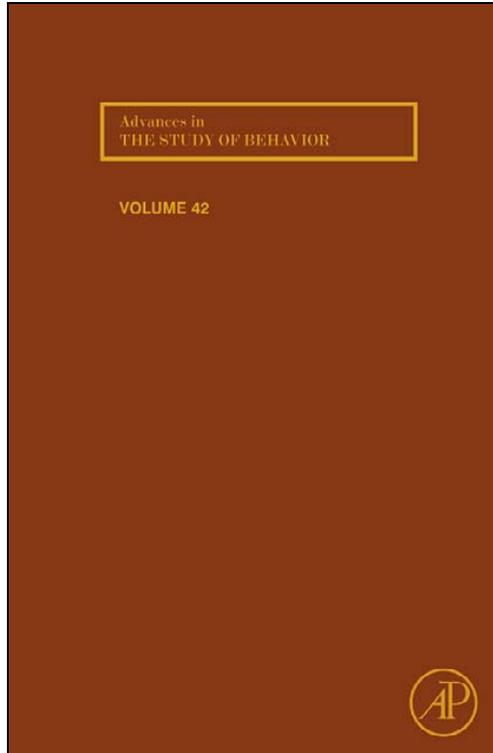


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Ecological Determinants of Social Systems: Perspectives on the Functional Role of Roosting Ecology in the Social Behavior of Tent-Roosting Bats

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I. INTRODUCTION

Most mammals use shelters on a daily or seasonal basis. Some species use preexisting structures, such as tree cavities, caves, and rock crevices, to provide protection from the sun, rain, or predators. Other species modify their environment in nontrivial ways to construct dens, nests, or burrows, which provide their occupants with a multitude of advantages. For example, among the approximately 1116 documented bat species, 30 are known to modify existing structures into shelters, or roosts, which provide not only protection from predators and inclement weather, but also sites for mating, caring for young, grooming, and feeding. Some of these modified structures include termite and ant nests, root masses, stems, and leaves (Kunz and Lumsden, 2003). Plant-modifying bats often alter the appearance of leaves, roots, and stems so that the resulting structure resembles a tent, and are thus referred to as tent-roosting or tent-making bats. However, not all plant-roosting bats alter the appearance of leaves or other plant structures in such a manner, nor do they exclusively use tents for roosting.

Tent-roosting bats comprise a polyphyletic group of both New and Old World origins. In the Paleotropics, at least six species from two families are known to modify plants into tents: *Balionycteris maculata*, *Cynopterus horsfieldii*, *C. brachyotis* Forest, *C. brachyotis* Sunda, and *C. sphinx*, from the family Pteropodidae, and *Scotophilus kuhlii*, from the family Vespertilionidae (Balasingh et al., 1995; Bhat and Kunz, 1995; Campbell et al., 2004; 2006b; Hodgkison et al., 2003; Rickart et al., 1989; Tan et al. 1997). In the Neotropics, the seven genera and 18 species known to construct or use tents

belong to a single family, Phyllostomidae (reviewed in [Kunz and Lumsden, 2003](#); [Rodríguez-Herrera et al., 2007b](#); [Muñoz-Romo and Herrera, 2003](#)). Notwithstanding their diversity and separate evolutionary origins, tent-roosting species exhibit many convergences in their morphology and ecology. First, most species are relatively small for their family. Pteropodid tent-making bats (i.e., *Balionycteris* and *Cynopterus*) have a body mass that ranges between 10 g and 60 g, representing the lower range of body masses for Pteropodidae (10–1500 g). Tent-roosting phyllostomids are also mostly comprised of small-bodied species (4–21 g), with a few exceptions (*Artibeus jamaicensis* and *A. lituratus*: 30–70 g), as the body masses for the entire family range between 4 g and 235 g. Tent-roosting bats also share great similarities in their diet, as most of them, except *S. kuhlii*, feed primarily on fruits ([Bumrungsri et al., 2007](#); [Rodríguez-Herrera et al., 2007b](#); [Tan et al., 1998](#)). They also modify leaves in a remarkably similar fashion, perhaps as a result of design constraints imposed by leaf size and shape, number and pattern of leaf veins, the position of petioles, and the number of stems ([Kunz et al., 1994](#)).

Since the first reports of tent-roosting behavior in bats by [Chapman \(1932\)](#) and [Barbour \(1932\)](#), there have been considerable advances in our understanding of this behavior. Many publications provide a detailed account of the plants used for roosting (e.g., [Rodríguez-Herrera et al., 2007b](#); [Timm, 1987](#)), the way in which these plants are modified (e.g., [Kunz et al., 1994](#); [Tan et al., 1997](#)), how bats select plants and leaves (e.g., [Choe and Timm, 1985](#); [Timm and Mortimer, 1976](#)), and the sex responsible for leaf modification (e.g., [Muñoz-Romo and Herrera, 2003](#); [Rodríguez-Herrera et al., 2007a](#)). While some of the older studies of tent-roosting bats provide information related to social behavior, such as group size and composition, more recent publications that use capture–recapture and radio-telemetry techniques present a more detailed account of the social behavior of these bats, including not only the size and composition of groups but also data on social cohesion and interactions among roosting groups ([Campbell et al., 2006a](#); [Chaverri et al., 2007a](#); [Muñoz-Romo et al., 2008](#); [Storz et al., 2000b](#)). However, despite the growing interest in the social behavior of tent-roosting bats, and the abundance of information regarding the roosting ecology and social behavior of many species, there have been few attempts to summarize findings on the social systems of tent-roosting bats, and to place them in an ecological context (but see [Campbell et al., 2006a](#) and [Campbell, 2008](#) for comparative analyses on the Old World genus *Cynopterus*). In this chapter, we compile ecological and behavioral data on Neotropical and Palearctic tent-roosting species to determine if the variation in social behavior observed in these bats may be explained by any of the components of their roosting ecology. For the purposes of this

review, a tent-roosting bat is defined as a species known to use plant parts such as leaves, roots, stems, and flower/fruit clusters that have been deliberately modified by bats.

In this chapter we first examine social systems and their components, focusing on diverse methodologies to define and categorize social organization, mating systems, and social structure. We address how ecological factors are known to influence social systems in diverse mammalian species, and explore the relationship between roosting resources and social behavior in bats. Next, we provide a detailed summary of the roosting ecology of diverse species of tent-roosting bats, focusing on roost diversity, abundance, distribution, construction, defense, and fidelity. We then address differences in group size, composition, and social cohesion in several species of tent-making bats, and attempt to understand the relationship between roosting ecology and social behavior by comparing species and populations, and by comparing the social behavior of these bats with the social behavior of other tropical species with different roosting habits. We conclude by summarizing the similarities and differences between tent-roosting species, with a discussion of some additional variables that may influence their social behavior. We also discuss how variation in social systems may influence mating strategies in tent-roosting bats.

A. DEFINING AND MEASURING SOCIAL SYSTEMS AND THEIR COMPONENTS

1. *Components of Social Systems and Basic Categorizations*

According to [Kappeler and van Schaik \(2002\)](#), social systems are composed of three distinct aspects, the social organization, the mating system, and the social structure. These authors define social organization as the size, sexual composition, and spatiotemporal cohesion of a society; the mating system as the subset of interactions that occur between mating partners and its resulting reproductive consequences; and the social structure as the patterns of social interactions and the resulting relationships among members of a society. Three basic social organizations are typically recognized: solitary, pair-living, and group-living ([Kappeler and van Schaik, 2002](#); [Lott, 1991](#)). Mating systems, on the other hand, are broadly categorized as monogamous when males and females typically mate with only one partner; polygynous when males mate with the same set of females in successive mating attempts; polyandrous when females mate with the same set of males in successive mating attempts; and promiscuous when either males or females mate with multiple members of the opposite sex and no long-term bond is established between mating partners ([Clutton-Brock, 1989](#)).

2. *Categorizing and Measuring Social Systems: Top-down and Bottom-up Approaches*

Developing a single classification scheme of social systems that can be applied to most taxa has been a difficult undertaking with relatively limited success. Categorization schemes developed for particular species or taxonomic groups may not be universally applicable, and methodological approaches often vary across studies. There is also extensive intraspecific variation in many features of societies, such as the number of associates (Bezanson et al., 2008; Borkowski and Furubayashi, 1998; Travis et al., 1995), mating system (Adamczak and Dunbar, 2008; Banks et al., 2005b; Davies and Lundberg, 1984), and stability of associations (Wiszniewski et al., 2009; Wittemyer et al., 2005). Thus, because categorization of social systems often depends on accurately quantifying these highly variable features, assigning a species to a narrowly defined social system based on measures of a single population may be a considerable misrepresentation.

Researchers have used two different approaches to measure social systems. Many sociobiologists, such as Wilson (1975), preferred a top-down perspective, in which animal societies were assigned to relatively broad categories that were divided somewhat arbitrarily. Unfortunately, the top-down approach does not always provide a clear representation of social structure, as many of the measures used to describe it, such as group size, may not be based on consistent or sound methodologies (Reiczigel et al., 2007), and because partitioning criteria could result in vague or inaccurate classifications (Whitehead, 2008). In contrast, ethologists such as Hinde (1976) proposed a bottom-up study of social systems. Hinde's work is based on dyadic interactions, which, if consistent, form the basis of relationships. The nature, quality, and patterning of these relationships form the basis of a population's social structure. This conceptual framework provides an elegant approach to analyze societies that is now widely used by ethologists and behavioral ecologists, and elements of all the three levels (interactions, relationships, and social structure) can be classified and subsequently used in comparative analyses to infer evolutionary processes.

3. *Measures of Social Structure*

Top-down and bottom-up approaches require that a subset of characteristics of societies be measured. Specific measures of social structure include demographic structure, rates of interaction, group size, closure and stability of groups, units or communities, stability of relationships, and differentiation of roles (Whitehead, 2008; Wilson, 1975). Demographic structure refers to the distribution of age, sex, and reproductive categories within a population, and understanding it is important given its influence on the

reproductive success of individuals and groups (Emlen and Oring, 1977; Treves, 2001). Interactions are instances in which the presence or behavior of one individual affects the behavior of another (Hinde, 1976). Thus, rates of interaction refer to how often these events occur among the same sets of individuals, and are important for understanding societies as they provide clues regarding disease transmission and information transfer (Böhm et al., 2008; Pacala et al., 1996; Vercauteren et al., 2007).

Group size is one of the most salient and most often studied features of animal societies. However, the way in which group size is measured and defined varies between authors and species. Most authors, for example, simply provide the mean and standard deviation of the number of individuals that occupy the same space at the same time. However, this measure is only helpful when group size has a normal distribution, which is rarely the case (Reiczigel et al., 2007). A more accurate representation of an individual's social environment is provided by the typical group size proposed by Jarman (1974), or crowding (sensu Reiczigel et al., 2007), which refers to the size of the group as experienced by any individual within that group. Hence, instead of using a single measure per group to calculate average group size, crowding provides a separate measure for all individuals, which can then be averaged across individuals to obtain the typical group size. Another difficulty with some of the measures of group size provided in the literature is that authors often define groups in different ways. In bats, for example, a set of terms that include aggregation, colony, group, and roosting group, have been used to define individuals using the same roost at the same time. In the case of individuals that do not always roost together, but that associate more often with one another than with other individuals in the population, authors have used terms such as social group, group, and colony (Kerth, 2008; Vonhof et al., 2004; Willis and Brigham, 2004).

Another important measure used to describe societies is the closure of social units, which refers to the rates of movement between relatively closed groups or communities. To measure rates of movement, however, it is necessary to first determine the composition of social units within populations. This is accomplished by using a set of agglomerative and divisive methods, such as hierarchical and network clustering, in which groups are defined based on measures of association strength between individuals (Newman and Girvan, 2004). Association strength, in turn, can help to quantify stability of associations by tracking temporal changes in dyadic associations using lagged association rates (Whitehead, 1995). Because group stability may significantly influence cooperation (Kun and Scheuring, 2009; Lusseau et al., 2003) and cooperation is known to improve fitness (Ryder et al., 2008; Wilkinson, 1984, 1992a), understanding and measuring the stability of associations is not a trivial undertaking.

B. RESOURCES AND SOCIAL SYSTEMS

Resource density and distribution are perhaps the most important ecological correlates of social systems. Resources may affect the demographic structure of populations when there are significant differences in dispersal behavior among males and females due to competition for scarce resources (Clark, 1978), particularly if there is also dispersal-associated mortality (Banks et al., 2005a). Severe environmental conditions or high population densities, which affect resource abundance and hence nutritional stress during pregnancy, can also have an effect on sex ratio as females may selectively produce offspring of the sex that provides the highest fitness return given the amount of resources available (Garroway and Broders, 2007a; Kruuk et al., 1999; Trivers and Willard, 1973). However, in addition to their effect on the demographic structure of populations, resources may also influence the sex ratio of groups. In primates, for example, multi-male groups are more common among species in which the number of females in a group is greater than 10 (Andelman, 1986). Because group size in these mammals may be influenced partly by the size and number of resource patches (Leighton and Leighton, 1982; Terborgh, 1983), it follows that characteristics of their feeding resources also influence group composition.

Group size is influenced by the balance between costs such as competition, aggression, and increased parasite loads (Alexander, 1974; Brown and Brown, 1986; Davies et al., 1991) and benefits such as predator avoidance, foraging enhancement, and thermoregulation (Beauchamp, 1998; Caraco and Wolf, 1975; Krause and Ruxton, 2002; Putaala et al., 1995; Seghers, 1974). Thus, patterns of resource abundance and distribution are strong determinants of group size (Macdonald, 1983). For example, increases in resource availability favor group formation and larger group size by decreasing the cost of sharing a territory with conspecifics (Johnson et al., 2002; Randall et al., 2005). Likewise, resource quality and quantity influence group size and composition via effects on population density (Chapman and Chapman, 1999; Hanya et al., 2004; Ostro et al., 2001; Raman 1997; Travis et al., 1995).

Resource abundance may also affect how individuals move among social units, such that whenever the resource is in short supply individuals will tend to disperse (Stradiotto et al., 2009; Wauters et al., 2005), decreasing the stability of groups or communities (Baird and Whitehead, 2000). The stability of relationships may also be influenced by the abundance of resources because weaker bonds form when resources are scarce due to increased competition (Wittemyer et al., 2005), and probably also because of an increase in the rates of aggressive encounters (Dubois and Giraldeau, 2005;

Dubois et al., 2003). Resource quality also affects interaction rates via its influence on range size and range overlap (Brashares and Arcese, 2002; Dahle and Swenson, 2003; McLoughlin et al., 2000).

C. ROOSTING ECOLOGY AND SOCIAL BEHAVIOR IN BATS

Diurnal roosts are one of the most important venues for social interactions in bats, and evidence suggests that most species encounter familiar conspecifics primarily at roost sites. For example, multiple social and reproductive activities, such as allogrooming (Kerth et al., 2003; Ortega and Maldonado, 2006; Wilkinson, 1986), allofeeding (Wilkinson, 1984, 1992a), nursing (Fleming et al., 1998; Kunz and Hood, 2000), and copulation (Chaverri and Kunz, 2006a; Keeley and Keeley, 2004; Zahn and Dippel, 1997), seem to occur almost exclusively at the roost. In addition to their role in social interactions, roosts also seem to be a valuable resource because they protect individuals from temperature extremes and predators (Ferrara and Leberg, 2005; Lausen and Barclay, 2006), they may be relatively scarce (Kunz, 1982; Kunz and Lumsden, 2003), they may be costly to construct and maintain (Balasingh et al., 1995; Kalko et al., 2006; Rodríguez-Herrera et al., 2007a), and many species have unique morphological specializations that restrict them to a single roost type (Riskin and Fenton, 2001; Thewissen and Etnier, 1995). Thus, it is no surprise that many bats actively defend roosts (Morrison, 1979; Ortega et al., 2008), territories within roosts (Davidson and Wilkinson, 2004), and roosting areas (Chaverri et al., 2007a; Fleming, 1988). Because roosts are the main venue for social interactions, are relatively scarce, and essential for protection, and because studies have found that diverse attributes of roosts exert a significant influence on social systems (e.g., Campbell et al., 2006a; Chaverri et al., 2007a, 2008; Hodgkison et al., 2003; Lausen and Barclay, 2006; Lundberg and Gerell, 1986), it seems reasonable to assume that roosts, and not food, are the most important determinants of social systems in many bat species. Notwithstanding studies have shown that the dispersion and abundance of feeding resources are also important correlates of social systems in bats (e.g., Bradbury and Vehrencamp, 1976, 1977). In fact, many species are known to engage in group defense of feeding territories (Barlow and Jones, 1997), while others cooperate during the location of food items (Dechmann et al., 2009; Wilkinson, 1992b; Wilkinson and Boughman, 1998), suggesting that foraging behavior may facilitate and promote sociality in many species (Safi and Kerth, 2007).

While little research has explicitly addressed how roosting resources influence the diverse social systems of bats, a few trends can be observed in comparisons between species that use different structures. Species using

large roosts, such as caves, typically live in colonies that can range from the hundreds to the millions (Betke et al., 2008; Churchill et al., 1997; Galindo et al., 2004; Hristov et al., 2010), whereas bats in similarly permanent but smaller structures, such as rock crevices, form small groups that typically do not exceed 40 individuals (Holloway and Barclay, 2000; Lausen and Barclay, 2002; Solick and Barclay, 2007; Vaughan and O'Shea, 1976). Hollow structures in plants also support colonies whose size is apparently correlated with the size of cavities. For example, tree cavities, which can measure up to 168,300 cm³ (Sedgeley and O'Donnell, 1999), may contain colonies of between 2 and 200 individuals (Kalcounis and Brigham, 1998; Kurta et al., 1993; Lumsden et al., 2002). In contrast, cavities within bamboo culm measure an average of 11,637 cm³, and are only known to hold up to 24 bats (Zhang et al., 2004). These trends are obvious not only between species, but also within them. For example, big brown bats (*Eptesicus fuscus*) roosting in rock crevices may live in groups ranging upward to 37 (Lausen and Barclay, 2002), whereas colonies in buildings range from 14 to 124 individuals (Davies et al., 1968).

Another characteristic of the social behavior of bats that has received some attention, particularly in more recent years, is the stability of associations and its correlation with roosting resources. In this respect, available data suggest that bats roosting in abundant structures, such as tree cavities and rock crevices, frequently switch roosts and roosting partners (Brigham, 1989; Garroway and Broders, 2007b; Kerth and König, 1999; Lausen and Barclay, 2002; Popa-Lisseanu et al., 2008; Willis and Brigham, 2004). In contrast, species that use less abundant roosts typically exhibit greater fidelity to such structures, with equivalent degrees of social cohesion (Brooke, 1997; Lewis, 1995; McCracken and Bradbury, 1981; Wilkinson, 1985). Some exceptions to this trend exist (e.g., Brosset, 1976; Vonhof et al., 2004), suggesting that other factors may also account for interspecific differences in social behavior.

D. NATURAL HISTORY OF TENT-ROOSTING BATS

1. *Paleotropical*

In the Paletropics, five species in the family Pteropodidae are known to construct tents. *Balionycteris maculata*, or the spotted-winged fruit bat, is a 13 g bat distributed throughout the Malay Peninsula, northern and western Borneo, Thailand, and Sumatra. It has a highly maneuverable flight, and is associated with old-growth forests. It feeds on fruits from at least 22 species of plants, but may also consume insects. Females are known to have two

pups per year, and they attain sexual maturity before one year of age. *Balionycteris maculata* roosts in cavities formed in ant and termite nests, and root masses of epiphytic ferns and gingers (Hodgkison and Kunz, 2006).

Cynopterus brachyotis, or the lesser dog-faced fruit bat, which has recently been subdivided in two evolutionary distinct ecotypes (i.e., Forest and Sunda; Campbell et al., 2004, 2006c, 2007), is distributed from southwest India and Sri Lanka to mainland southeast Asia, and throughout Indonesia and the Philippines (Corbet and Hill, 1992). *Cynopterus brachyotis* Sunda is a 32–42 g bat that is abundant in disturbed habitats, while the smaller *C. brachyotis* Forest weighs 24–37 g and is restricted to forested habitats (Campbell et al., 2006a, 2007). The diet of *C. brachyotis* consists of fruits from 54 plant species, and also includes leaves and stamens from diverse taxa (Tan et al., 1998). *Cynopterus brachyotis* Sunda uses a diversity of roosts, including fan palm tents, root and stem tents, and spaces under unmodified leaves (Campbell et al., 2006b; Tan et al., 1997). *Cynopterus brachyotis* Forest uses both modified and unmodified leaves for roosting (Campbell et al., 2006b).

Cynopterus horsfieldii, or Horsfield's fruit bat, occurs from southern Thailand throughout peninsular Malaysia, Sumatra, Java, and Borneo. It weighs from 55 to 59 g, and is seasonally polyestrous and reproductively asynchronous. This bat is a habitat generalist, occupying diverse lowland habitats from primary forests to agricultural areas and suburban parks. *Cynopterus horsfieldii* feeds on fruits and pollen, and roosts under foliage, rock and limestone cavities, and in caves. This bat apparently modifies foliage roosts in an opportunistic manner (Campbell and Kunz, 2006).

Cynopterus sphinx, or short-nosed fruit bat, is distributed through Pakistan, India and Sri Lanka to southern China, the Malay Peninsula, Sumatra, Java, Borneo, Sulawesi, Timor, and the smaller islands in the Malay Archipelago. This bat weighs between 38 and 46 g, and is seasonally polyestrous, producing a maximum of two young per year. Females become sexually active during their first year of age. *Cynopterus sphinx* is relatively common throughout its range, and may prefer cultivated habitats in drier regions. Its diet includes fruits, leaves, and flowers from at least 31 species of plants. The short-nosed fruit bat uses a diversity of roosting structures, including aerial roots, tree hollows, foliage, buildings, caves, and also constructs leaf and stem tents (Storz and Kunz, 1999).

The other species known to use modified leaves for roosting in the Paleotropics is *Scotophilus kuhlii*, or Asiatic yellow bat (family Vespertilionidae). Little information exists regarding the life history, ecology, and behavior of this bat. *Scotophilus kuhlii* weighs approximately 20 g, and is distributed from Pakistan to Taiwan, south to Sri Lanka and western Malaysia, southeast to the Philippines, and in Aru Islands in Indonesia (Wilson and Reeder, 2005). This insectivorous species is found in primary

and secondary forests, in rural and urban areas. It roosts in buildings, caves, hollow trees, crevices, dry leaves, and in leaf tents (Bates and Harrison, 1997; Rickart et al., 1989).

2. Neotropical

All known tent-roosting species in the Neotropics are members of the family Phyllostomidae, or leaf-nosed bats. The genus *Artibeus* contains the largest number of tent-roosting phyllostomids, which accounts for half the species known to use tent-roosts in the New World. Species in the *Artibeus* genus known to roost in tents are *anderseni*, *cinereus*, *glaucus*, *gnomus*, *jamaicensis*, *lituratus*, *phaeotis*, *toltecus*, and *watsoni*. This group of bats is distributed from the central regions of Mexico, through Central America, to southeastern Brazil. *Artibeus jamaicensis* also occurs in the Greater and Lesser Antilles (Rodríguez-Durán, 2010; Rodríguez-Herrera et al., 2007b). Most species are relatively small-bodied, weighing 5–20 g, with the exception of *A. jamaicensis* and *A. lituratus*, whose body mass may range up to 51 and 73 g, respectively. All species in this genus are known to primarily consume fruit, but a few eat leaves, pollen, nectar, and occasionally insects (Rex et al., 2010). The nine species of tent-making *Artibeus* occur in a wide diversity of habitats, including primary and secondary humid and dry forests, clearings, and plantations (LaVal and Rodríguez, 2002; Reid, 1997). Females in this genus typically exhibit a seasonal bimodal polyestry, with parturitions occurring mostly during the dry season and beginning of the wet season (Chaverri and Kunz, 2006a; LaVal and Rodríguez, 2002; Ortega and Castro-Arellano, 2001; Timm, 1985). Almost all *Artibeus* are obligate tent-roosters, except for *A. jamaicensis*, *A. lituratus*, and *A. toltecus*, which may use unmodified foliage, caves, buildings, and hollow trees (Kunz et al., 1983; Ortega and Castro-Arellano, 2001; Rodríguez-Herrera et al., 2007b; Webster and Jones 1982). *Artibeus lituratus* is an interesting exception to the typical tent-making behavior of most tent-roosting bats. This species is often not considered a tent-roosting species because it has never been observed using the characteristic architectural patterns described by Kunz et al. (1994). However, this bat exhibits a leaf-modifying behavior, in which individuals puncture the medial region of the lamina in a pleurocostal-ellipsoidal pattern, that undoubtedly results in an improvement of the leaf-roost (Muñoz-Romo and Herrera, 2003; Muñoz-Romo et al., 2008), and will be accordingly treated as a tent-roosting species for the purposes of this review.

Ectophylla alba, or the Honduran white bat, and *Mesophylla macconnelli*, the little yellow-faced bat, are the smallest of all tent-roosting species, weighing 5.5 and 6.5 g, respectively. *Ectophylla alba* is known only from the Caribbean lowlands of Central America, as far north as eastern Honduras south to western Panama. *Mesophylla macconnelli* is distributed from the

southern parts of Central America through northern South America. These two species appear to exhibit bimodal seasonal polyestry, but little is known about their reproductive patterns. They are mostly found in primary lowland tropical moist and humid forests, and feed primarily on fruits. *Ectophylla alba* roosts exclusively in tent-roosts, whereas *M. macconnelli* uses tent-roosts and unmodified foliage (Kunz and Pena, 1992; Timm, 1982).

Platyrrhinus helleri, or Heller's broad-nosed bat, is a medium-sized bat with an average body mass of 15 g. It is distributed from southern Mexico south through Central and South America to Peru, Bolivia, and Amazonian and central Brazil. Some specimens have been reported from Trinidad (Clarke et al., 2005). Reproduction appears to be bimodal seasonal polyestry, with births occurring during the last part of the dry season and then again in the middle of the wet season. It is most often captured in humid tropical primary forests, and feeds primarily on fruits that grow in the forest canopy. *Platyrrhinus helleri* roosts in caves, tunnels, bridges, in foliage, under branches, and in tent-roosts (Ferrell and Wilson, 1991; Tello and Velazco, 2003).

Uroderma bilobatum, or Peter's tent-making bat, and *U. magirostrum*, or brown tent-making bat, are medium-sized bats (12–21 g) distributed along the lowlands of southern Mexico, south to Peru, Bolivia, and southeastern Brazil. Both species occur in deciduous and evergreen forests, but *U. bilobatum* is also found in secondary woodlands and fruit groves. Like most other tent-roosting bats, *U. bilobatum* exhibits a bimodal seasonal polyestry, with births occurring during the dry and early rainy seasons. Most authors report a frugivorous diet for *U. bilobatum*, although it may also feed on pollen, nectar, and insects associated with flowers and fruits. Little is known about the reproductive biology and feeding habits of *U. magirostrum*. Both species have been observed only in tent-roosts (Baker and Clark, 1987; Reid, 1997).

Three species of the genus *Vampyressa* are known to use tent-roosts: *V. nymphaea*, *V. pusilla*, and *V. thyone*. These are relatively small bats (6–16 g) known from southeastern Nicaragua through northwestern Ecuador (*V. nymphaea*); from southern Mexico through Central America to Bolivia, Peru, Venezuela, and the Guyanas (*V. thyone*); and in eastern Paraguay and southeastern Brazil (*V. pusilla*). A bimodal seasonal polyestry and a frugivorous diet are presumed for all three species. These bats have been captured in a variety of habitats, mostly in primary forests, but also in yards, orchards, croplands, and swamps. The only known roosting sites for these three species are tents (Lewis and Wilson, 1987; Reid, 1997; Rodríguez-Herrera et al., 2007b).

Rhinophylla pumilio, or dwarf little fruit bat, is the only tent-roosting Neotropical bat that does not belong to the subfamily Stenodermatinae. This relatively small bat (7–13 g), a member of the subfamily Carollinae, is a relatively common species found in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Surinam, and Venezuela. *Rhinophylla*

pumilio is most often captured in primary and secondary forests, but it can also be observed in pastures and orchards. Its diet is mostly composed of small-seeded understory and mid-canopy fruits, but other fruits with larger seeds are also consumed, as well as pollen. It is most often found roosting in tents, but may also use culverts, thatched roofs, and unmodified leaves (Rinehart and Kunz, 2006; Rodríguez-Herrera et al., 2007b).

II. ROOSTING ECOLOGY OF TENT-MAKING BATS

A. ROOST DIVERSITY

At least 100 species of plants, representing 24 families, are known to be used by tent-roosting bats. Most bats use less than five species of plants for tent-roosting, while one bat, *A. watsoni*, has been observed and/or captured in up to 42 different plant species (Campbell et al., 2006b; Hodgkison et al., 2003; Kunz et al., 1994; Muñoz-Romo and Herrera, 2003; Rickart et al., 1989; Rodríguez-Herrera et al., 2007b; Storz and Kunz, 1999; Tan et al., 1997). The majority of plant species used by tent-roosting bats belong to the families Araceae (arums) and Arecaceae (palms), and one salient feature of these families is that many species have leaves that are usually quite large. For example, the talipot palm (*Corypha umbraculifera*) has round leaves that can grow up to 2.4 m long and 3.6 m wide (Table I).

The plant structure most often used for roosting is the leaf, which bats modify by chewing the veins and/or midribs (Kunz et al., 1994; Rodríguez-Herrera et al., 2007a). This results in the collapse of leaves, or leaflets, and in the formation of an enclosed structure that varies in size and shape depending on the plant and on the bats' behavior (Kunz et al., 1994; Tan et al., 1997). In addition to leaves, which are most commonly used by bats in the Neotropics, some Paleotropical species also modify stems, fruit and flower clusters, and root masses in seven species of plants to form an enclosure (Bhat and Kunz, 1995; Tan et al., 1997; Hodgkison et al., 2003; Fig. 1).

B. ROOST ABUNDANCE AND DISTRIBUTION

Tent-roosts are regarded as one of the most abundant structures used by bats for roosting, compared to caves, buildings, tree cavities, and rock crevices (Lewis, 1995). In fact, many of the plants typically used by tent-roosting bats can be quite common in tropical forests. For example, lowland primary forests of northeastern Costa Rica are known to have densities of 2200 plants per ha of three palms that are used by tent-roosting bats: *Asterogyne martiana*, *Bactris hondurensis*, and *Geonoma cuneata*

TABLE I
TYPE OF ROOST, TENT STYLES, AND THE SIZE OF UNMODIFIED LEAVES AND TENTS OF SOME OF THE PLANTS USED BY
TENT-ROOSTING BATS AS DIURNAL ROOSTS.

| Family | Species | Roost | | Tent | | Bat | Group size | | References |
|-----------|--|-------------------|--------------------|-----------|---------|----------------------------|------------|-------|--|
| | | Type ^a | Style ^b | Leaf | Tent | | Mean | Range | |
| Araceae | <i>Anthurium ravenii</i> | LT | 1 | 43 × 38 | 40 × 28 | <i>A. watsoni</i> | 1.8 | 1–3 | Chaverri and Kunz (2006b), Choe and Timm (1985) |
| | <i>Philodendrum grandipes</i> | LT | 1 | 34 × 28 | | <i>A. watsoni</i> | 1.9 | 1–5 | Chaverri and Kunz (2006b) |
| | <i>Philodendrum popenoei</i> | LT | 1 | 31 × 24 | | <i>A. watsoni</i> | 2.4 | 2–4 | Chaverri and Kunz (2006b) |
| | <i>Philodendrum pterotum</i> | LT | 1 | 80 × 60 | | <i>A. watsoni</i> | 2.6 | 1–6 | Chaverri and Kunz (2006b) |
| | <i>Rhodospatha wendlandii</i> | LT | 1 | 55 × 25 | | <i>A. watsoni</i> | 1.8 | 1–5 | Chaverri and Kunz (2006b) |
| | <i>Scindapsus aureus</i> | LT | 1 | 100 × 45 | | <i>C. brachyotis</i> Sunda | | 1–2 | Tan et al. (1997) |
| | <i>Scindapsus aureus</i> | UL | | 100 × 45 | | <i>C. brachyotis</i> Sunda | | 1–2 | Tan et al. (1997) |
| | <i>Asterogyne martiana</i> | LT | 2 | 88 × 21 | | <i>A. watsoni</i> | 2.1 | 1–4 | Chaverri and Kunz (2006b) |
| Arecaceae | <i>Astrocaryum macrocalyx</i> ^c | LT | 2 | | 50 × 17 | <i>M. macconnelli</i> | 3.3 | 1–7 | Foster (1992) |
| | <i>Astrocaryum sciophilum</i> ^c | LT | 2 | | | <i>M. macconnelli</i> | 4 | 2–7 | Simmons and Voss (1998) |
| | <i>Astrocaryum sciophilum</i> ^c | LT | 2 | | | <i>R. pumilio</i> | 2.8 | 1–5 | Simmons and Voss (1998) |
| | <i>Astrocaryum standleyanum</i> ^c | LT | 2 | 62 × 18 | | <i>A. watsoni</i> | 2.1 | 1–4 | Chaverri and Kunz (2006b) |
| | <i>Borassus flabellifer</i> | LT | 3 | | 20 × 20 | <i>C. brachyotis</i> Sunda | | 1–5 | Tan et al. (1997) |
| | <i>Cocos nucifera</i> | LT | 6 | | | <i>U. bilobatum</i> | 2.3, 4.9 | 1–23 | Lewis (1992), Timm and Lewis (1991) |
| | <i>Corypha umbraculifera</i> | LT | 3 | 248 × 368 | | <i>C. sphinx</i> | | 3–8 | Storz and Kunz (1999) |
| | <i>Corypha utan</i> | LT | 3 | 220 × 255 | 50 × 31 | <i>C. brachyotis</i> Sunda | | 1–18 | Tan et al. (1997) |
| | <i>Cryosophila guagara</i> | LT | 3 | 110 × 160 | | <i>A. watsoni</i> | 2.34 | 1–4 | Chaverri and Kunz (2006b) |
| | <i>Elaeis guineensis</i> | UL | | | | <i>C. brachyotis</i> Sunda | | 3–5 | Tan et al. (1997) |
| | <i>Livistona chinensis</i> | LT | 3 | 125 × 125 | 22 × 17 | <i>C. brachyotis</i> Sunda | | 1–14 | Tan et al. (1997) |
| | <i>Livistona chinensis</i> | UL | | 125 × 125 | | <i>C. brachyotis</i> Sunda | | 1–5 | Tan et al. (1997) |
| | <i>Livistona rotundifolia</i> | LT | 3 | 125 × 125 | 19 × 20 | <i>C. brachyotis</i> Sunda | | 1–10 | Tan et al. (1997) |
| | <i>Livistona saribus</i> | LT | 3 | 149 × 203 | 22 × 16 | <i>C. brachyotis</i> Sunda | | 1–3 | Tan et al. (1997) |
| | <i>Pritchardia pacifica</i> | LT | 3 | 120 × 100 | 50 × 59 | <i>U. bilobatum</i> | | 1–56 | Barbour (1932) |

(Continued)

TABLE I (Continued)

| Family | Species | Roost | Tent | Size (cm) | | | Group size | | References |
|---------------|---------------------------------------|-------------------|--------------------|-----------|-----------|----------------------------|------------|-------------------|---|
| | | Type ^a | Style ^b | Leaf | Tent | Bat | Mean | Range | |
| | <i>Washingtonia</i> sp. | ML | | 90 × 130 | | <i>A. lituratus</i> | 5.3 | 2–14 | Muñoz-Romo and Herrera (2003), Muñoz-Romo et al. (2008) |
| Liliaceae | <i>Dracaena fragrans</i> | LT | 5 | 85 × 7 | | <i>C. brachyotis</i> Sunda | | 1–6 | Tan et al. (1997) |
| Annonaceae | <i>Polyalthia longifolia</i> | ST | | | 637 × 140 | <i>C. sphinx</i> | 3 | 1–11 | Storz et al. (2000a) |
| Asteraceae | <i>Vernonia scandens</i> | ST | | | 558 × 157 | <i>C. sphinx</i> | 5.3 | 1–20 ^d | Balasingh et al. (1995) |
| Heliconiaceae | <i>Heliconia imbricata</i> | LT | 4 | 180 × 40 | | <i>A. watsoni</i> | 2.75 | 1–8 | Chaverri and Kunz (2006b) |
| | <i>Heliconia imbricata/pogonantha</i> | LT | 4 | 100 × 20 | | <i>E. alba</i> | 5.42 | 1–17 | Brooke (1990) |
| | <i>Heliconia latispatha</i> | LT | 4 | 62 × 25 | | <i>A. watsoni</i> | 2.33 | 1–3 | Chaverri and Kunz (2006b) |
| Cyclanthaceae | <i>Asplundia alata</i> | LT | 2 | 82 × 30 | | <i>A. watsoni</i> | 2.1 | 1–7 | Chaverri and Kunz (2006b) |
| | <i>Asplundia sleeperae</i> | LT | 2 | 90 × 43 | | <i>M. macconnelli</i> | 3 | | Rodríguez-Herrera et al., 2007b |
| | <i>Carludovica palmata</i> | LT | 3 | 55 × 55 | | <i>A. watsoni</i> | 2.2 | 1–5 | Chaverri and Kunz (2006b) |
| Marantaceae | <i>Calathea lutea</i> | LT | 1 | 90 × 40 | | <i>A. watsoni</i> | 2.97 | 1–7 | Chaverri and Kunz (2006b) |
| Musaceae | <i>Musa paradisiaca</i> | LT | 4 | 120 × 21 | | <i>A. phaeotis</i> | 3 | 1–7 | Timm (1987) |
| | <i>Musa paradisiaca</i> | LT | 4 | 129 × 21 | | <i>A. watsoni</i> | 2.65 | 1–7 | Chaverri and Kunz (2006b) |
| | <i>Musa paradisiaca</i> | LT | 7 | 213 × 93 | | <i>U. bilobatum</i> | 4.5 | 1–8 | Timm (1987) |
| Piperaceae | <i>Piper</i> sp. | LT | 1 | 25 × 12 | | <i>A. watsoni</i> | 1.33 | 1–2 | Chaverri and Kunz (2006b) |

We only include species for which data on the size of roosting groups using that specific plant have been published. Size of tents is provided by cited reference(s), but sources for the size of leaves, which include on-line herbarium specimens and botanical books, are not cited. Group size refers to the mean and range of individuals roosting in the same tent at the same time (i.e., roosting group). When more than one study presents data of group size for a single species of plant, we provide both results. Measures of leaf and leaf-tent size are length × width, while measures of stem tents are height of interior crown × vertical length of tent cavity.

^aLT = leaf tent, ML = modified leaf, ST = stem tent, UL = unmodified leaf.

^b1 = apical, 2 = bifid, 3 = palmate umbrella, 4 = boat, 5 = conical, 6 = pinnate, 7 = paradox.

^cWe provide measures for terminal leaflets only, as these are the ones used by bats.

^dAdults only.

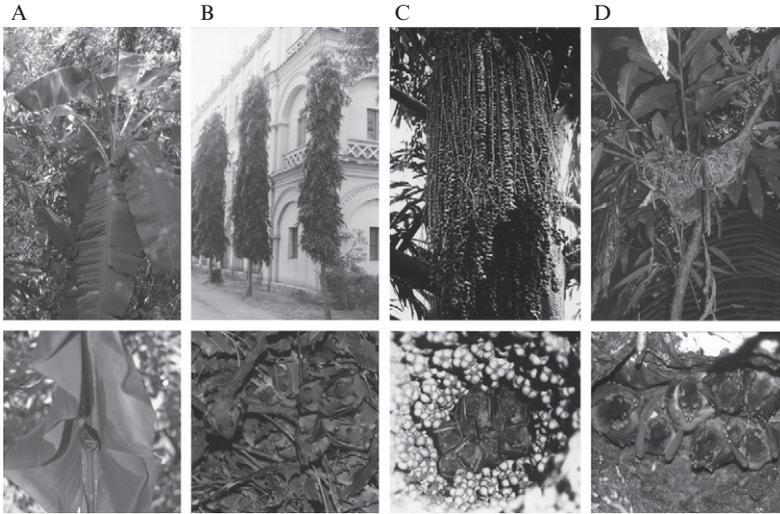


FIG. 1. Four types of tent-roosts: leaf tent constructed by *Artibeus watsoni* and occupied by a single male in *Musa paradisiaca* (A); stem tent constructed by *Cynopterus sphinx* and occupied by a harem group in the mast tree, *Polyalthia longifolia* (B); fruit cluster modified by *C. sphinx* and occupied by a harem group in the kitul palm, *Caryota urens* (C); and excavated root mass of the epiphytic ginger (*Asplenium nidus*) occupied by a harem group of *Balionycteris maculata* (D). Photographs by G. Chaverri, J. Balasingh, K. H. Tan, and R. Hodgkison, respectively.

(Aguilar Barquero and Jiménez Hernández, 2009). Marantaceae, a family of herbaceous understory plants that is often used by tent-roosting bats in the Neotropics (Rodríguez-Herrera et al., 2007b), occurs in densities averaging 1800 individuals per ha in *terra firme* tropical rain forests near Manaus, Brazil (Costa, 2006). Similarly, families that account for the greatest ground herb coverage in a lowland Amazonian forest in Ecuador include Araceae, Marantaceae, and Heliconiaceae, which are commonly used as roosting resources by tent-making bats (Poulsen and Balslev, 1991). However, not all plants used by tent-roosting bats are abundant. In their study of *Cynopterus sphinx*, Storz et al. (2000a) mapped the location of mast trees (*Polyalthia longifolia*) in an area measuring approximately 1 km in diameter, and found 330 trees. This corresponds to a density of only four mast trees per ha. Similarly, Rickart et al. (1989) found only 10 *Livistona rotundifolia* trees at their study site of approximately 1256 ha, which corresponds to a density of 0.008 such trees per ha.

Although some of the plants that are typically used by tent-roosting bats for roosting are very abundant, tent-roosts are not equally frequent. Tents used by *Artibeus watsoni* in southwestern Costa Rica, for example, occur in

densities of eight tent-roosts per ha (Chaverri et al., 2008). Similarly, tent roosts constructed by *C. sphinx* in the dense foliage of mast trees in southern India have a density of 0.5 per ha (Storz et al., 2000a), and a total of 10 roosts, or the equivalent of 0.007 tents per ha, were used by *S. kuhlii* in Luzon Island, the Philippines (Rickart et al., 1989). Tent availability may not only differ between species, but also among populations of the same species. For example, tents constructed in *Heliconia* plants by *E. alba* at two sites in northeastern Costa Rica occur in densities of 0.56 and 2.56 tent-roosts per ha (Rodríguez-Herrera et al., 2008). The number of roosts used by individuals at different sites, which may be an indication of the overall availability of this resource, may also differ in other species. In southwestern Costa Rica, for example, tent availability for several populations of *A. watsoni* ranges between 5 and 23 per ha (Chaverri et al., 2007b).

In terms of spatial dispersion, there is very little information on how roosting resources of tent-making bats are distributed across the landscape. Timm and Lewis (1991) studying *U. bilobatum* in a coconut grove observed that occupied tents appeared to be clumped within the study area, which they attribute to the distribution of preferred trees. Campbell et al. (2006a) estimated the dispersion of available roosts for *C. brachyotis* Sunda and *C. brachyotis* Forest, and observed that significant deviations from random patterns were inferred for the former but not for the latter. However, the dispersion of roosting resources in *C. brachyotis* Forest also had a tendency towards a clumped rather than a random pattern.

C. ROOST CONSTRUCTION AND DEFENSE

The process of roost construction is one of the most appealing yet poorly studied aspects of the roosting ecology and behavior of tent-making bats. To date, tent construction has been observed and described only in three species. The first report of such behavior came from Balasingh et al. (1995), who observed a single male of the short-nosed fruit bat (*C. sphinx*) in the act of roost construction in *Vernonia scandens*, the curtain creeper. This male chewed and severed more than 300 separate stems for a period of 30 days, primarily during the night. After the tent was completed and occupied by females, the male continued to modify some of the stems. The second report of roost construction was published by Muñoz-Romo and Herrera (2003), who observed the “leaf-modifying” behavior of *A. lituratus*. These authors recorded several males puncturing the leaf frond of the palm *Washingtonia* sp. Unlike the tent-making behavior of other species, these punctures did not result in the collapse of the outer leaf surface, as the bats did not cut the leaf’s veins. The most recent report of roost construction was that of Rodríguez-Herrera et al. (2007a) in the Honduran white bat *E. alba*. These authors observed, for

the first time, females in the act of tent construction. A pregnant female who engaged in roost construction repeatedly punctured the side of the leaf's central vein, and also punctured the central region of the leaf, probably to facilitate landing.

Roost construction is thought to be a relatively costly behavior, which authors presume, based on direct observations of roost construction and on observations of the state of roosts being constructed, can take from one to 50 nights to complete, depending on the structure being modified. Shorter periods are associated with leaf tents whose veins are relatively soft and easier to sever, whereas longer periods are required for more complex stem tents constructed by the Paleotropical genus *Cynopterus* (Balasingh et al., 1995; Barbour, 1932; Bhat and Kunz, 1995; Brooke, 1990; Tan et al., 1997). Because roost construction is such a time-consuming activity, many authors believe that male tent-making bats invest time and energy in constructing and defending these structures because they can attract mating partners (e.g., Balasingh et al., 1995; Hodgkison et al., 2003; Kunz and McCracken, 1996; Muñoz-Romo and Herrera, 2003). In fact, studies show that periods of roost construction may coincide with the breeding season (Balasingh et al., 1995), which could increase male reproductive success.

Behavioral observations of tent-roosting bats suggest that males may exhibit one or several roost-defense tactics. For example, male *C. sphinx* uses saliva to mark their roosts, and also chase intruding males (Balasingh et al., 1995), while male *C. brachyotis* Sunda and *C. sphinx* spread their wings in response to threats (Balasingh et al., 1995; Tan et al., 1997). Males may also defend roosting resources by foraging near tent-roosts, thereby increasing roost surveillance (Balasingh et al., 1995; Chaverri et al., 2007c; Hodgkison et al., 2003). Most male tent-roosting bats also exhibit greater fidelity to diurnal roosts than females, which may decrease the probability of roost appropriation by competing males (Balasingh et al., 1995; Campbell et al., 2006a; Chaverri et al., 2007b; Muñoz-Romo et al., 2008; Storz et al., 2000a). Other species seem to defend not only specific tents, but also areas in which several tents may be present (Chaverri et al., 2007a). Interestingly, males defend tents even when females are absent (Balasingh et al., 1995), suggesting that tents are more defensible than groups of females (Storz et al., 2000a).

D. ROOST FIDELITY

Although many authors have described the movement of tent-making bats among roosting sites, few have provided quantitative measures of roost fidelity. Regarding short-term roost fidelity, some authors report that individuals tend to switch tents almost on a daily basis (Table II). In a six-day study, Timm and Lewis (1991) recorded the distribution of unmarked bats

TABLE II
 VARIATION IN THE SOCIAL AND ROOSTING BEHAVIOR OF NEOTROPICAL (N) AND PALEOTROPICAL (P) TENT-ROOSTING BATS.

| Bat | Dist. | Mass (g) | Group | | | Roost | | | References |
|-----------------------|-------|----------|-----------------------|--------------------------|-----------|----------------|---------|----------|--|
| | | | Size | Composition ^c | Stability | Construct | Defense | Fidelity | |
| <i>A. jamaicensis</i> | N | 36–48 | 1.5 (1–4) | ♀♀/♂, ♂♂ | ? | ♂ ^d | ? | L | Foster and Timm (1976), Kunz and Pena (1992), Morrison (1979), Ortega and Castro-Arellano (2001) |
| <i>A. lituratus</i> | N | 70 | 5.3 (2–14) | ♀♀/♂ | M | ♂ | ♂ | L, I, >♂ | Muñoz-Romo and Herrera (2003), Muñoz-Romo et al. (2008) |
| <i>A. watsoni</i> | N | 11 | 2.4 (1–8) | ♀♀/♂, ♀♀, ♂♂ | L | ♂ ^d | ? | L, I, >♂ | Chaverri and Kunz (2006a), Chaverri and Kunz (2006b), Chaverri et al. (2008) |
| <i>E. alba</i> | N | 5–6 | 5.4 (1–17) | ♀♀/♂, ♀♀/♂♂, ♂♂ | H | ♀, ♂ | ? | M, G | Brooke (1990), Rodríguez-Herrera et al. (2007a), Rodríguez-Herrera et al. (2007b), Timm and Mortimer (1976), Timm (1982) |
| <i>M. macconnelli</i> | N | 6.5 | 3.3 (1–7) | ♀♀/♂, ♀♀/♂♂, ♂♂ | M | ? | ? | M, G | Foster (1992), Koepcke (1984), Kunz and Pena (1992), Rodríguez-Herrera et al. (2007b), Simmons and Voss (1998) |
| <i>R. pumilio</i> | N | 8–9 | 2.6 (1–5) | ♀♀/♂ | ? | ? | ? | L | Charles-Dominique (1993), Simmons and Voss (1998) |
| <i>U. bilobatum</i> | N | 13–20 | 2.3 (1–56), .9 (1–23) | ♀♀/♂, ♀♀, ♂♂ | L | ♂ ^d | ? | L, I | Barbour (1932), Kunz and McCracken (1996), Lewis (1992), Timm and Lewis (1991) |

| | | | | | | | | | |
|--------------------------------|---|-------|--|----------|---|----------------|---|----------------|--|
| <i>B. maculata</i> | P | 13 | 5.6 (1–14) | ♀♀/♂ | H | ♂ ^d | ♂ | H, I, >♂ | Hodgkison et al. (2003) |
| <i>C. brachyotis</i> Forest | P | 24–37 | 1.6 (1–4) ^a | ♀♀/♂, ♀♀ | H | ? | ? | M, G, ♀ = ♂ | Campbell et al. (2006a) |
| <i>C. brachyotis</i> Sunda | P | 32–42 | 3.5 (2–7), 2.37 (1–17) ^a | ♀♀/♂ | M | ♂ ^d | ♂ | H, I, >♂ | Campbell et al. (2006a), Campbell et al. (2006b), Tan et al. (1997) |
| <i>C. horsfieldi</i> | P | 50–70 | 3.75 (3–6) | ♀♀/♂, ♀♀ | L | ? | ♂ | L, I, >♀ | Campbell et al. (2006b), Tan et al. (1999) |
| <i>C. sphinx</i> | P | 40–70 | 3.9 (1–19), 9.9 (2–38) ^b | ♀♀/♂ | L | ♂ | ♂ | M, I, >♂ | Balasingh et al. (1995), Bhat and Kunz (1995), Campbell et al. (2006b), Storz et al. (2000b) |

Group size refers to the mean (range) number of adult males and females, plus young, roosting in the same tent at the same time (i.e., roosting group), unless otherwise noted. When more than one study presented data of group size, we have provided both results. Group stability is categorized based on whether significant changes in group composition occur daily (L), every week (M), or when group composition remains relatively constant for more than one month (H). Construct and defense refer to the sex responsible for constructing and defending the tent-roost, respectively. Fidelity refers to the short-term movement of bats among roosts, with low fidelity (L) representing species in which most members of a roosting group switch tents daily; medium fidelity (M) representing species in which few members move daily, or those in which most individuals switch approximately every week; and high fidelity (H) representing species in which only a few individuals switch every week, or those in which most individuals remain in the same tent for more than two weeks. When data are available, we also indicate whether males or females exhibit greater fidelity to roosts, and whether individuals switch roosts primarily as a group (G) or individually (I).

^aHarem size (i.e., number of adult females in group).

^bAdults only.

^c♀♀/♂ = harem group, ♀♀/♂♂ = multimale/multifemale groups, ♀♀ = female-only groups, ♂♂ = male-only groups.

^dCircumstantial evidence of tent construction.

in 13 tents, and observed that the number of individuals in each tent varied considerably from one day to the next. A similar trend was observed by Chaverri and Kunz (2006b) studying *A. watsoni*, as most radio-tracked individuals switched roosts on a daily basis. Timm and Mortimer (1976) noted that *E. alba* used the same tent for more than one day only on two occasions. Other tent-roosting species, particularly those in the Paleotropics, seem to exhibit greater short-term fidelity to their tent-roosts. For example, *C. brachyotis* Forest is known to use a single roost continuously for up to 30 days, and *C. brachyotis* Sunda may remain for up to 48 days at the same roost (Campbell et al., 2006a). *Cynopterus sphinx* has also been observed to use one tent-roost continuously for over 15 days (Storz et al., 2000a). While species differ in how faithful they are to particular tents, they all seem to make use of alternative roost-sites located in the vicinity (Chaverri and Kunz, 2006b; Kunz and McCracken, 1996; Muñoz-Romo et al., 2008; Storz et al., 2000a; Tan et al., 1997).

In addition to the differences in roost fidelity, species may also differ in whether they switch tents as a group or individually. In their study of *E. alba*, Timm and Mortimer (1976) observed that adjacent roosts were simultaneously abandoned and reoccupied by groups of the same size, suggesting that most individuals in a single group may relocate in a synchronized manner. Other studies show that while the entire group does not switch roosts simultaneously, some individuals seem to remain together despite their constant tent-switching. For example, in their study of *C. brachyotis* Forest, Campbell et al. (2006a) observed that female–male pairs moved among roosting sites in a coordinated fashion. Similarly, Chaverri et al. (2008) report that despite constant switching among roost sites, some male–female pairs remained continuously associated for more than three months.

Some of the social and ecological correlates of roost fidelity in tent-making bats include sex, reproductive status, gregariousness, and roost availability. In this respect, most studies report that males exhibit greater fidelity to tent-roosts than females (Storz et al., 2000a; Hodgkison et al., 2003; Campbell et al., 2006a; Chaverri et al., 2007b; Muñoz-Romo et al., 2008; Table II), most likely because these structures are costly to construct and because they provide a means of attracting potential mating partners (Kunz and McCracken, 1996; Kunz et al., 1994). Reproductive status of females may also explain roost fidelity of males, as the latter apparently spend a large proportion of the night inside the tent when females are experiencing a postpartum estrous (Balasingh et al., 1995). Gregariousness also seems to promote roost fidelity, as solitary individuals exhibit less fidelity to tent roosts than gregarious ones (Campbell et al., 2006a; Kunz and McCracken, 1996; Tan et al., 1997). Results from comparative studies

also suggest that roost availability is an important correlate of roost fidelity. In their study of several populations of *A. watsoni*, Chaverri et al. (2007b) found that individuals using areas in which tents were readily available switched roosts more often than individuals residing in areas with scarcer roosting resources. Similarly, Campbell et al. (2006a) reported greater roost fidelity in *C. brachyotis* Sunda compared to *C. brachyotis* Forest, and while they did not correlate roost availability to roost fidelity directly, their findings of greater roost availability for *C. brachyotis* Forest (Campbell et al., 2006b) suggest that the differences among species may be partly explained by the availability of roosts.

Despite the fact that tents are commonly regarded as ephemeral structures (e.g., Lewis, 1995), many studies report tent-roosts lasting up to several years. For example, tents constructed by *C. sphinx* in mast trees may be used for up to one year (Balasingh et al., 1995), and tents in the flower/fruit clusters of kitul palms (*Caryota urens*) may remain serviceable for up to four years (Storz et al., 2000b). *Cynopterus brachyotis* Sunda may use tent-roosts for periods of more than 10 months, even in leaf-tents (Tan et al., 1997), and *B. maculata*'s use of cavities in root masses may last for over 13 months (Hodgkison et al., 2003). Other leaf-tents, such as those constructed in the palm trees *Sabal mauritiiformis* and *Washingtonia* sp., are also known to last for periods of up to nine and 12 months, respectively (Kunz and McCracken, 1996; Muñoz-Romo et al., 2008). Similarly, *A. watsoni* may use tents constructed in palms and aroids for over 16 months, although roosts constructed in leaves of Heliconiaceae, Marantaceae, and Musaceae may not even last one month (Chaverri and Kunz, 2006b). However, Brooke (1990) reports that *E. alba* may use tent-roosts in *Heliconia* sp. for up to 45 days.

III. SOCIAL BEHAVIOR IN TENT-MAKING BATS

A. GROUP SIZE

Compared to many other species of bats, most tent-roosting bats form relatively small roosting groups of less than 20 individuals (Tables I and II). For example, the average size of tent-roosting groups in *A. jamaicensis* and *C. brachyotis* Forest is less than 1.6 individuals, with a maximum of five individuals observed in the same roost (Campbell et al., 2006a; Kunz and McCracken, 1996). Other species with group sizes of fewer than 10 individuals per roost include *A. watsoni*, *M. macconnelli*, *R. pumilio*, and *C. horsfieldi* (Chaverri et al., 2008; Simmons and Voss, 1998; Tan et al., 1999). However, not all tent-roosting species exhibit such small group sizes.

For example, *E. alba* and *C. brachyotis* Sunda may roost in groups of almost 20 individuals (Brooke, 1990; Campbell et al., 2006a), whereas *C. sphinx* and *U. bilobatum* may roost in groups of over 40 individuals (Barbour, 1932; Storz et al., 2000b). As with many other species of bats, solitary tent-roosting individuals are typically male (Chaverri et al., 2008; Tan et al., 1997).

While studies conducted by different authors in different populations indicate that the upper-limit of group size varies among species, there is also evidence for considerable intraspecific variation in group size (Fig. 2). In four different studies, group size for *U. bilobatum* varied from 1 to 6 (Kunz and McCracken, 1996), 1 to 23 (Timm and Lewis, 1991), 1 to 17 (Lewis, 1992), and 1 to 56 (Barbour, 1932). In addition, each of these studies also reports significant differences in the size of groups observed each day. For example, Timm and Lewis (1991) found, in one single day, 11 groups that had 1, 2, 4, 6, 8, 11, and 23 bats. A similar pattern was observed by Balasingh et al. (1995) and Storz et al. (2000b), who recorded groups of 1–19

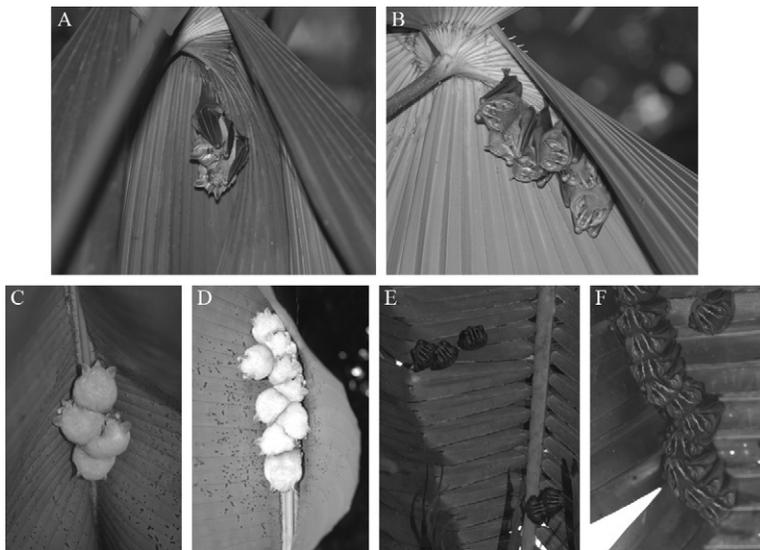


FIG. 2. Three tent-roosting bats of the Neotropics using leaf-tents. (A) Male and female *Artibeus watsoni* roosting in an umbrella tent constructed in *Carludovica palmata*. (B) Harem group of *A. watsoni* roosting in *C. palmata*. (C) Small *Ectophylla alba* group roosting in a boat tent constructed in *Heliconia imbricata*. (D) Large *E. alba* group roosting in *H. imbricata*. (E) Small *Uroderma bilobatum* group roosting in a pinnate tent constructed in *Cocos nucifera*. (F) Medium-sized *U. bilobatum* group roosting in *C. nucifera*. Photographs by G. Chaverri (A–E) and M. Sagot (F).

and 2–38 adult *C. sphinx* per roost, respectively. Interestingly, significant interseasonal variation in the size of *C. sphinx* groups also occurs between the wet and dry seasons, with a mean increase of seven individuals per group during the latter (Storz et al., 2000b).

B. GROUP COMPOSITION

One of the most salient features of the social behavior of tent-roosting bats is that roosting groups are commonly composed of one male and one to several females. This pattern of roost composition has been recorded in every species for which data are available (Table II). Many authors refer to these groups as “harems” (Campbell et al., 2006a; Hodgkison et al., 2003; Kunz and McCracken, 1996; McCracken and Wilkinson, 2000; Muñoz-Romo et al., 2008; Storz et al., 2000b). However, studies report multi-male/multifemale groups in *E. alba* and *M. macconnelli* (Brooke, 1990; Simmons and Voss, 1998), and male-only “bachelor” groups in tent-making *A. jamaicensis*, *A. watsoni*, *M. macconnelli*, and *U. bilobatum* (Chaverri et al., 2008; Foster and Timm, 1976; Lewis, 1992; Rodríguez-Herrera et al., 2007b).

While roosting groups in tent-making bats rarely contain more than one adult male, social groups may be composed of several females that share tents within an area and several males that use a specific set of roosts (Balasingh et al., 1995; Campbell et al., 2006a; Chaverri et al., 2008; Muñoz-Romo et al., 2008; Storz et al., 2000b). These social groups may even be formed by an equal proportion of males, evenly distributed along many tents, and females, which tend to exhibit a more clumped distribution (Storz et al., 2000a,b). An interesting exception to this pattern is *C. brachyotis* Forest, whose social groups are typically composed of one male and up to five females. These individuals, like many other tent-roosting bats, are not always found roosting in the same tent at the same time (Campbell et al., 2006a).

C. GROUP COHESION

A common characteristic of tent-roosting bat societies is the relatively low short-term stability of roosting groups. In some species, individuals switch roosting partners almost on a daily basis, resulting in relatively low association patterns. For example, in the Neotropical bat *A. watsoni*, radio-tracked individuals typically spend approximately 31% of the time roosting together (Chaverri et al., 2008). Similarly, in *A. lituratus*, females move constantly between tents within a restricted area, which results in females spending less than 50% of their time with a given male (Muñoz-Romo et al., 2008). Dyads in other species spend longer periods of time together, but still

switch roosting companions regularly. In *C. brachyotis* Sunda, for example, while many dyads spend less than 30% of their time in association, many others remain together for periods of 25 consecutive days or more (Campbell et al., 2006a). *Cynopterus brachyotis* Forest associations are more stable, with most individuals spending over 70% of the study period with the same roost mates. Moreover, the composition of roosting groups varies little in this species, as the same group members may remain together for up to 24 days (Campbell et al., 2006a).

Despite the frequent switching of individuals among roost sites and roost companions, social groups of tent-roosting bats seem to be more stable, with a few long-lasting relationships. In *C. brachyotis* Sunda and Forest, for example, individuals continue to associate with the same members of their social group for periods of two months or more (Campbell et al., 2006a). This same pattern has been observed in other species including *A. watsoni*, *A. lituratus*, and *C. sphinx* (Chaverri et al., 2008; Muñoz-Romo et al., 2008; Storz et al., 2000b). In terms of overall duration of associations, most long-term relationships formed among social group members seem to be those of male–female dyads (Campbell et al., 2006a; Chaverri et al., 2008). For example, in their 2-year-long study of the social behavior of *C. sphinx*, Storz et al. (2000b) observed that a few females were found with the same male and within the same roost one year after their initial capture. They noted, however, that subsets of females also remained cohesive throughout reproductive periods. Because these females remained as roost mates despite their continuous tent-switching, Storz and colleagues suggest that associations are maintained actively because of individual preferences, and not passively due to roost membership.

IV. FUNCTIONAL ROLE OF ROOSTING ECOLOGY IN THE SOCIAL BEHAVIOR OF TENT-ROOSTING BATS

A. GROUP SIZE AND ROOSTING ECOLOGY

1. *Roost Size and Quality*

Several characteristics of tent-roosts may account for some observed differences in roosting group size among species and populations. In terms of roost size, several authors have suggested that larger tents should be able to contain more individuals, while smaller ones should be able to support only a few (Kunz et al., 1994; Timm and Clauson, 1990). This correlation between group and roost sizes was observed in the short-nosed fruit bat (*C. sphinx*) by Balasingh et al. (1995), who studied the dimensions of stem tents and the number of females roosting in each of

these structures. These authors argue that females may use roost characteristics, such as the height of interior crown and vertical length of tent cavity, to assess tent quality, increasing the probability that more females will simultaneously use the best available structure. Other studies, however, have found no significant relationship between the dimensions of roost cavities and group size (Hodgkison et al., 2003). Another study conducted on 338 roosting groups of *A. watsoni* captured in 25 different plant species, ranging from the small *Piper* leaves to the large palm *Cryosophila guagara*, found that the size of groups did not differ significantly between tent-roost plant species (Chaverri and Kunz, 2006b). Notwithstanding, while very small leaves of the genus *Piper* never supported more than two individuals, other much larger tents constructed in *Heliconia imbricata* and *Musa paradisiaca* often contained up to eight individuals (Table I).

Across species, it appears that there is some correlation between the size of tents and the size of roosting groups (Table I). For example, bats that use relatively small tents, such as those constructed in apical tents of Araceae and Piperaceae, in the bifid tents in the terminal leaflets of palms, or in small palmate umbrella tents in palms and Cyclanthaceae, typically roost in groups of no more than 10 individuals (Chaverri and Kunz, 2006b; Choe and Timm, 1985; Tan et al., 1997). Other bats that use medium-sized roosts, such as those constructed in boat or large palmate umbrella tents, often form groups of over 10 individuals. *Cynopterus brachyotis* Sunda roosting in *Corypha utan*, for example, has been observed in groups of up to 18 individuals, and *E. alba* in *H. imbricata* may form groups of 17 individuals (Brooke, 1990; Tan et al., 1997). Interestingly, *U. bilobatum* has been observed roosting in very large groups of 56 individuals in the palm *Pritchardia pacifica* (Barbour, 1932), whose tents are only slightly larger than those formed in *C. utan*. Other records of large groups (20 or more bats) have been made exclusively in very large tent-roosts, such as those formed in the pinnate leaves of *Cocos nucifera*, or in stem tents of the curtain creeper, *V. scandens* (Balasingh et al., 1995; Lewis, 1992; Timm and Lewis, 1991).

Although roost size may set an upper limit on the number of bats that can simultaneously use a single tent, many tent-roosts typically hold smaller groups than they seem structurally capable of supporting (see Storz et al., 2000a and Timm and Lewis, 1991). Thus, it is possible that other characteristics can make particular tent-roosts more attractive, promoting the formation of larger groups. In *A. lituratus*, for example, males using modified leaves that exhibit greater resistance to weather conditions, greater structural support, enhanced protection against predators, and darker areas for roosting, typically spend less time alone and associate with a larger number of females (Muñoz-Romo et al., 2008). Similarly, roosts that have been

modified into tent-roosts often exhibit better protection against rain (Choe, 1994; Timm and Lewis, 1991), and thus may be greatly sought out by bats, or at least more so than unmodified leaves. This may explain why *C. brachyotis* Sunda roosting in leaf-tents of the palm *Livistona chinensis* forms larger groups than bats using unmodified leaves of the same species (Tan et al., 1997).

2. Roost Abundance

Although resource abundance is known to affect group formation and size (see earlier sections), few studies of tent-making bats have directly established an association between roost availability and group size. In their study of *C. brachyotis* Forest and *C. brachyotis* Sunda, Campbell et al. (2006a,b) recorded a lower abundance of roost sites, and larger group sizes, for the latter species. Similarly, in a comparative study of the social systems of Palearctic tent-roosting bats, Campbell (2008) showed that populations inhabiting areas of lower roost abundance, such as those of *C. sphinx* in Palayamkottai and Pune (India), and *C. brachyotis* Sunda in Bangi (Peninsular Malaysia), roost in larger groups than populations that inhabit areas with more roosting resources. Populations of the Neotropical tent-making bat *A. watsoni* also differ in roosting group size according to differences in the abundance of roosting resources. At their study site in Golfito (Costa Rica), Chaverri and Kunz (2006b) observed significantly larger groups and fewer roosting resources than at their other site in Corcovado (Costa Rica). These authors report population densities of up to five times higher in Golfito than in Corcovado which, coupled with fewer roosting resources, may increase home range overlap (Chaverri et al., 2007a), facilitating the formation of larger groups. A larger population and fewer roost sites may also be partly responsible for the increase in harem size during the dry season in *C. sphinx* at Pune (Storz et al., 2000b).

3. Roost Distribution

The only study that has directly addressed the effect of resource dispersion on group size in bats is that of Campbell et al. (2006a). These authors measured the spatial distribution of available roosts and its relationship with female group size, roost fidelity, and the strength of associations in *C. brachyotis* Forest and Sunda. At their study sites in Peninsular Malaysia, they found that roosts used by *C. brachyotis* Sunda were clumped, and group sizes were relatively large. However, roost distribution was more evenly spaced in *C. brachyotis* Forest, and groups were smaller. Although the evidence is scant, these results suggest that the size of harems in tent-roosting bats may be somewhat related to the distribution of roosts, such that relatively uniform distributions restrict the aggregation of a large

number of females around particular tents, while highly clumped roosts promote female aggregations and hence larger harem sizes (Campbell et al., 2006a).

B. GROUP COMPOSITION AND ROOSTING ECOLOGY

Most studies of tent-making bats agree that the patterns of group formation, and the resulting relationship in the number of females and males within roosts, are determined by the construction and defense of the tent-roost *per se*. Because roost construction is primarily a male behavior (see earlier sections), tent roosts are thought to provide a defensible resource used by males to attract mating partners and to deter potential competitors (e.g., Hodgkison et al., 2003; Kunz and McCracken, 1996; Muñoz-Romo and Herrera, 2003; Storz et al., 2000b; Tan et al., 1999). This results in a harem-like social organization in which single adult males roost with one or several adult females (see Table II and references therein). However, not all tent-roosts are occupied by single-male/multifemale groups. Because harem groups typically contain several females, and since the demographic structure of tent-roosting populations is characterized by a relatively even number of females and males (Storz et al., 2000a), adult males are frequently found roosting alone (Chaverri et al., 2008; Muñoz-Romo et al., 2008; Storz et al., 2000b). In addition, while most studies of tent-making bats do not report multimale groups, a few authors have observed such groups (e.g., Brooke, 1990; Chaverri et al., 2008; Lewis, 1992; Rodríguez-Herrera et al., 2007b). These authors found that male-only groups formed only in the absence of females in the area or particular roost.

In addition to harem, single-male, and multimale roosting groups, tent-roosting bats may also be found in female-only groups (Table II). Females may roost alone for extended periods of time independent of their reproductive status (Campbell et al., 2006a), or they may actively seek the company of male roost-partners primarily during the mating season, resulting in a greater proportion of female-only groups during the nonbreeding season. In *A. watsoni*, for example, female-only groups are uncommon during the months of February and December (Chaverri et al., 2008), which coincides with the period of greatest sexual activity (Chaverri and Kunz, 2006a). This difference in group composition between seasons, however, is most notable at one study site (i.e., Golfito; Fig. 3). Because this particular site has few roosting resources yet higher population densities (Chaverri and Kunz, 2006b), it is reasonable to assume that single tents located within a male's territory are not large enough to simultaneously accommodate all females in the area, resulting in many female-only groups. During the breeding season, however, it may be difficult for territorial males

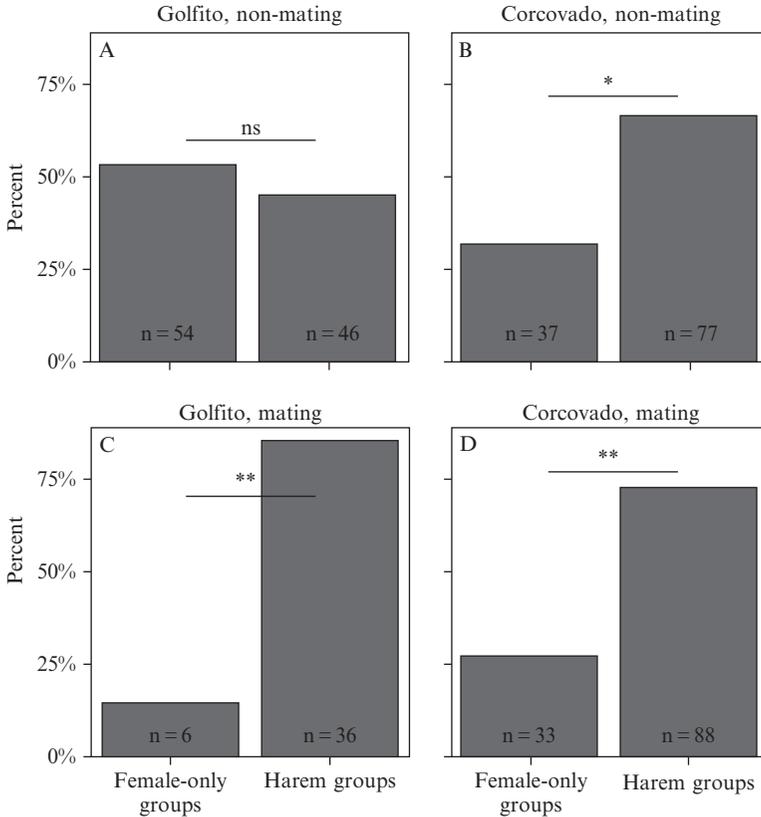


FIG. 3. Percent of female-only and harem groups of *A. watsoni* at two sites in southwestern Costa Rica (Golfito and Corcovado; G. Chaverri, unpublished data). Data are divided among the mating and nonmating seasons. Significant ($P \leq 0.05$) and highly significant ($P \leq 0.01$) differences among adjacent categories are represented by * and **, respectively.

to deter all possible male competitors, especially if females seek their company as a means to secure copulations, which could result in fewer numbers of female-only groups. Interestingly, tent-roosting bats that primarily defend tent-roosts and not roosting areas characteristically lack female-only groups (Storz et al., 2000a).

The least common form of roost association in tent-roosting bats is the multimale/multifemale group, which has been recorded in only two Neotropical species: *E. alba* and *M. macconnelli* (Table II). Mixed-sex groups have been observed in *M. macconnelli* by Simmons and Voss (1998). These authors reported a group containing two adult males and five adult females, and another composed by one male and two females. Similarly, in her study

of the social organization of *E. alba*, Brooke (1990) observed multimale/multifemale roosting groups prior to parturition. However, immediately following parturition, and during the postpartum estrous, groups were composed of single adult males and multiple adult females, plus their dependent young. While no data are yet available regarding roost construction in *M. macconnelli*, and little is known about roost construction in most tent-making species (see earlier sections), it is noteworthy that the only species for which a female's role in roost construction is known to be equally, or even more, significant than that of the male's (i.e., *E. alba*; Rodríguez-Herrera et al., 2007a) is also one of the few tent-roosting species for which roosting group composition differs from the typical harem-like pattern. Thus, unlike most tent-making male bats, whose access to mating opportunities seem to be achieved by some form of resource defense, male *E. alba* may monopolize mating opportunities by defending groups of females, and not tent-roosts.

C. GROUP COHESION AND ROOSTING ECOLOGY

Comparisons among species suggest several patterns in the relationship between social cohesion and the roosting ecology of tent-making bats. First, bats that exhibit low roost fidelity typically switch roosting partners almost daily, as observed in *A. watsoni*, *U. bilobatum*, *C. horsfieldi*, and *C. sphinx* (see Table II and references therein). This finding suggests that clustering at roost sites may be primarily determined in these species by the use of common roosting areas, and not by active choice of roost partners (Chaverri et al., 2007a). Second, species that exhibit high roost fidelity, such as *C. brachyotis* Sunda, may not exhibit correspondingly high fidelity to roosting partners, which could be explained by a roost-switching behavior in which individuals, and not groups, move among roost-sites (Campbell et al., 2006a). As before, this pattern suggests passive, rather than active, association at preferred roosts. Greater group stability in a species where individuals move among roost-sites independently of each other indicates that roost availability may be the primary determinant of roost, and consequently group, switching behaviors.

Another interesting pattern in terms of social cohesion and roost fidelity is that, despite relatively constant switching of roosts in *E. alba*, *M. macconnelli*, and *C. brachyotis* Forest, groups seem relatively stable (Table II). Studies conducted in these three species report that movement among roost sites typically occurs collectively (Brooke, 1990; Campbell et al., 2006a; Foster, 1992; Timm and Mortimer, 1976), indicating that, unlike other tent-roosting bats, association at roost sites may be explained by actively maintained associations, and not simply by roost membership. While no

studies have yet addressed the causes for group-mediated roost-switching behaviors in the latter three species, authors suggest that spatially dispersed and relatively ephemeral roosts could potentially result in low encounter rates among roost members. Thus, by actively maintaining associations with other group members, individuals increase the probabilities of securing mating opportunities during the brief periods of sexual receptivity (Campbell et al., 2006a). Because *E. alba* is known to engage in communal nursing and tent construction (Brooke, 1990; Rodríguez-Herrera et al., 2007a), stable associations in this species are advantageous as they could favor cooperation among group members (St-Pierre et al., 2009).

Studies conducted in different populations of tent-roosting bats reveal that some of the observed differences in group stability within species may be explained by patterns of resource abundance and distribution. Populations of *A. watsoni* in southwestern Costa Rica, for example, inhabit areas with relatively large differences in the abundance of tent-roosts (Chaverri and Kunz, 2006b). In areas of low roost availability, individuals continuously associate with the same partners within the same tent for more than a week, while roost and group switching occur daily in areas where roost abundance is significantly higher (Chaverri et al., 2007b, 2008). Roost availability may affect group cohesion in this species through its effect on movement patterns, such that individuals in areas of low roost abundance may be unable to use many tents, forcing them to remain together longer (Chaverri et al., 2007a). Similar results were obtained by Campbell et al. (2006a), who examined social stability of *C. brachyotis* Forest and *C. brachyotis* Sunda at two different sites in northern peninsular Malaysia (Perlis State Park and Taiping). These authors report greater association indices among pairs of bats inhabiting the Taiping site, which is also the site where fewer roosts were observed (Campbell et al., 2006b).

V. SOCIAL SYSTEMS IN TENT-MAKING BATS COMPARED TO OTHER TROPICAL SPECIES

A survey of available data on the social systems of tropical bats suggests that the relatively small and labile harem group structure that characterizes tent-making bats is rare in non-tent-making species. For example, in their study of five emballonurid bats in Costa Rica and Trinidad, Bradbury and Vehrencamp (1976) found that these species typically live in very cohesive multimale/multifemale groups. Like tent-roosting species, some of these insectivorous bats (i.e., *Saccopteryx leptura* and *Peropteryx kappleri*) also cluster in relatively small groups of less than 10 individuals in tree boles and fallen logs. Others that use tree boles and tree cavities (i.e., *Rhynchonycteris*

naso and *Saccopteryx bilineata*), however, roost in groups of up to 45 individuals. The cave-dwelling species, *Balantiopteryx plicata*, was observed in groups of 50–200 bats. In their study of the bat fauna at Paracou, French Guiana, [Simmons and Voss \(1998\)](#) extensively sampled roost sites and found roosting groups for 20 species in a diversity of structures, including bridges, fallen logs, and tree cavities. Most of the species sampled formed small (i.e., < 10 individuals), mixed-sex aggregations, while only three species exhibited a combination of a harem-like group composition and small group sizes similar to those found in tent-making bats. Unfortunately, no long-term data were collected to determine if any of these three species exhibited similar patterns of social lability as those found in tent-making species. Other tropical species that exhibit small group sizes include *Neoromicia nanus* and *Thyroptera tricolor*. These species roost in the developing tubular leaves of plants of the order Zingiberales, and form mixed-sex groups no larger than 14 individuals ([Happold and Happold, 1996](#); [Vonhof et al., 2004](#)). Unlike tent-roosting bats, which typically form aggregations, species that roost beneath unmodified palm fronds, stems and branches, and unmodified foliage of canopy and subcanopy trees, such as *Artibeus intermedius*, *Dobsonia minor*, *Nyctimene robinsoni*, and *Syconycteris australis*, are most commonly found roosting solitarily ([Bonaccorso et al., 2002](#); [Evelyn and Stiles, 2003](#); [Spencer and Fleming, 1989](#); [Winkelman et al., 2000](#)).

There are, however, some examples of species with similar patterns of group size, composition, and stability. For example, the short-tailed fruit bat, *Carollia perspicillata*, forms tight clusters of 1–18 adult females and a single adult male inside caves. Similar to tent-roosting bats, males of *C. perspicillata* defend roost-sites within the cave against intruding males, and exhibit greater site fidelity than females. These females also regularly switch roost sites and males ([Fleming, 1988](#)). The Jamaican fruit-eating bat, *A. jamaicensis*, exhibits a harem-like social organization when it uses roosts other than tents ([Kunz et al., 1983](#)). For example, groups roosting in hollow trees are composed by one adult male and 4–11 adult females and their young, and most groups using solution cavities in caves are formed by 4–18 females and a single male. However, unlike tent-making bats, larger groups in the latter structures may also contain another adult male, and individuals at both structures exhibit high roost fidelity and low female turnover rates among harem groups ([Morrison, 1979](#); [Ortega and Arita, 1999](#)).

The few species that use nonplant materials for roost construction exhibit a very similar social system as that observed in tent-roosting bats. For example, in addition to modifying the root masses of epiphytes, *Balionycteris maculata* also constructs roosts in ant and termite nests. These bats

exhibit a social system that is consistent across roost types, and which is comprised of relatively small, labile harem groups (Hodgkison et al., 2003). Another species known to modify termite nests is the Neotropical insectivorous bat *Lophostoma silviculum* (Kalko et al., 2006). Roosting groups in this species are usually formed by one adult male and up to six females, plus subadults and young. A few bachelor groups have also been observed, and larger groups, unlike tent-making bats, may be composed of several adult males and females. Like most tent-roosting bats, individual males are thought to be primarily responsible for roost construction (Dechmann et al., 2005).

Although most tent-roosting species studied to date have relatively low group stability and intergroup movements independent of other roost members, three species exhibit a unique pattern in which stable associations persist despite constant roost-site switching: *E. alba*, *M. macconnelli*, and *C. brachyotis* Forest. Although no data exist as to whether *M. macconnelli* and *C. brachyotis* Forest engage in any sort of cooperative behaviors, it is noteworthy that non-tent-making species in which some form of cooperation exists also have stable group composition. For example, *T. tricolor* is one of the few species known to maintain highly cohesive groups despite daily roost-switching (Vonhof et al., 2004). In this species, individuals that have located suitable roost sites vocalize in response to calls emitted by flying conspecifics, which results in the location of roost sites and group companions by the latter (Chaverri et al., 2010). The common vampire bat (*Desmodus rotundus*) also forms long-term nonrandom associations which could facilitate allofeeding and allogrooming (Wilkinson, 1984, 1985, 1986). Similarly, the greater spear-nosed bat (*Phyllostomus hastatus*) forms very cohesive female groups that associate for several years (McCracken and Bradbury, 1981). Individuals cooperate by attracting group members to foraging sites, which may ultimately result in the defense of predictable food sources (Wilkinson and Boughman, 1998). Information transfer of food location may also favor the formation of cohesive female groups in the fishing bat *Noctilio leporinus*, which are known to persist for several years (Brooke, 1997).

VI. CONCLUSIONS

Given the theoretical and empirical evidence that similar ecological and morphological characteristics often result in convergent behaviors (Clutton-Brock, 1989; Emlen and Oring, 1977; Macdonald, 1983; Pérez-Barbería et al., 2007), it is not surprising to observe many similarities in the social behavior of tent-roosting bats. In this respect, studies confirm that most tent-making species exhibit a social system in which roosting groups

are composed of a single adult male and one to several adult females. Individuals in these roosting groups often move between roosts, resulting in relatively low roost fidelity and in the exchange of group members. Despite these similarities among species, studies also show that a few tent-roosting bats do not seem to conform to the typical harem-like, and labile, composition of roosting groups, but exhibit instead groups that may contain several adult males and females that maintain stable associations regardless of constant roost-site switching. Moreover, comparative studies have confirmed that intraspecific variation exists in the social behavior of some tent-making species. This suggests that the unique histories of populations, the adaptation of individuals to specific local conditions, and the idiosyncratic nature of dyadic relations can result in highly variable social systems among species and populations (Chapman and Rothman, 2009; Eisenberg et al., 1972; Entwistle et al., 2007).

Our survey of the literature suggests that most of the variation in the social behavior within and among tent-roosting species may be explained by the size, abundance, and distribution of roosting resources. Groups that occupy larger, scarcer, and clumped roosts form larger aggregations than those using smaller, abundant, and dispersed roosts. This pattern is similar to that observed in other species of bats, in which hundreds of individuals cluster at larger, scarcer, and clumped roosts such as caves and buildings, while small aggregations form at smaller, more abundant, and dispersed roosts such as unmodified foliage. The abundance of tent-roosts may also largely determine group cohesion in most tent-roosting species, as very abundant resources apparently facilitate roost switching, and individuals that change roosts are often also more likely to change roost partners. Interestingly, the fact that individuals switch roosts whenever these are available suggests high costs of roost-site fidelity and/or large benefits of roost switching. By moving between roosting sites, individuals may avoid high parasite loads (Lewis, 1995; Reckardt and Kerth, 2005; ter Hofstede and Fenton, 2005), minimize the chance of their predators locating them (Fenton et al., 1994; Winkelmann et al., 2000), decrease the energy spent commuting to foraging areas (Fleming, 1988; Kunz, 1982; Wilkinson, 1985), allow individuals to become familiar with alternative roosts in case the primary roost is destroyed or disturbed (Lewis, 1995), and promote long-term relationships between social group members spread over many roosts within a given area (Willis and Brigham, 2004).

Most studies of tent-making bats seem to agree that the modification of plant structures by males results in a resource that is (1) sufficiently attractive to encourage its use over other unmodified plant structures, (2) sufficiently costly to construct to merit its defense, and (3) sufficiently rare to facilitate female clumping. This results in the typical harem-like social

organization observed in most tent-roosting species. By reducing the cost of construction, communal roost building probably discourages male tent defense, resulting in multimale/multifemale associations at roost sites. However, why some species of tent-making bats engage in communal roost construction while others do not remains unknown. One possibility is that other essential resources are sufficiently scarce that engaging in roost construction would be prohibitively costly for a single individual. Interestingly, the only species known to engage in communal roost construction is *E. alba*, which is also known to feed on a single species of fig tree (*Ficus colubrinae*; Brooke, 1990) that is relatively scarce in Neotropical lowland forests (Condit et al., 1996).

Researchers have postulated that polygyny should prevail in tent-roosting bats because when males modify leaves into tents, the resulting roost functions as both a critical and defensible resource (Kunz and McCracken, 1996; McCracken and Wilkinson, 2000), thus generating resource defense polygyny (Emlen and Oring, 1977). Accordingly, males that successfully recruit females to roost sites should have greater reproductive success than non-harem males, and the variance in mating success among the former should be proportional to the distribution of females among roost-sites. In fact, two studies confirm that in some tent-roosting bats, harem males sire the majority of offspring, and that variance in male mating success is correlated with the distribution of females among roosts (Chaverri et al., 2008; Storz et al., 2001). Because paternity analyses have been conducted only in two tent-roosting species, understanding how species and population-level variation in social behavior influences genetic mating system remains elusive. For example, we still do not know how patterns of reproductive synchrony, social cohesion, roost distribution, and foraging may influence the ability of harem males to mate with females within their tent-roosts (Campbell, 2008). Most interestingly, the patterns of parentage among species with multimale/multifemale roosting groups are still unknown.

The observed relationships between the roosting ecology and the social behavior of tent-making bats suggest that these resources play a considerable role in the evolution of social behavior in these volant mammals. However, ecological and behavioral data are still lacking for many tent-roosting species. Of the 30 bats known to roost in tents, detailed data on the diversity, abundance, and distribution of plants used for roosting are available for less than 10 species, four of which are in the Paleotropical genus *Cynopterus*. Even within *Cynopterus*, the question of how variation in roost type (i.e., modified vs. unmodified) and female group cohesion impacts on variance in male mating success remains unanswered. In the Neotropics, where diversity of tent-making in bats is the greatest, available data are extremely scant. For example, there exist almost no data on roost diversity,

abundance, distribution, and fidelity for more than half of the species known to roost in tents, and detailed information regarding social behavior is absent for the majority. Knowledge of the patterns of roost construction and defense is also deficient for most species in the Old and New World. Similarly, the demographic structure, reproductive patterns, foraging behavior, and patterns of interactions are almost entirely unknown for any species. In addition to the paucity of data, as noted, most authors report patterns of roost fidelity and social cohesion in very different ways, making intra- and interspecific comparisons challenging. Thus, to improve our understanding of the role of roosting ecology in the social behavior of tent-making bats, it is necessary to collect basic information for most species and to do so in a consistent manner.

Tent-making bats comprise a group with diverse evolutionary origins whose ecology has converged in the use of a unique roosting structure. This provides an excellent opportunity to test hypotheses regarding the effects of roosting ecology in the evolution of social behavior independent of phylogenetic affiliations. The studies summarized in this chapter represent a first step toward understanding how resources influence the social behavior of these fascinating mammals. But the lack of congruence in research methodologies, lack of attention to interpopulation variation, and taxonomic biases, coupled with the advent of recent genetic and analytical methodologies, present a great opportunity for further research. In particular, the use of computational advances such as the analysis of patterns of dyadic associations or social network analysis, by providing a mechanism for visualizing and quantifying social relationships, has the potential to revolutionize how we think about and categorize social structure. These methods can provide a more thorough and quantitative perspective on the roosting ecology and social behavior of any species, and their use will likely make it possible to answer many of the remaining questions on the functional role of roosting ecology in shaping the social behavior of bats.

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