | | | | | | | | | | | | | |
| % of studies that showed positive selection | | | 78 | | 84 | 73 | 76 | 20 | 78 | 36 | 86 | | | |

Note. Sex = M & F if both sexes investigated or F (Mat) if roosts largely from females and young during the maternity season. Types of cavity were coded thus: CR = crevice in bark; H = hollow; UB = under bark; ? = reference does not specify if roosts are in cavities or under bark. Variables assessed for selection are as follows: + = positive selection; 0 = used at random; - = negative selection; ellipses dots = the characteristic was not measured or not compared statistically with availability. "Other" refers to other measured variables, included here only if selection was shown: 1 = trunk height and surface; 2 = % stem remaining; 3 = number of limbs; 4 = amount of rot; 5 = number of cavities per tree; 6 = cavity type and dimension; 7 = cavity microclimate; 8 = height of cavities aboveground; 9 = height of roost tree in relation to canopy; 10 = distance to nearest tree of same or greater height; 11 = distance to nearest tree as tall as roost; 12 = distance to nearest neighboring tree; 13 = distance to nearest available/cavity tree; 14 = distance from water; 15 = distance from forest edge; 16 = slope.

* Also includes a small number of foliage roosts. Note that only the November sample is included in this analysis as the May sample was largely from foliage roosts.



Figure 1.3. *A*, Maternity roost of *Nyctophilus geoffroyi* in a snag of a river red gum (*Eucalyptus camaldulensis*) in Australia; arrow denotes roost opening (photo by L. Lumsden); *B*, Douglas fir snags (*Pseudotsuga menziesii*) provide roosting cavities for a maternity colony of *Lasionycteris noctivagans* in British Columbia, Canada (photo by M. Vonhof).

species roost in cavities with large basal openings (e.g., *Desmodus rotundus* [Wilkinson 1985], *Rhinolophus hildebrandti* [Fenton and Rautenbach 1986], *Noctilio albiventris* [Fenton et al. 1993], and *Nycteris thebaica* [Aldridge et al. 1990]).

In the Neotropics, where *Saccopteryx bilineata* typically roosts in relatively accessible buttress cavities (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976) they may remain active to avoid predators (Genoud and Bonaccorso 1986). Alertness, however, does not guarantee protection from predators, as observed by Arendt (1986) when a St. Lucia boa (*Boa constrictor*) captured a *Brachyphylla cavernarum* that unsuccessfully retreated upward into a large tree cavity. That some tropical species select cavities with large openings may reflect the fact that thermal constraints generally are less than in temperate regions where well-insulated cavities should offer important thermoregulatory advantages.

A number of variables have been measured to assess selection at the level of the roost tree and in the immediate vicinity of the tree (roost stand; table 1.1). As predicted by Vonhof and Barclay (1996) and Brigham et al. (1997), most, but not all, bat species that have been studied select trees that are large in diameter, taller than surrounding trees, and relatively uncluttered by adjacent vegetation. Vonhof and Barclay (1996) and Betts (1998) suggest three benefits of such roosts: (1) increased conspicuousness and hence ease of bats finding the roost tree; (2) reduced predation risk; and (3) maintenance of an optimal microclimate. Tall trees with an open canopy generally experience elevated exposures to solar radiation that may increase the energetic benefits to bats.

In general, bats are not likely to discriminate between tree species per se but, rather, select trees based on the specific characteristics of the cavities associated with a particular species (Sedgeley and O'Donnell 1999b). Notwithstanding, the species of tree was an important variable in several studies (e.g., Boonman 2000; Sedgeley and O'Donnell 1999b; Vonhof 1996). This may reflect the fact that some species provide better insulation than others. Using infrared thermal imaging, Rieger (1996) showed that beech trees (*Fagus sylvatica*) used as roosts by *Myotis daubentonii* remained warmer during the day and night than other tree species. The size of the tree appears to influence the microclimate in the cavity roost, and thus large trees are often selected as roosts (table 1.1). Slender trunks offer less insulation against extreme temperatures than do large ones (Alder 1994; Gellman and Zielinski 1996; Sluiter et al. 1973).

The amount of bark present on a tree also appears to influence the internal microclimate of the roost, with thicker bark providing the greatest insulation (Nicolai 1986). Dead trees are generally less well insulated than live ones owing to a lack of bark and a lower water content (Maeda 1974). Dead trees often contain more cavities than do live ones; and many of the studies summarized in table 1.1 noted that most roost trees were dead, although this varied among tree species and areas. Some trees, such as conifers, generally do not form cav-

ities until they begin to decay, whereas species such as eucalypts form cavities when they are alive and healthy. Thus, in the case of eucalypts, although dead trees are not categorically avoided, certain bat species roost primarily in live trees (Lumsden et al. 2002b).

Not only do bats select particular trees as roost sites, they may also select particular parts of the forest in which to roost. Several studies have compared variables within the roost stand to other areas of the forest, with the majority showing selection for one or more of these variables (table 1.1). For example, in North America, areas around roosts of *Lasionycteris noctivagans* had more roost-type trees, a lower canopy cover, shorter understory, and less vegetative cover than did random plots (Campbell et al. 1996). In southeastern Australia, *Nyctophilus geoffroyi* and *Chalinolobus gouldii* selected areas of forest that contained high densities of their respective preferred roost trees (Lumsden et al. 2002a).

Selection can also occur at the landscape scale with roosts of some species being closer to water (Boonman 2000; Ormsbee and McComb 1998), closer to the forest edge (Boonman 2000; Sedgely and O'Donnell 1999b), or associated with other landscape elements (Lumsden et al. 2002a). In the Netherlands, Boonman (2000) found that *Nyctalus noctula* and *Myotis daubentonii* roosted closer to the edge of forested areas than was expected from randomly chosen cavities and suggested that these trees may experience greater exposure to solar radiation, resulting in warmer cavities. Moreover, bats that foraged outside the forested area were able to reduce the time and energy spent flying through the forest.

How dependent bats are on certain characteristics of roosts can be explored by determining ways that a single species reacts to the availability of roost resources. Dependence on certain characteristics would be indicated if some variables were consistently selected in different environments. If variables were used selectively it might indicate that the bats were more flexible in their use of these characteristics. Selection of roosts by *Vespadelus pumilus* was investigated at two sites in eastern Australia with different disturbance histories: old-growth and regenerating forest (Law and Anderson 2000). At sites where numerous large, old trees were available, bats selected those in preference to smaller trees. In the regenerating forest, the remaining dead trees and large trees in an adjacent area were preferentially used as roosts. In addition, understory trees, such as blackwood (*Acacia melanoxylon*), which forms cavities at a smaller tree diameter were used as roost sites. Although these understory trees were present in the old-growth forest, they were not used as roosts when more suitable cavities were available.

Trees selected by bats may not only vary regionally and by area but also intraspecifically by sex and season. Roosts selected by maternity colonies may be different from those used during the nonbreeding period. Adult males and nonreproductive females tend to select cooler roost sites at temperatures that

allow them to enter torpor, thus minimizing energy expenditure (Hamilton and Barclay 1994; Kerth et al. 2000). During the nonbreeding season in southeastern Australia, both males and females of *Nyctophilus geoffroyi* occupy a wide range of structures, including buildings, under bark, and within cavities in relatively small trees. Within the same area, females selected large dead trees during the maternity period that were more than twice the diameter of those selected at other times (Lumsden et al. 2002b). The location of a roost within a given landscape may also vary between maternity and nonbreeding periods. Maternity roosts of *Chalinolobus tuberculatus* (Sedgeley and O'Donnell 1999b) and *N. geoffroyi* (Lumsden et al. 2002a) were located closer to the forest edge than were nonbreeding roosts.

Several studies have investigated roost use during the breeding season, but they have seldom separated data by reproductive status or age (e.g., Brigham et al. 1997; Callahan et al. 1997; Kalcounis and Brigham 1998; Ormsbee and McComb 1998). While it can be expected that pregnant and lactating females both would require a warm microclimate to enhance the rapid growth of the fetus and young, distinguishing use of roosts between these groups can reveal differences in their requirements at these times. For example, Kerth et al. (2000) found that pregnant females of *Myotis bechsteinii* preferred significantly cooler roosts than did lactating females.

Are Tree Cavities Limited Resources for Bats?

Long-term studies on roost selection and detailed information on the availability of roosts are needed to determine whether roosts are limiting to bats. Because many species of bats show strong selection for particular types of roosts, tree cavities may be limiting depending on their relative abundance (Crampton and Barclay 1998). From observations on cavity and tree selection by *Chalinolobus tuberculatus*, Sedgeley and O'Donnell (1999a) determined that only 1.3% of trees contained cavities that were suitable as roosts. Based on the density of suitable trees, they calculated that more than 3,000 potential roost trees were present in their study area. Although colonies of *C. tuberculatus* shifted roost sites almost every day and rarely reused roosts (O'Donnell 2000), they concluded that roosts were relatively abundant (Sedgeley and O'Donnell 1999a).

Little information is available on competition between different bat species and whether they partition available roost resources. Several studies have compared different species in areas where they may have access to the same tree cavities. In some situations, no differences in roost characteristics were found between sympatric species (Crampton and Barclay 1998; Vonhof 1996), whereas significant differences were found in other situations, which had larger sample sizes (Boonman 2000; Lumsden et al. 2002b). Perkins (1996) suggested that local distribution, species composition, and population size of bats in managed forests in North America were related to interspecific com-

petition for limited roost sites. There is also evidence that other vertebrate and invertebrate species compete for roosts and, at times, may evict bats from tree cavities (e.g., Maeda 1974; Mason et al. 1972; Sedgely and O'Donnell 1999a; Start 1998; Tidemann and Flavel 1987).

Spaces beneath Exfoliating Bark

Spaces that form beneath exfoliating bark (fig. 1.4) also provide alternate roosting sites to cavities in branches and tree trunks for some species. In North America, crevices beneath exfoliating bark are used predominantly by *Myotis* spp. (e.g., *M. californicus* [Brigham et al. 1997], *M. evotis* [Vonhof and Barclay 1996, 1997], *M. septentrionalis* [Foster and Kurta 1999], *M. sodalis* [Humphrey et al. 1977; Kurta et al. 1993, 1996], and *M. volans* [Vonhof and Barclay 1996]; fig. 1.4A) and by *Lasionycteris noctivagans* (Mattson et al. 1996; Vonhof and Barclay 1996). In Australia, spaces beneath exfoliating bark are predominantly used as roosts by *Nyctophilus* spp. (e.g., *N. arnhemensis* [Churchill 1998], *N. bifax* [Lunney et al. 1995], *N. geoffroyi* [Hosken 1996; Lumsden et al. 2002b; Taylor and Savva 1988], *N. gouldi* [Lunney et al. 1988; Tidemann and Flavel 1987], and *N. timoriensis* [Churchill 1998]). In the Neotropics, spaces beneath

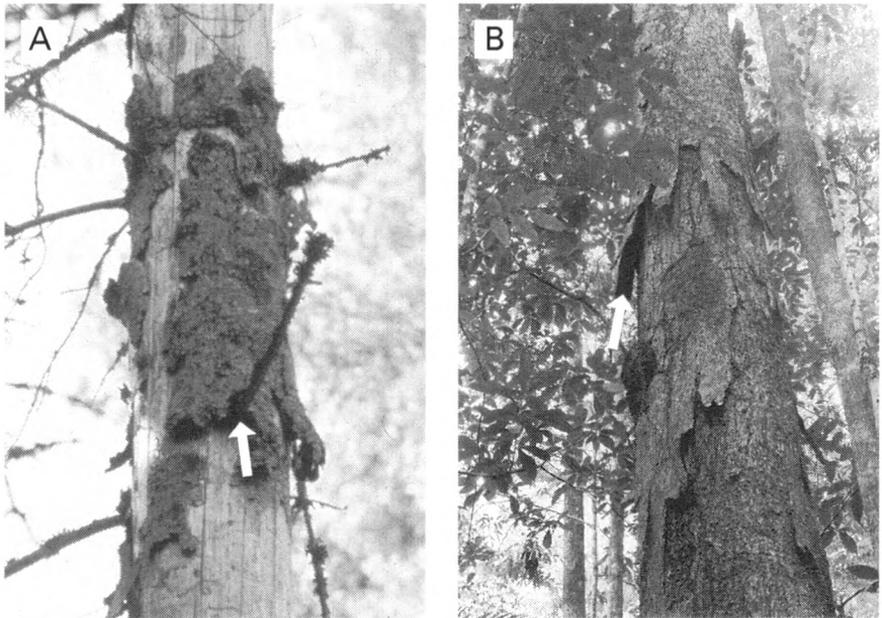


Figure 1.4. A, Exfoliating bark (arrow) on a Douglas fir snag (*Pseudotsuga menziesii*) used as a day roost by *Myotis volans* in British Columbia (photo by M. Vonhof); B, exfoliating bark (arrow) on a living grignon tree (*Ocotea rubra*) used as day roosts by *Artibeus obscurus* in French Guiana (from Simmons and Voss 1998; photo by R. Voss).

exfoliating bark are used as day roosts by *Artibeus obscurus* (Simmons and Voss 1998; fig. 1.4B). To our knowledge, no species are known to roost exclusively beneath exfoliating bark.

Exfoliating bark is present on some live trees but is more common on dead trees. Roosts beneath exfoliating bark are generally more ephemeral than tree cavities, with some lasting only a few months, although others may persist for several years (Humphrey et al. 1977). For some North American tree species (e.g., shagbark hickory [*Carya ovata*] and grignon [*Ocoetea rubra*]), exfoliating bark typically persists for the life of the tree and, thus, potentially provides more roost permanency than does bark on dead trees. One of the risks of roosting beneath exfoliating bark, however, is illustrated by an observation made by Kurta (1995), who witnessed a strip of bark falling into water from a dead tree with a torpid male *Eptesicus fuscus* still attached.

Roost sites beneath exfoliating bark may have different thermal properties than tree cavities and usually are climatically less stable (Crampton and Barclay 1998). The roost microclimate may be influenced by the insulative properties of the bark (Nicolai 1986), the size of the tree, and the amount of solar exposure it receives (Kurta et al. 1996; Vonhof and Barclay 1997). Where roost sites have been compared to available spaces beneath exfoliating bark, bats generally select sites that are thermally stable (Kurta et al. 1996; Vonhof and Barclay 1997).

Little empirical data are available on predation rates on bats that occupy exfoliating bark roosts. Wunder and Carey (1996) suggested that bats that roost beneath exfoliating bark may be more susceptible to predation than those that roost in tree cavities. However, bats are more likely to escape from beneath exfoliating bark if there are alternate routes of exit. Further investigations are needed to determine if predation is an important variable in the selection of roosts beneath exfoliating bark. Despite the apparent disadvantages of roosting in ephemeral sites, including suboptimal microclimates and, perhaps, increased risks of predation, a number of species actively select roosts beneath exfoliating bark, even in situations where tree cavities are abundant (e.g., Foster and Kurta 1999; Lumsden et al. 2002b). This suggests that, for some species, there are benefits to roosting in these situations or that at least the occupants incur no additional costs.

Interspecific competition for roosts by bats may be less for those that roost beneath exfoliating bark than those that roost in tree cavities. Only a small percentage of bat species use roosts beneath exfoliating bark, despite the fact that these roosts may be more abundant in some situations. In a study conducted in a wetland area of North America, with numerous dead trees, two species of *Myotis* that roosted beneath exfoliating bark were examined, with characteristics of roost trees compared to evaluate possible competition between the two species (Foster and Kurta 1999; Kurta et al. 1993, 1996). *Myotis sodalis* roosted exclusively beneath exfoliating bark on dead green ash (*Fraxinus* sp.) trees

with low canopy cover. Although *M. septentrionalis* roosts had similar characteristics, this species exhibited a broader roosting niche. A greater variety of cavity types, tree species, decay stages, and amount of canopy cover was used by *M. septentrionalis*. Where roosts were abundant, there was little overlap in the actual trees that were used by these two species, although Foster and Kurta (1999) suggested that interspecific interactions may exist in areas with lower availability. In addition to competition between bat species, there may be competition with other vertebrates and invertebrates (e.g., Kurta and Foster 1995).

Rather than concealing themselves beneath exfoliating bark, some species roost in narrow crevices between heavily furrowed folds of bark or in the narrow spaces formed between two touching tree trunks. In Canada, *L. noctivagans* has been observed roosting in such crevices during their northward migration (Barclay et al. 1988). The bats were well concealed, as they were wedged into the crevices with both their dorsal and ventral surfaces in contact with the substrate. These roosts provided shelter from rain, wind, and possibly predators and were cool enough to allow bats to enter torpor. Despite appearing to be opportunistic in choice of roost sites, individual *L. noctivagans* selected older willow trees with large circumferences as they provided more crevices than did younger trees.

Exposed Boles

A few species, most notably members of the Emballonuridae, roost in relatively exposed areas on the sides of tree boles, beneath fallen trees, and on branches and similar structures (bridges) suspended over water (Bradbury 1977b; Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976; Goodwin and Greenhall 1961; Simmons and Voss 1998). Emballonurids often assume stereotypical postures, but are largely inconspicuous to observers because of their cryptic coloration and mottled pelage. For example, *Rhynchonycteris naso* and *Saccopteryx leptura* commonly roost on the open boles of trees in small harem groups, often spaced in a vertical row, one above the other (fig. 1.5). Colonies of *R. naso* range from three to 45 individuals, whereas those of *S. leptura* are generally smaller, ranging from two to nine individuals. Colonies of both species use several alternative roosts, between which the entire group may move as a unit (Bradbury and Vehrencamp 1976). Other Neotropical emballonurids, such as *Centronycteris maximiliani*, *Cormura brevirostris*, *Peropteryx kappleri*, *P. macrotis*, and *P. leucoptera*, are known to roost in small groups beneath trunks and buttresses of fallen trees (LaVal 1977; Simmons and Voss 1998).

Cavities in Bird Nests

A limited number of bat species (primarily members of the Vespertilionidae, Molossidae, and Emballonuridae) use abandoned bird nests as roost sites (Dalquest and Walton 1970; Schulz 1997). For some bats, bird nests constructed



Figure 1.5. Small harem group of *Saccopteryx bilineata* roosting on the exposed bole of a lowland rainforest tree in Panama (photo by M. D. Tuttle). The bats are cryptic as viewed against the lichen-covered bark.

from plant material serve as primary roost resources, but, for others, they are used only opportunistically. Schulz (1997) reviewed use of abandoned bird nests by bats and found that three types of nests were primarily used as roosts: hanging nests; open cup-shaped nests; and enclosed mud nests (some of which include plant material mixed with soil).

In tropical areas of Africa, Asia, and Australia, members of the genera *Kerivoula* and *Murina* commonly roost in suspended bird nests (Schulz 1997). These nests are dome-shaped structures constructed from long pieces of vegetation such as bark, rootlets, leaves, ferns, and palm fibers (fig. 1.6). Schulz (2000) suggested that roosts located in suspended bird nests may be less sus-



Figure 1.6. Suspended bird nest used as a day roost by *Kerivoula papuensis* in Australia, with a modified opening at the base (photo by C. Taylor).

ceptible to predation from terrestrial, climbing, and aerial predators than other types of roosts.

In Australia, the majority of *Kerivoula papuensis* roosts have been found in the abandoned hanging nests of brown gerygones (*Gerygone mouki*) and yellow-throated scrub wrens (*Sericornis citreogularis* [Schulz 1995, 2000]). These roosts were mostly occupied by single males or females, with a maximum group size of eight individuals. No breeding activity of bats was recorded in these nests, suggesting that they may not provide the required roost microclimate for raising young (Schulz 2000). When birds originally construct these nests they have a side entrance. However, each nest used as a roost by *K. papuensis* contained a hole in the base (fig. 1.6). This led Schulz (2000) to suggest that bats modify these nests to make them more suitable as roosting sites.

This modification allows an unobstructed view of the ground below and a quick exit route in response to disturbance. He suggested that such modifications were similar to those made by tent-making bats observed in some Neotropical and Palearctic species (Kunz et al. 1994). In particular, they resembled the stem tents made by *Cynopterus sphinx* in vines (Balasingh et al. 1995) and flower/fruit clusters (Bhat and Kunz 1995; Storz et al. 2000a, 2000b).

Murina florium has also been recorded roosting in suspended bird nests in Australia, with seven of the 11 roosts observed in nests of the yellow-throated scrub wren and the fern wren (*Oreoscopus gutturalis* [Schulz and Hannah 1998]). The scrub wren nests, also used by *K. papuensis*, all included a basal hole modification; however, the nests of the fern wren, which were not used by *K. papuensis*, were unmodified.

In Africa, *Kerivoula argentata* and *K. lanosa* roost alone, or in small groups of up to six individuals, in the disused hanging nests of masked and spectacled weaverbirds (*Ploceus velatus* and *P. ocularis*) and scarlet-chested sunbirds (*Nectarinia senegalensis* [Skinner and Smithers 1990]). In India, *Kerivoula picta* roost in nests of the baya weaverbird (*Ploceus philippinus* [Sharma 1986]). All roosts of *K. picta* were in incomplete nests, with no bats found in the large number of completed nests that were examined.

In contrast to hanging nests, mud nests are predominantly made from soil but may include plant parts. Generally, these nests are used opportunistically by bat species that typically roost in other structures. Two basic forms of mud nests include open-cup structures and enclosed bottle-shaped structures, which are made by swallows and swiftlets. These are constructed in both natural and artificial situations, such as along stream banks, under rock overhangs, under bridges, and in road culverts. In the southwestern United States, *Myotis velifer* has been observed roosting throughout the year in open-cup nests of barn swallows (*Hirundo rustica*) and cave swallows (*Petrochelidon fulva* [Jackson et al. 1982; Pitts and Scharninghausen 1986; Ritzi et al. 1998]) and enclosed, bottle-shaped nests constructed by cliff swallows (*P. pyrrhonota* [Buchanan 1958; Manning et al. 1987; Pitts and Scharninghausen 1986]). *Tadarida brasiliensis* also roosts in the bottle-shaped nests constructed by cliff swallows, although it appears to use these roosts more opportunistically (Buchanan 1958; Pitts and Scharninghausen 1986).

In Australia, Schulz (1998) surveyed 5,175 bottle-shaped mud nests constructed by fairy martins (*Hirundo ariel*) and located 204 bats representing eight species (all vespertilionids) at a frequency of 3.9 bats per 100 nests. *Myotis macropus*/*M. moluccarum* and *Vespardelus troughtoni* were the most frequently recorded species, making up 83% of the individuals present. Group size ranged from one to 21 individuals.

Cavities in Bamboo Culm

Roosting within the culm of bamboo has been reported primarily for four species of vespertilionids from Southeast Asia: *Eudiscopus denticulus*, *Glischropus tylopus*, *Tylonycteris pachypus*, and *T. robustula* (Kock and Kovac 2000; Kofron 1994; Medway and Marshall 1970). Each is a small species (3.5–10 g) with thickened thumb pads (see fig. 1.15) that assist in gripping the smooth inner surface of the internode cavities of bamboo culm. *Tylonycteris pachypus*, *T. robustula*, and *E. denticulus* have extremely flattened skulls, an adaptation that facilitates access to roosts with small openings. Anecdotal records of other Asian bats roosting in bamboo culm include *Glischropus javanus* (Chasen 1939), *Kerivoula papillosa* (Bates and Harrison 1997), *Myotis hasseltii* (Lekagul and McNeely 1977), *Pipistrellus mimus* (Lekagul and McNeely 1977), and *P. paterculus* (Bates and Harrison 1997).

In their study on roosting habits of *T. pachypus* and *T. robustula* in Malaysia, Medway and Marshall (1970, 1972) located 448 roosting groups in the internodes of standing, green culms of the bamboo *Gigantochloa scortechninii*. Openings to the roosting chambers were all narrow vertical slits formed by the pupation chambers and emergence holes of the leaf beetle *Lasiochila goryi*. Although there was broad overlap in physical dimensions of roosts used by both bat species, there were significant differences in diameter of the culm and the length and width of the opening. The smaller *T. pachypus* was able to use roosts with narrower openings, from which *T. robustula* was excluded. Both species showed selection in the types of roosts used compared to their availability in the area. Bats selected roosts that had openings located in the lower half of the cavity. Although 28% of roosts were used by both species on different occasions, only once were the two species found roosting together. Group sizes ranged from one to 20 individuals for *T. pachypus* (average 4.9) and from one to 32 for *T. robustula* (average 3.5). Maternity groups sometimes consisted entirely of females, but many contained a single adult male (Medway and Marshall 1970). The number of potential roosts in the study area greatly exceeded the number used by bats, and individuals frequently changed roost sites on a daily basis.

In Thailand, *Eudiscopus denticulus* also roosts in small groups in internode cavities of the bamboo *Gigantochloa* sp. (Kock and Kovac 2000). Bats roost in the upper part of the cavity, apparently clinging to the inner surface with the adhesive disks on their feet and wrists. Kofron (1994) observed four groups of *Glischropus tylopus* roosting in dead bamboo culms in Brunei, northwest Borneo. Each group formed a social unit, consisting primarily of adult females and young. All roosts were approximately 2 m above the ground in bamboo culms that were 4.6–4.8 cm in diameter, and with openings less than 2.5 cm wide. Openings were either made or modified by beetles or by a gnawing rodent.

Foliage

Trees and understory plants provide roosting opportunities for a wide range of species, many of which are frugivorous or nectarivorous. Old World fruit bats, particularly members of the genus *Pteropus*, often roost on exposed branches within the tree canopy (fig. 1.7A; see review in Pierson and Rainey 1992). Most species are strongly colonial, although some are solitary or roost in small family groups. In large colonies, roost sites (camps) may include a number of adjacent trees (Pierson and Rainey 1992; Ratcliffe 1932). *Pteropus* spp. typically show long-term fidelity to traditional roost sites, particularly those that remain undisturbed (Pierson and Rainey 1992; Ratcliffe 1932; Wiles 1987). Several camps in Australia have been used repeatedly for more than 80 yr (Lunney and Moon 1997).

Old World megachiropterans roost in a wide range of habitats. *Pteropus vampyrus*, one of the largest megachiropterans, exemplifies this variation. In Malaysia, *P. vampyrus* has been recorded in lowland coastal areas, roosting in rainforest, mangroves, and coconut groves (Davis 1962; Goodwin 1979; Lim 1966; Payne et al. 1985). In Indonesia, on the island of Pulau Rambut, this bat roosts in kedoya (*Amoora aphanamixis*) and kepuh trees (*Sterculia foetida* [Wiriosoepartha et al. 1986]) and, on Sumatra, in cultivated kapok trees (*Ceiba pentandra* [Davison 1992]).

The specific criteria that *Pteropus* spp. use to select roost sites are poorly understood. However, canopy structure, physical features of the surrounding area, and location with respect to feeding habitat appear to be important variables. Ratcliffe (1932) specified seclusion and protection from the sun. Richards (1990a) evaluated 17 variables to characterize roost sites and roost environments of *P. conspicillatus* and found that distance to nearest rainforest accounted for 75.1% of the sample variance. Pierson and Rainey (1992) suggested that protection from strong winds and access to updrafts were important criteria for roost selection. Among six variables evaluated in a multivariate model, canopy height and height of emergent trees were the most important variables in explaining roosting sites used by *P. alecto* and *P. scapularis* (Tidemann et al. 1999).

In the relatively intact forests of tropical Australia, the presence of water appears to be a major factor influencing roost selection by *P. alecto*, with roosts typically located in riparian habitats, especially during the dry season (Loughland 1998; Tidemann et al. 1999). When ambient temperatures increase during the rainy season, roosts are mostly located in rainforest habitat, with smaller numbers in mangrove and bamboo forests. In rainforest habitat, *P. alecto* roosts in the shade beneath the dense forest canopy, but during the dry season individuals that roost in the deciduous bamboo forest are exposed directly to sunlight (Palmer and Woinarski 1999). Tidemann et al. (1999) suggested that initial colonization of roosts by *P. alecto* was random when roost vegetation is



Figure 1.7. A, Colony of *Pteropus poliocephalus* roosting in a partially defoliated emergent tree in Australia; B, small group of *P. poliocephalus* roosting on defoliated branches (photos by P. Eby); C, mother and young *Lasius cinereus* roosting on a branch of a spruce tree in North America (photo by M. D. Tuttle); D, three young *Lasius borealis* roosting on a branch of a maple tree in North America (photo by T. H. Kunz).

not limiting, but factors such as human predation, cyclones, and fires may influence their persistence.

For many island species of the Pteropodidae, and to a lesser extent populations in mainland areas, the influence of external forces such as habitat loss and hunting pressure may mask the influence of habitat preferences on roost location in pteropodids. For example, existing roosts of both *P. livingstonii* in the Comores Islands and *P. samoensis* in American Samoa are concentrated in montane forests on steep slopes (Brooke et al. 2000; Craig et al. 1994; Reason and Trehwella 1994). These current roosting habits may reflect avoidance of increased hunting pressure in highly fragmented lowland forests more than a preference for steep montane vegetation.

The emergent trees used by highly gregarious species, such as *Pteropus* and *Eidolon*, are often defoliated by their occupants (Banack 1996; Bonaccorso 1998; Brooke et al. 2000; Flannery 1995; Goodwin 1979; Jones 1972; Kitchener et al. 1990; Nelson 1965; Okon 1974; fig. 1.7B). Bonaccorso (1998) suggested that defoliated branches in roost trees might facilitate visual observations of social partners, rivals, or approaching aerial predators. Reduced foliage cover also exposes roosting animals to sunlight, wind, and rain. When exposed to the hot sun during the day, individuals often cool themselves by flapping their wings, licking their chest and wings, and panting (Nelson 1965; Neuweiler 1969; Ochoa and Kunz 1999). In cool weather or during heavy rain, large pteropodids almost completely wrap themselves with their wings (Lekagul and McNeely 1977; Ochoa and Kunz 1999).

Some species of small, foliage-roosting megachiropterans are associated with specific types of plants. For example, in peninsular Malaysia, the day roosts of *Cynopterus horsfieldi* appear associated with the availability of the epiphytic bird's nest fern (*Asplenium nidus*). Leaf shelters are formed when older, dry leaves of this fern droop downward creating a skirt of dead leaves, beneath which *C. horsfieldi* roosts (Tan et al. 1997).

Little is known about factors that influence the distribution and abundance of foliage-roosting microchiropterans, although availability and dispersion of plants and characteristics of foliage appear important (Kunz 1982, 1996; Morrison 1980). The leaved canopies of both temperate and tropical trees provide roost sites for a number of species. The roosting habits of foliage-roosting microchiropterans seem to reflect the structure and composition of local forest communities (Constantine 1958, 1959, 1966; Menzel et al. 1998; Morrison 1980; Schulz and Hannah 1998; Simmons and Voss 1998).

Foliage-roosting microchiropterans roost in a range of situations, including epiphytes, beneath unmodified live and dead leaves and in the foliage of tree ferns. In northern Australia, *Murina florium* roosts in vertically suspended clusters of dead leaves (Schulz and Hannah 1998). These roosts are typically located in the rainforest understory close to breaks in the forest canopy. Most

roosts are occupied by singletons, however, a group of 12 bats was observed in the curled base of a suspended dead palm leaf (*Archontophoenix* sp. [Schulz and Hannah 1998]).

Members of the vespertilionid genus *Lasiurus* typically roost among leaves in densely foliated tree canopies (Constantine 1958, 1966; Hutchinson and Lacki 2000; Kurta and Lehr 1995; Mager and Nelson 2001; McClure 1942; Menzel et al. 1998; Saugey et al. 1998; Shump and Shump 1982; Webster et al. 1980). Roosts have been recorded from a range of both conifers (fig. 1.7C) and hardwoods (fig. 1.7D) and usually consist of individuals or small family groups.

Within their roosts, lasiurines typically cling to leaf petioles or the tips of small branches (Menzel et al. 1998). Constantine (1966) identified three types of shelters used by *Lasiurus borealis* and *L. cinereus* in agricultural areas in the midwestern United States (Iowa): an inverted bowl-shaped canopy made of tree branches infiltrated with grapevines that provided structural rigidity; a dense, leafy overhang of new succulent growth; and a dense tuft of older, non-succulent leaves.

The roosting habits of *L. borealis* and *L. seminolus* in the southeastern United States (Georgia) were quantitatively investigated by Menzel et al. (1998) to determine which variables influenced roost site selection and how this varied among the two species. Roost trees of both species were significantly taller and had larger diameters than did surrounding trees. *Lasiurus borealis* roosted predominantly in hardwoods, which tended to have smaller diameters than the conifers used by *L. seminolus*. Moreover, the understory and canopy vegetation in the vicinity of *L. borealis* roosts showed a greater diversity than those occupied by *L. seminolus*. Mager and Nelson (2001) quantified roost variables for *L. borealis* and found that this species showed a preference for large trees, nearly 80% of which exceeded 30 cm in diameter. They also suggested, as did Constantine (1966) and Menzel et al. (1998), that canopies of more mature trees provided a high degree of protective cover for foliage-roosting bats.

The roosting height of *L. borealis* within a tree may vary geographically and between tree species (Constantine 1958, 1966; McClure 1942; Mager and Nelson 2001; Menzel et al. 1998), although roosting height may reflect methodological differences among studies. Constantine (1966), who based his research on direct observations, found that solitary *L. borealis* generally roosted relatively low in the tree, whereas small family groups were more often observed on branches higher in the canopy. He suggested that selection of high roosts by adult females with young may provide greater concealment from terrestrial predators, avoid disturbances from activity on the ground that might dislodge young, and permit young a greater opportunity to conduct initial flights (Constantine 1966). Using radiotelemetry, Mager and Nelson (2001) reported that most roosts of *L. borealis* were more than 5 m above the ground and

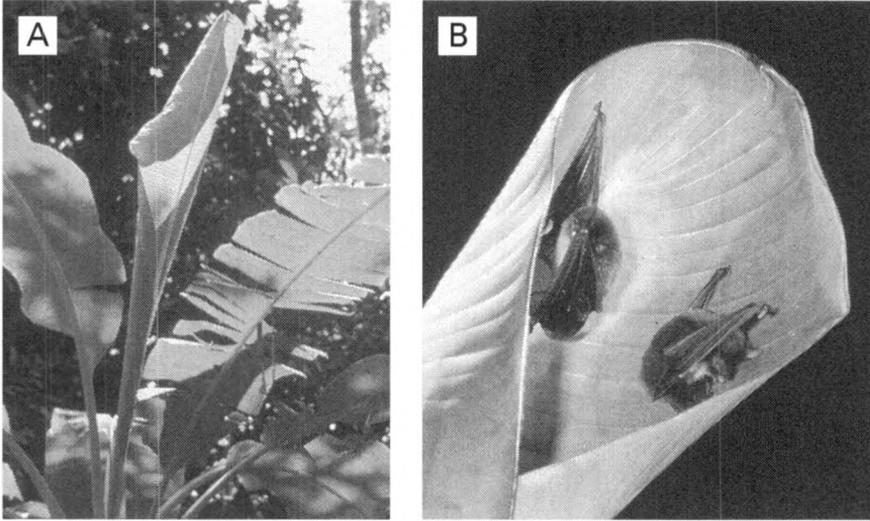


Figure 1.8. A, Furled banana leaf (*Musa* sp.) used as a day roost by *Thyroptera tricolor*; B, two *T. tricolor* clinging to the inner, moist surface near the opening of a furled banana leaf used as a day roost (photos by M. D. Tuttle).

located within 1.5 m of the edge of the crown, with few branches nearby that would obstruct flight.

Furled Leaves

Some foliage-roosting microchiropterans in the Old and New World occupy cylindrical spaces formed by furled leaves (fig. 1.8). Species that utilize these roosts have highly specialized foot and thumb pads that enable them to cling to the smooth upper surfaces of leaves (*Myotis bocagei* [Baagøe 1978; Brosset 1976], *M. mystacinus* [Medway 1983], *Myzopoda aurita* [Findley and Wilson 1974], *Pipistrellus nanus* [Happold and Happold 1990, 1996; LaVal and LaVal 1977], *Thyroptera discifera* and *T. tricolor* [Findley and Wilson 1974]). These morphological specializations may make it impossible for them to cling to rough surfaces, but the typical head-up posture inside a furled leaf may be ideal for detecting potential predators (Findley and Wilson 1974).

The growth form of wild banana leaves (*Musa* spp. and *Strelitzia* spp.) and similar-shaped leaves (*Heliconia* spp.) and the geographic distribution of these species may have an important effect on the local distribution of bats that roost in furled leaves. The Neotropical disk-winged bats, *T. discifera* and *T. tricolor* routinely occupy furled leaves of *Heliconia* spp. and *Calathea* spp., both within the forest and in forest clearings (Findley and Wilson 1974; Goodwin and Greenhall 1961; Wimsatt and Villa-R 1970). Occupied leaves are predomi-

nantly found in areas that are shaded for part of the day. Findley and Wilson (1974) found that most *T. tricolor* roosts were in furled leaves with the diameter of the opening between 50 and 100 mm. In Natal, South Africa, *Pipistrellus nanus* typically roosts in furled leaves of domesticated banana plants (*Musa* spp.), but may have used leaves of wild banana (*Strelitzia nicolai*) before domesticated varieties were introduced (LaVal and LaVal 1977).

Furled leaves are highly ephemeral roosts, with the leaves typically opening (unfurling) in 1–3 d. This necessitates the frequent movement to nearby furled leaves (Brosset 1976; Findley and Wilson 1974; Happold and Happold 1990, 1996; LaVal and LaVal 1977). Despite being from different biogeographic regions and phylogenetic groups, the behavior of different species that roost in furled leaves is remarkably similar, suggesting behavioral convergence in these distantly related taxa.

Furled leaves are typically occupied by singletons or small groups of bats. In Malaysia, colony sizes of *Myotis mystacinus* range from one to eight individuals (Medway 1983), whereas in Costa Rica, groups of *T. tricolor* range from one to nine, with each roosting group occupying an exclusive area (Findley and Wilson 1974). In Malawi (east-central Africa) males of *P. nanus* often roost alone or in small multifemale groups, with exclusive maternity colonies formed during the breeding season (Happold and Happold 1990).

Tents

Diversity of Bats That Roost in "Tents"

Among the 19 species of bats known to roost in or construct tents (table 1.2), 15 are members of the New World family Phyllostomidae, three are members of the Old World family Pteropodidae, and one is a member of the Vespertilionidae (Kunz et al. 1994; Hodgkison et al., in press). One direct observation (Balasingh et al. 1995) and several indirect observations support the hypothesis that some tents are indeed made by bats (Brooke 1990; Chapman 1932; Choe and Timm 1985; Kunz et al. 1994; Kunz and McCracken 1996; Tan et al. 1997; Timm 1987). Notwithstanding, it remains unclear whether all bat species that have been observed roosting in tents are responsible for their construction.

Tent-making and tent-roosting behaviors are restricted to relatively small-bodied species because larger bats (especially the larger megachiropterans) could not be supported or adequately concealed by altered leaves, or they would not be sufficiently agile to fly in the physically cluttered environments often associated with tents in the forest understory (Kunz et al. 1994). Among the 15 species of Neotropical bats known to roost in or thought to construct tents, body masses range from 8 to 50 g, and each feeds largely on small fruits, although some also may feed on nectar, pollen, leaves, and insects (Gardner 1977). In the Paleotropics, the three megachiropterans species (*Balionycteris*

Table 1.2. Biogeographic and phylogenetic patterns in tent architecture and tent-roosting/tent-making behavior in Paleotropical and Neotropical bats

| Biogeographic Region and Suborder/Family/Subfamily/Species | Architectural Style of Tent | | | | | | | |
|--|-----------------------------|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| Paleotropics | X | X | | X | | | | X |
| Megachiroptera: | | | | | | | | |
| Pteropodidae: | | | | | | | | |
| Pteropodinae: | | | | | | | | |
| <i>Balionycteris maculata</i> | | | | | | | | X |
| Cynopterus: | | | | | | | | |
| <i>C. brachyotis</i> | X | X | | X | | | | X |
| <i>C. sphinx</i> | | X | | | | | | X |
| Microchiroptera: | | | | | | | | |
| Vespertilionidae: | | | | | | | | |
| <i>Scotophilus kuhlii</i> | X | | | | | | | |
| Neotropics | X | X | X | X | X | X | X | |
| Microchiroptera: | | | | | | | | |
| Phyllostomidae: | | | | | | | | |
| Carollinae: | | | | | | | | |
| <i>Rhinophylla pumilio</i> | | | X | X | | | | |
| Stenodermatinae: | | | | | | | | |
| Artibeus: | | | | | | | | |
| <i>A. anderseni</i> | | | | | | | | X |
| <i>A. cinereus</i> | | X | | X | X | X | X | |
| <i>A. glaucus</i> | | | | | X | | | |
| <i>A. gnomus</i> | | | | X | | | | |
| <i>A. jamaicensis</i> | | X | X | X | | | | |
| <i>A. phaeotis</i> | | | | X | X | | X | |
| <i>A. toltecus</i> | | | | X | | | | |
| <i>A. watsoni</i> | | X | X | X | X | | X | |
| <i>Ectophylla alba</i> | | | | X | | | X | |
| <i>Mesophylla macconnelli</i> | | | | X | X | X | | |
| Urodema: | | | | | | | | |
| <i>U. bilobatum</i> | | X | X | X | X | X | X | X |
| <i>U. magnirostrum</i> | | | X | | | | | |
| Vampyressa: | | | | | | | | |
| <i>V. nymphaea</i> | | | X | | | | | |
| <i>V. pusilla</i> | | | | X | | | | |

Note. Architectural styles of tents are as follows: 1 = conical; 2 = palmate umbrella; 3 = pinnate; 4 = apical; 5 = bifid; 6 = pyramid; 7 = boat; 8 = stem (after Kunz et al., 1994).

maculata, *Cynopterus brachyotis* and *C. sphinx*) that occupy tents range in body mass from approximately 18 to 65 g (Hodgkison et al., in press; T. H. Kunz, personal observation; Storz et al. 2001) and feed almost exclusively on understory fruits, flowers, nectar, and leaves (Bhat 1994; Boon and Corlett 1989; Elangovan et al. 1999, 2000; Hodgkison 2002; Marshall 1985; Ruby et al. 2000; Tan et al. 1998).

In the only published report of a tent-roosting vespertilionid, Rickart et al. (1989) found singletons and small groups of *Scotophilus kuhlii* beneath modified and collapsed fronds of *Livistona rotundifolia* in the Philippines. Al-

though roosting groups of this bat were common, it is unclear whether this species constructed these tents or parasitized existing ones that were made by other species (Kunz et al. 1994). *Cynopterus brachyotis* and *C. sphinx* are sympatric with *S. kuhlii* and both species are known to roost in or construct umbrella tents similar to those occupied by *S. kuhlii*.

Tent-Roost Architecture

The eight architectural styles of tents (table 1.2; fig. 1.9) generally reflect the size and shape of the leaf and the number of veins and/or plications chewed or the plant part that is modified (e.g., leaves, stems, root masses). Kunz et al. (1994) suggested that the resulting architectural style of bat tents in leaves is more a consequence of leaf shape than of the behavioral repertoire of the bat constructing the tent. An exception to this may be the tents of *Ectophylla alba*, all of which are constructed from one basic leaf shape (oblong) modified into a characteristic boat-shaped structure (Brooke 1990).

Existing classifications of tent architecture (table 1.2) offer a convenient way to organize the diversity of plant taxa used by bats in tent construction (table 1.3). Although future observations will no doubt require modification of this scheme, it provides a useful framework for comparing the architectural styles of tents constructed by species that are from different biogeographic regions and that have different evolutionary histories. The relatively limited number of leaf forms and plant structures in the subcanopy of Neotropical and Paleotropical forests should limit the kinds of architectural styles of tents that can be constructed by bats. For example, circular, semicircular, and ovoid cuts appear to be the only ways that bats can effectively modify palmate-shaped leaves into effective tents. Similarly, oblong leaves of *Heliconia* spp. and *Musa* spp. are most commonly modified into tents when cuts are made parallel to the midrib to form a boat-shaped tent, although the paradox tent appears to be an exception (Kunz et al. 1994; Timm 1987). Chewed basal veins in ovoid leaves of *Philodendron* spp. and similar leaf forms invariably form apical tents, whereas the chewed petioles and/or midribs in a rosette of six to 14 leaves on understory saplings form conical tents. When bats sever the innermost stems of pendulous flower/fruit clusters, vines, and root masses, this invariably creates cavities and bell-shaped enclosures known as stem tents.

Some variation in tent architecture may occur if a leaf is modified by more than one bat species. For example, a large epiphyte, *Anthurium jenmanii*, was observed alternately occupied by small harem groups of *Artibeus cinereus* and *Mesophylla macconnelli* (T. H. Kunz and G. F. McCracken, unpublished data). This large, oblong leaf was modified with a long cut parallel to the midrib, characteristic of boat-style tents typically used by *A. cinereus*. Superimposed on this tent leaf were two J-shaped cuts that were similar to those observed in bifid and paradox tents. The only types of leaf architecture reported for

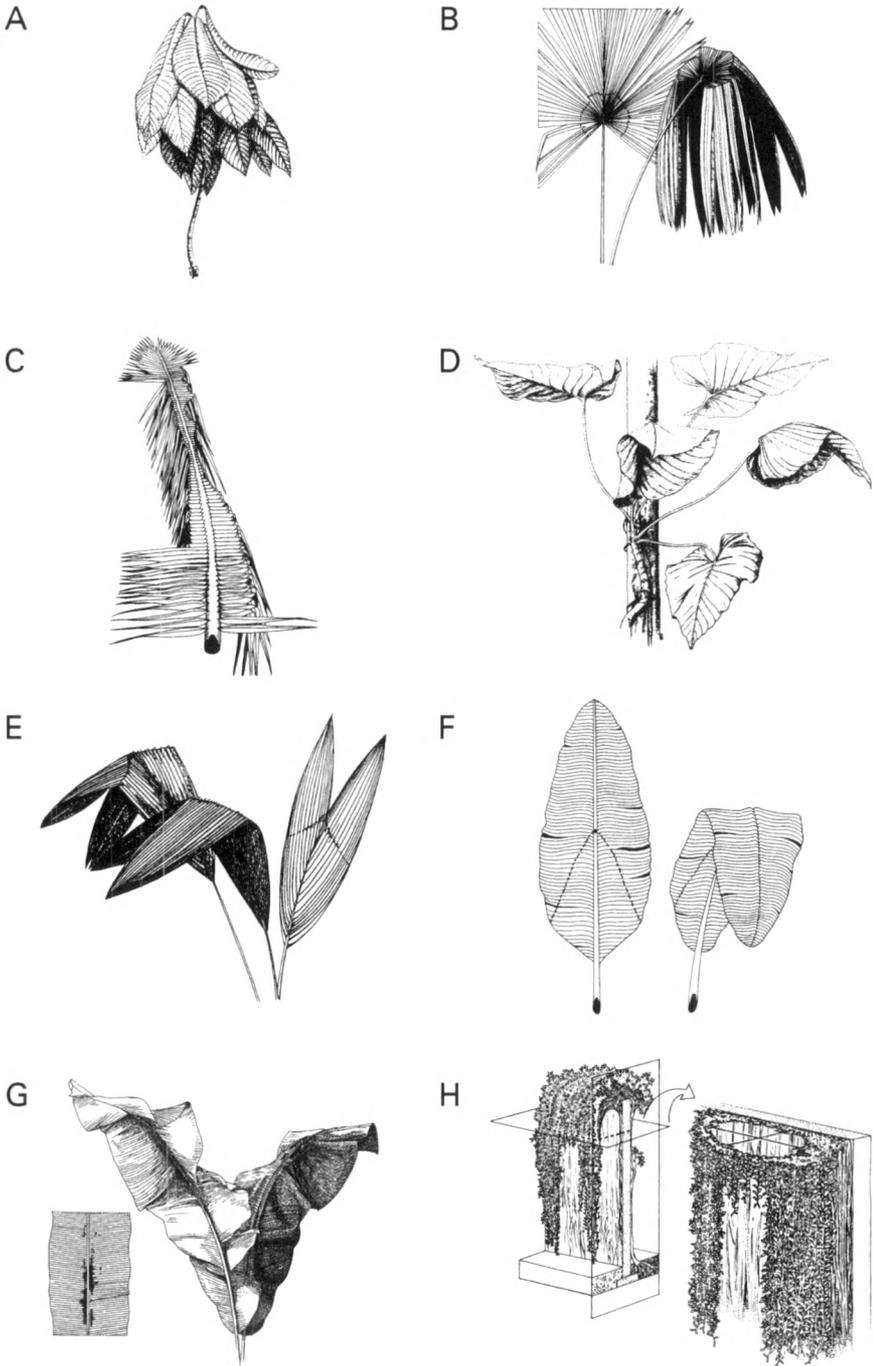


Figure 1.9. Eight architectural styles of tents constructed by tent-making bats. A, Conical tent (unidentified sapling); B, palmate umbrella tent (*Sabal mauritiformis*); C, pinnate tent (*Scheelea rostrata*); D, apical tent (*Philodendron ornatum*); E, bifid tent (*Cocos nucifera*); F, paradox tent (*Musa* sp.); G, boat tent (*Heliconia* sp.); and H, stem tent (*Polyalthia longifolia*) (illustrations by E. Rooks, from Kunz et al. 1994).

Table 1.3. (continued)

| Bat Suborder/ Family/Species | Plant Family | Plant Species | Tent Style | References |
|---------------------------------|----------------|---|---------------------------------|---|
| Microchiroptera: | | | | |
| Phyllostomidae: | | | | |
| <i>Artibeus</i> : | | | | |
| <i>A. anderseni</i> | Heliconiaceae | <i>Heliconia</i> sp. | 7 | Timm 1987 |
| <i>A. cinereus</i> | Araceae | <i>Anthurium jenmanii</i> <i>Philodendron fragrantissimum</i> <i>Philodendron ornatum</i> <i>Philodendron simsi</i> <i>Xanthosoma urudipes</i> <i>Xanthosoma</i> sp. <i>Heliconia</i> sp. | 6 4 4 4 4 4 7 | Kunz et al. 1994 Kunz et al. 1994 Kunz et al. 1994 Kunz et al. 1994 Kunz et al. 1994 Timm 1987 Kunz et al. 1994 |
| | Heliconiaceae | <i>Musa</i> sp. | ? | Goodwin and Greenhall 1961 |
| | Musaceae | <i>Astrocaryum sciophilum</i> | 5 | Simmons and Voss 1998 |
| | Palmae | <i>Coccoloba latifolia</i> <i>Cocos nucifera</i> <i>Manicaria saccifera</i> Unspecified <i>Xanthosoma</i> sp. | 4 4 5 ? 4 | Kunz et al. 1994 Kunz et al. 1994 Kunz et al. 1994 Goodwin and Greenhall 1961 Timm 1987 |
| <i>A. glaucus</i> | Araceae | <i>Monstera lechleriana</i> | 4 | Timm 1987; Timm and Clauson 1990 |
| <i>A. gnomus</i> | Araceae | <i>Philodendron</i> sp. A <i>Philodendron</i> sp. | 4 4 | Charles-Dominique 1993 Simmons and Voss 1998 |
| | Sterculiaceae | <i>Sterculia</i> sp. | 4 | Charles-Dominique 1993 |
| | Strelitziaceae | <i>Phenakospermum guyanense</i> | 4 | Simmons and Voss 1998 |
| | Araceae | <i>Philodendron fragrantissimum</i> | 4 | Kunz et al. 1994 |
| | Palmae | <i>Coccothrinax barbadensis</i> <i>Sabal mauritiformis</i> <i>Scheelea rostrata</i> | 2 2 3 | Kunz et al. 1994 Kunz et al. 1994 Foster and Timm 1976 |
| | Rubiaceae | <i>Pentagonia dommel-smithii</i> | 4 | Brooke 1990; Kunz et al. 1994 |
| <i>A. phaeotis</i> | Araceae | <i>Philodendron mediocostatum</i> | 4 | Kunz et al. 1994 |
| | Heliconiaceae | <i>Heliconia imbricata</i> | 7 | Barbour 1932 |
| | Musaceae | <i>Musa</i> × <i>paradisiana</i> | 7 | Timm 1987 |
| | Palmae | Unidentified | 5 | Kunz et al. 1994 |

Table 1.3. (continued)

| Bat Suborder/ Family/Species | Plant Family | Plant Species | Tent Style | References |
|---|---------------------------------|-------------------------------------|---|--|
| <i>Mesophylla macconnelli</i> | Araceae | <i>Anthurium jenmanii</i> | 6 | Kunz et al. 1994 |
| | | <i>Philodendron fragrantissimum</i> | 4 | Kunz et al. 1994 |
| | Palmae | <i>Xanthosoma</i> sp. | 4 | Koepcke 1984 |
| | | <i>Astrocaryum macrocalyx</i> | 5 | Foster 1992 |
| | | <i>Astrocaryum sciophilum</i> | 5 | Charles-Dominique 1993; Simmons and Voss 1998 |
| | | <i>Geonoma</i> sp. | 5 | Koepcke 1984 |
| | | Unidentified palm | ? | Ermoms 1990 |
| | Araceae | <i>Philodendron melinonii</i> | 4 | Charles-Dominique 1993 |
| | | <i>Philodendron ornatum</i> | 4 | Charles-Dominique 1993 |
| | | <i>Rhodospathia latifolia</i> | 4 | Charles-Dominique 1993 |
| Heliconiaceae | <i>Heliconia</i> sp. | 4 | Zortéa 1995 | |
| Musaceae | <i>Musa</i> sp. | 4 | Zortéa 1995 | |
| Palmae | <i>Astrocaryum sciophilum</i> | 5 | Charles-Dominique 1993; Simmons and Voss 1998 | |
| | <i>Atalea ataleoides</i> | 5 | Charles-Dominique 1993 | |
| Sterculiaceae | <i>Sterculia</i> sp. | 4 | Charles-Dominique 1993 | |
| Strelitziaceae | <i>Phenakospermum guyanense</i> | 4 | Simmons and Voss 1998 | |
| <i>Uroderma:</i> <i>U. bilobatum</i> | Araceae | <i>Philodendron fragrantissimum</i> | 2 | Kunz et al. 1994 |
| | Cyclantaceae | <i>Carludovica palmata</i> | 2 | Kunz et al. 1994; Timm 1987 |
| | Flacourtiaceae | <i>Carpotroche platyptera</i> | 1 | Kunz et al. 1994 |
| | Heliconiaceae | <i>Heliconia imbricata</i> | 7 | Kunz et al. 1994 |
| | | <i>Heliconia latispatha</i> | 7 | Kunz et al. 1994 |
| | Moraceae | <i>Cecropia</i> sp. | ? | Buchanan 1969 |
| | Musaceae | <i>Musa</i> sp. | 6 | Kunz et al. 1994; Timm 1987 |
| | | <i>Musa</i> sp. | ? | Buchanan 1969 |
| | Palmae | <i>Coccothrynx barbadosis</i> | 2 | Kunz and McCracken 1996; Kunz et al. 1994 |
| | | <i>Cocos nucifera</i> | 3 | Lewis 1992; Timm and Clauson 1990; Timm and Lewis 1991 |
| | | <i>Cocos nucifera</i> | 5 | Barbour 1932 |
| | | <i>Cocos nucifera</i> | ? | Goodwin and Greenhall 1961 |
| | | <i>Livistona chinensis</i> | 2 | Barbour 1932 |
| | | <i>Mantecaria saccifera</i> | 5 | Kunz et al. 1994 |

| | | | |
|---------------------------|----------------------------------|-------|--|
| | <i>Pritchardia pacifica</i> | 2 | Barbour 1932 |
| | <i>Scheelea rostrata</i> | 3 | Timm 1987 |
| | <i>Sabal mauritiformis</i> | 2 | Buchanan 1969; Goodwin and Greenhall 1961; Kunz et al. 1994; Timm 1987 |
| | Unidentified | ? | Bloedel 1955 |
| | <i>Coccoloba manzanillensis</i> | 1 | Chapman 1932 |
| | <i>Phenakospermum guyanense</i> | 4 | Simmons and Voss 1998 |
| | <i>Astrocaryum murumuru</i> | 3 | Timm 1987 |
| <i>U. magirostrum</i> | <i>Pentagonia donnel-smithii</i> | 4 | Brooke 1987 |
| <i>Vampyressa:</i> | <i>Philodendron macrophylla</i> | 4 | Kunz et al. 1994 |
| <i>V. nymphaea</i> | <i>Philodendron</i> sp. | 4 | Timm 1984 |
| <i>V. pusilla</i> | <i>Heliconia spathocircinata</i> | 4 (7) | Zortéa and De Brito 2000 |
| | <i>Heliconia richardiana</i> | 4 (7) | Zortéa and De Brito 2000 |
| | <i>Rhodospatha wendlandii</i> | 4 | Kunz et al. 1994 |
| Vespertilionidae: | <i>Livistona rotundifolia</i> | 2 | Rickart et al. 1989 |
| <i>Scotophilus kuhlii</i> | | | |

Note. Some bats may roost in tents that they do not construct. Tent style: 1 = conical; 2 = palmate umbrella; 3 = palmate umbrella; 4 = pinnate; 5 = bifid; 6 = paradox; 7 = boat; 8 = stem (after Kunz et al. 1994).

M. macconnelli (Foster 1992; Koepcke 1984) include the J-shaped cuts (characteristic of bifid tents) and those in which the basal veins have been chewed (as in apical tents).

Considering the relatively temporary nature of tents and the number of veins, stems, or roots that must be modified to construct such structures, the cost of construction should vary depending on the architectural style and number of tents that are made (Kunz et al. 1994). The number of leaf veins that some tent-making bats modify varies from three to four in apical tents of *Philodendron* spp. (Kunz et al. 1994) to more than 60 in palmate umbrella tents constructed in *Sabal* sp. and *Prichardia* sp. or bifid and pinnate tents in *Coccoloba nucifera* (Kunz et al. 1994; Timm 1987). Tents constructed in the leaves of succulent aroids such as *Philodendron* spp. are probably completed in a single night. By contrast, tents constructed in palmate leaves, where large numbers of veins and plications are chewed, may take several days to complete (Barbour 1932; Kunz and McCracken 1996). Construction of stem tents by *C. sphinx* may take several months to complete (Balasingh et al. 1995).

Another small (12–18 g) megachiropteran (*Balionycteris maculata*) in peninsular Malaysia is known to modify root masses of the epiphytic ginger (*Asplenium nidus*) and bird's nest fern (*Hedychium longicornutum*) by severing roots and excavating soil to create roosting cavities (Hodgkison et al., in press; fig. 1.10).

Convergence in Tent-Roosting Behavior

The striking similarities in tent architecture among the Old World pteropodids and the New World phyllostomids (fig. 1.11) supports an interpretation of convergence in tent-making and tent-roosting behavior. For example, oval-shaped or round tent crowns in palmate leaves of *Livistona rotundifolia* (attributed to the Old World megachiropteran *C. sphinx* and *C. brachyotis*) and similar-shaped tents in palmate leaves of *Coccothrinax barbadensis* (attributed to the New World microchiropteran *Artibeus jamaicensis*) are nearly identical (Kunz et al. 1994).

Convergence in bat-tent architecture may be a consequence of similarity in leaf morphology, but observations that members of taxa with divergent evolutionary histories (Megachiroptera and Microchiroptera) are capable of modifying similar leaf forms in nearly identical ways supports an interpretation of behavioral convergence (Kunz et al. 1994). Because tent-making species are relatively small (<65 g) and largely frugivorous, they are probably subjected to similar selection pressures relating to foraging and roosting behavior in the structurally similar forests in which they have evolved.

Among the Megachiroptera, the close ancestral affiliations and similar roosting habits of *C. sphinx* and *C. brachyotis* suggest that tent-making behavior may have evolved only once in this genus and, thus, could be expected in other members of this taxon (Kunz et al. 1994). The roosting habits of other

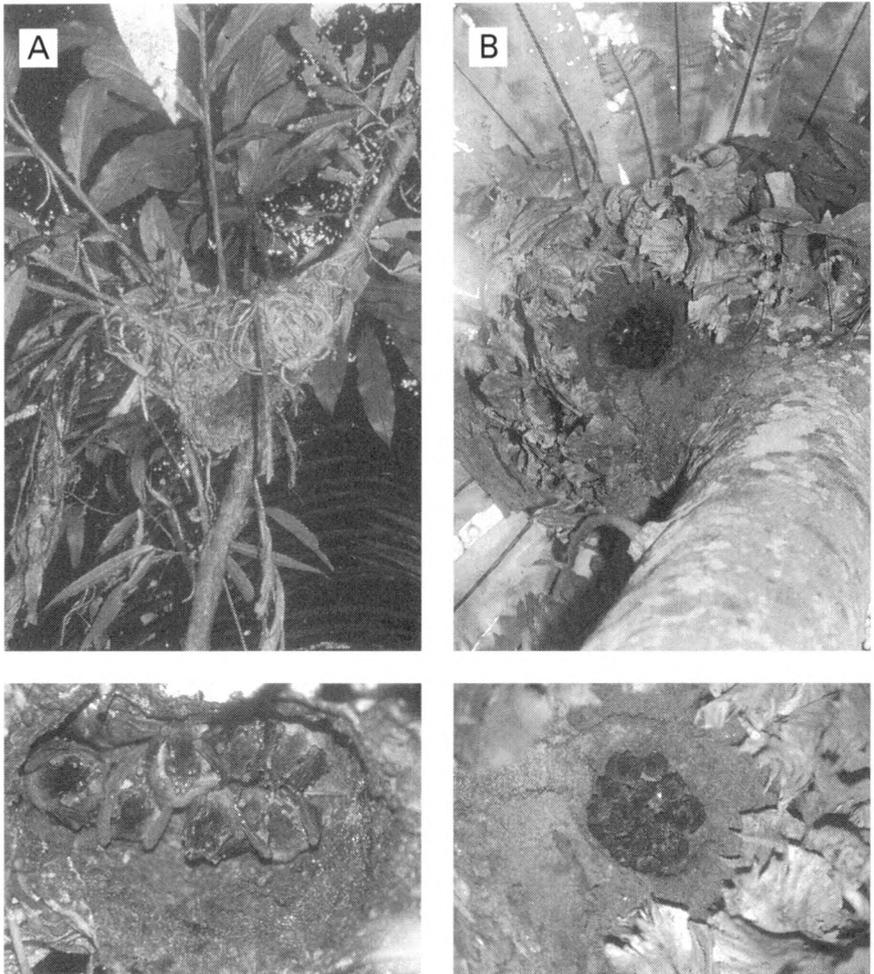


Figure 1.10. A, Excavated root mass of the epiphytic ginger, *Asplenium nidus* (top), occupied by a harem group of *Balionycteris maculata* (bottom); B, excavated root mass of a bird's nest fern, *Hedychium longicornutum* (top), occupied by a small harem group of *B. maculata* (bottom) (photos by R. Hodgkison).

species of *Cynopterus* have not been fully described, but future investigations are needed to test the hypothesis that tent-making behavior is a trait shared by other members of the genus (Kunz et al. 1994).

With the exception of *Rhinophylla pumilio* (subfamily Caroliinae), all New World tent-roosting species belong to the subfamily Stenodermatinae (tribe Stenodermatini). However, existing phylogenies for the Phyllostomidae (Baker et al. 1989, 2000; Lim 1993; Owen 1987, 1988; reviewed in Wetterer et al. 2000)

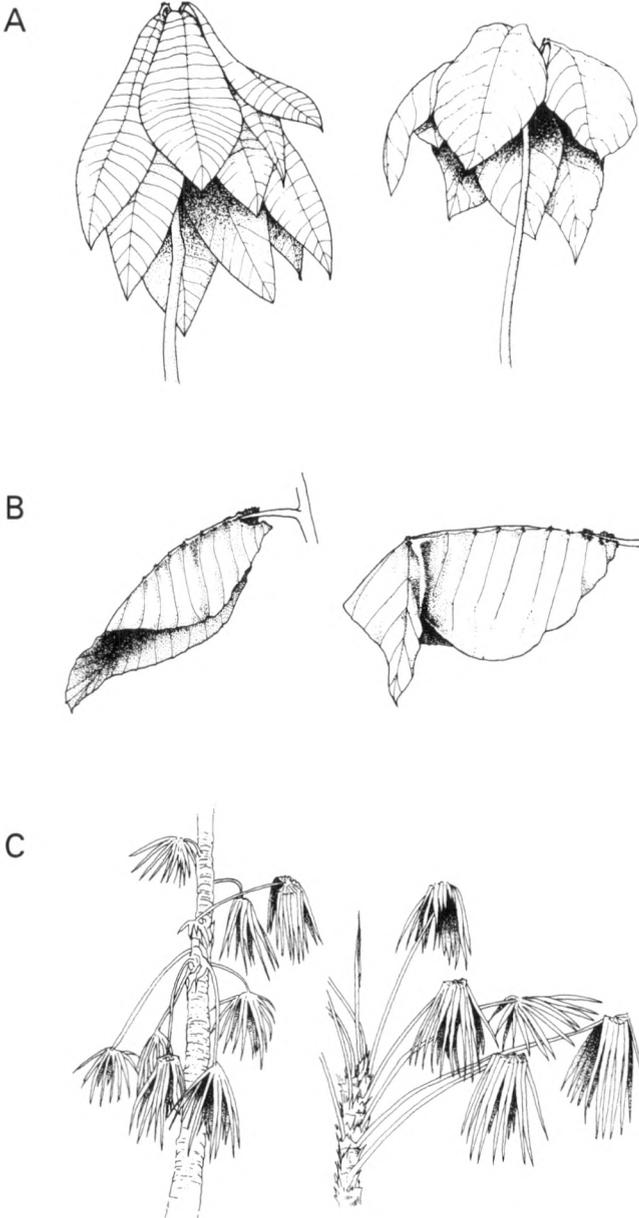


Figure 1.11. Convergence in bat-tent architecture in the Paleotropics (Indonesia) (left) and Neotropics (Costa Rica) (right). A, Conical tents, unidentified Anacardiaceae (left), *Carpotroche platyptera* (right); B, apical tents, *Dillenia beccariana* (left) and *Pentogonia donnel-smithii* (right); and C, palmate umbrella tents, *Livistonia rotundifolia* (left) and *Carludovica palmata* (right) (illustrations by E. Rooks, after Kunz et al. 1994).

are not sufficiently developed to establish whether tent-making/tent-roosting bats share a common ancestor. Of the 18 genera recognized in the tribe Stenodermatini, Owen's (1987) proposed assignment of *Demanura* is herein included with *Artibeus*, and the genus *Mesophylla* is judged distinct from *Ectophylla* (Lim 1993).

Tent-making/roosting behavior in the Phyllostomidae has been reported for six genera—*Artibeus* (*Dermanura*), *Ectophylla*, *Mesophylla*, *Rhinophylla*, *Uroderma*, and *Vampyressa*. Using Lim's (1993) phylogeny for the Phyllostomidae, tent-making/roosting habits may have evolved three or four times (see Kunz et al. 1994). A similar conclusion is made if we accept Wetterer et al.'s (2000) phylogeny of the Phyllostomidae. If we use Baker et al.'s (2000, fig. 2) phylogeny on which to map tent-roosting/tent-making bats, five clades are recognized with tent-roosting/tent-making traits. One clade includes *Artibeus* (*Dermanura*), a second includes *Ectophylla*, a third includes *Mesophylla* and *Vampyressa pusilla*, a fourth includes *Uroderma* and *Vampyressa bidens*, and a fifth clade includes *Rhinophylla*.

Given the provisional nature of each phylogeny, especially at the species level, one cannot rule out the possibility that tent-making/roosting behavior in the Phyllostomidae may have evolved only once, especially if the trait was present in a taxon ancestral to these groups (Kunz et al. 1994). Alternatively, its apparent absence in other members of the Stenodermatinae (e.g., *Chiroderma*, *Enchisthenes*, *Platyrrhinus*, *Surnira*, and *Vampyrodes*) may reflect the subsequent loss of these traits or, perhaps, that they have not yet developed in these taxa.

A complicating factor in attempting to assess phylogenetic relationships among tent-roosting/tent-making species is that some bats may parasitize tents initially made by others (Brooke 1987; Charles-Dominique 1993; Foster 1992; Kunz et al. 1994; Simmons and Voss 1998; Timm 1987). Charles-Dominique (1993) suggested that *Rhinophylla pumilio* occupied tents that were constructed by other species—perhaps *Mesophylla macconnelli* or *Artibeus gnomus*—and thus may not construct their own tents (also see Simmons and Voss 1998). Further studies should be designed to distinguish among tent-making and tent-roosting species.

Why Do Bats Construct and/or Roost in Tents

Relative to other types of foliage roosts, tents provide several potential benefits to their occupants. These include greater protection from inclement weather (rain, wind, and direct solar radiation), increased protection from visually oriented predators, avoidance of parasites, proximity to food resources, and increased energy economy (Bhat and Kunz 1995; Brooke 1987, 1990; Kunz et al. 1994; Kunz and McCracken 1996; Tan et al. 1999; Timm 1987; Timm and Lewis 1991; Timm and Mortimer 1976). Tent-making behavior presumably evolved because individuals benefit from the investment made in their construction and because the benefits outweigh the costs that bats may have incurred in their construction (Kunz et al. 1994).

Several investigators have suggested that the mating system of tent-roosting bats is based on roost-defense polygyny (Balasingh et al. 1995; Brooke 1990; Kunz and McCracken 1996; reviewed in McCracken and Wilkinson 2000). When males modify leaves and other plant parts into tents, they create spaces that can be potentially defended against intruding males more effectively than they could if they occupied unmodified foliage (Balasingh et al. 1995; Kunz and McCracken 1996). If we assume that tents are constructed by males, and males recruit females for mating (Balasingh et al. 1995), important benefits of tent construction would be that the tents are attractive to females and that either the tent or females can be defended by the harem males (Balasingh et al. 1995; Kunz and McCracken 1996; Storz et al. 2000a). If tent architecture is perceived by females as an extension of a male's phenotype, then a male would benefit if females selected those traits when choosing a mate.

What characteristics of plants do bats select when they modify leaves and other plant parts into tents? If tent quality is an important factor in female choice, tents constructed in the most physically vigorous leaves may be an important criterion for attracting females (Stoner 2000). Height above the ground, age, and angle of the leaf are important factors. *Artibeus watsoni* and *A. cinereus* typically select leaves for tent construction that are approximately 1.5–5 m above the ground, even though other leaves may be available (Choe and Timm 1985; Stoner 2000). Brooke (1987) noted that *Vampyressa nymphaea* showed a preference for young leaves, presumably because they were softer (more succulent) and thus easier to modify. *Ectophylla alba* appears to select *Heliconia* leaves for tent construction based on height above the ground and angle of the petiole (Brooke 1990; Timm and Mortimer 1976). Thus, males may judge the suitability of leaves and other plant parts for tent construction based on their degree of protection from inclement weather and predators, but they may also increase the potential for polygyny and their ability to defend tents (and female occupants) against intrusions by other males.

The hypothesis that tents provide protection from rain was supported experimentally by Choe (1994), who placed cotton balls beneath unmodified leaves. He found that the cotton balls placed beneath tents were less saturated with rainwater compared to those beneath unmodified leaves. Some plant species in which tents are constructed have characteristics that may increase protection from potential predators. Stoner (2000) found that *A. watsoni* chose understory palms (*Astergyne martiana*) that were taller and had thicker petioles and longer leaves than a random selection of plants and suggested that larger leaves provided safer roosting sites from terrestrial predators. Large leaves and the presence of spines on the rachis may increase protection from visually oriented predators (Charles-Dominique 1993; Simmons and Voss 1998; Stoner 2000). In addition, bats that roost in tents with long slender petioles are more likely to be alerted to approaching predators (e.g., snakes and scansorial primates), whose body masses and activity may disturb the surrounding foliage (Boinski and Timm 1985; Timm and Mortimer 1976).

There have been no systematic studies comparing rates of predation on bats that occupy unmodified foliage versus tents. Because tents offer their occupants unobstructed views of their environment below, bats should be alert to a predator approaching from the ground and may be able to escape before being attacked (Brooke 1990; Kunz and McCracken 1996). Tent-roosting bats generally are alert in their tents—which may further reduce risks of predation. In addition, the construction and occupancy of a number of tents within a bat's home range, as observed in *M. macconnelli*, may confer advantages to bats if it introduces a degree of uncertainty into the search tactics of a potential predator (Foster 1992). That tent-making behavior originated solely as an antipredator strategy (see Boinski and Timm 1985), however, is doubtful, since other benefits are more compelling.

Some visually oriented predators may learn to recognize tents and, thus, use an acquired search image to increase their chances of locating tents in which bats roost. Anecdotal observations have revealed that tent-roosting bats are occasionally taken by squirrel monkeys (*Saimiri oerstedii* and *S. sciureus* [Boinski and Timm 1985; Souza et al. 1997]) and by white-faced capuchin monkeys (*Cebus capucinus* [Perry 1994]). Moreover, some bats that were disturbed by squirrel monkeys were subsequently preyed on by double-toothed kites (*Harpagus bidentatus* [Boinski and Timm 1985]). In India, tents of *Cynopterus sphinx* are sometimes harassed by known or suspected predators, such as jungle crows (*Corvus macrorhynchos*), house crows (*C. splendens*), rat snakes (*Ptyas mucosus*), or spectacled cobras (*Naja naja* [Storz et al. 2000b]). However, based on the evolutionary success of tent-roosting/tent-making bats, the benefits of tent-roosting appear to outweigh the disadvantages of occasional predation.

Theoretically, enclosed spaces should trap metabolic heat and thus increase the temperature inside an occupied roost, thereby reducing a bat's daily energy expenditure. Although thermoregulatory benefits may accrue to cavity-roosting bats in temperate regions (Kurta 1985), the hypothesis that tents in tropical areas provide thermoregulatory benefits to their occupants remains to be tested. Relative to the enclosed spaces of a tree or building cavity, leaves generally have low insulative properties. However, even the partially enclosed space of a tent cavity could reduce both heat and water losses due to convective forces. If wind velocity in foliage roosts is 18%–30% less than the velocity outside of roosts (see Walsberg 1986), then tent-roosting bats could benefit energetically.

Timm (1987) suggested that tents might play a role in controlling ectoparasites, but this would only benefit bats if they regularly moved to alternate sites when parasite infestations increased. This may be the situation for some species but not for others. Several species, including groups of *Ectophylla alba*, *Cynopterus sphinx*, and *C. brachyotis* may occupy the same tent continuously for several weeks during the maternity period (Balasingh et al. 1995; Brooke 1990; Tan et al. 1997). Abandonment of tents may be more associated with the breakup of the maternity roost than with a buildup of parasites. Timm's (1987)

hypothesis may apply only to those species that regularly move among several alternate tents (e.g., small stenodermines that roost in apical tents).

Several authors have qualitatively examined the amount of foliage clutter around occupied and unoccupied tents, noting that occupied tents had the least amount of adjacent clutter (Brooke 1990; Kunz and McCracken 1996). The open space beneath tents not only provides a clear view of approaching predators (Brooke 1987, 1990) but also offers bats unimpeded access to and from the tent as they depart to and return from foraging bouts (Balasingh et al. 1995; Kunz 1982; Kunz et al. 1994; Kunz and McCracken 1996). Easy access to tents on the wing may also be one tent characteristic that females use to judge tent quality. For example, Balasingh et al. (1995) found that the largest harems of *C. sphinx* occupied stem tents that had the least amount of clutter around the opening.

Cavities in Arboreal Termite and Ant Nests

At least four species of Neotropical microchiropterans (Phyllostomidae: *Tonatia silvicola*, *T. carrikeri*, *T. brasiliense*, and *Phyllostomus hastatus*), one Australian vespertilionid (*Murina florium*), and one megachiropteran (*Balionycteris maculata*) have been observed roosting in excavated arboreal ant nests (Clague et al. 1999; Goodwin and Greenhall 1961; Handley 1966, 1976; Hodgkison et al., in press; Kalko et al. 1999; McCarthy et al. 1992; fig. 1.12). Whether Neotropical bats modify these nests or exploit cavities created by trogons (*Trogon* sp.), orange-chinned parakeets (*Brotogeris* sp.), or other species (Kalko et al. 1999) remains to be determined.

In Panama, termite nests occupied by *T. silvicola* were active and located approximately 5–7 m above the ground (Kalko et al. 1999). Each nest was excavated from below with a space approximately 30–40 cm deep (Kalko et al. 1999). The size of day-roosting groups of *T. silvicola* was typically small, ranging from four to five individuals, often including a single male. Some day roosts were used at night (as feeding roosts), and males tended to forage near these sites. The proximity of a male *T. silvicola* to its day roost and the presence of several females suggest the possibility of harem formation (Kalko et al. 1999).

In peninsular Malaysia, *Balionycteris maculata* also has been observed roosting in nests of the arboreal ant *Crematogaster aboenini* (fig. 1.12) and are excavated similarly to the way some tent-making bats modify fruit/flower clusters, leaves, vines, and root masses. These excavated structures are often occupied by single adult males and small harem groups of *B. maculata* ranging from four to eight bats, although groups as large as 20 individuals have been observed (Hodgkison et al., in press; Lim 1966). It is not known how or when these excavations occur, although Hodgkison et al. (in press) postulated that bats use their teeth and/or claws to scrape away soil and nest material, perhaps similarly to the way they excavate soil around root masses (see fig. 1.10).



Figure 1.12. Arboreal ant nest (*Crematogaster ebinina*) excavated by and used as a day roost by *Balionycteris maculata* (photo by R. Hodgkison). Excavated basal opening is shown with an arrow.

Morphological and Behavioral Adaptations for Roosting

The opportunistic and sometimes obligate use of cavities and foliage as roosts frequently involves specialized behavioral and morphological adaptations of bats (Fenton 1992a; Kunz 1982, 1996). The cranium and postcranial skeleton may be under strong selection pressures from a bat's roosting environment (Bennett 1993; Fenton 1992a; Kunz 1982). Some microchiropterans that seek shelter in tree crevices and bamboo culm have evolved modified cranial, pelvic, and pectoral structures that coincide with an extraordinary ability to crawl through small spaces (Fenton 1992a). For example, *Tylonycteris pachypus*

and *T. robustula* have strongly flattened crania that facilitate access to the interior spaces of bamboo culm (Medway and Marshall 1972).

Many bats have evolved specialized thumbs and feet for roosting. Megachiropterans often assume pendant postures by hanging from one or both feet, facilitated by a specialized locking mechanism (Bennett 1993). Species in the genera *Pteropus*, *Eidolon*, and *Epomophorus* are especially adept at using their thumbs and claws for climbing among branches (Nelson 1965; Neuweiler 1969; Wickler and Seibt 1976). By contrast, some foliage-roosting microchiropterans, such as *Lavia frons*, are less agile in roosting situations and select relatively open sites for roosting that are relatively free of surrounding vegetation (Wickler and Uhrig 1969).

Some microchiropterans have specialized thumb and footpads or suction pads that predispose them for certain roosting situations (fig. 1.13). The highly specialized thumb and footpads in *Myzopoda aurita*, *Thyroptera discifera*, and *T. tricolor* make it possible for them to cling to the smooth upper surfaces of furled leaves (Schliemann and Mags 1978; Wilson 1978; Wilson and Findley 1977). Similarly, the modifications of the foot and thumb pads of *Thyroptera pachypus* and *T. robustula* facilitate entry and exit through small openings on smooth bamboo culm and allow them to cling to the interior of the culm cavity (Kunz 1982; Medway and Marshall 1972; Schliemann and Hoerber 1978).

Cryptic markings are pronounced in several species of both Old and New World foliage-roosting bats (Bonaccorso 1998; Kunz 1982), and these traits presumably confer a selective advantage in certain roosting situations. Some foliage roosting bats are well concealed in their roosting places by either real or apparent color. The reddish and yellowish coloration of some lasiurine bats (e.g., *Lasiurus borealis* and *L. intermedius*) that roost in the foliage of deciduous trees may confer protection from predators. The greenish wings of *Paranyctimene raptor* provides an effective camouflage in foliage (Bonaccorso 1998). The white pelage of *Ectophylla alba* assumes a greenish appearance as the light that transmits through leaves casts a green light on these tent-making bats (Brooke 1990)—perhaps making them less readily detected by visually oriented predators.

The so-called painted bats of the genus *Kerivoula* typically have long, thick, woolly pelage that ranges in color from yellow to bright orange and scarlet (Allen 1939; Dobson 1877; Fenton 1992a; Nowak 1994; Schulz 2000). Similarly, the pelage of other temperate and tropical plant-roosting bats are colored with hues of yellow, orange, and red, resembling fruits and leaves. The contrasting lighter colors around the head and neck (mantle) of some megachiropterans suggests a type of countershading that may confer a certain degree of crypsis (Bonaccorso 1998; Dobson 1877; Flannery 1995; Novick 1977). Similarly, the mottled and woolly pelage of *Rhynconycteris naso*, which roosts in small groups on the exposed boles of tropical trees (Bradbury and

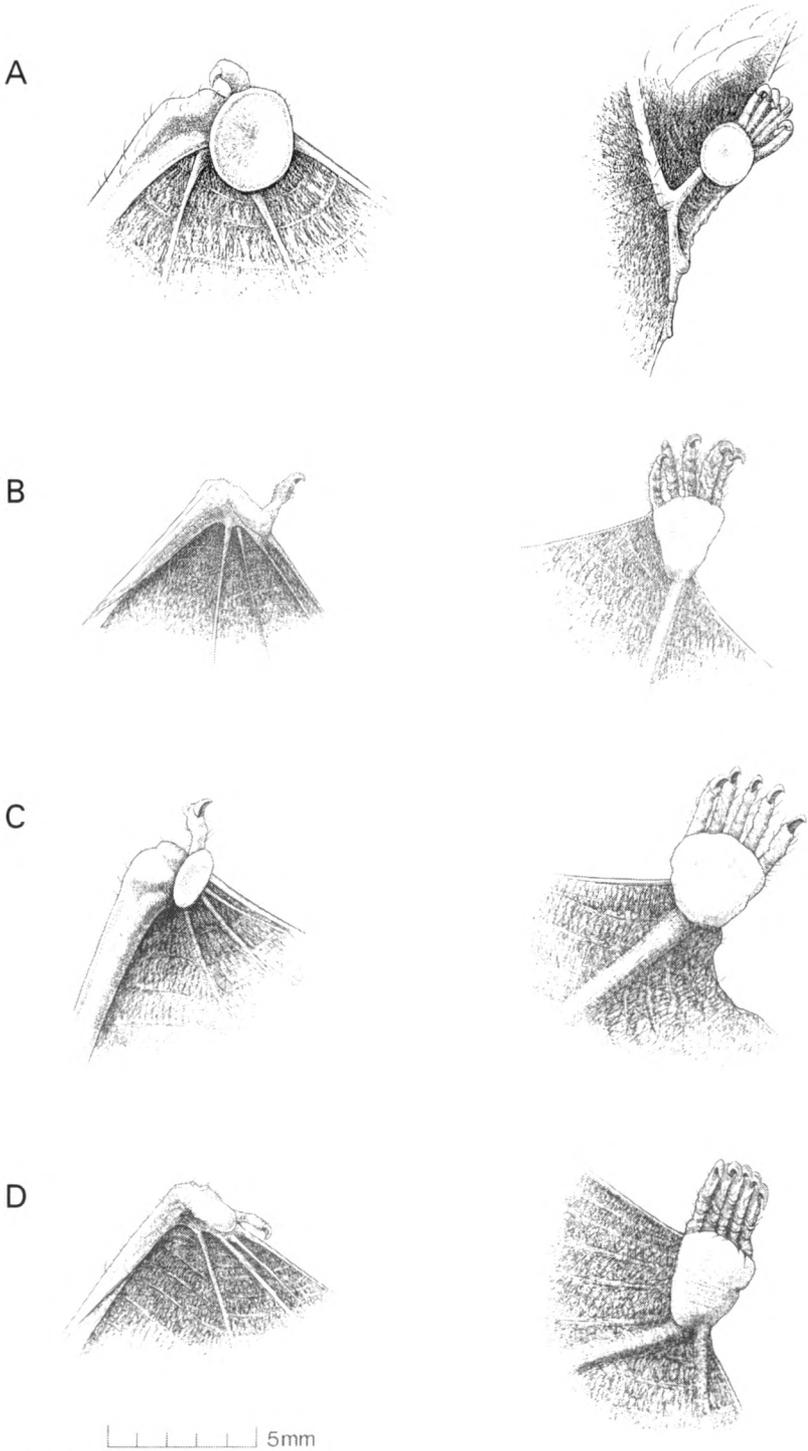


Figure 1.13. Morphological specializations of wrists and feet in (A) *Thyroptera tricolor*, (B) *Pipistrellus nanus*, (C) *Tylonycteris pachypus*, and (D) *Glischropus tylopus*, used for roosting on the smooth inner surfaces of bamboo culms or furled leaves. (Illustrations by P. Esty, from Kunz 1982.)

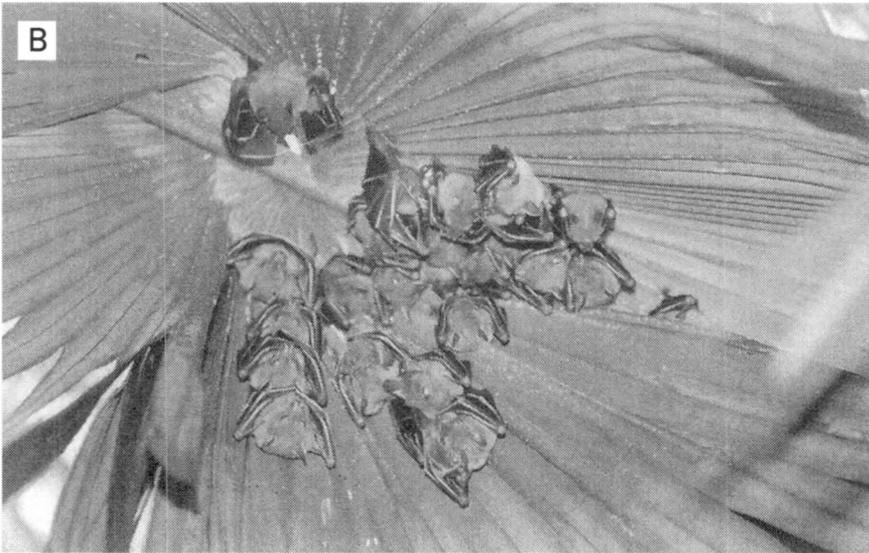
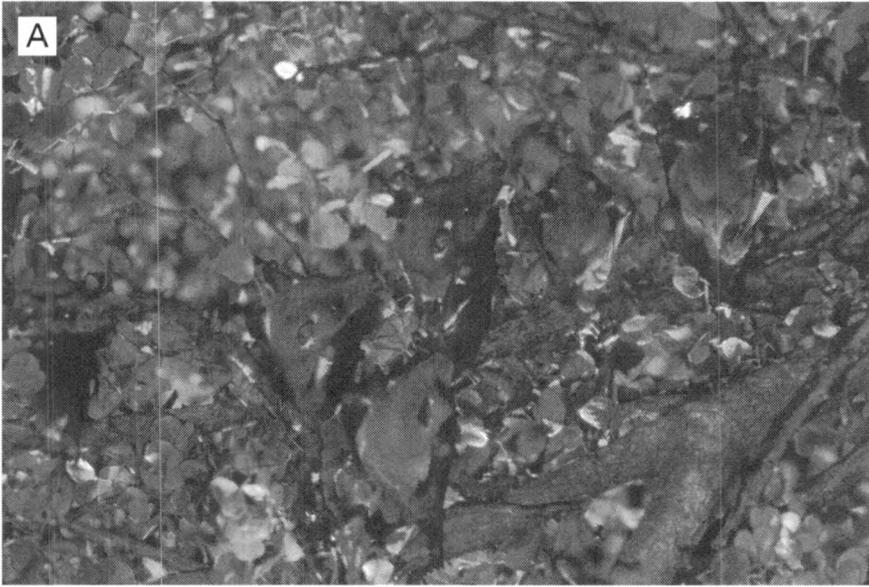


Figure 1.14. *A*, Cryptic pelage marking of *Epomophorus* sp. roosting in foliage. White ear and shoulder patches disguise the appearance of the bats as observed from below in the sun-flecked canopy (from Fenton 1992b; photo by M. B. Fenton); *B*, contrasting metacarpels and phalanges of *Cynopterus brachyotis* disrupt the uniform pattern of wings against the veins and plications of palm fronds (photo by T. H. Kunz).

Vehrencamp 1976), may be of benefit by camouflaging these bats from potential predators (see fig. 1.5).

Other foliage-roosting bats may be concealed with disruptive marking on their pelage or wings, such as the spotted pattern on the wings and ears of *Nyctimene albiventer* (Bonaccorso 1998). Similarly, the reticulate markings on the wings of *Chalinolobus variegatus*, the white dorsal stripe and patches on the head and shoulders of the vespertilionid *Scotomanes ornatus*, and the white ear spots, mottled wings, and contrasting metacarpels and phalanges of *Epomophorus wahlbergi*, *Cynopterus sphinx*, and *C. brachyotis* may function as disruptive patterns in roosting situations (fig. 1.14) and, thus, potentially protect them from visually oriented predators (Fenton 1992b; Lekagul and McNeely 1977; Nowak 1994; Rosevear 1965).

Concealment of bats in foliage also may be enhanced by certain roosting habits. The near motionless postures sometimes observed in *Syconycteris australis* (Bonaccorso 1998; Law 1993), *Pteropus poliocephalus* (Nelson 1965), *Epomops franqueti* and *Micropteropus pusillus* (Jones 1972), *Lavia frons* (Kingdon 1974), *Epomophorus gambianus* (Marshall and McWilliam 1982), *Nyctimene major* (Nowak 1994), *N. robinsoni* (Spencer and Fleming 1989), and *Lasiurus borealis* and *L. seminolus* (Constantine 1958, 1959, 1966), where they are shrouded by their wings, giving them the appearance of dead leaves, may reduce detection by potential predators.

Schulz (1999) described an unusual behavior in the foliage-roosting species *Murina florium*, which he termed "leaf wrapping." An individual would drag a leaf over its body and hold it in place using the hindfoot and thumb, thus obscuring the body from view. This behavior may provide shelter from sunlight and rain and reduce vulnerability to predation.

Colony Size

Colony sizes of bats roosting in cavities or foliage vary considerably. Although intraspecific differences exist, a number of species that roost in cavities typically form small colonies of fewer than 10 individuals (table 1.4). The size of colonies may reflect the social structure of a particular species, such as harem formation in *Artibeus jamaicensis* (Morrison 1979) or monogamous pairs in *Vampyrus spectrum* (Vehrencamp et al. 1977). Other species form larger groups, for example, in Kenya, up to 80 individuals of the megadermatid *Cardioderma cor* roost in hollow baobab trees (Vaughan 1976; see fig. 1.1D). Some cavity-roosting species form very large groups, such as *Hipposideros caffer*, with colonies of more than 1,000 individuals (Kingdon 1974), and *Mystacina tuberculata*, where up to 4,500 individuals have been found in a single tree cavity in New Zealand (Lloyd and McQueen 1997).

Bats that roost beneath exfoliating bark are often solitary or form small groups (e.g., Crampton and Barclay 1998; Mattson et al. 1996; Menzel et al.

Table 1.4. Mean colony size, roost fidelity, and roost area of selected species of bats roosting in tree cavities or beneath exfoliating bark

| Species | Country | Mean Colony Size | Roost Fidelity | Roost Area | References |
|----------------------------------|--------------|------------------|----------------|------------|---|
| Mystacinidae: | | | | | |
| <i>Mystacinia</i> sp. | New Zealand | A, C | B | ... | O'Donnell et al. 1999 |
| <i>Mystacinia tuberculata</i> | New Zealand | C | ... | B | Lloyd and McQueen 1997; Daniel and Williams 1984 |
| Noctilionidae: | | | | | |
| <i>Noctilio albiventris</i> | Costa Rica | ... | C | B | Fenton et al. 1993 |
| Phyllostomidae: | | | | | |
| <i>Artibeus jamaicensis</i> | Panama | A | C | A | Morrison 1979 |
| <i>Desmodus rotundus</i> | Costa Rica | A | C | B | Wilkinson 1985 |
| <i>Vampyrum spectrum</i> | Costa Rica | A | C | ... | Vehrencamp et al. 1977 |
| Rhinolophidae: | | | | | |
| <i>Rhinolophus hildebrandti</i> | South Africa | B | C | ... | Fenton and Rautenbach 1986 |
| Vespertilionidae: | | | | | |
| <i>Chalinolobus tuberculatus</i> | New Zealand | B | A | A | O'Donnell and Sedgely 1999 |
| <i>Eptesicus fuscus</i> | Canada, USA | B | B | A | Betts 1996; Brigham 1991; Kalcounis and Brigham 1998 |
| <i>Lasionycteris noctivagans</i> | Canada, USA | A, B | B | A | Betts 1996; Crampton and Barclay 1998; Mattson et al. 1996; Vonhof and Barclay 1996 |
| <i>Myotis californicus</i> | Canada | B | A | A | Brigham et al. 1997 |
| <i>Myotis daubentonii</i> | Switzerland | B | A | B | Rieger 1996 |
| <i>Myotis evotis</i> | Canada | A | A | A | Vonhof and Barclay 1996; Waldien et al. 2000 |
| <i>Myotis lucifugus</i> | Canada | B | B | B | Barclay and Cash 1985; Crampton and Barclay 1998 |
| <i>Myotis septentrionalis</i> | USA | A, B | A | A | Foster and Kurta 1999; Sasse and Pekins 1996 |
| <i>Myotis sodalis</i> | USA | A, B | B, C | A | Humphrey 1977; Kurta et al. 1993, 1996 |
| <i>Myotis volans</i> | Canada, USA | A, C | B | A | Chung-MacCoubrey 1996; Ormsbee 1996; Vonhof and Barclay 1996 |
| <i>Nyctalus lasiopterus</i> | Japan | B | B | ... | Maeda 1974 |
| <i>Nyctalus noctula</i> | Germany | A, C | A | B | Kronwitter 1988; van Heerdt and Sluiter 1965; Sluiter et al. 1973 |
| <i>Nycticeius humeralis</i> | USA | A | A | ... | Menzel et al. 2001 |
| <i>Nyctophilus bifax</i> | Australia | A | A | A | Lunney et al. 1995 |
| <i>Nyctophilus geoffroyi</i> | Australia | A | A | A | Hosken 1996 |
| <i>Nyctophilus gouldi</i> | Australia | A | A | A | Lunney et al. 1988; Tidemann and Flavel 1987 |
| <i>Scotophilus borbonicus</i> | Zimbabwe | A | A | A | Fenton 1983; Fenton and Rautenbach 1986 |
| <i>Vespadelus darlingtoni</i> | Australia | B | | A | Herr and Klomp 1999 |
| <i>Vespadelus pumilus</i> | Australia | A, B | A | A | Law and Anderson 2000 |

Note. Mean colony sizes: A < 10; B = 11–100; C > 100 individuals. Roost fidelity: A = shifting roost on average every 1–2 d; B = shifting every 3–10 d; C = shifting > 10 d. Roost area is the mean distance between consecutive roosts: A < 400m; B > 400m. Ellipses dots indicate that the characteristic was not measured.

2001; Vonhof and Barclay 1997). In some situations, the physical area beneath exfoliating bark may limit the number of individuals, although colony sizes of up to 50 individuals have been reported (e.g., *Myotis sodalis* [Humphrey et al. 1977; Kurta et al. 1996] and *M. volans* [Baker and Phillips 1965]).

Maternity roosts generally contain more individuals than do nonbreeding roosts, with increased energy conservation expected owing to clustering behavior of females and young (Roverud and Chappell 1991). At times, lactating females may resort to solitary roosting to facilitate entry into torpor after unsuccessful foraging bouts or if their energetic balance is close to a critical threshold (O'Donnell and Sedgely 1999). Males more often than females roost alone in cavities (Law and Anderson 2000).

Clustering behavior is important for temperate species that hibernate in tree cavities. *Nyctalus noctula*, one of the few European species that hibernates in tree cavities, can tolerate lower temperatures when clustered. Sluiter et al. (1973) found that clusters of approximately 100 individuals could survive for at least 53 d when the roost temperature was below 0°C. In contrast, single individuals were usually forced to arouse from hibernation at these temperatures.

Degrees of coloniality vary among species of *Pteropus* (Pierson and Rainey 1992). In Western and American Samoa, *P. tonganus* forms year-round colonies comprising several thousand individuals (Brooke et al. 2000; Cox 1983; Wilson and Engbring 1992). The closely related *P. samoensis* occupies the same islands, but it is solitary or roosts in loose aggregations of up to a dozen individuals (Brooke et al. 2000; Cox 1983; Rainey 1998; Wilson and Engbring 1992). In the Philippines and peninsular Malaysia, roosting groups of *P. vampyrus* typically consist of fewer than 100 individuals (Lim 1966). However, a colony of approximately 15,000 was observed in a mangrove forest in southwestern Borneo (Lyon 1911), and in Indonesia one colony was estimated to include as many as 21,000 individuals (Wiriosoepartha et al. 1986). In eastern Australia, colonies of *P. poliocephalus* range from a few hundred to 200,000 individuals (Eby 1991; Eby et al. 1999; fig. 1.15A). Estimates of the number of individuals in large camps are relatively crude and may be subject to observer error (see Garnett et al. 1999).

Some foliage-roosting megachiropterans exhibit a gregarious phase during one season but may roost alone or form small groups at other times. In some regions, the reduction or breakup of large aggregations of pteropodids has been attributed to the decrease in abundance of flower blossoms and fruits, suggesting that the stimulus for dispersal and nongregarious behavior reflects depletion of local food resources (Fleming and Eby, this volume; Palmer and Woinarski 1999; Richards 1995; Thomas 1983).

Mixed species roosts are common in some species of *Pteropus*. In Papua New Guinea, *P. conspicillatus* has been observed roosting with *P. hypomelanus* (Bonaccorso 1998). In the Philippines, *P. vampyrus* has been observed sharing

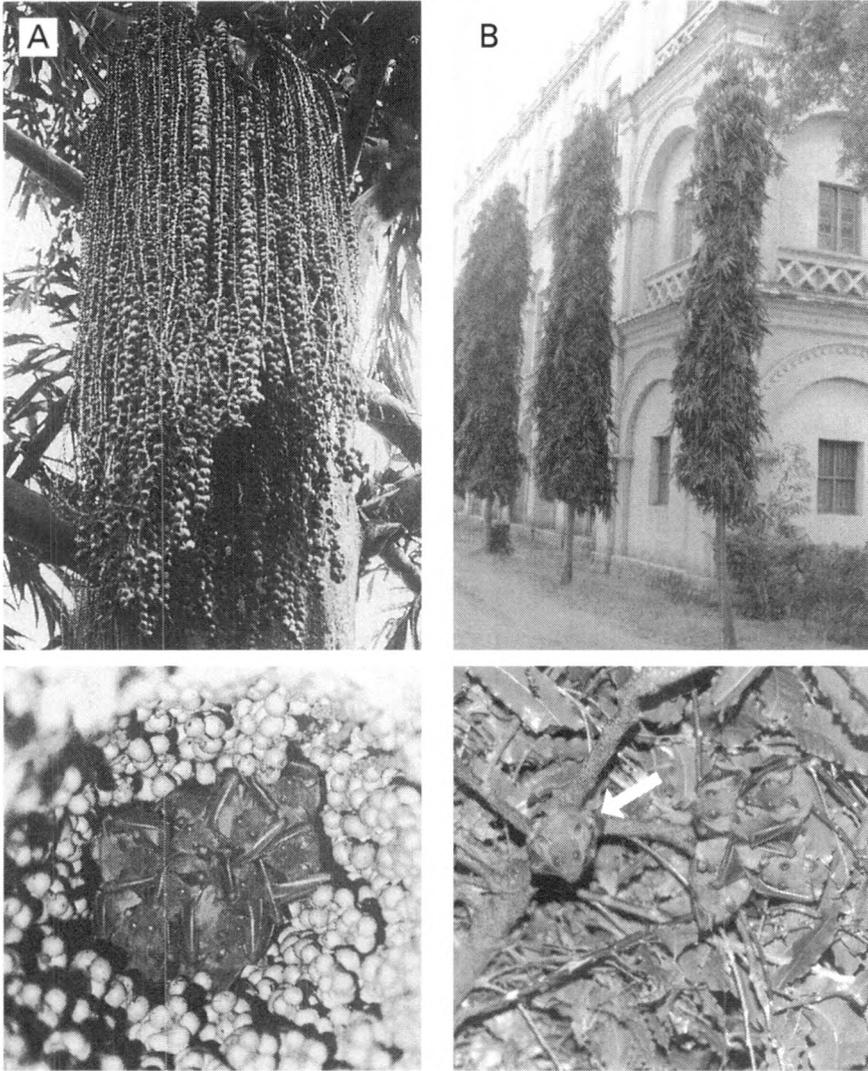


Figure 1.15. Two types of stem tents (top) constructed by *Cynopterus sphinx*, occupied by small harem groups (bottom) in (A) kital palm fruit cluster (*Caryota urens*) and (B) mast tree (*Polyalthia longifolia*). Arrow in bottom right photo show positions of harem male (photos by K. H. Tan and J. Balasingh, respectively).

roosts with *Acerodon jubatus* in groups ranging from several hundred to about 150,000 individuals (Heideman and Heaney 1992; Mudar and Allen 1986). In Australia, *P. poliocephalus*, *P. alecto*, and *P. scapulatus* sometimes form mixed groups that exceed 50,000 individuals (Eby et al. 1999; Ratcliffe 1932; Tidemann et al. 1999; fig. 1.16B). In contrast to the large members of the Pteropodidae,

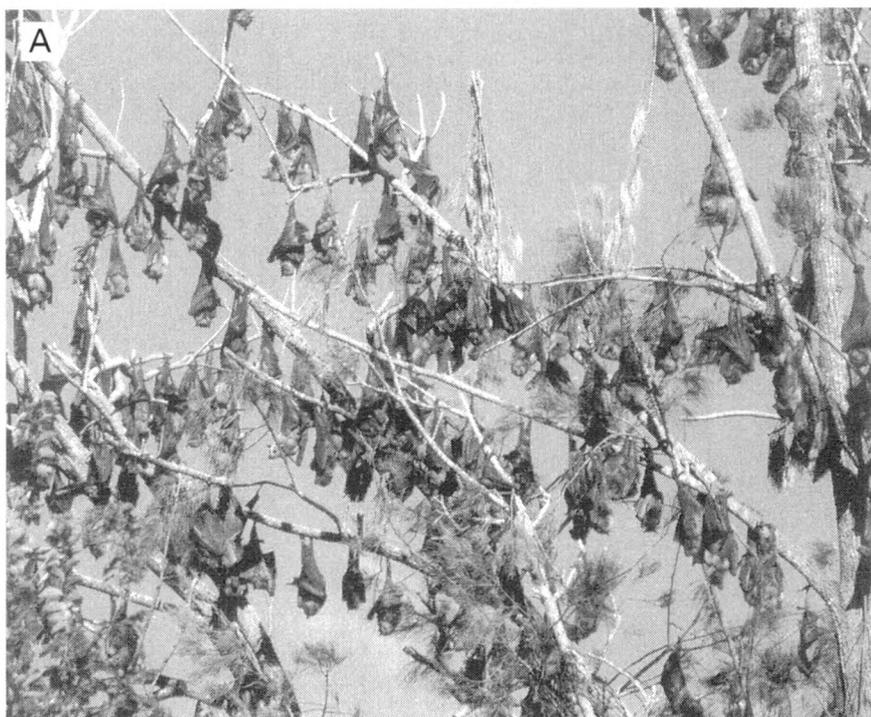


Figure 1.16. A, Colony of *Pteropus poliocephalus* roosting on branches of a partially defoliated trees in eastern Australia (photo by P. Birt); B, mixed colony *P. poliocephalus*, *P. alecto*, and *P. scapulatus* occupying defoliated trees in southeast Queensland, Australia (photo by T. Allofs).

smaller species of fruit and nectar feeding bats of both the New and Old Worlds are often solitary or form small groups (Bonaccorso 1998; Fenton et al. 1985; Morrison 1980; Tan et al. 1999).

Roost Fidelity

Bats exhibit a wide range of fidelity to their roosts. This variation is often reflected in the type of roost, life history stage, and form of social organization (Bradbury 1977b; Lewis 1995; McCracken and Wilkinson 2000). Bats that roost in relatively permanent roosts generally exhibit higher levels of fidelity compared to those that roost in more ephemeral situations (Lewis 1995). Although many species of cavity- and foliage-roosting bats show low fidelity to specific roost sites, they often exhibit high levels of fidelity to roost areas, with individuals moving among several alternate roosts. A number of reasons for roost lability have been proposed, including reduced probability of predation, lower ectoparasite loads, familiarity with different roost microclimates, disturbance, and decreased commuting costs to foraging areas (Lewis 1995).

Available data on roost fidelity for species that roost in tree cavities or beneath exfoliating bark generally can be grouped into three categories (table 1.4): species that, on average, shift roost sites every 1–2 d; those that shift every 3–10 d; and species that remain in the same roost for more than 10 d. These data indicate that 12 species (50%) shift roost sites almost every day. Six species, while still moving regularly, remain in the same roost for up to 10 d. Five species remain faithful to one roost for long periods: *Artibeus jamaciensis*, *Desmodus rotundus*, *Noctilio albiventris*, *Rhinolophus hildebrandti*, *Vampyrum spectrum*. Interestingly, each of the latter species often roost in large basal cavities in live trees. A number of species in which individuals shift roost sites regularly alternate between a core number of preferred roost trees (e.g., *Nyctalus noctula* [Kronwitter 1988], *Myotis daubentonii* [Rieger 1996], and *M. sodalis* [Callahan et al. 1997; Kurta et al. 1996]). In contrast, a new roost tree was occupied almost every day by colonies of *Chalinolobus tuberculatus*, with all individuals usually abandoning the roost together (O'Donnell and Sedgely 1999).

Bats that roost beneath exfoliating bark often show low levels of fidelity, which may be associated with the relatively ephemeral nature of these sites (Kurta et al. 1996; Lewis 1995). Movements to alternate roosts may occur every 1–2 d (e.g., Grindal 1999; Kurta et al. 1996; Mattson et al. 1996; Menzel et al. 2001), although longer occupations have been reported, especially during the maternity period (Humphrey et al. 1977). Kurta et al. (1996) found that pregnant female *M. sodalis* shifted roosts more often than did lactating or nonreproductive females. They suggested that pregnant females moved to reacquaint themselves with suitable roosts after returning from overwintering sites, whereas lactating females reduced shifting due to the added cost of moving young.

Several species roost beneath exfoliating bark during the nonbreeding season but abandon these sites in favor of tree cavities during the maternity period, as observed in *Lasionycteris noctivagans* (Mattson et al. 1996; Vonhof and Barclay 1996), *Nyctophilus geoffroyi* (Lumsden et al. 2002b), and *Nycticeus humeralis* (Menzel et al. 2001). Other species, such as *M. sodalis* (Callahan et al. 1977; Humphrey et al. 1977; Kurta et al. 1993, 1996) and *M. californicus* (Brigham et al. 1997), do, however, occupy roosts beneath exfoliating bark throughout the maternity period.

Lactating females typically shift roosts less often than nonbreeding individuals do, and this may reflect the energetic costs of moving nonvolant young between roosts or the limited availability of roosts suitable for rearing young (Kurta et al. 1996; Mattson et al. 1996; Menzel et al. 2001; Vonhof and Barclay 1996). In contrast, females in maternity roosts of some species, such as *C. tuberculatus* (O'Donnell and Sedgely 1999), shift as often as nonbreeding individuals, suggesting that, for these species, the benefits of shifting roosts outweigh the energetic costs. Roost sites were abundant in O'Donnell and Sedgely's (1999) study, which may indicate that the availability of suitable maternity roosts in other areas influences the rate of roost switching.

When individuals shift roosts, it is usually to one nearby. A number of studies have found that the mean distance between consecutive tree cavity or bark roosts is fewer than 400 m (table 1.4), although the distance between others may reach several kilometers (Kronwitter 1988; Rieger 1996). Distances between consecutive roosts are usually less than the distances between all roost sites and foraging areas, suggesting that being closer to foraging areas is not the reason for cavity-dwelling bats shifting among different roosts (Kurta et al. 1996; Lumsden et al. 2002a; O'Donnell 2001; Wilkinson 1985).

Roost fidelity in foliage-roosting vespertilionids, such as *Lasiurus borealis* and *L. seminolis*, is generally low, with individuals rarely using the same roost on consecutive days (Mager and Nelson 2001; Menzel et al. 1998). Menzel et al. (1998) reported that *L. borealis* and *L. seminolis* spent an average of 1.2 and 1.7d, respectively, in any one roost. Although both species moved frequently, roosts of *L. borealis* were located within a significantly larger area (2.6 ha) than those of *L. seminolis* (0.2 ha). Mager and Nelson (2001) found that 82% of the *L. borealis* roosts that they observed on consecutive days were less than 100 m apart.

Seasonal shifts in the roosting habitats of some foliage-roosting bats are associated with annual cycles of temperature or rainfall. In Australia, male and female *Syconycteris australis* shift from winter roosts in the warmer and moister rainforest edge and littoral rainforests to summer roosts in the cooler interior forests (Law 1993). Law postulated that this behavior allowed *S. australis* to avoid the relatively cool temperatures inside the forests in winter, as well as the hot temperatures of the forest exterior from spring through autumn. The moderate temperatures, high moisture-laden sea breezes, and buffering capacity of the forest appear to protect these bats from seasonal extremes.

Similarly, the foliage-roosting microchiropteran *Nyctophilus bifax* in eastern Australia shifts its roost location from the forest interior in late spring to the forest edge in late autumn, suggesting that local movements of this species make it possible for individuals to avoid high temperatures in spring–autumn and low temperatures in winter (Lunney et al. 1995).

Traditional roosts of most pteropodids are used seasonally, often in response to climatic variation and the availability of food (Fleming and Eby, this volume; Law 1993; Loughland 1998; Nelson 1965; Okon 1974; Parry-Jones and Augee 1991; Ratcliffe 1932; Thomas 1983; Vardon and Tidemann 1999). In West Africa, three species (*Eidolon helvum*, *Myonycteris torquata*, and *Nanonycteris veldkampii*) migrate in response to the seasonal availability of food (Thomas 1983). *Pteropus poliocephalus* migrates distances of up to 750 km along the east coast of Australia in response to seasonal fruiting and flowering phenologies (Eby 1991; Spencer et al. 1991). Although some colonies of *P. conspicillatus* move seasonally between sites, most remain in the same general areas showing a strong affinity for rainforest trees year round (Richards 1990a). In contrast, *P. alecto* moves between roosts seasonally, from bamboo and mangrove habitats in the dry season to rainforest in the wet season (Palmer and Woinarski 1999).

Day roosts of the African species *Epomophorus wahlbergi* are commonly located in riverine or gallery forests (Fenton 1992b; Fenton et al. 1985; Wickler and Seibt 1976). Typically, three to six individuals roost in groups spaced a few centimeters apart. Roost switching appears to be common, with entire groups moving several meters or more every 5–6 d. By contrast, *Epomophorus gambianus* forms colonies ranging from a few to 50–100 well-spaced individuals in the crowns of trees (Jones 1972; Marshall and McWilliam 1982). In Australia and Papua New Guinea, *Nyctimene robinsoni* and *Syconycteris australis* roost alone in dense rainforest foliage (Spencer and Fleming 1989; Law 1993; Winkelmann et al. 2000). *Syconycteris australis* shows little fidelity to specific roosts, and roost sites are seldom occupied for more than a single day (Law 1993).

Influence of Roost Selection on Social Organization and Mating Systems

Our understanding of how the roosting environment influences social biology and mating systems of bats is in its infancy. Research on several species has revealed a wide range of mating systems in foliage-roosting bats, including leks in *Hypsignathus monstrosus* (Bradbury 1977a); multimale/multifemale groups in *Epomophorus wahlbergi* (Wickler and Seibt 1976); seasonally variable, single male/multifemale aggregations in *Pteropus seychellensis* (Cheke and Dahl 1981); year-round harems with labile female groups in *P. mariannus* and *P. tonganus* (Grant and Banack 1999; Wiles 1987), *Cynop-*

terus sphinx (Balasingh et al. 1995; Storz et al. 2000b), and *C. brachyotis* (Tan et al. 1997); seasonally variable, multimale/multifemale groups in *P. poliocephalus* (Nelson 1965); year-round, multimale/multifemale groups in *P. giganteus* (Neuweiler 1969); and monogamy in *P. samoensis* (Banack 1996; Craig et al. 1994).

One hypothesis for the evolution of polygyny is that resources are limiting (Clutton-Brock 1989; Emlen and Oring 1977). When breeding females are distributed among defensible roosts (mating territories), the potential for polygyny will depend on the site fidelity (or group cohesion) of the females. In American Samoa, observations on *P. tonganus* indicate that this species roosts in large colonies, ranging upward to several thousand individuals. Within these colonies year-round harem groups are formed, averaging 5.3 females per male, with males, either singly or in groups, occupying roosts on trees surrounding reproductive females (Grant and Banack 1999). Harems typically roost in trees that are devoid of leaves. When bats roost in live trees, males typically remove leaves from roost areas, and scent mark specific roost sites, which they defend from conspecifics. Harem boundaries are delineated by the branching patterns of the roost trees. Grant and Banack (1999) suggested that the mating system of *P. tonganus* had elements of both resource defense (tree roosts) and female defense polygyny. In contrast, the sympatric *P. samoensis* typically roosts alone or in monogamous pairs (Banack 1996; Craig et al. 1994; Pierson and Rainey 1992).

Cynopterus sphinx is one of the best-studied megachiropterans with respect to the effect of roost resources on its mating system. Observations suggest that tents are constructed by single males and that these males are joined by one or more females once a tent is completed (Balasingh et al. 1995; Bhat and Kunz 1995; Storz et al. 2000a, 2000b). Solitary bats that have been observed constructing tents are invariably males (Storz et al. 2000b), and tent construction appears to occur several weeks or months before the arrival of females (Storz and Kunz 2000). The unique characteristics of stem tents (fig. 1.15, also figs. 1.9H and 1.10) make it possible for males to defend these semienclosed structures and their female occupants from incursions by other males (Balasingh et al. 1995; Bhat and Kunz 1995; Hodgkison et al., in press; Kunz and McCracken 1996; Storz et al. 2000a, 2000b).

The question of whether female tent-making bats select roostmates on the basis of tent quality or some characteristic of the male deserves further study. Based on an analysis of several tent variables, neither Balasingh et al. (1995) nor Storz et al. (2000a, 2000b) found a significant relationship between these variables and group size in *C. sphinx*. Notwithstanding, group size varies seasonally, with larger harem groups forming in the dry season than in the wet season (Storz et al. 2000b). Other observations suggest that variation in harem size may be largely influenced by transient movements of females among adjacent roosts (Storz et al. 2000a).

Tents that *C. sphinx* construct in flower/fruit clusters of the kital palm may persist for several years, and harem males may retain breeding tenure for up to four breeding seasons at these sites (Storz et al. 2000b). Males and females generally remain faithful to one colony (a spatial array of several tents), but individuals often switch roosts from one breeding period to another (Storz et al. 2000b). Limited availability of roosts is not sufficient to explain harem group formation in female *C. sphinx* (Storz et al. 2000b). Because males construct and occupy tents in the absence of females, Storz et al. (2000b) suggested that the male mating strategy was based on territorial defense of roosts rather than on direct defense of labile female groups. Thus, the mating system of *C. sphinx*, as in other polygynous bat species (see McCracken and Wilkinson 2000), can be attributed largely to variation in behavioral cohesiveness of reproductively active females (Balasingh et al. 1995; Storz et al. 2000b).

The relationship between roosting ecology, roost fidelity, and mating systems has also been studied extensively in *Artibeus jamaicensis*, as this species is known to form harems in tree cavities (Morrison 1979; Morrison and Handley 1991; Morrison and Morrison 1981), caves (Kunz et al. 1983; Ortega and Arita 2000), and tents (Kunz and McCracken 1996; Foster and Timm 1976; Timm 1987). Morrison (1979) postulated a mating system based on resource defense polygyny, largely based on his observations that tree cavities (see fig. 1.1B) were limited resources on Barro Colorado Island, Panama. He suggested that a polygynous mating system would not be expected in caves and foliage roosts because these resources were not limiting. Kunz et al. (1983) tested this hypothesis by examining the group size and social organization of *A. jamaicensis* in a cave environment in Puerto Rico. Their observations indicated that caves with solution cavities offered resources to *A. jamaicensis* that were potentially limiting as well as defensible, supporting the hypothesis that such caves provided potential for the evolution of polygyny in this species. Subsequently, Kunz and McCracken (1996) observed social groups of tent-roosting *A. jamaicensis* in palmate umbrella tents in Trinidad and, similarly, described this as a polygynous mating system based on the ability of males to defend these roosts. Adult males roosted singly or in larger groups composed of one male (rarely two) and from one to 10 females. During parturition and lactation, females and young roosted separately from males.

Available data on other foliage-roosting and cavity-roosting species strongly suggest a predominance of female-biased social groups. Multi-female/single male groups of *Ectophylla alba* form following parturition (Brooke 1990). The presence of single males in the tent immediately following parturition, but not at other times, suggests a postpartum estrus in this species. Whether males defend the leaf as a resource to gain access to females has not been determined (Brooke 1990). Observations that some males are found in bachelor groups suggests that harem males may prevent other males

from gaining access to the tents or to females during the receptive period of females.

Patterns of year-round harem maintenance have been reported for other polygynous species (McCracken and Wilkinson 2000), including *Saccopteryx bilineata*, which typically roosts in the semidarkened spaces of buttress cavities that form in large, tropical trees (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976; Voigt et al. 2001). Colonies range upward to 42 individuals, and within these colonies, males defend territories of 1–3 m² of vertical surface in the buttress cavity during the day. Females are distributed among these territories, forming harems of one to eight individuals per male (Bradbury and Vehrencamp 1976). Movements by males between colonies are less frequent than by females. Odor appears to play an important role in this and other harem-forming emballonurids (Voigt and Helversen 1999). Harem males of *S. bilineata* disseminate odors by salting and fanning them from a proptagial sac while in the roost and during energetically costly hovering displays before females. Females subsequently choose among the territorial males with whom they may mate (Voigt and Helversen 1999).

The mating system of *Pipistrellus nanus* also appears to be strongly influenced by its roosting habits. When roosting in furled leaves, males are seldom found together with females and their young during parturition and lactation (Happold and Happold 1996). At other times of the year, adults roost both singly and in small groups of up to 12 individuals. Where adult males roost with females, there is usually only a single male present. Males may exclude other males from their roosts, but it is not clear how and why this exclusion occurs. Group composition is relatively labile, but some males attract more females than do others.

Pipistrellus nanus exhibits little fidelity to specific roosts but, instead, shows fidelity to clumps of banana plants (Happold and Happold 1996). Males show higher fidelity to the clumps of banana plants than do females, but no relationship was found between the reliability of clumps and number of females recruited. Females seem to be attracted to males independent of roost quality, and males and females roost with several potential mates in succession, with no evidence for sustained bonding (Happold and Happold 1996). Furled banana leaves were not limiting in this area, with less than 50% of the available roosts occupied at any time. Because competition was minimal for these roosts, males did not have a mechanism for demonstrating their relative fitness to females, and thus Happold and Happold (1996) suggested a promiscuous mating system for this species.

Myotis bocagei also roosts in furled banana leaves (*Musa* spp.) and forms harems with stable female membership, with male tenure extending up to 1 yr or more (Brosset 1976). Differences in mating system between *M. bocagei* and *P. nanus* may reflect the fact that females of *M. bocagei* are not simultaneously

receptive, as they are in *P. nanus* (Happold and Happold 1996). Intraspecific differences also occur, as when *P. nanus* roosts in thatched roofs, males defend territories and form harems (O'Shea 1980). Thus, the mating system in *P. nanus* varies depending on the availability of semipermanent thatch roosts, on the one hand (O'Shea 1980), and the relative ephemeral roosts in banana leaves, on the other (Happold and Happold 1996).

Relationships between Roosting and Foraging Behavior

Night Roosts

Night roosts play an important functional role in the foraging ecology of bats. They are used as resting places between foraging bouts, promote digestion and energy conservation, provide retreats from predators and inclement weather, provide places to ingest food transported from nearby feeding areas, function as feeding perches for sit-and-wait predators, and serve as places that promote social interactions and information transfer (Kunz 1982).

A wide range of structures are used by bats as night roosts, including buildings, bridges, caves, mines, or rock surfaces (reviewed in Kunz 1982). Comparatively little is known about night roosts in tree cavities or in vegetation. Some bats return to their day roost at night (e.g., *Nyctalus noctula* [Kronwitter 1988], *Pipistrellus nanus* [O'Shea 1980], and *Tonatia silvicola* [Kalko et al. 1999]). Harem males of *Cynopterus sphinx* and *C. brachyotis* typically roost in tents during the day and night, although females use separate feeding roosts at night (Balasingh et al. 1995; Bhat and Kunz 1995; Elangovan et al. 1999; Tan et al. 1997).

Cavity-roosting bats sometimes select night roosts separate from their day roost (e.g., *Eptesicus fuscus* [Brigham 1991] and *Scotophilus (borbonicus) leucogaster* [Fenton 1983]). Night roosts may be located in the vicinity of feeding areas to reduce the energetic cost of returning to the day roost and to minimize the associated risk of predation (Kunz 1982). The distance to foraging areas and the prevailing weather conditions may influence whether individuals return to the day roost following feeding bouts (Shiel et al. 1999). Brigham (1991) compared the proportion of times that separate night roosts were used by *E. fuscus* for individuals foraging at different distances from the diurnal roost. When bats foraged less than 1 km from the day roost, they used alternate night roosts 25% of the time. In contrast, when bats foraged up to 4 km away, they used night roosts 60% of the time.

The proportion of the night spent in night roosts varies both daily and seasonally in relation to reproductive condition, prey density, and ambient temperature. Long night-roosting periods in *Myotis lucifugus* that roost in buildings are generally associated with cool nights and low prey densities (Anthony et al. 1981). Females return to the day roost most frequently when

they have dependent young that require feeding during the night (Racey 1982). Once young bats are independent, females increasingly use separate night roosts (Anthony et al. 1981).

Feeding roosts are used by bats that "capture" food elsewhere and retreat to a roost to consume the food. In this way, plant-visiting species that use feeding roosts away from source trees make an important contribution to seed dispersal (Boon and Corlett 1989; Morrison 1978a; Richards 1990b). Feeding roosts are used extensively by both mega- and microchiropteran frugivores. Small, canopy-feeding, foliage-roosting bats may harvest fruits and carry them to nearby feeding roosts (Bhat 1994; Boon and Corlett 1989; Charles-Dominique 1993; Elangovan et al. 1999; Law 1993; Spencer and Fleming 1989). This may be a form of antipredator behavior (Fenton et al. 1985; Kunz 1982; Spencer and Fleming 1989) or perhaps avoidance behavior in response to conspecifics at food sources (Richards 1990b, 1995). Heithaus and Fleming (1978) estimated that individual *Carollia perspicillata* made 40–50 trips a night between fruiting trees and feeding roosts.

Feeding roosts of small species are often located in dense vegetation and are thus relatively inaccessible to terrestrial predators (Morrison 1978a). In contrast, larger pteropodids, which are less vulnerable to predation, generally remain in the food tree where they consume the fruit and nectar located at that site (Richards 1990b; Thomas and Fenton 1978). *Pteropus conspicillatus* in northern Australia exhibits what Richards (1990b) termed a "raider vs. resident strategy" at feeding sites. Dominant individuals establish feeding territories in fruit trees early in the evening until the tree is full of feeding bats. Later in the night, when other bats attempt to join the feeding group, these individuals are evicted by the residents. Fruit taken by the raiders before escaping from the aggression of residents is taken elsewhere to be consumed (Richards 1990b).

Some insectivorous and carnivorous microchiropterans use feeding roosts, often when their prey is too large to consume in flight. These "sit-and-wait" predators use feeding perches, where individuals hang from vantage points while scanning their surroundings for both vertebrate and invertebrate prey (Audet et al. 1991; Csada 1996; Schulz 1986). Forays to pursue prey are typically brief, with a bat returning to its original perch to consume the item (Vaughan and Vaughan 1986). Species that use this foraging strategy are predominantly gleaning bats with low wing loading and low aspect ratios (e.g., *Hipposideros didactyla* [Pavey 1998], *Lavia frons* [Vaughan and Vaughan 1986], *Macroderma gigas* [Tidemann et al. 1985], *Megaderma lyra* [Audet et al. 1991], *Nycteris grandis* [Fenton et al. 1990], *Rhinolophus hildebrandti* [Fenton and Rautenbach 1986], *R. rouxi* [Neuweiler et al. 1987], *Tonatia silvicola* [Kalko et al. 1999], and *Trachops cirrhosus* [Kalko et al. 1999]). Hunting from feeding perches may be a way to minimize foraging costs and allow capture of heavy prey relative to the bat's body mass without incurring high costs of flight (Audet et al. 1991).

Nocturnal calling roosts are common among male epomophorine bats in Africa (e.g., *Epomophorus wahlbergi* [Wickler and Seibt 1976] and *Hypsignathus monstrosus* [Bradbury 1977a]). Males typically space themselves apart hanging from small branches and undertake extensive periods of calling and displaying to attract females. Several species of microchiropterans use calling or "singing" roosts. Males of *Nyctalus noctula* in Europe spend considerable time during the mating season, calling from their roost to attract females (Alcalde 1999; Kronwitter 1988). Singing roosts used by *Mystacina tuberculata* in New Zealand are usually located in small trees within 100 m of day roosts (Daniel 1990; O'Donnell et al. 1999). Single bats call from the openings of small cavities for periods of 10–40 min. The repetitive, high-intensity song is audible to the human ear for up to 50 m. Other bats visit these calling sites, some of which are allowed to enter the cavity while others are repelled aggressively.

Relationships among Roosts and Foraging Areas

The relationship among roosts and foraging areas is influenced by several factors, including roost type, the availability of roosts, food and water, flight morphology, colony size, and reproductive cycles. Small microchiropterans often commute less than several kilometers between roost sites and foraging areas (e.g., Brigham et al. 1997; Campbell et al. 1996; Sasse and Pekins 1996; Schulz and Hannah 1998). However, radiotelemetry studies indicate that many species of bats fly greater distances and have larger home ranges than previously recognized and sometimes forage at distances ranging from 10 to 30 km from roost sites (Arlettaz 1999; Barclay 1989; O'Donnell 2001; Pierson 1998). In these situations, especially where roost sites are limiting, bats select optimal roosting sites and optimal foraging areas and appear not to minimize commuting distances to reduce energetic costs (Brigham 1991; Fenton et al. 1985; Lumsden et al. 2002a). Although home ranges may be large, individuals often concentrate their nightly activity in localized areas rather than foraging over the entire range (O'Donnell 2001; O'Donnell et al. 1999; Robinson and Stebbings 1997).

Flight morphology and body size have been used to interpret foraging ranges of bats, with larger species and those with high aspect ratios (narrow, pointed wings) likely to commute greater distances to forage (Fenton 1997; Jones et al. 1995). However, some species do not conform to these predictions. For example, in New Zealand, *Chalinolobus tuberculatus* (10 g) and *Mysticina tuberculata* (15 g) both fly considerably further from their roost than predicted, up to 19 and 24 km, respectively (O'Donnell 2001; O'Donnell et al. 1999). Different flight patterns may be used for commuting from roosts sites compared to those for foraging. Some species (e.g., *Myotis emarginatus* and *M. myotis* in Europe [Arlettaz 1999; Audet 1990; Krull et al. 1991] and *Nyctophilus geoffroyi* and *Hipposideros* spp. in Australia [Lumsden et al. 2002a; Pavey and Burwell 2000]) use a slow maneuverable flight pattern while foraging but employ

a faster and more direct flight when commuting, a strategy that may enable them to commute greater distances.

Proximity to food resources may also be an important determinant in roost site selection for some species. Bats that use roost types that are abundant (e.g., foliage) are more likely to move their day roosts in response to food availability. The roosting and foraging behavior of small, solitary, foliage-roosting, and fruit-eating pteropodids differ from what is often observed in the larger, gregarious species. *Micropteropus pusilla*, *Epomops buettikorkeri*, and *Epomophorus wahlbergi* from Africa roost alone or in small groups and feed near their roosts in the forest canopy (Fenton et al. 1985; Thomas 1982; Wickler and Seibt 1976). *Nyctimene robinsoni* and *Syconycteris australis* from Australasia forage mostly in the subcanopy of rainforests, and generally roost near food trees used on the previous night (Law 1993; Spencer and Fleming 1989; Winkelmann et al. 2000).

In contrast, large gregarious megachiropterans such as *Eidolon*, *Pteropus*, and *Acerodon* often form large colonies that are located many kilometers from feeding areas (Eby 1996; Nelson 1965; Palmer and Woinarski 1999; Richards 1995; Tidemann, et al. 1999). Large pteropodids, in particular, are highly mobile, and their roosting and foraging behavior appear to be adaptations to fruit and nectar sources that are patchy in time and space (Fleming and Eby, this volume; Palmer and Woinarski 1999).

To examine the influence of food availability on the foraging distances of a New World plant-visiting bat, Morrison (1978b) compared the commuting distances of *Artibeus jamaicensis* in two areas with different densities of figs (*Ficus* spp). On Barro Colorado Island, Panama, where figs were abundant, females commuted 0.6 km, whereas they commuted 8 km in Chamela, Mexico, where figs were much less common. Cavity-roosting females returned to the same roost even after shifting foraging areas, and Morrison (1978b) suggested that, if suitable roosts were scarce, commuting a longer distance to a food resource may cost less than searching for a suitable roost near the new foraging site. After Hurricane Hugo devastated Puerto Rico in 1989, population levels of *Stenoderma rufum* declined by 70%, and, in response to the lower food availability, individuals home ranges increased fivefold. This increased the cost of commuting and foraging, in terms of time and energy, and may have affected their reproductive success (Gannon and Willig 1994).

Proximity to water appears to be an important consideration in roost site selection by bats (Campbell et al. 1996; Mattson et al. 1996; Ormsbee and McComb 1998). Some species of insectivorous bats concentrate foraging directly over or in the vicinity of water (e.g., Bogdanowicz 1994; Brigham 1991; Jaberg et al. 1998), and hence the energetic costs of commuting may be reduced when roosts are located nearby. Water is also required for drinking by many species (Kurta et al. 1989, 1990), which is reflected in the concentration of bats observed at watering holes in arid and semiarid regions (e.g.,

Lumsden and Bennett 1995; Szewczak et al. 1998). Some bats also visit watering holes to obtain nutrients such as calcium and sodium, which may otherwise be limiting resources, especially during pregnancy and lactation (Barclay 1995).

The number of individuals in a roost may influence the distance that bats need to travel to find food. Refuging theory (Hamilton and Watt 1970) predicts that some individuals in a refuge should commute farther than others to minimize competition. Solitary roosting species should have little competition for food close to their roost, whereas food resources may be limiting around large communal roosts. In Western and American Samoa, *Pteropus samoensis*, which roost singly or in small groups, forage largely in the same area in which they roost (Brooke et al. 2000; Cox 1983; Rainey 1998; Wilson and Engbring 1992). In contrast, the sympatric *P. tonganus*, which roosts in colonies of several thousand individuals, commutes long distances from roosting sites to foraging areas (Richmond et al. 1998; Wilson and Engbring 1992).

Reproductive condition may influence foraging behavior, with higher energetic demands on females during the breeding season. Lactating females typically forage closer to their roost sites than do pregnant or nonbreeding females, presumably to reduce the time and energetic cost of returning to suckle young during the night (e.g., *Chalinolobus tuberculatus* [O'Donnell 2001], *Nyctalus leisleri* [Shiel et al. 1999], *Nyctophilus bifax* [Lunney et al. 1995], and *Plecotus auritus* [Fuhrmann and Seitz 1992]). However, some species fly similar or greater distances (e.g., *Chalinolobus gouldii* [Lumsden et al. 2002a], *Lasiurus cinereus* [Barclay 1989], and *Nyctophilus geoffroyi* [Lumsden et al. 2002a]), suggesting that for these species the energetic benefits of foraging in optimal feeding areas outweigh the commuting costs.

The time spent by females in the day roost during the night varies throughout the lactation period in response to the thermoregulatory abilities of the young and the type of roost selected. For example, the exposed foliage roosts used by *L. cinereus* may require females to spend more time with their young early in lactation to keep them warm (Barclay 1989). As young develop, the time that females spend roosting declines and the length of foraging bouts increases. Once young *Chalinolobus tuberculatus* commence flying, females may commute greater distances to foraging areas to reduce competition for food resources within the vicinity of the roost while the flight capabilities of the young develop (O'Donnell 2001).

Distances between roosts and foraging areas of the large pteropodids also can differ between sexes. In northern Australia, females of *P. alecto* are restricted to one roost when they have dependent young (Palmer and Woinarski 1999; Palmer et al. 2000). Females in large colonies may not have the flexibility to change to alternate roosts, especially if the cost of transport would place the young and mother at risk of predation. By contrast, males are less constrained in their roost selection. If food patches are widely spaced due to forest frag-

mentation, this may be an important factor in limiting areas that can be used as roosting sites (Eby 1991; Palmer and Woinarski 1999).

Conservation of Cavity and Foliage Roosting Bats

Bat populations continue to decline in many parts of the world (Hutson et al. 2001; Kunz and Pierson 1994; Kunz and Racey 1998; Mickleburgh et al. 1992; Racey and Entwistle, this volume; Wilson and Graham 1992). Factors that contribute to these declines vary regionally, but deforestation and conversion of native habitats to intensive agriculture or other human developments pose the greatest threats. Deforestation has reduced the availability of many important roost resources, and loss of such roosts is having an enormous impact on the density and distribution of local bat faunas.

In the Indo-Pacific region, Asia and Australia, where more than 60% of megachiropterans live on islands and in coastal habitats, deforestation is the most important factor contributing to their decline (Law 1996; Racey and Entwistle, this volume; Rainey 1998; Uzzurum 1998). Pressures resulting from unchecked human population growth in some countries, and the custom of land tenure in others (Whewell 1992), have contributed considerably to the loss of tropical forests (Arita and Ortega 1998; Marinho-Filho and Sazima 1998; Uzzurum 1998). Some roosting and foraging habitats of bats are being severely altered or are being made uninhabitable (Rainey 1998; Robertson 1992). For example, mangrove forests, which serve as important habitats for several island and coastal species of pteropodids, are largely being destroyed for the woodchip industry (Robertson 1992; Start and Marshall 1976), aquaculture, or commercial development (A. Zubaid, personal communication).

Reductions in some populations of pteropodids on tropical islands have been attributed to the direct and indirect impacts of periodic typhoons (Craig et al. 1994; Lemke 1992; Pierson et al. 1996; Rainey 1998). In addition to bats being killed during these storms, food and roosting resources may be severely depleted, resulting in the fragmentation of camps into smaller groups and a reduction in the recruitment of young animals (Banack 1996; Rainey 1998; Richards 1990a; Robertson 1992). On some islands in the western Indian Ocean, the combined effect of deforestation and typhoons has severely threatened the existence of already endangered faunas (Cheke and Dahl 1981; Craig et al. 1994; Reason and Trehwella 1994). Overhunting by humans and predation by the introduced brown tree snake (*Boiga irregularis*) have also had an impact on local populations of some species of *Pteropus* (Craig et al. 1994; Mickleburgh et al. 1992; Rainey 1998).

The capacity of colonial *Pteropus* to roost in modified habitats varies widely. Species such as *P. niger* on Mauritius (Cheke and Dahl 1981) and *P. samoensis* in American Samoa (Pierson et al. 1996) roost mostly in primary forests. In the highly fragmented landscapes of eastern Australia, *P. poliocephalus*, *P. alecto*,

and *P. scapulatus* commonly roost in small patches of remnant lowland vegetation surrounded by agricultural land or urban development (Lunney and Moon 1997; Parry-Jones and Augee 2001). While these species show high fidelity to traditional camps, they may use alternate roosts when existing vegetation is cleared or made uninhabitable (Lunney and Moon 1997; Tidemann et al. 1999).

Conservation strategies for many temperate species must address seasonal and geographical variation in their roosting habits (Pierson 1998; Racey 1998; Racey and Entwistle, this volume). Some temperate species hibernate in caves and rock crevices in winter (Barbour and Davis 1969) but roost in tree cavities or beneath exfoliating bark in warm months (Barclay and Brigham 1996). Thus, protecting only their summer roosts is inadequate for the conservation of these species. For example, population declines reported for the endangered *Myotis sodalis* were initially attributed to disturbances at caves, where this species hibernates. But while most of the critical hibernacula have now been protected, populations have continued to decline. Only recently have efforts been made to focus attention on protecting summer roosts and foraging habitats. Species dependence on cavity roosts may vary geographically. For example, *Eptesicus fuscus* is commonly associated with buildings in eastern North America (Kunz and Reynolds, in press) but appears to depend more on tree cavities in western North America (Betts 1996; Brigham 1991; Vonhof 1996).

Protection of forests that provide important roost and food resources for bats should be an important conservation goal (Pierson 1998). Densities of tree-cavity-roosting species are greater in old-growth stands, where structural diversity provides a range of roosting options (Barclay and Brigham 1996). Current forest management practices that favor even-age monospecific stands, short rotation times, and selective removal of dead and dying trees reduce the availability of roosting habitat of cavity-roosting species (Barclay and Brigham 1996). Unless efforts are made to reverse these forest management practices, expected declines in bat populations and species richness are likely to have serious consequences for ecosystem function (Pierson 1998).

In western Europe, deforestation and habitat fragmentation have long threatened the conservation of bats and other wildlife (Bright 1993). In Great Britain, few contiguous forest habitats exist, which limits the availability of suitable roosting sites for tree-cavity bats. In other parts of Europe, however, some forests are sufficiently mature or protected to provide suitable habitat for species that roost in tree cavities (e.g., *Nyctalus noctula* [Boonman 2000] and *Myotis bechsteinii* and *M. daubentonii* [Kerth et al. 2000]). Notwithstanding, these and other European bat species also roost in manmade structures (Entwistle et al. 1997; Kerth et al. 2000; Schober and Grimmerger 1989; Swift 1998) or in boxes designed for birds (Benzal 1991) and bats (Stebbing and

Walsh 1985; Swift 1998). The successful use of bat houses in Europe and North America (Tuttle and Hensley 1993), in providing roosting habitats for bats that traditionally roost in tree cavities, is a conservation management practice that is expected to increase as forest management practices reduce the availability of natural tree cavities.

Many cavity-roosting species move among roost sites on a regular basis, using a number of trees within a defined roost area (Barclay and Brigham 1996, Lewis 1995; O'Donnell and Sedgely 1999). As a result, high densities of suitable roost trees are required (Kerth et al. 2000; Lumsden and Bennett 2000). Such roosts are most likely to occur in large, contiguous stands of mature forest. Suitable roosts are liable to be present in lower abundance in areas managed for timber production and in agricultural areas. Little is known about the impact of reduced densities of roost trees or the affect of roosting in suboptimal tree roosts. However, Brigham and Fenton (1986) demonstrated that reproductive success in *E. fuscus* was lower in suboptimal building roosts, and this also may be the case for bats that roost in tree cavities. The use of artificial bat houses (which may mimic natural tree cavities) provide a model for testing the effects of different roost variables on reproductive success (Kerth et al. 2000).

Forest management practices that focus on retaining high densities of roost trees should benefit cavity-roosting species. Management should focus on maintaining potential roost trees that are easily accessible to bats and have moderate to high levels of exposure to solar radiation (e.g., snags that protrude above the canopy, in canopy gaps, and adjacent to forest clearings [Barclay and Brigham 1996; Waldien et al. 2000]). The concentration of snags in clusters may be beneficial to some species (Waldien et al. 2000). Methods that promote the creation of snags and accelerate cavity formation need to be considered as management options (Bull and Partridge 1986; Carey and Sanderson 1981; Lewis 1998). Because small cavities form as precursors to larger ones, bats may be among the first cavity-using species to colonize rejuvenating forests (Barclay and Brigham 1996; Tidemann and Flavel 1987). In part, this reflects the strong commuting abilities of bats, which gives them an advantage over nonvolant mammals in exploiting newly available habitat (Rawlinson et al. 1992; Whitaker and Jones 1994). Species that roost beneath exfoliating bark may be able to recolonize forests earlier than species dependent on large cavities (see Kunz 1996; Mackowski 1984). In addition, as many species have large home ranges and travel considerable distances between roost sites and foraging areas, the environment in which they live needs to be evaluated and managed at the landscape scale (Barclay and Brigham 1996; Lumsden et al., in press a).

In some regions, such as Africa and India, the collection of firewood by people has increasingly become an important factor in forest destruction and

modification. When human populations exceed the carrying capacity of local ecosystems, natural habitats are readily converted into deserts and wasteland (Racey and Entwistle, this volume). Overgrazing by elephants and other wildlife that are restricted to reserves in parts of Africa has led to irreversible changes in woodlands on which bats depend for both roosts and food (Fenton and Rautenbach 1998). Although some fruit-eating and insectivorous bats in tropical regions may be relatively common in urban and agricultural areas, far removed from forested areas, the numbers of endemic species in these regions have become severely reduced. In the Philippines, where there is a relatively high degree of endemism, endemic fruit bats have not been reported from urban orchards and agricultural areas (Utzurum 1995, 1998). Notwithstanding, some species such as *Cynopterus brachyotis* and *C. sphinx* have become relatively common and exploit a wide variety of human-altered habitats for roosting, including buildings in urban areas, as well as trees in orchards and gardens (Balasingh et al. 1995; Bhat 1994; Bhat and Kunz 1995; Boon and Corlett 1989; Tan et al. 1997; Utzurum 1998).

Plantings of ornamental trees in some urban areas have provided new roosting (and feeding) opportunities for some foliage-roosting species (e.g., *Cynopterus sphinx* [Balasingh et al. 1995; Bhat and Kunz 1995], *C. brachyotis* [Tan et al. 1997], *C. horsfield* [Tan et al. 1999], *Lasiurus xanthinus* [Constantine 1998], and *Scotophilus kuhlii* [Rickart et al. 1989]). The use of palm "skirts" as a roost resource appears to be important for *L. xanthinus* in the southeastern United States, as recent range extensions have been reported where ornamental palms have been planted (Constantine 1998). Similarly, plantings of ornamental palms along boulevards and in residential areas in the Old World tropics may not only provide opportunities for range expansion, but may also support increased densities of bats that use these roost resources (Tan et al. 1997).

Future conservation efforts for bats in both temperate and tropical ecosystems must include protection of roost resources. In large measure, this can best be accomplished by focusing on protecting large forest reserves and suitable corridors for seasonal migrants (Fleming and Eby, this volume). Many of the megachiropterans that form large aggregations at traditional roost sites disperse seasonally over great distances, and their protection requires management strategies that focus on the protection of movement corridors as well as on local habitats that provide both roosts and food resources. The protection of forest habitats that provide such resources should be a high priority for conservation biologists (Racey and Entwistle, this volume). Because island and coastal ecosystems have experienced the most severe pressures from deforestation and commercial development, increased efforts are needed to protect these fragile ecosystems (Rainey 1998).

Island and peninsular species that show high levels of endemism (Corbet and Hill 1992; Heaney 1986; Pierson and Rainey 1992; Rodriguez-Duran and

Kunz 2001) and have evolved highly dependent, and sometimes obligate, relationships with the local flora are most vulnerable (Kunz 1996). The loss of "keystone" or "pivotal" species can lead to an ever-increasing cascade of extinctions (Cox et al. 1991; Howe 1984; Mills et al. 1993; Myers 1986; Rainey et al. 1995). The enumeration (Crome and Richards 1988; Francis 1990; Zubaid 1993) and protection of biological diversity in temperate and tropical forest ecosystems, especially on islands and in coastal ecosystems, remains one of the greatest challenges to conservation biologists.

Acknowledgments

We are grateful to S. Churchill, P. Eby, A. Kurta, C. O'Donnell, E. D. Pierson, and M. Schulz for suggestions on the manuscript and to T. Allofs, J. Balasingh, P. Birt, P. Eby, P. Espy, M. B. Fenton, R. Hodgkison, L. Lumsden, D. H. Morrison, E. Rooks, C. Taylor, K. H. Tan, M. D. Tuttle, T. A. Vaughan, M. Vonhof, and R. Voss for sharing their photographs and illustrations that were used in this chapter. We also thank Cari Watkins, who assisted in the preparation of the final manuscript and illustrations. Kunz's research on roosting ecology has been supported by the U.S. National Science Foundation, the National Geographic Society, and the Lube Foundation, and Lumsden's research has been supported by the Arthur Rylah Institute.

Literature Cited

- Alcalde, J. T. 1999. New ecological data on the noctule bat (*Nyctalus noctula* Schreber, 1774) (Chiroptera, Vespertilionidae) in two towns of Spain. *Mammalia*, 63:273–280.
- Alder, H. 1994. Erste erfahrungen mit dem data logger: Ereigniszählung vor baumhöhlenquartieren von wasserfledermausen, *Myotis daubentonii*, bei gleichzeitiger messung mikroklimatischer werte. *Mitteilungen der Naturforschenden Gesellschaft Schaffhausen*, 39:119–133.
- Aldridge, H. D. J. N., M. Orbist, H. G. Merriam, and M. B. Fenton. 1990. Roosting, vocalizations, and foraging by the African bat *Nycteris thebaica*. *Journal of Mammalogy*, 71:242–246.
- Allen, G. M. 1939. *Bats*. Harvard University Press, Cambridge, Mass.
- Anthony, E. L. P., M. H. Stack, and T. H. Kunz. 1981. Night roosting and the nocturnal time budget of the little brown bat, *Myotis lucifugus*: effects of reproductive status, prey density, and environmental conditions. *Oecologia*, 51:151–156.
- Arendt, W. J. 1986. Bat predation by the St. Lucia boa (*Boa constrictor orophias*). *Caribbean Journal of Science*, 22:219–220.
- Arita, H. T., and J. Ortega. 1998. The middle American bat fauna: conservation in the Neotropical-Nearctic border. Pp. 295–308 *in*: *Bat Biology and Conservation* (T. H. Kunz and P. A. Racey, eds.). Smithsonian Institution Press, Washington, D.C.
- Arlettaz, R. 1999. Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. *Journal of Animal Ecology*, 68:460–471.

- Audet, D. 1990. Foraging behavior and habitat use by a gleaning bat, *Myotis myotis* (Chiroptera: Vespertilionidae). *Journal of Mammalogy*, 71:420–427.
- Audet, D., D. Krull, G. Marimuthu, S. Sumithran, and J. B. Singh. 1991. Foraging behavior of the Indian false vampire bat, *Megaderma lyra* (Chiroptera: Megadermatidae). *Biotropica*, 23:63–67.
- Baagøe, J. S. 1978. Observations on the biology of the banana bat, *Pipistrellus nanus*. Pp. 275–282 in: *Proceedings of the Fourth International Bat Research Conference* (R. J. Olembo, J. B. Castelino, and F. A. Mutere, eds.). Kenya National Academy for Advancement of Arts and Sciences, Kenya Literature Bureau, Nairobi.
- Baker, R. H., and C. J. Phillips. 1965. Mammals from El Navado de Colima, Mexico. *Journal of Mammalogy*, 46:691–693.
- Baker, R. J., C. S. Hood, and R. Honeycutt. 1989. Phylogenetic relationships and classification of the higher categories of the New World bat family Phyllostomidae. *Systematic Zoology*, 38:228–238.
- Baker, R. J., C. A. Porter, J. C. Patton, and T. A. Van Den Bussche. 2000. Systematics of bats of the family Phyllostomidae based on Rag2 DNA sequences. *Occasional Papers, Museum of Texas Tech University*, 202:1–16.
- Balasingh, J., S. Isaac, and R. Subbaraj. 1993. Tent-roosting by the frugivorous bat *Cynopterus sphinx* (Vahl 1797) in southern India. *Current Science*, 65:418.
- Balasingh, J., J. Koilraj, and T. H. Kunz. 1995. Tent construction by the short-nosed fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae) in southern India. *Ethology*, 100:210–229.
- Banack, S. A. 1996. Flying foxes, genus *Pteropus*, in the Samoan Islands: interactions with forest communities. Ph.D. Dissertation. University of California, Berkeley.
- Barbour, R. W., and W. H. Davis. 1969. *Bats of America*. University Press of Kentucky, Lexington.
- Barbour, T. 1932. A peculiar roosting habit of bats. *Quarterly Review of Biology*, 7:307–312.
- Barclay, R. M. R. 1989. The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. *Behavioral and Ecological Sociobiology*, 24:31–37.
- Barclay, R. M. R. 1995. Does energy or calcium availability constrain reproduction in bats? *Symposia of the Zoological Society of London*, no. 67:245–258.
- Barclay, R. M. R., and R. M. Brigham, eds. 1996. *Bats and Forests Symposium*, October 19–21, 1995, Victoria, British Columbia, Canada. British Columbia Ministry of Forests, Victoria.
- Barclay, R. M. R., and K. J. Cash. 1985. A noncommensal maternity roost of the little brown bat (*Myotis lucifugus*). *Journal of Mammalogy*, 66:782–783.
- Barclay, R. M. R., P. A. Faure, and D. R. Farr. 1988. Roosting behavior and roost selection by migrating silver-haired bats (*Lasionycteris noctivagans*). *Journal of Mammalogy*, 69:821–825.
- Bates, P. J. J., and D. L. Harrison. 1997. *Bats of the Indian Subcontinent*. Harrison Zoological Museum, Sevenoaks, Kent.
- Becking, R. W. 1982. *Pocket Flora of the Redwood Forest*. Island Press, Covelo, Calif.
- Bennett, A. F., L. F. Lumsden, and A. O. Nicholls. 1994. Tree hollows as a resource for wildlife in remnant woodlands: spatial and temporal patterns across the northern plains of Victoria, Australia. *Pacific Conservation Biology*, 1:222–235.
- Bennett, M. 1993. Structural modifications involved in the fore and hind limb grip

- of some flying foxes (Chiroptera: Pteropodidae). *Journal of Zoology (London)*, 229:237–248.
- Benzal, J. 1991. Population dynamics of the brown long-eared bat (*Plecotus auritus*) occupying bird boxes in a pine forest plantation in central Spain. *Netherlands Journal of Zoology*, 41:241–249.
- Bernard, E. 1999. Notes on a colony of *Peropteryx leucoptera* (Emballonuridae) in Brazil. *Bat Research News*, 40:37–38.
- Betts, B. J. 1996. Roosting behaviour of silver-haired bats (*Lasionycteris noctivagans*) and big brown bats (*Eptesicus fuscus*) in northeast Oregon. Pp. 55–61 in: *Bats and Forests Symposium*, October 19–21, 1995, Victoria, British Columbia, Canada (R. M. R. Barclay and R. M. Brigham, eds.). British Columbia Ministry of Forests, Victoria.
- Betts, B. J. 1998. Roosts used by maternity colonies of silver-haired bats in northeastern Oregon. *Journal of Mammalogy*, 79:643–650.
- Bhat, H. R. 1994. Observations of the food and feeding behavior of *Cynopterus sphinx* Vahl (Chiroptera, Pteropodidae) at Pune, India. *Mammalia*, 58:363–370.
- Bhat, H. R., and T. H. Kunz. 1995. Altered flower/fruit clusters of the kitul palm used as roosts by the short-nosed fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae). *Journal of Zoology (London)*, 235:597–604.
- Bloedel, P. 1955. Observations on life histories of Panama bats. *Journal of Mammalogy*, 36:232–235.
- Bogdanowicz, W. 1994. *Myotis daubentonii*. *Mammalian Species*, 475:1–9.
- Boinski, S., and R. M. Timm. 1985. Predation by squirrel monkeys and double-toothed kites on tent-making bats. *American Journal of Primatology*, 9:121–127.
- Bonaccorso, F. J. 1998. *Bats of Papua New Guinea*. Conservation International, Washington, D.C.
- Boon, P. P., and R. T. Corlett. 1989. Seed dispersal by the lesser short-nosed fruit bat (*Cynopterus brachyotis*, Pteropodidae, Megachiroptera). *Malayan Nature Journal*, 42:251–256.
- Boonman, M. 2000. Roost selection by noctules (*Nyctalus noctula*) and Daubenton's bats (*Myotis daubentonii*). *Journal of Zoology (London)*, 251:385–389.
- Bradbury, J. W. 1977a. Lek mating behavior in the hammer-headed bat. *Zeitschrift für Tierpsychologie*, 45:225–255.
- Bradbury, J. W. 1977b. Social organization and communication. Pp. 1–72 in: *Biology of Bats* (W. A. Wimsatt, ed.). Academic Press, New York.
- Bradbury, J. W., and L. H. Emmons. 1974. Social organization of some Trinidad bats. I. Emballonuridae. *Zeitschrift für Tierpsychologie*, 36:137–183.
- Bradbury, J. W., and S. L. Vehrencamp. 1976. Social organization and foraging in emballonurid bats. I. Field studies. *Behavioral Ecology and Sociobiology*, 1:337–381.
- Brigham, R. M. 1991. Flexibility in foraging and roosting behaviour by the big brown bat (*Eptesicus fuscus*). *Canadian Journal of Zoology*, 69:117–121.
- Brigham, R. M., and M. B. Fenton. 1986. The influence of roost closure on the roosting and foraging behaviour of *Eptesicus fuscus* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology*, 64:1128–1133.
- Brigham, R. M., M. J. Vonhof, R. M. R. Barclay, and J. C. Gwilliam. 1997. Roosting behavior and roost-site preferences of forest-dwelling California bats (*Myotis californicus*). *Journal of Mammalogy*, 78:1231–1239.
- Bright, P. 1993. Habitat fragmentation and predictions for British mammals. *Mammal Review*, 230:101–111.

- Brooke, A. P. 1987. Tent selection, roosting ecology and social organization of the tent-making bat, *Ectophylla alba*, in Costa Rica. *Journal of Zoology* (London), 221:11–19.
- Brooke, A. P. 1990. Tent construction and social organization in *Vampyressa nymphaea* (Chiroptera: Phyllostomidae) in Costa Rica. *Journal of Tropical Ecology*, 3:171–175.
- Brooke, A. P., C. Solek, and A. Tualalelei. 2000. Roosting behavior of colonial and solitary flying foxes in American Samoa (Chiroptera: Pteropodidae). *Biotropica*, 32:338–350.
- Brosset, A. 1976. Social organization in the African bat, *Myotis bocagei*. *Zeitschrift für Tierpsychologie*, 42:50–56.
- Buchanan, F. M. 1969. Bats of the Arima Valley, Trinidad, W.I. Privately published. Asa Wright Nature Centre, Trinidad and Tobago, 53 pp.
- Buchanan, M. 1958. *Tadarida* and *Myotis* occupying cliff swallow nests. *Journal of Mammalogy*, 39:434–435.
- Bull, E. L., and A. D. Partridge. 1986. Methods of killing trees for use by cavity nesters. *Wildlife Society Bulletin*, 14:142–146.
- Callahan, E. V., R. D. Drobney, and R. L. Clawson. 1997. Selection of summer roosting sites by Indiana bats (*Myotis sodalis*) in Missouri. *Journal of Mammalogy*, 78:818–825.
- Campbell, L. A., J. G. Hallett, and M. A. O'Connell. 1996. Conservation of bats in managed forests: use of roosts by *Lasionycteris noctivagans*. *Journal of Mammalogy*, 77:976–984.
- Carey, A. B., and H. R. Sanderson. 1981. Routing to accelerate tree-cavity formation. *Wildlife Society Bulletin*, 9:14–21.
- Chapman, F. M. 1932. A home-making bat. *Natural History*, 32:555–556.
- Charles-Dominique, P. 1993. Tent use by the bat *Rhinophylla pumilio* (Phyllostomidae: Carollinae) in French Guiana. *Biotropica*, 25:111–116.
- Chasen, F. N. 1939. Four new mammals from Java. *Treubia*, 17:185–188.
- Cheke, A. S., and J. F. Dahl. 1981. The status of bats on western Indian Ocean islands, with special reference to *Pteropus*. *Mammalia*, 45:205–238.
- Choe, J. C. 1994. Ingenious design of tent roosts by Peter's tent-making bat, *Uroderma bilobatum* (Chiroptera: Phyllostomidae). *Journal of Natural History*, 28:731–737.
- Choe, J. C., and R. M. Timm. 1985. Roosting site selection by *Artibeus watsoni* (Chiroptera: Phyllostomidae) on *Anthurium ravenii* (Araceae) in Costa Rica. *Journal of Tropical Ecology*, 1:241–247.
- Chung-MacCoubrey, A. L. 1996. Bat species composition and roost use in pinyon-juniper woodlands of New Mexico. Pp. 118–123 in: *Bats and Forests Symposium*, October 19–21, 1995, Victoria, British Columbia, Canada (R. M. R. Barclay and R. M. Brigham, eds.). British Columbia Ministry of Forests, Victoria.
- Churchill, S. 1998. *Australian Bats*. Reed New Holland, Sydney.
- Clague, C. I., R. B. Coles, O. J. Whybird, H. J. Spencer, and P. Flemons. 1999. The occurrence and distribution of the tube-nosed insectivorous bat (*Murina florium*) in Australia. *Proceedings of the Linnean Society of New South Wales*, 121:175–191.
- Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *Journal of Wildlife Management*, 44:773–786.
- Clutton-Brock, T. H. 1989. Mammalian mating systems. *Proceedings of the Royal Society of London B*, 236:339–372.
- Constantine, D. G. 1958. Ecological observations on lasiurine bats in Georgia. *Journal of Mammalogy*, 39:64–70.

- Constantine, D. G. 1959. Ecological observations on lasiurine bats in the North Bay area of California. *Journal of Mammalogy*, 40:13–15.
- Constantine, D. G. 1966. Ecological observations of lasiurine bats in Iowa. *Journal of Mammalogy*, 47:34–41.
- Constantine, D. G. 1998. Range extensions of ten species of bats in California. *Bulletin of the Southern California Academy of Sciences*, 97:49–75.
- Corbet, G. B., and J. E. Hill. 1992. *Mammals of the Indo-Malayan Region: A Systematic Review*. British Museum Publications, Oxford University Press, London.
- Cox, P. A. 1983. Observations on the natural history of Samoan bats. *Mammalia*, 47:519–523.
- Cox, P. A., T. Elmquist, E. D. Pierson, and W. E. Rainey. 1991. Flying foxes as strong interactors in South Pacific island ecosystems: a conservation hypothesis. *Conservation Biology*, 5:448–454.
- Craig, P., P. W. Trail, and T. E. Morrell. 1994. The decline of fruit bats in American Samoa due to hurricanes and overhunting. *Biological Conservation*, 69:261–266.
- Crampton, L. H., and R. M. R. Barclay. 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conservation Biology*, 12:1347–1358.
- Crome, F. H. J., and G. C. Richards. 1988. Bats and gaps: microchiropteran community structure in a Queensland rainforest. *Ecology*, 69:1960–1969.
- Csada, R. 1996. *Cardioderma cor*. *Mammalian Species*, 519:1–4.
- Dalquest, W. W., and D. W. Walton. 1970. Diurnal retreats of bats. Pp. 162–187 *in*: *About Bats* (B. H. Slaughter and D. W. Walton, eds.). Southern Methodist University Press, Dallas.
- Daniel, M. J. 1990. Order Chiroptera. Pp. 114–137 *in*: *The Handbook of New Zealand Mammals* (C. M. King, ed.). Oxford University Press, Auckland.
- Daniel, M. J., and G. R. Williams. 1984. A survey of the distribution, seasonal activity and roost sites of New Zealand bats. *New Zealand Journal of Ecology*, 7:9–25.
- Davis, D. D. 1962. Mammals of the lowland rainforest of North Borneo. *Bulletin of the National Museum, Singapore*, 31:1–129.
- Davison, G. W. H. 1992. *Pteropus vampyrus malaccensis*. Pp. 142–143 *in*: *Old World Fruit Bats: An Action Plan for the Family Pteropodidae* (S. P. Mickleburgh, A. M. Hutson, and P. A. Racey, eds.). International Union for Conservation of Nature and Natural Resources Survival Commission, Gland, Switzerland.
- Dobson, G. E. 1877. Protective mimicry among bats. *Nature*, 15:354.
- Eby, P. 1991. Seasonal movements of grey-headed flying foxes, *Pteropus poliocephalus* (Chiroptera: Pteropodidae), from two maternity camps in northern New South Wales. *Wildlife Research*, 18:547–559.
- Eby, P. 1996. Interactions between the grey-headed flying fox, *Pteropus poliocephalus* (Chiroptera: Pteropodidae) and its diet plants—seasonal movements and seed dispersal. Ph.D. Thesis, University of New England, Armidale, New South Wales.
- Eby, P., G. Richards, L. Collins, and K. Parry-Jones. 1999. The distribution, abundance and vulnerability to population reduction of the grey-headed flying fox *Pteropus poliocephalus* in New South Wales. *Australian Zoologist*, 31:240–253.
- Elangovan, V., G. Marimuthu, and T. H. Kunz. 1999. Temporal patterns of individual and group foraging behaviour in the short-nosed fruit bat, *Cynopterus sphinx*, in south India. *Journal of Tropical Ecology*, 15:681–687.

- Elangovan, V., G. Marimuthu, and T. H. Kunz. 2000. Nectar feeding behavior of the short-nosed fruit bat, *Cynopterus sphinx* (Pteropodidae). *Acta Chiropterologica*, 2:1–5.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* (Washington, D.C.), 197:215–223.
- Emmons, L. H. 1990. *Neotropical Rainforest Mammals: A Field Guide*. University of Chicago Press, Chicago.
- Entwistle, A. C., P. A. Racey, and J. R. Speakman. 1997. Roost selection by the brown long-eared bat (*Plecotus auritus*). *Journal of Applied Ecology*, 34:399–408.
- Fenton, M. B. 1983. Roosts used by the African insectivorous bat, *Scotophilus leucogaster* (Chiroptera: Vespertilionidae). *Biotropica*, 15:129–132.
- Fenton, M. B. 1992a. *Bats. Facts on File*, New York.
- Fenton, M. B. 1992b. Pelage patterns and crypsis in roosting bats: *Taphozous mauritanus* and *Epomophorus* species. *Koedoe*, 35:49–55.
- Fenton, M. B. 1997. Science and the conservation of bats. *Journal of Mammalogy*, 78:1–14.
- Fenton, M. B., D. Audet, D. C. Dunning, J. Long, C. B. Merriam, D. Pearl, D. M. Syne, B. Adkins, S. Pedersen, and T. Wohlgenant. 1993. Activity patterns and roost selection by *Noctilio albiventris* (Chiroptera: Noctilionidae) in Costa Rica. *Journal of Mammalogy*, 74:607–613.
- Fenton, M. B., R. M. Brigham, A. M. Mills, and I. L. Rautenbach. 1985. The roosting and foraging areas of *Epomophorus wahlbergi* (Pteropodidae) and *Scotophilus viridis* (Vespertilionidae) in Kruger National Park, South Africa. *Journal of Mammalogy*, 66:461–468.
- Fenton, M. B., and I. L. Rautenbach. 1986. A comparison of the roosting and foraging behaviour of three species of African insectivorous bats (Rhinolophidae, Vespertilionidae and Molossidae). *Canadian Journal of Zoology*, 64:2860–2867.
- Fenton, M. B., and I. L. Rautenbach. 1998. Impacts of ignorance and human and elephant populations on the conservation of bats in African woodlands. Pp. 261–270 *in*: *Bat Biology and Conservation* (T. H. Kunz and P. A. Racey, eds.). Smithsonian Institution Press, Washington, D.C.
- Fenton, M. B., I. L. Rautenbach, S. E. Smith, C. M. Swanepoel, J. Grosell, and J. van Jaarsveld. 1994. Raptors and bats: threats and opportunities. *Animal Behaviour*, 48:9–18.
- Fenton, M. B., C. M. Swanepoel, R. M. Brigham, J. Cebek, and M. B. C. Hickey. 1990. Foraging behavior and prey selection by large slit-faced bats (*Nycteris grandis*; Chiroptera: Nycteridae). *Biotropica*, 22:2–8.
- Findley, J. S., and D. E. Wilson. 1974. Observations on Neotropical disk-winged bats, *Thyroptera tricolor* Spix. *Journal of Mammalogy*, 55:562–571.
- Finney, M. A. 1991. Ecological effects of prescribed and simulated fire on the coast redwood (*Sequoia sempervirens*). Ph.D. Dissertation. University of California, Berkeley.
- Flannery, T. 1995. *Mammals of the South-West Pacific and Moluccan Islands*. Reed Books, Chatswood, New South Wales.
- Foster, M. S. 1992. Tent roosts of Macconnelli's bat (*Vampyressa macconnelli*). *Biotropica*, 24:447–454.
- Foster, M. S., and R. M. Timm. 1976. Tent-making by *Artibeus jamaicensis* (Chiroptera: Phyllostomatidae) with comments on plants used by bats for tents. *Biotropica*, 8:65–269.

- Foster, R. W., and A. Kurta. 1999. Roosting ecology of the northern bat (*Myotis septentrionalis*) and comparisons with the endangered Indiana bat (*Myotis sodalis*). *Journal of Mammalogy*, 80:659–672.
- Francis, C. M. 1990. Trophic structure of bat communities in the understorey of lowland dipterocarp rain forest in Malaysia. *Journal of Tropical Ecology*, 6:421–431.
- Fuhrmann, M., and A. Seitz. 1992. Nocturnal activity of the brown long-eared bat (*Plecotus auritus* L., 1758): data from radio-tracking in the Lenneberg forest near Mainz (Germany). Pp. 538–548 *in*: *Wildlife Telemetry: Remote Monitoring and Tracking of Animals* (I. G. Priede and S. M. Swift, eds.). Ellis Horwood, New York.
- Gaisler, J., V. Hanak, and J. Dungel. 1979. A contribution to the population ecology of *Nyctalus noctula* (Mammalia: Chiroptera). *Prirodovedne Prace Ustavu Ceskoslovenske Akademie Ved Brne*, 13:1–38.
- Gannon, M. R., and M. R. Willig. 1994. The effects of Hurricane Hugo on bats of the Luquillo Experimental Forest of Puerto Rico. *Biotropica*, 26:320–331.
- Gardner, A. L. 1977. Feeding habits. Pp. 393–350 *in*: *Biology of Bats of the New World Family Phyllostomatidae* (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Pt. 2. Special Publications, the Museum, Texas Tech University, 13. Texas Tech Press, Lubbock.
- Garnett, S., O. Whybird, and H. Spencer. 1999. The conservation status of the spectacled flying fox *Pteropus conspicillatus* in Australia. *Australian Zoologist*, 31:38–50.
- Gellman, S. T., and W. J. Zielinski. 1996. Use by bats of old-growth redwood hollows on the north coast of California. *Journal of Mammalogy*, 77:255–265.
- Genoud, M., and F. J. Bonaccorso. 1986. Temperature regulation, rate of metabolism, and roost temperature in the greater white-lined bat *Saccopteryx bilineata* (Emballonuridae). *Physiological Zoology*, 59:49–54.
- Gibbons, P. 1994. Sustaining key old-growth characteristics in native forests used for wood production: retention of trees with hollows. Pp. 59–84 *in*: *Ecology and Sustainability of Southern Temperate Ecosystems* (T. W. Norton and S. R. Dovers, eds.). Commonwealth Scientific and Industrial Research Organization, East Melbourne.
- Goodwin, G. G., and A. M. Greenhall. 1961. A review of bats of Trinidad and Tobago. *Bulletin of the American Museum of Natural History*, 122:187–302.
- Goodwin, R. E. 1979. The bats of Timor: systematics and ecology. *Bulletin of the American Museum of Natural History*, 163:73–122.
- Grant, G. S., and S. A. Banack. 1999. Harem structure and reproductive behavior of *Pteropus tonganus* in American Samoa. *Australian Mammalogy*, 21:111–120.
- Grindal, S. D. 1999. Habitat use by bats, *Myotis* spp., in western Newfoundland. *Canadian Field-Naturalist*, 113:258–263.
- Hamilton, I. M., and R. M. R. Barclay. 1994. Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). *Canadian Journal of Zoology*, 72:744–749.
- Hamilton, W. J., III, and K. E. F. Watt. 1970. Refuging. *Annual Review of Ecology and Systematics*, 1:263–286.
- Handley, C. O., Jr. 1966. Checklist of the mammals of Panama. Pp. 753–795 *in*: *Ectoparasites of Panama* (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago.
- Handley, C. O., Jr. 1976. Mammals of the Smithsonian Venezuelan Project. *Brigham Young University Science Bulletin, Biological Series*, 20:1–91.

- Happold, D. C. D., and M. Happold. 1990. The domiciles, reproduction, social organization and sex ratios of the banana bat *Pipistrellus nanus* (Chiroptera, Vespertilionidae) in Malawi. *Zeitschrift für Säugetierkunde*, 55:145–160.
- Happold, D. C. D., and M. Happold. 1996. The social organization and population dynamics of leaf-roosting banana bats, *Pipistrellus nanus* (Chiroptera, Vespertilionidae), in Malawi, east-central Africa. *Mammalia*, 60:517–544.
- Heaney, L. R. 1986. Biogeography of the mammals of Southeast Asia: estimates of colonization, extinction, and speciation. *Biological Journal of the Linnean Society*, 28:127–165.
- Heideman, P. D., and L. R. Heaney. 1992. *Pteropus vampyrus lanensis*. Pp. 141–142 in: *Old World Fruit Bats: An Action Plan for the Family Pteropodidae* (S. P. Mickleburgh, A. M. Hutson, and P. A. Racey, eds.). International Union for Conservation of Nature and Natural Resources Survival Commission, Gland, Switzerland.
- Heithaus, E. R., and T. H. Fleming. 1978. Foraging movements of a frugivorous bat, *Carollia perspicillata* (Phyllostomatidae). *Ecological Monographs*, 48:127–143.
- Herr, A. 1998. Aspects of the ecology of insectivorous forest-dwelling bats (Microchiroptera) in the western slopes of the Australian alps. Ph.D. Thesis. Charles Sturt University, Albury, Australia.
- Herr, A., and N. I. Klomp. 1999. Preliminary investigation of roosting habitat preferences of the large forest bat *Vespadelus darlingtoni* (Chiroptera, Vespertilionidae). *Pacific Conservation Biology*, 5:208–213.
- Hodgkison, R. 2001. The ecology of fruit bats (Chiroptera: Pteropodidae) in a Malaysian lowland dipterocarp forest, with particular reference to the spotted-winged fruit bat (*Balionycteris maculata*, Thomas). Ph.D. Dissertation. University of Aberdeen, Aberdeen.
- Hodgkison, R., S. T. Balding, A. Zubaid, and T. H. Kunz. In press. Roosting ecology and social organization of the spotted-winged fruit bat, *Balionycteris maculata*, Thomas (Chiroptera: Pteropodidae) in a Malaysian lowland dipterocarp forest. *Journal of Tropical Ecology*.
- Hosken, D. J. 1996. Roost selection by the lesser long-eared bat, *Nyctophilus geoffroyi*, and the greater long-eared bat, *N. major* (Chiroptera: Vespertilionidae) in *Banksia* woodlands. *Journal of the Royal Society of Western Australia*, 79:211–216.
- Howe, H. F. 1984. Implications of seed dispersal by animals for tropical reserve management. *Biological Conservation*, 30:261–281.
- Humphrey, S. R. 1975. Nursery roosts and community diversity of Nearctic bats. *Journal of Mammalogy*, 56:321–346.
- Humphrey, S. R., A. R. Richter, and J. B. Cope. 1977. Summer habitat and ecology of the endangered Indiana bat, *Myotis sodalis*. *Journal of Mammalogy*, 58:334–346.
- Hutchinson, J. T., and M. J. Lacki. 2000. Selection of day roosts by red bats in mixed mesophytic forests. *Journal of Wildlife Management*, 64:87–94.
- Hutson, A. M., S. P. Mickleburgh, and P. A. Racey. 2001. *Microchiropteran Bats: Global Status Survey and Conservation Action Plan*. IUCN/SSC Chiroptera Specialist Group. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- Ingles, L. G. 1953. Observations on Barro Colorado Island mammals. *Journal of Mammalogy*, 34:266–268.
- Jaberg, C., C. Leuthold, and J.-D. Blant. 1998. Foraging habitats and feeding strategy of

- the parti-coloured bat *Vespertilio murinus* L., 1758 in western Switzerland. *Myotis*, 36:51–61.
- Jackson, J. A., B. J. Schardien, C. D. Cooley, and B. E. Rowe. 1982. Cave *Myotis* roosting in barn swallow nests. *Southwestern Naturalist*, 27:463–464.
- Janzen, D. H. 1976. Why tropical trees have rotten cores. *Biotropica*, 8:110.
- Jones, C. 1972. Comparative ecology of three pteropid bats in Rio Muni, West Africa. *Journal of Zoology (London)*, 167:353–370.
- Jones, G., P. L. Duverge, and R. D. Ransome. 1995. Conservation biology of an endangered species: field studies of greater horseshoe bats. *Symposia of the Zoological Society London*, no. 67:309–324.
- Kalcounis, M. C., and R. M. Brigham. 1998. Secondary use of aspen cavities by tree-roosting big brown bats. *Journal of Wildlife Management*, 62:603–611.
- Kalcounis, M. C., and K. R. Hecker. 1996. Intraspecific variation in roost-site selection by little brown bats (*Myotis lucifugus*). Pp. 81–90 in: *Bats and Forests Symposium*, October 19–21, 1995 Victoria, British Columbia, Canada (R. M. R. Barclay and R. M. Brigham, eds.). British Columbia Ministry of Forests, Victoria.
- Kalko, E. K. V., D. Friemel, C. O. Handley, Jr., and H.-U. Schnitzler. 1999. Roosting and foraging behavior of two Neotropical gleaning bats, *Tonatia silvicola* and *Trachops cirrhosus* (Phyllostomidae). *Biotropica*, 31:344–353.
- Kaufman, L. 1988. The role of developmental crises in the formation of buttresses: a unified hypothesis. *Evolutionary Trends in Plants*, 2:39–51.
- Kerth, G., K. Weissmann, and B. König. 2000. Day-roost selection in female Bechstein's bats (*Myotis bechsteinii*): a field experiment to determine the influence of roost temperature. *Oecologia (Berlin)*, 126:1–9.
- Kingdon, J. 1974. *East African Mammals*. Vol. 2. Pt. A. Insectivores and Bats. Academic Press, London.
- Kitchener, D. J., Boeadi, I. Charlton, and Maharadatunkamsi. 1990. Wild mammals of Lombok Island: Nusa Tenggara, Indonesia: systematics and natural history. *Records of the Western Australian Museum, Supplement no. 33*:1–129.
- Kock, D., and D. Kovac. 2000. *Eudiscopus dentalus* (Osgood 1932) in Thailand with notes on its roost (Chiroptera: Vespertilionidae). *Zeitschrift für Säugetierkunde*, 65:1121–1123.
- Koepcke, J. 1984. "Blattzelte" als Schlafplätze der Fledermaus *Ectophylla macconnelli* (Thomas, 1901) (Phyllostomidae) im tropischen Regenwald von Peru. *Säugetierkundliche Mitteilungen*, 31:123–126.
- Kofron, C. P. 1994. Bamboo-roosting of the thick-thumbed pipistrelle bat (*Glischropus tylopsus*) in Borneo. *Mammalia*, 58:306–309.
- Kronwitter, F. 1988. Population structure, habitat use, and activity patterns of the noctule bat, *Nyctalus noctula* Schreib. 1774 (Chiroptera: Vespertilionidae) revealed by radio-tracking. *Myotis*, 26:23–85.
- Krull, D., A. Schumm, W. Metzner, and G. Neuweiler. 1991. Foraging areas and foraging behavior in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). *Behavioral Ecology and Sociobiology*, 28:247–253.
- Kunz, T. H. 1982. Roosting ecology of bats. Pp. 1–55 in: *Ecology of Bats* (T. H. Kunz, ed.). Plenum Press, New York.
- Kunz, T. H. 1996. Obligate and opportunistic interactions of Old-World tropical bats and plants. Pp. 37–65 in: *Conservation and Faunal Biodiversity in Malaysia*

- (Z. A. A. Hasan and Z. Akbar, eds.). Penerbit Universiti Kebangsaan Malaysia, Bangi.
- Kunz, T. H., P. V. August, and C. D. Burnett. 1983. Harem social organization in cave-roosting *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Biotropica*, 15:133–138.
- Kunz, T. H., M. S. Fujita, A. P. Brooke, and G. F. McCracken. 1994. Convergence in tent architecture and tent-making behavior among Neotropical and Palearctic bats. *Journal of Mammalian Evolution*, 2:57–78.
- Kunz, T. H., and G. F. McCracken. 1996. Tents and harems: apparent defence of foliage roosts by tent-making bats. *Journal of Tropical Ecology*, 12:121–137.
- Kunz, T. H., and E. D. Pierson. 1994. Bats of the world—an introduction. *In: Bats of the World* (R. W. Nowak, ed.). Johns Hopkins University Press, Baltimore.
- Kunz, T. H., and P. A. Racey, eds. 1998. *Bat Biology and Conservation*. Smithsonian Institution Press, Washington, D.C.
- Kunz, T. H., and D. S. Reynolds. In press. Bat colonies in buildings. *In: Monitoring Trends in Bat Populations of the U.S. and Territories: Problems and Prospects* (T. J. O'Shea and M. A. Bogan, eds.). U.S. Geological Survey, Biological Resources Division, Information and Technology Report, Washington, D.C.
- Kurta, A. 1985. External insulation available to a non-nesting mammal, the little brown bat (*Myotis lucifugus*). *Comparative Biochemistry and Physiology A, Comparative Physiology*, 8:413–420.
- Kurta, A. 1995. Bark roost of a male big brown bat (*Eptesicus fuscus*). *Bat Research News*, 35:63.
- Kurta, A., G. P. Bell, K. A. Nagy, and T. H. Kunz. 1989. Water balance of free-ranging little brown bats (*Myotis lucifugus*) during pregnancy and lactation. *Canadian Journal of Zoology*, 67:2468–2472.
- Kurta, A., and R. Foster. 1995. The brown creeper (Aves: Certhiidae): a competitor of bark-roosting bats? *Bat Research News*, 36:6–7.
- Kurta, A., D. King, J. A. Teramino, J. M. Stribley, and K. J. Williams. 1993. Summer roosts of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. *American Midland Naturalist*, 129:132–138.
- Kurta, A., T. H. Kunz, and K. A. Nagy. 1990. Energetics and water flux of free-ranging big brown bats (*Eptesicus fuscus*) during pregnancy and lactation. *Journal of Mammalogy*, 71:59–65.
- Kurta, A., and G. C. Lehr. 1995. Lasiurus ega. *Mammalian Species*, 515:1–7.
- Kurta, A., K. J. Williams, and R. Mies. 1996. Ecological, behavioral, and thermal observations of a peripheral population of Indiana bats (*Myotis sodalis*). Pp. 102–117 *in: Bats and Forests Symposium*, October 19–21, 1995, Victoria, British Columbia, Canada (R. M. R. Barclay and R. M. Brigham, eds.). British Columbia Ministry of Forests, Victoria.
- LaVal, R. K. 1977. Notes on some Costa Rican bats. *Brenesia*, 10/11:77–83.
- LaVal, R. K., and M. L. LaVal. 1977. Reproduction and behavior of the African banana bat, *Pipistrellus nanus*. *Journal of Mammalogy*, 58:403–410.
- Law, B. S. 1993. Roosting and foraging ecology of the Queensland blossom bat, *Syconycteris australis*, in north-eastern New South Wales: flexibility in response to seasonal variation. *Wildlife Research*, 20:419–431.
- Law, B. S. 1996. The ecology of bats in south-east Australian forests and potential impacts of forestry practices: a review. *Pacific Conservation Biology*, 2:363–374.

- Law, B. S., and J. Anderson. 2000. Roost preferences and foraging ranges of the eastern forest bat, *Vespadelus pumilus* under two disturbance histories in northern New South Wales. *Austral Ecology*, 24:352–367.
- Lekagul, B., and J. A. McNeely. 1977. Mammals of Thailand. Association for the Conservation of Wildlife, Bangkok.
- Lemke, T. O. 1992. State of the Marianas fruit bat (*Pteropus mariannus*) in the northern Mariana islands north of Saipan. Pp. 68–93 in: *Pacific Island Flying Foxes: Proceedings of an International Conservation Conference* (D. E. Wilson and G. L. Graham, eds.). U.S. Fish and Wildlife Service, Biological Report 90 (23), Washington, D.C.
- Lewis, J. C. 1998. Creating snags and wildlife trees in commercial forest landscapes. *Western Journal of Applied Forestry*, 13:97–101.
- Lewis, S. E. 1992. Behavior of Peter's tent making bat, *Uroderma bilobatum*, at maternity roosts in Costa Rica. *Journal of Mammalogy*, 73:541–546.
- Lewis, S. E. 1995. Roost fidelity of bats: a review. *Journal of Mammalogy*, 76:481–496.
- Lim, B. K. 1993. Cladistic reappraisal of Neotropical stenodermatine bat phylogeny. *Cladistics*, 9:147–165.
- Lim, L. B. 1966. Abundance and distribution of Malaysian bats in different ecological habitats. *Federation Museum Journal*, 9:60–73.
- Lindenmayer, D. B., R. B. Cunningham, C. F. Donnelly, M. T. Tanton, and H. A. Nix. 1993. The abundance and development of cavities in *Eucalyptus* trees: a case study in the montane forests of Victoria, southeastern Australia. *Forest Ecology and Management*, 60:77–104.
- Lloyd, B., and S. McQueen. 1997. Roosting behaviour of *Mystacina tuberculata* in central North Island, New Zealand. *Australasian Bat Society Newsletter*, 7:57.
- Loughland, R. A. 1998. Mangal roost selection by the flying-fox *Pteropus alecto* (Mega-chiroptera: Pteropodidae). *Marine and Freshwater Research*, 49:351–352.
- Lumsden, L. F., and A. F. Bennett. 1995. Bats of a semiarid environment in south-eastern Australia: biogeography, ecology and conservation. *Wildlife Research*, 22:217–240.
- Lumsden, L. F., and A. F. Bennett. 2000. Bats in rural landscapes: a significant but largely unknown faunal component. Pp. 42–50 in: *Balancing Conservation and Production in Grassy Landscapes: Proceedings of the Bushcare Grassy Landscapes Conference*, Clare, South Australia, 19–21 August 1999 (T. Barlow and R. Thorburn, eds.). Environment Australia, Canberra.
- Lumsden, L. F., A. F. Bennett, and J. E. Silins. 2002a. Location of roosts of the lesser long-eared bat *Nyctophilus geoffroyi* and Gould's wattled bat *Chalinolobus gouldii* in a fragmented landscape in south-eastern Australia. *Biological Conservation*, 106:237–249.
- Lumsden, L. F., A. F. Bennett, and J. E. Silins. 2002b. Selection of roost sites by the lesser long-eared bat (*Nyctophilus geoffroyi*) and Gould's wattled bat (*Chalinolobus gouldii*) in south-eastern Australia. *Journal of Zoology (London)*, 257:207–218.
- Lunney, D., J. Barker, T. Leary, D. Priddel, R. Wheeler, P. O'Connor, and B. Law. 1995. Roost selection by the north Queensland long-eared bat *Nyctophilus bifax* in littoral rainforest in the Iluka World Heritage Area, New South Wales. *Australian Journal of Ecology*, 20:532–537.
- Lunney, D., J. Barker, D. Priddel, and M. O'Connell. 1988. Roost selection by Gould's long-eared bat, *Nyctophilus gouldi* Tomes (Chiroptera: Vespertilionidae), in logged forests on the south coast of New South Wales. *Australian Wildlife Research*, 15:375–384.

- Lunney, D., and C. Moon. 1997. Flying foxes and their camps in the remnant rainforests of northeast New South Wales. Pp. 247–277 in: Australia's Ever-Changing Forests. III. Proceedings of the Third National Conference on Australian Forest History (J. Darvel, ed.). Centre for Resource and Environmental Studies, Canberra.
- Lyon, M. W. 1911. Mammals collected by Dr. W. L. Abbott on Borneo. Proceedings of the United States National Museum, 40:53–146.
- Mackowski, C. M. 1984. The ontogeny of hollows in Blackbutt (*Eucalyptus pilularis*) and its relevance to the management of forests for possums, gliders and timber. Pp. 553–567 in: Possums and Gliders (A. P. Smith and I. D. Hume, eds.). Surrey Beatty & Sons, Chipping Norton, Sydney.
- Maeda, K. 1974. Eco-ethologie de la grande noctule, *Nyctalus lasiopterus*, a Sappora, Japon. Mammalia, 38:461–487.
- Mager, K. J., and T. A. Nelson. 2001. Roost-site selection by eastern red bats (*Lasiurus borealis*). American Midland Naturalist, 145:120–126.
- Manning, R. W., J. K. J. Jones, Jr., R. R. Hollander, and C. Jones. 1987. Notes on distribution and natural history of some bats on the Edward Plateau and in adjacent areas of Texas. Texas Journal of Science, 39:279–285.
- Marinho-Filho, J., and I. Sazima. 1998. Brazilian bats and conservation biology. Pp. 282–294 in: Bat Biology and Conservation (T. H. Kunz and P. A. Racey, eds.). Smithsonian Institution Press, Washington, D.C.
- Marshall, A. G. 1985. Old World phytophagous bats (Megachiroptera) and their food supply: a survey. Zoological Journal of the Linnean Society, 29:115–135.
- Marshall, A. G., and A. N. McWilliam. 1982. Ecological observations on epomophorine fruit-bats (Megachiroptera) in West Africa savanna woodland. Journal of Zoology (London), 198:53–67.
- Mason, C. F., R. E. Stebbings, and G. P. Winn. 1972. Noctules (*Nyctalus noctula*) and starlings (*Sturnus vulgaris*) competing for roosting holes. Journal of Zoology (London), 166:467.
- Mattson, T. A., S. W. Buskirk, and N. L. Stanton. 1996. Roost sites of the silver-haired bat (*Lasiorycteris noctivagans*) in the Black Hills, South Dakota. Great Basin Naturalist, 56:247–253.
- Mawson, P. R., and J. L. Long. 1994. Size and age parameters of nest trees used by four species of parrot and one species of cockatoo in south-west Australia. Emu, 94:149–155.
- Mayle, B. A. 1990. A biological basis for bat conservation in British woodlands—a review. Mammal Review, 20:159–195.
- McCarthy, T. G. A., A. L. Gardner, and C. O. Handley, Jr., 1992. *Tonatia carrikeri*. Mammalian Species, 407:1–4.
- McClure, H. E. 1942. Summer activities of bats (genus *Lasiurus*) in Iowa. Journal of Mammalogy, 23:430–434.
- McCracken, G. F., and G. S. Wilkinson. 2000. Bat mating systems. Pp. 321–362 in: The Reproductive Biology of Bats (E. G. Crichton and P. H. Krutzsch, eds.). Academic Press, New York.
- Medway, Lord. 1983. The Wild Mammals of Malaya. 2d ed. Oxford University Press, Kuala Lumpur.
- Medway, Lord, and A. G. Marshall. 1970. Roost-site selection among flat-headed bats (*Tylonycteris* spp.). Journal of Zoology (London), 161:237–245.
- Medway, Lord, and A. G. Marshall. 1972. Roosting associations of flat-headed bats, *Ty-*

- lonycteris* species (Chiroptera: Vespertilionidae) in Malaysia. *Journal of Zoology* (London), 168:463–482.
- Menzel, M. A., T. C. Carter, B. R. Chapman, and J. Laerm. 1998. Quantitative comparison of tree roosts used by red bats (*Lasiurus borealis*) and Seminole bats (*L. seminolus*). *Canadian Journal of Zoology*, 76:630–634.
- Menzel, M. A., T. C. Carter, W. M. Ford, and B. R. Chapman. 2001. Tree-roost characteristics of subadult and female adult evening bats (*Nycticeius humeralis*) in upper coastal plain of South Carolina. *American Midland Naturalist*, 145:112–119.
- Mickleburgh, S., P. A. Racey, and A. M. Hutson, eds. 1992. Old World Fruit Bat Action Plan. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- Mills, L. S., M. E. Soulé, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. *BioScience*, 43:219–224.
- Morrison, D. W. 1978a. Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. *Ecology*, 59:716–723.
- Morrison, D. W. 1978b. Influence of habitat on the foraging distances of the fruit bat, *Artibeus jamaicensis*. *Journal of Mammalogy*, 59:622–624.
- Morrison, D. W. 1979. Apparent male defense of tree hollows in the fruit bat, *Artibeus jamaicensis*. *Journal of Mammalogy*, 60:11–15.
- Morrison, D. W. 1980. Foraging and day-roosting dynamics of canopy fruit bats in Panama. *Journal of Mammalogy*, 61:20–29.
- Morrison, D. W., and C. O. Handley, Jr. 1991. Roosting behavior. Pp. 131–136 in: *Demography and Natural History of the Common Fruit Bat, Artibeus jamaicensis*, on Barro Colorado Island, Panama (C. O. Handley, Jr., D. E. Wilson, and A. L. Gardner, eds.). Smithsonian Contributions in Zoology, no. 511, Smithsonian Institution Press, Washington, D.C.
- Morrison, D. W., and S. H. Morrison. 1981. Economics of harem maintenance by a Neotropical bat. *Ecology*, 62:864–866.
- Mudar, K. M., and M. S. Allen. 1986. A list of bats from northeastern Luzon, Philippines. *Mammalia*, 50:219–225.
- Myers, N. 1986. Tropical deforestation and a megaextinction spasm. Pp. 394–409 in: *Conservation Biology: The Science of Scarcity and Diversity* (M. E. Soulé, ed.). Sinauer Associates, Sunderland, Mass.
- Nelson, J. E. 1965. Behaviour of Australian Pteropodidae (Megachiroptera). *Animal Behaviour*, 8:544–557.
- Neuweiler, G. 1969. Verhaltensbeobachtungen an einer indischen Flughundkolonie (*Pteropus g. giganteus* Brunn). *Zeitschrift für Tierpsychologie*, 26:166–199.
- Neuweiler, G., W. Metzner, U. Heilmann, R. Rubsamen, M. Eckrich, and H. H. Costa. 1987. Foraging behavior and echolocation in the rufous horseshoe bat (*Rhinolophus rouxi*) of Sri Lanka. *Behavioral Ecology and Sociobiology*, 20:53–67.
- Nicolai, V. 1986. The bark of trees: thermal properties, microclimate and fauna. *Oecologia* (Berlin), 69:148–160.
- Novick, A. 1977. Acoustic orientation. Pp. 73–287 in: *Biology of Bats*. Vol. 3 (W. A. Wimsatt, ed.). Academic Press, New York.
- Nowak, R. M. 1994. *Walker's Bats of the World*. Johns Hopkins University Press, Baltimore.
- Ochoa, H., and T. H. Kunz. 1999. Behavioral thermoregulation in the island flying fox *Pteropus hypomelanus*. *Journal of Thermal Biology*, 24:15–20.

- O'Donnell, C. F. J. 2000. Cypitic local populations in a temperate rainforest bat *Chalinolobus tuberculatus* in New Zealand. *Animal Conservation*, 3:287–297.
- O'Donnell, C. F. J. 2001. Home range and use of space by *Chalinolobus tuberculatus*, a temperate rainforest bat from New Zealand. *Journal of Zoology (London)*, 253: 253–264.
- O'Donnell, C. F. J., J. Christie, C. Corben, J. A. Sedgely, and W. Simpson. 1999. Rediscovery of short-tailed bats (*Mystacina* sp.) in Fiordland, New Zealand: preliminary observations of taxonomy, echolocation calls, population size, home range, and habitat use. *New Zealand Journal of Ecology*, 23:21–30.
- O'Donnell, C. F. J., and J. A. Sedgely. 1999. Use of roosts by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate rainforest in New Zealand. *Journal of Mammalogy*, 80:913–923.
- Okon, E. E. 1974. Fruit bats at Ife: their roosting and food preferences. *Nigerian Field*, 39:33–40.
- Ormsbee, P. C. 1996. Characteristics, use, and distribution of day roosts selected by female *Myotis volans* (long-legged myotis) in forested habitat of the Central Oregon Cascades. Pp. 124–131 in: *Bats and Forests Symposium*, October 19–21, 1995 Victoria, British Columbia, Canada (R. M. R. Barclay and R. M. Brigham, eds.). British Columbia Ministry of Forests, Victoria.
- Ormsbee, P. C., and W. C. McComb. 1998. Selection of day roosts by female long-legged myotis in the central Oregon Cascade Range. *Journal of Wildlife Management*, 62:596–603.
- Ortega, J., and H. T. Arita. 2000. Defense of females by dominant males of *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Ethology*, 106:395–407.
- O'Shea, T. J. 1980. Roosting, social organization and annual cycle in a Kenya population of the bat *Pipistrellus nanus*. *Zeitschrift für Tierpsychologie*, 53:171–195.
- Owen, R. D. 1987. Phylogenetic analysis of the bat subfamily Stenodermatinae (Mammalia: Chiroptera). Special Publications, the Museum, Texas Tech University, 26:1–65.
- Owen, R. D. 1988. Phenetic analysis of the bat subfamily Stenodermatinae (Chiroptera: Phyllostomidae). *Journal of Mammalogy*, 69:795–810.
- Palmer, C., O. Price, and C. Bach. 2000. Foraging ecology of the black flying fox (*Pteropus alecto*) in the seasonal tropics of the Northern Territory, Australia. *Wildlife Research*, 27:169–178.
- Palmer, C., and J. C. Z. Woinarski. 1999. Seasonal roosts and foraging movements of the black flying fox (*Pteropus alecto*) in the Northern Territory: resource tracking in a landscape mosaic. *Wildlife Research*, 26:823–838.
- Parry-Jones, K. A., and M. L. Augée. 1991. Food selection by grey-headed flying foxes (*Pteropus poliocephalus*) occupying a summer colony site near Gosford, New South Wales. *Wildlife Research*, 18:111–124.
- Parry-Jones, K. A., and M. L. Augée. 2001. Factors affecting the occupation of a colony site in Sydney NSW by the grey-headed flying-fox, *Pteropus poliocephalus* (Pteropodidae). *Austral Ecology*, 26:47–55.
- Pavey, C. R. 1998. Colony sizes, roost use and foraging ecology of *Hipposideros diadema reginae*, a rare bat from tropical Australia. *Pacific Conservation Biology*, 4:232–239.
- Pavey, C. R., and C. J. Burwell. 2000. Foraging ecology of three species of hipposiderid bats in tropical rainforest in north-east Australia. *Wildlife Research*, 27:283–287.

- Payne, J., C. M. Francis, and K. Phillips. 1985. A Field Guide to the Mammals of Borneo. Sabah Society, Kota Kinabalu, Sabah, Malaysia.
- Perkins, J. M. 1996. Does competition for roosts influence bat distribution in a managed forest? Pp. 164–172 *in*: Bats and Forests Symposium, October 19–21, 1995 Victoria, British Columbia, Canada (R. M. R. Barclay and R. M. Brigham, eds.). British Columbia Ministry of Forests, Victoria.
- Perry, S. 1994. Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capucinus*. *Primates*, 35:409–415.
- Phillips, W. W. 1924. A Guide to the Mammals of Ceylon. Pt. 1. *Ceylon Journal of Science*, 13:1–63.
- Pierson, E. D. 1998. Tall trees, deep holes, and scarred landscapes: conservation biology of North American bats. Pp. 309–325 *in*: Bat Biology and Conservation (T. H. Kunz and P. A. Racey, eds.). Smithsonian Institution Press, Washington, D.C.
- Pierson, E. D., T. Elmquist, W. E. Rainey, and P. A. Cox. 1996. Effects of tropical cyclonic storms on flying fox populations on the South Pacific islands of Samoa. *Conservation Biology*, 10:438–451.
- Pierson, E. D., and W. E. Rainey. 1992. The biology of flying foxes of the genus *Pteropus*: a review. Pp. 1–17 *in*: Pacific Island Flying Foxes: Proceedings of an International Conservation Conference (D. E. Wilson and G. Graham, eds.). U.S. Fish and Wildlife Service, Biological Report, 90 (23), Washington, D.C.
- Pitts, R. M., and J. J. Scharninghausen. 1986. Use of cliff swallow and barn swallow nests by the cave bat, *Myotis velifer*, and the free-tailed bat, *Tadarida brasiliensis*. *Texas Journal of Science*, 38:265–266.
- Rabe, M. J., T. E. Morrell, H. Green, J. deVos, and C. R. Miller. 1998. Characteristics of ponderosa pine snag roosts used by reproductive bats in northern Arizona. *Journal of Wildlife Management*, 62:612–621.
- Racey, P. A. 1982. Ecology of bat reproduction. Pp. 57–104 *in*: Ecology of Bats (T. H. Kunz, ed.). Plenum Press, New York.
- Racey, P. A. 1998. Ecology of European bats in relation to their conservation. Pp. 249–260 *in*: Bat Biology and Conservation (T. H. Kunz and P. A. Racey, eds.). Smithsonian Institution Press, Washington, D.C.
- Rainey, W. E. 1998. Conservation of bats on remote Indo-Pacific Islands. Pp. 326–341 *in*: Bat Biology and Conservation (T. H. Kunz and P. A. Racey, eds.). Smithsonian Institution Press, Washington, D.C.
- Rainey, W. E., E. D. Pierson, T. Elmquist, and P. A. Cox. 1995. The role of pteropodids in oceanic island ecosystems of the Pacific. *Symposia of the Zoological Society of London*, no. 67:47–62.
- Raphael, M. G., and M. L. Morrison. 1987. Decay and dynamics of snags in the Sierra Nevada, California. *Forest Science*, 33:774–783.
- Ratcliffe, F. 1932. Notes on the fruit bats (*Pteropus* spp.) of Australia. *Journal of Animal Ecology*, 1:32–57.
- Rawlinson, P. A., R. A. Zann, S. van Balen, and I. W. B. Thornton. 1992. Colonization of the Krakatau islands by vertebrates. *GeoJournal*, 28:225–231.
- Reason, P. F., and W. J. Trehwella. 1994. The status of *Pteropus livingstonii* in the Comores. *Oryx*, 28:107–114.
- Reid, F. A. 1997. A Field Guide to the Mammals of Central America and Southeast Mexico. Oxford University Press, New York.

- Richards, G. C. 1990a. The spectacled flying-fox, *Pteropus conspicillatus* (Chiroptera: Pteropodidae) in north Queensland. 1. Roost sites and distribution patterns. *Australian Mammalogy*, 13:17–24.
- Richards, G. C. 1990b. The spectacled flying-fox, *Pteropus conspicillatus*, (Chiroptera: Pteropodidae) in north Queensland. 2. Diet, seed dispersal and feeding ecology. *Australian Mammalogy*, 13:25–31.
- Richards, G. C. 1995. A review of ecological interactions of fruit bats in Australian ecosystems. *Symposia of the Zoological Society of London*, no. 67:76–96.
- Richards, P. W. 1996. *The Tropical Rain Forest*. 2d ed. Cambridge University Press, Cambridge.
- Richmond, J. Q., S. A. Banack, and G. S. Grant. 1998. Comparative analysis of wing morphology, flight behaviour, and habitat use in flying foxes (Genus: *Pteropus*). *Australian Journal of Zoology*, 46:283–289.
- Rickart, E. A., P. D. Heideman, and R. C. B. Utzurrum. 1989. Tent-roosting by *Scotophilus kuhlii* (Chiroptera: Vespertilionidae) in the Philippines. *Journal of Tropical Ecology*, 5:433–436.
- Rieger, V. I. 1996. Wie nutzen wasserfledermause, *Myotis daubentonii* (Kuhl, 1817), ihre tagesquartiere? (How do Daubenton's bats, *Myotis daubentonii* (Kuhl, 1817), use their day roosts?). *Zeitschrift für Säugetierkunde*, 61:202–214.
- Ritzi, C. M., C. W. Walker, and R. L. Honeycutt. 1998. Utilization of cave swallow nests by the cave myotis, *Myotis velifer*, in central Texas. *Texas Journal of Science*, 50:175–176.
- Robertson, P. B., 1992. Small islands, natural catastrophes, and rapidly disappearing forests: a high vulnerability recipe for island populations of flying foxes. Pp. 41–45 in: *Pacific Island Flying Foxes: Proceedings of an International Conservation Conference* (D. E. Wilson and G. L. Graham, eds.). U.S. Fish and Wildlife Service, Biological Report 90 (23), Washington, D.C., 176 pp.
- Robinson, M. F., and R. E. Stebbings. 1997. Home range and habitat use by the serotine bat, *Eptesicus serotinus*, in England. *Journal of Zoology (London)*, 243:117–136.
- Rodriguez-Duran, A., and T. H. Kunz. 2001. Biogeography of West Indian bats: an ecological perspective. Pp. 353–366 in: *Biogeography of the West Indies* (C. A. Woods, ed.). CRC Press, Boca Rotan, Fla.
- Rosevear, D. R. 1965. *The Bats of West Africa*. British Museum (Natural History), London.
- Roverud, R. C., and M. A. Chappell. 1991. Energetic and thermoregulatory aspects of clustering behavior in the Neotropical bat *Noctilio albiventris*. *Physiological Zoology*, 64:1527–1541.
- Ruby, J., P. T. Nathan, J. Balasingh, and T. H. Kunz. 2000. Chemical composition of leaves and fruits eaten by short-nosed fruit bat, *Cynopterus sphinx* (Megachiroptera). *Journal of Chemical Ecology*, 26:2825–2841.
- Sasse, D. B., and P. J. Pekins. 1996. Summer roosting ecology of northern long-eared bats (*Myotis septentrionalis*) in the White Mountain National Park. Pp. 91–101 in: *Bats and Forests Symposium*, October 19–21, 1995 Victoria, British Columbia, Canada (R. M. R. Barclay and R. M. Brigham, eds.). British Columbia Ministry of Forests, Victoria.
- Saughey, D. A., B. G. Crump, R. L. Vaughn, and G. A. Heidt. 1998. Notes on the natural history of *Lasiurus borealis* in Arkansas. *Journal of the Arkansas Academy of Science*, 52:92–98.

- Schliemann, H., and M. Hoerber. 1978. The structure and function of the pads on the thumb and foot of *Tylonycteris*. Pp. 39–50 in: Proceedings of the Fourth International Bat Research Conference (R. J. Olembo, J. B. Castelino, and F. A. Mutere, eds.). Kenya National Academy for Advancement of Arts and Sciences, Kenya Literature Bureau, Nairobi.
- Schliemann, H., and B. Mags. 1978. *Myzopoda aurita*. Mammalian Species, 116:1–2.
- Schober, W., and E. Grimberger. 1989. A Guide to the Bats of Britain and Europe. Hamlyn, London.
- Schulz, M. 1986. Vertebrate prey of the ghost bat, *Macroderma gigas*, at Pine Creek, Northern Territory. *Macroderma*, 2:59–62.
- Schulz, M. 1995. Utilisation of suspended bird nests by the golden-tipped bat (*Kerivoula papuensis*) in Australia. *Mammalia*, 59:280–283.
- Schulz, M. 1997. Bats in bird nests in Australia: a review. *Mammal Review*, 27:69–76.
- Schulz, M. 1998. Bats and other fauna in disused fairy martin *Hirundo ariel* nests. *Emu*, 98:184–191.
- Schulz, M. 1999. Leaf wrapping behavior in the flute-nosed bat *Murina florium*. *Bat Research News*, 40:6–8.
- Schulz, M. 2000. Roosts used by the golden-tipped bat, *Kerivoula papuensis* (Chiroptera: Vespertilionidae). *Journal of Zoology (London)*, 250:467–478.
- Schulz, M., and D. Hannah. 1998. Relative abundance, diet and roost selection of the tube-nosed insect bat, *Murina florium*, on the Atherton Tablelands, Australia. *Wildlife Research*, 25:261–271.
- Sedgeley, J. A. 2001. Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. *Journal of Applied Ecology*, 38:425–438.
- Sedgeley, J. A., and C. F. J. O'Donnell. 1999a. Factors influencing roost cavity selection by a temperate rainforest bat (*Chalinolobus tuberculatus*, Vespertilionidae) in New Zealand. *Journal of Zoology (London)*, 249:437–446.
- Sedgeley, J. A., and C. F. J. O'Donnell. 1999b. Roost selection by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate New Zealand rainforest and its implications for the conservation of bats in managed forests. *Biological Conservation*, 88:261–276.
- Sharma, S. K. 1986. Painted bats and nests of Baya weaver bird. *Journal of the Bombay Natural History Society*, 81:196.
- Shiel, C. B., R. E. Shiel, and J. S. Fairley. 1999. Seasonal changes in the foraging behaviour of Leisler's bats (*Nyctalus leisleri*) in Ireland as revealed by radio-telemetry. *Journal of Zoology (London)*, 249:347–358.
- Shump, K. A., and A. U. Shump. 1982. *Lasiurus cinereus*. Mammalian Species, 185:1–5.
- Simmons, N. B., and R. S. Voss. 1998. The mammals of Paracou, French Guiana: a Neotropical lowland rain forest fauna. Pt. 1. Bats. *Bulletin of the American Museum of Natural History*, no. 237, 219 pp.
- Skinner, J. D., and R. H. N. Smithers. 1990. The Mammals of the Southern African Sub-region. University of Pretoria, Pretoria.
- Sluiter, J. W., A. M. Voute, and P. F. van Heerdt. 1973. Hibernation of *Nyctalus noctula*. *Periodicum Biologorum*, 75:181–188.
- Souza, L. L., S. Ferrari, and A. L. Pina. 1997. Feeding behavior and predation of a bat by *Saimiri sciureus* in a semi-natural Amazonian environment. *Folia Primatologica*, 68:194–198.

- Speakman, J. R. 1991. The impact of predation by birds on bat populations in the British Isles. *Mammal Review*, 21:123–142.
- Spencer, H. J., and T. H. Fleming. 1989. Roosting and foraging behaviour of the Queensland tube-nosed bat, *Nyctimene robinsoni* (Pteropodidae). Preliminary radio-tracking observations. *Australian Wildlife Research*, 16:413–420.
- Spencer, H. J., C. Palmer, and K. Parry-Jones. 1991. Movements of fruit bats in eastern Australia, determined by using radiotracking. *Wildlife Research*, 18:463–468.
- Start, A. N. 1998. Do rainbow lorikeets evict bats? *Western Australian Naturalist*, 22:123–124.
- Start, A. N., and A. G. Marshall. 1976. Nectarivorous bats as pollinators of trees in West Malaysia. Pp. 141–150 in: *Tropical Trees: Variation, Breeding, and Conservation* (J. Burley and B. T. Styles, ed.). Academic Press, London.
- Stebbings, R. E., and J. T. Walsh. 1985. *Bat Boxes*. Fauna and Flora Preservation Society, London, 15 pp.
- Stoner, K. 2000. Leaf selection by the tent-making bat *Artibeus watsoni* in *Asterogyne martiana* palms in southwestern Costa Rica. *Journal of Tropical Ecology*, 16:151–157.
- Storz, J. F., J. Balasingh, H. R. Bhat, P. T. Nathan, D. P. S. Doss, A. A. Prakash, and T. H. Kunz. 2001. Clinal variation in body size and sexual dimorphism in an Indian fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae). *Biological Journal of the Linnean Society*, 72:17–31.
- Storz, J. F., J. Balasingh, P. T. Nathan, K. Emmanuel, and T. H. Kunz. 2000a. Dispersion and site fidelity in a tent-roosting population of the short-nosed fruit bat (*Cynopterus sphinx*). *Journal of Tropical Ecology*, 16:1–18.
- Storz, J. F., H. R. Bhat, and T. H. Kunz. 2000b. Social structure of a polygynous tent-making bat, *Cynopterus sphinx* (Megachiroptera). *Journal of Zoology (London)*, 251:151–165.
- Storz, J. F., and T. H. Kunz. 2000. *Cynopterus sphinx*. *Mammalian Species*, 613:1–8.
- Swift, S. M. 1998. *Long-eared Bats*. T & A. D. Poyser, Ltd., London.
- Szewczak, J. M., S. M. Szewczak, M. L. Morrison, and L. S. Hall. 1998. Bats of the White and Inyo Mountains of California-Nevada. *Great Basin Naturalist*, 58:66–75.
- Tan, K. H., A. Zubaid, and T. H. Kunz. 1997. Tent construction and social organization in *Cynopterus brachyotis* (Muller) (Chiroptera: Pteropodidae) in peninsular Malaysia. *Journal of Natural History*, 31:1605–1621.
- Tan, K. H., A. Zubaid, and T. H. Kunz. 1998. Food habits of *Cynopterus brachyotis* (Muller) (Chiroptera: Pteropodidae) in peninsular Malaysia. *Journal of Tropical Ecology*, 14:299–307.
- Tan, K. H., A. K. Zubaid, and T. H. Kunz. 1999. Roost selection and social organisation in *Cynopterus horsfieldi* (Chiroptera: Pteropodidae). *Malayan Nature Journal*, 53:295–298.
- Taylor, R. J., and N. M. Savva. 1988. Use of roost sites by four species of bats in state forest in south-eastern Tasmania. *Australian Wildlife Research*, 15:637–645.
- Thomas, D. W. 1982. The ecology of an African savanna fruit bat community: resource partitioning and role in seed dispersal. Ph.D. Thesis. University of Aberdeen, Aberdeen.
- Thomas, D. W. 1983. The annual migrations of three species of West African fruit bats (Chiroptera: Pteropodidae). *Canadian Journal of Zoology*, 61:2266–2272.
- Thomas, D. W., and M. B. Fenton. 1978. Notes on the dry season roosting and foraging

- behaviour of *Epomophorus gambianus* and *Rousettus aegyptiacus* (Chiroptera: Pteropodidae). *Journal of Zoology* (London), 186:403–406.
- Tidemann, C. R., and S. C. Flavel. 1987. Factors affecting choice of diurnal roost sites by tree-hole bats (Microchiroptera) in south-eastern Australia. *Australian Wildlife Research*, 14:459–473.
- Tidemann, C. R., D. M. Priddel, J. E. Nelson, and J. D. Pettigrew. 1985. Foraging behaviour of the Australian ghost bat, *Macroderma gigas* (Microchiroptera: Megadermatidae). *Australian Journal of Zoology*, 33:705–713.
- Tidemann, C. R., M. J. Vardon, R. A. Loughland, and P. J. Brocklehurst. 1999. Dry season camps of flying-foxes (*Pteropus* spp.) in Kakadu World Heritage Area, North Australia. *Journal of Zoology* (London), 247:155–163.
- Timm, R. M. 1994. Tent construction by *vampyressa* in Costa Rica. *Journal of Mammalogy*, 65:166–167.
- Timm, R. M. 1987. Tent construction by the bats of the genera *Artibeus* and *Uroderma*. *Fieldiana, Zoology* (Special issue: Studies in Neotropical mammalogy: essays in honor of Philip Hershkovitz, ed. B. D. Patterson and R. M. Timm), n.s., no. 39: 187–212.
- Timm, R. M., and B. L. Clauson. 1990. A roof over their feet. *Natural History*, 3:55–58.
- Timm, R. M., and S. E. Lewis. 1991. Tent construction and use by *Uroderma bilobatum* in coconut palms (*Cocos nucifera*) in Costa Rica. *Bulletin of the American Museum of Natural History* (Special issue: Contributions to mammalogy in honor of Karl F. Koopman, ed. T. A. Griffiths and D. Klingener), 206:251–260.
- Timm, R. M., and J. Mortimer. 1976. Selection of roost sites by Honduran white bats, *Ecotophylla alba* (Chiroptera: Phyllostomatidae). *Ecology*, 57:385–389.
- Tuttle, M. D. 1970. Distribution and zoogeography of Peruvian bats, with comments on natural history. *University of Kansas Science Bulletin*, 49:45–86.
- Tuttle, M. D. 1976. Collecting techniques. Pp. 71–88 *in*: *Biology of Bats of the New World Family Phyllostomatidae* (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Pt. 1. Special Publications, the Museum, Texas Tech University, 13. Texas Tech Press, Lubbock.
- Tuttle, M. D., and D. Hensley. 1993. Bat houses: the secrets of success. *Bats*, 11:3–14.
- Utzurum, R. C. B. 1995. Feeding ecology of Philippine fruit bats: patterns of resource use and seed dispersal. *Symposia of the Zoological Society of London*, no. 67:63–78.
- Utzurum, R. C. B. 1998. Geographic patterns, ecological gradients, and the maintenance of tropical fruit bat diversity. The Philippine model. Pp. 342–353 *in*: *Bat Biology and Conservation* (T. H. Kunz and P. A. Racey, eds.). Smithsonian Institution Press, Washington, D.C.
- van Heerdt, P. F., and J. W. Sluiter. 1965. Notes on the distribution and behavior of the noctule bat (*Nyctalus noctula*) in the Netherlands. *Mammalia*, 29:463–477.
- Vardon, M. J., and C. R. Tidemann. 1999. Flying-foxes (*Pteropus alecto* and *P. scapulatus*) in the Darwin region, north Australia: patterns in camp size and structure. *Australian Journal of Zoology*, 47:411–423.
- Vaughan, T. A. 1976. Nocturnal behavior of the African false vampire bat (*Cardioderma cor*). *Journal of Mammalogy*, 57:227–248.
- Vaughan, T. A., and R. P. Vaughan. 1986. Seasonality and the behavior of the African yellow-winged bat. *Journal of Mammalogy*, 67:91–102.

- Vehrencamp, S. L., F. G. Stiles, and J. W. Bradbury. 1977. Observations on the foraging behavior and avian prey of the Neotropical carnivorous bat, *Vampyrum spectrum*. *Journal of Mammalogy*, 58:469–478.
- Verschuren, J. 1957. *Ecologie, biologie, et systématique des Chiroptères. Exploration du Parc National de la Garamba*. no. 7 (Mission H. de Saeger). Institut des Parcs Nationaux du Congo Belge, Brussels.
- Verschuren, J. 1966. Introduction à la écologie et a la biologie des Chiroptères. Pp. 25–65 in: *Exploration du Parc National Albert*, no. 2 (Mission F. Bouliere et J. Verschuren, 1957–1961). Fasc. 2. Institut des Parcs Nationaux du Congo Belge, Brussels.
- Voigt, C. C., and O. von Helversen. 1999. Storage and display of odour by male *Saccopteryx bilineata* (Chiroptera, Emballonuridae). *Behavioral Ecology and Sociobiology*, 47:29–40.
- Voigt, C. C., O. von Helversen, R. Michener, and T. H. Kunz. 2001. The economics of harem maintenance in the sac-winged bat, *Saccopteryx bilineata* (Emballonuridae). *Behavioral Ecology and Sociobiology*, 50:31–36.
- Vonhof, M. J. 1996. Roost-site preferences of big brown bats (*Eptesicus fuscus*) and silver-haired bats (*Lasionycteris noctivagans*) in the Pend d'Oreille Valley in southern British Columbia. Pp. 62–80 in: *Bats and Forests Symposium, October 19–21, 1995 Victoria, British Columbia, Canada* (R. M. R. Barclay and R. M. Brigham, eds.). British Columbia Ministry of Forests, Victoria.
- Vonhof, M. J., and R. M. R. Barclay. 1996. Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. *Canadian Journal of Zoology*, 74:1797–1805.
- Vonhof, M. J., and R. M. R. Barclay. 1997. Use of tree stumps as roosts by the western long-eared bat. *Journal of Wildlife Management*, 61:674–684.
- Waldien, D. L., J. P. Hayes, and E. B. Arnett. 2000. Day-roosts of female long-eared *Myotis* in western Oregon. *Journal of Wildlife Management*, 64:785–796.
- Walsberg, G. E. 1986. Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. *Auk*, 103:1–7.
- Webster, W. D., J. K. Jones, and R. J. Baker. 1980. *Lasiurus intermedius*. *Mammalian Species*, 132:1–3.
- Wetterer, A. L., M. V. Rockman, and N. B. Simmons. 2000. Phylogeny of phyllostomid bats (Mammalia: Chiroptera): data from diverse morphological systems, sex chromosomes, and restriction sites. *Bulletin of the American Museum of Natural History*, 248:1–200.
- Whewell, G. D. 1992. Flying foxes in the Solomon Islands. Pp. 102–104 in: *Pacific Island Flying Foxes: Proceedings of an International Conservation Conference* (D. E. Wilson and G. L. Graham, eds.). U.S. Fish and Wildlife Service, Biological Report 90 (23), Washington, D.C., 176 pp.
- Whitaker, R. J., and S. J. Jones. 1994. The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *Journal of Biogeography*, 21:245–258.
- Whitmore, T. C. 1998. *An Introduction to Tropical Rain Forests*. 2d ed. Oxford University Press, Oxford.
- Wickler, W., and U. Seibt. 1976. Field studies of the African fruit bat, *Epomophorus wahlbergi*, with special reference to male calling. *Zeitschrift für Tierpsychologie*, 40:345–376.

- Wickler, W., and D. Uhrig. 1969. Verhalten und Ökologische Nische der Gelflügelgedermaus, *Lavia frons* (Geoffroy) (Chiroptera, Megadermatidae). *Zeitschrift für Tierpsychologie*, 26:726–736.
- Wiles, G. J. 1987. Current research and future management of Mariannus fruit bats (Chiroptera: Pteropodidae) on Guam. *Australian Mammalogy*, 10:93–95.
- Wilkinson, G. S. 1985. The social organization of the common vampire bat. I. Pattern and cause of association. *Behavioral Ecology and Sociobiology*, 17:111–121.
- Wilson, D. E., 1978. Thyroptera discifera. *Mammalian Species*, 104:1–3.
- Wilson, D. E., and J. Engbring. 1992. The flying foxes *Pteropus samoensis* and *Pteropus tonganus*: status in Fiji and Samoa. Pp. 74–101 in: *Pacific Island Flying Foxes: Proceedings of an International Conservation Conference* (D. E. Wilson and G. L. Graham, eds.). U.S. Fish and Wildlife Service, Biological Report 90 (23), Washington, D.C.
- Wilson, D. E., and J. S. Findley. 1977. Thyroptera tricolor. *Mammalian Species*, 71:1–3.
- Wilson, D. E., and G. L. Graham, eds. 1992. *Pacific Island Flying Foxes: Proceedings of an International Conservation Conference*. U.S. Fish and Wildlife Service, Biological Report 90 (23), Washington, D.C.
- Wimsatt, W. A., and B. Villa-R. 1970. Locomotor adaptations in the disc-winged bat, *Thyroptera tricolor*. *American Journal of Anatomy*, 129:89–119.
- Winkelman, J. R., F. J. Bonaccorso, and T. L. Strickler. 2000. Home range of the southern blossom bat, *Syconycteris australis*, in Papua New Guinea. *Journal of Mammalogy*, 81:408–414.
- Wiriosopartha, A. S., A. S. Mukhtar, and M. Bismark. 1986. Habitat and population study of flying foxes *Pteropus vampyrus* in relation with coastal birds conservation in Pulau Rambut Nature Reserve. *Buletin Penelitan Hutan*, 479:17–27 (in Malay, English summary).
- Wunder, L., and A. B. Carey. 1996. Use of the forest canopy by bats. *Northwest Science*, 70:79–85.
- Zielinski, W. J., and S. T. Gellman. 1999. Bat use of remnant old-growth redwood stands. *Conservation Biology*, 13:160–167.
- Zortéa, M. 1995. Observations on tent-using in the carolline bat *Rhinophylla pumilio* in southeastern Brazil. *Chiroptera Neotropical*, 1:2–4.
- Zortéa, M., and F. A. De Brito. 2000. Tents used by *Vampyressa pusilla* (Phyllostomidae) in southeastern Brazil. *Journal of Tropical Ecology*, 16:475–480.
- Zubaid, A. 1993. A comparison of the bat fauna between primary and fragmented secondary forest in peninsular Malaysia. *Mammalia*, 57:202–206.