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Roost making in bats

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Structures created by animals can serve many purposes. Spiders weave intricate webs to trap prey; beavers engineer complex networks of dams to alter waterways; male bower birds construct and decorate elaborate bowers to attract mates. Animal architecture ranges widely in function, but by far the most common use is shelter. Animals can spend a large amount of time in their shelters, and this is often where they both sleep and rear young, two of the most vulnerable states in animal lives. To optimize the safety and suitability of refuges available to them, many animals have become architects and create their own shelters, ranging from simple holes in the ground to the large complex nests of some social insects.

Building or modifying a structure to create a refuge, however, requires time and energy, and understanding this behaviour in a social and ecological context is key to understanding the selection pressures that shape it. Though animal architecture is taxonomically widespread, reviews of animal architecture often focus on birds and insects. Few researchers discuss, let alone parameterize and model, the advantages and disadvantages of shelter construction in mammals.

Bats are the second largest order of mammals with more than 1400 species described to date, and exhibit stunning diversity in ecology, social systems, behaviour, and morphology. All bats depend on suitable shelters or ‘roosts’ as they rest during the day, and often also between foraging bouts at night. Bat shelters have to fulfil specific microclimate and accessibility requirements, and their availability both limits species distribution ranges and is crucial for successful conservation. For example, the fact that so many bats aggregate in just a few suitable caves has had a dramatic influence on the spread in North America of white-nose syndrome, a devastating fungal infection that has caused local extinction of many bat populations. Because of their limited availability and importance, roosts are often tightly linked with social systems and mating strategies, and can shape reproductive success, parasite loads, behaviour and multiple other aspects of bat life history.

Despite the pivotal role roosts play in the life of bats, to date only few bat species are known to build their own roosts, presumably because adaptation to flight has left little room for digging or otherwise modifying the environment with the forelimbs or hindlimbs, a common roost construction approach in other taxa. Indeed, most roost construction observed to date in bats is done with the teeth. In this Primer, we review roost making in bats, discuss how this behaviour is linked to ecological and social correlates, and highlight convergent behaviours in bat roost construction across the Old and New World.

Diversity of roosts constructed by bats

Given how rare bat roost making is, the diversity of bat roost constructions is striking. Unlike many birds and insects, no known species of bat constructs its roosts from scratch. With rare exceptions, bats do not dig burrows, or move and combine material; instead, they modify existing structures to make them more suitable for roosting. While roost making is by far most common in the large and diverse Neotropical family of leaf-nosed bats (Phyllostomidae), species from at least three other families, Old World fruit bats (Pteropodidae), vesper bats (Vespertilionidae), and short-tailed bats (Mystacinidae), have also been documented to construct roosts, indicating that this behaviour has evolved several times in this mammalian order. Below we discuss types of bat-made roosts, what is known about their costs and benefits, and their associated social behaviours. We identify gaps in our knowledge and potential avenues for fruitful investigation.

The modification of hanging bird nests (Figure 1A) is a roost making strategy used by several species of vesper bats in the genera of *Kerivoula*, *Murina* and *Phoniscus* in the tropical regions of Africa, Asia and Australia.

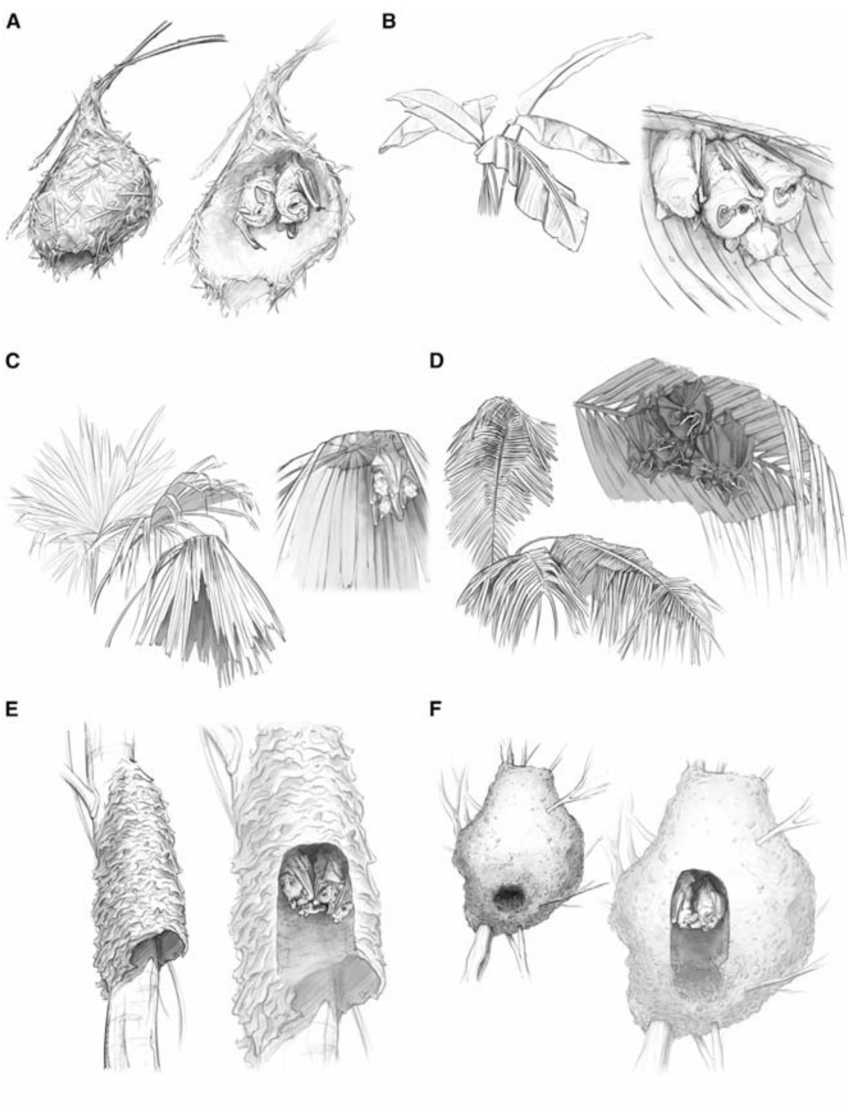

Figure 1. Roost construction strategies in Old (left) and New World bat species (right).
(A) Damara woolly bats (*Kerivoula argentata*) roosting in a modified *Euplectes* weaver bird nest in Mozambique. (B) Honduran white bats (*Ectophylla alba*) roosting in a tent made from a modified *Heliconia* leaf in Costa Rica. Convergent use of modified palm fronds in (C) greater short-nosed fruit bats (*Cynopterus sphinx*) in India, and (D) Peter's tent-making bats (*Uroderma bilobatum*) in Panama. Excavation of the active nests of social insects in (E) spotted-winged fruit bats (*Balionycteris maculata*) in an ant nest in Malaysia, and (F) pygmy round-eared bats (*Lophostoma brasiliense*) in a termite nest in Trinidad. Illustrations by Javier Lázaro.

These bats add a circular opening at the base of a hanging bird nest, which allows them efficient access and quick escape in case of predator approach. Bats use hanging nests from a wide range of bird species, including yellow-throated scrubwrens (*Sericornis citreogularis*) and brown gerygones (*Gerygone mouki*) in Australia, spectacled weavers (*Ploceus ocularis*) and scarlet-chested sunbirds (*Chalcomitra senegalensis*) in Africa, and baya weavers (*Ploceus philippinus*) in Asia. While in most cases bats use abandoned bird nests as their roosts, golden-tipped bats (*Phoniscus papuensis*; formerly *Kerivoula papuensis*) in Australia occasionally occupy multi-tiered nests together with *S. citreogularis*. The bats create an entrance to a chamber in the lower part of the nest while the birds occupy the chamber above. This concurrent habitation only occurs during the bird breeding season; after the scrubwren nestlings fledge, all the birds leave, and the bats can continue to occupy the nest alone.

All bird-nest-roosting bat species also use other types of roosts and may only modify bird nests opportunistically. Interestingly, in contrast to other bat-constructed roosts, modified bird nests are usually occupied by just one or a small number of individual bats and do not seem to be used during the reproductive period. Roosting behaviour in the genus *Kerivoula* is remarkable, not only because it is one of only a few genera in the large family of vesper bats known to alter structures, but also because a species in this genus uses even more exceptional roosts: *K. hardwickii* roost inside the pitchers of carnivorous plants in the genus *Nepenthes* and have developed specialized pads on their wrists to adhere to the smooth inner surface of the pitchers. A mutualism has evolved, with the bats providing the plant with nitrogen through its faeces, and the plant reducing the amount of digestive fluid in its pitchers, which allows space for the bats to roost. Though *K. hardwickii* does not modify its pitcher plant roosts, its unusual roosting strategy is characteristic of the diversity in roosting behaviour found across this interesting genus.

Other roost constructions in the family Vespertilionidae include observations of Geoffroy's bats, *Myotis emarginatus*, roosting in a cavity in a haystack, and common noctule bats, *Nyctalus noctula*, roosting in a cavity in styrofoam insulation. In both cases, scattered material suggested that the cavities were excavated by the bats. Although purely anecdotal, these observations indicate a greater potential for roost making among vesper bats, and call attention to the need for increased study.

The most varied and abundant type of roosts constructed by bats are leaf-tents. At least 22 species of bats, most of them New World leaf-nosed bats (family Phyllostomidae), chew on the major veins of large leaves or palm fronds of live plants to create a more enclosed space (Figure 1B–D). Numerous stereotyped leaf-tent architectures have been described, with remarkable convergence in the leaf-tents constructed by Neotropical and Paleotropical bat species, perhaps reflecting a convergence in the leaf morphologies available in these tropical forest understories. The advantages of these tents are manyfold: the tents protect from strong weather conditions, including intense sun, rain, and wind; they conduct vibrations that serve as an early warning system for predator approach; and they help to visually camouflage the bats roosting in them. Tents occupied by bats are warmer than unoccupied tents or unmodified leaves, resulting in measurable energy savings. However, the leaves that leaf-tents are made of often last only a few months, with bats abandoning the roost as its structure degrades, requiring tent-making bats to switch roosts more often than bats roosting in more permanent structures such as caves or tree holes.

Similar to New World leaf-tents are the modified plant structures created by some Old World fruit bats (family Pteropodidae), especially the genus of short-nosed bats (*Cynopterus,* Figure 1C). Species in this genus create roosts by modifying vegetation such as clusters of fruits, flowers, leaves, stems and root clumps. No *Cynopterus* species are obligate modified-roost users; all use alternative, non-modified roosts as well. In addition to modifying plant material (Figure 2A–D), another species of Old World fruit bat, the spotted-winged bat (*Balionycteris maculata*), also excavates arboreal ant (Figures 1E and 2E,F) and termite nests, creating a basal cavity which is accessed from below. Worldwide, 15 species of bats have been documented roosting in termite nests, but only few, such as *B. maculata*, actively excavate these roosts, even if only facultatively. But there is a genus of bats that takes this a step further.

At least four of seven species in the New World genus of round-eared bats (*Lophostoma)* roost in excavated termite nests (Figures 1F and 2G–J). In the species that has been studied most extensively, *L. silvicolum*, males have been observed excavating and maintaining cavities in arboreal nests of a single termite species, *Nasutitermes corniger*. These bats never use any other type of roost and desert the cavity when the termite colony dies. It has been speculated that these bats have an olfactory camouflage that not only causes the termites to ignore them but also protects them from the ants (*Dolichoderus bispinosus*) that co-inhabit up to 62% of these termite nests. Another species of *Lophostoma*, *L. kalkoae*, has been documented roosting in excavated *Azteca* ant nests, an aggressive ant genus from the same subfamily. The relationship between bats, termites and ants, and the question of what came first, excavating ant or termite nests, is one of many interesting areas in bat roosting behaviour requiring further study.

Finally, a unique form of terrestrial roost construction has been reported for the New Zealand lesser short-tailed bat (*Mystacina tuberculata*). While *M. tuberculata* usually roosts in unmodified tree cavities, this species has been found in cavities in the soft rotten wood of fallen trees. Excavation behaviour has not been directly observed, but the floors of these cavities were covered with pieces of wood marked with what appeared to be bat tooth-marks. Another highly unusual roosting behaviour has been observed for this species: *M. tuberculata* have been documented roosting in excavated holes in the banks of volcanic pumice. Reports on bat-made terrestrial roosts remain equivocal and call for more investigation. The fact that until recently New Zealand was free from ground predators, with no terrestrial mammals except for bats, may have allowed these unusual forms of roost making to evolve.

Who makes roosts?

Ground roosting is not the only remarkable component of the roosting behaviour of *M. tuberculata*. Another is that this species occurs in the temperate zone. Nearly all roost-making bat species are tropical or subtropical. This is not surprising — the number of bat species that use ephemeral and exposed roosts decreases as one moves away from the equator. Bats in temperate zones tend to roost in well-buffered structures such as caves, crevices, tree holes and human-made structures, which offer more stable conditions and better protection from adverse weather conditions. In contrast to the more permanent roosting structures used by most bats in temperate areas, the structures that most roost-making bats

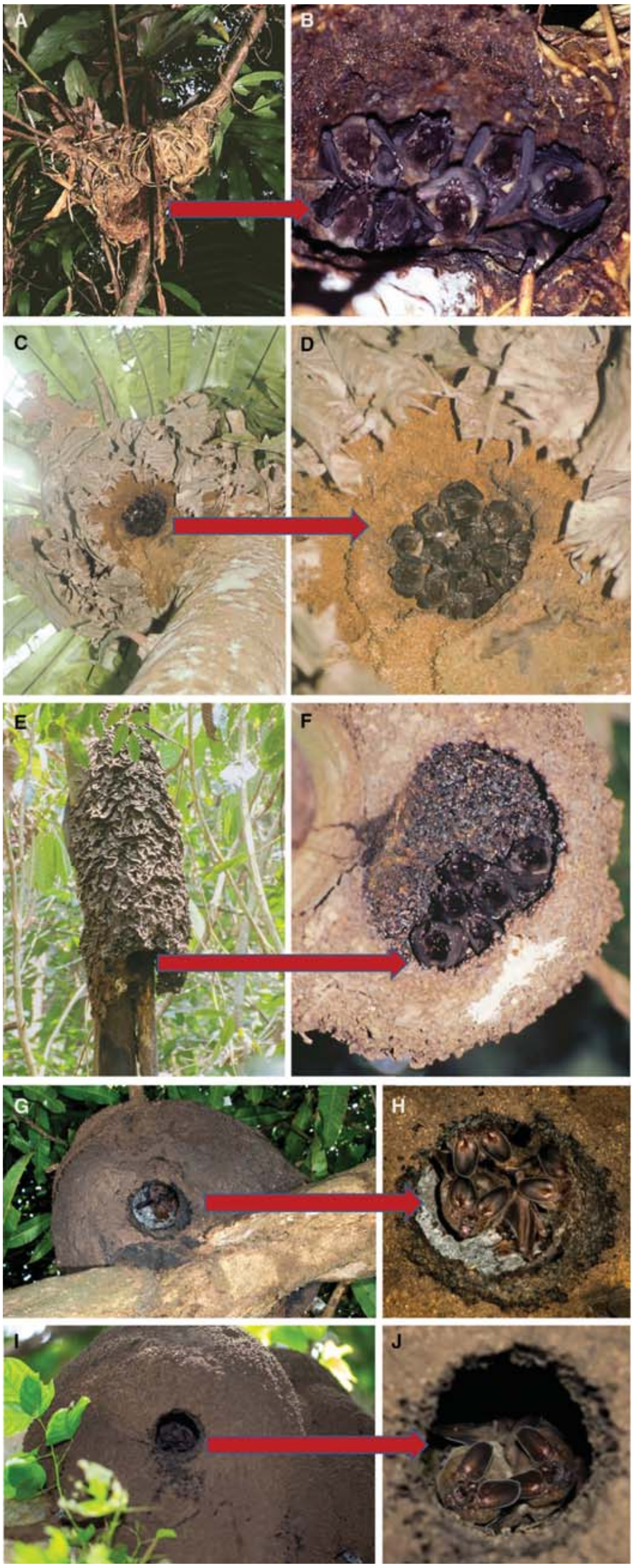

Figure 2. Bat roosts formed by excavating cavities.

(A) The root mass of an epiphytic ginger (*Hedychium longicornutum*) inhabited by (B) a harem of spotted-winged fruit bats (*Balionycteris maculata*) in Malaysia. (C) The root mass of an epiphytic fern (*Asplenium nidus*) with (D) a roosting group of *B. maculata* in Malaysia. (E) An active arboreal ant (*Crematogaster ebinina*) nest used as a roost site by (F) *B. maculata* in Malaysia. (G) A live termite (*Nasutitermes corniger*) nest in Trinidad occupied by (H) pygmy round-eared bats (*Lophostoma brasiliense*). (I) A live termite (*N. corniger*) nest occupied by (J) white-throated round-eared bats (*L. silvicolum*) in Panama. Photos A–F courtesy of Robert Hodgkison; photos G–J courtesy of Merlin Tuttle (MerlinTuttle.org).

use in warmer climates usually consist of leaves or other forms of vegetation that are ephemeral and need to be replaced frequently.

Phylogenetically, roost making is spread out among bats and has evolved multiple times. It has then been conserved among relatively closely related species. In the Old World fruit bats (Pteropodidae), for example, all tent-making species known to date (species in the genus *Cynopterus* and the single species *B. maculata*) belong to the subfamily Cynopterinae. All New World tent-making bats belong to the family Phyllostomidae, with at least 16 species in the subfamily Stenodermatinae; a single species, the dwarf little fruit bat (*Rhinophylla pumilio*), is in the closely related subfamily Rhinophyllinae. Interestingly, like the Old World roost-making pteropodid species, all New World tent-roosting species are fruit eaters. A single species from the insectivorous family Vespertilionidae has been documented to occasionally also roost in leaf-tents: the lesser Asiatic yellow bat (*Scotophilus kuhlii*) in the Philippines. Report of this behaviour is the only case of an insect-eating bat roosting in leaf-tents, and there is debate as to whether this species constructs its own roosts or parasitizes the roosts of other bats, highlighting the need for increased detailed study of bats worldwide.

A review by Tom Kunz, one of the first researchers to look for patterns in roost-making behaviour among bats, estimated that only a subset of the species in the genera that contain roost-making species actually make roosts. He pointed out that this estimate is likely to be inaccurate, on the one hand underestimated because of how little we know about many bat species, many of which use several roost types, and on the other hand overestimated because some species found in leaf-tents may be using abandoned tents made by other bat species, or may even actively expel them. Especially for larger bats that are not obligate leaf-tent roosters but also roost in caves or tree holes, leaf-tent roost eviction is likely common.

To understand bat-modified roosts, direct observations of roost construction are key, but rare. The actual process of modifying a leaf to make a tent has been observed only in a few species. In Honduran white bats (*Ectophylla alba*; Figures 1B and 3C,D), both sexes construct the roost. In Peter's tent-making bats (*Uroderma bilobatum*, Figures 1D and 3A) and great fruit-eating bats (*Artibeus lituratus*), the leaf is modified by the harem male. In greater short-nosed fruit bats (*Cynopterus sphinx*; Figures 1C and 3B) in southern India, and lesser short-nosed fruit bats (*C. brachyotis*) in Malaysia, single males sever stems, branches and leaf petioles to construct roosting cavities, a process that can take over a month. Once completed, these roosts are occupied by this harem male, together with females and their pups.

Among Old World insect-eating bats of the family Vespertilionidae, three genera (*Kerivoula*, *Murina*, and *Phoniscus*) make basal holes in hanging bird nests. While several bat species have been documented roosting in social insect nests, nest excavation has only been observed in two bat lineages to date: the Old World pteropodid *B. maculata* and the New World genus *Lophostoma*. And in case of the rare terrestrial excavation behaviour reported in *M. tuberculata*, roost-making is restricted to the only extant representative of its family.

Bats range in size from 2 g to over 1 kg but, to date, roost modification has only been documented in small to mid-sized bats, with the heaviest known leaf-modifying bats weighing approximately 70 g (*A. lituratus*). It is notable that in the comparatively large-bodied Old World fruit bats (Pteropodidae), only relatively smaller species roost in modified shelters (*Cynopterus* spp., with masses up to 60 g, and *B. maculata,* around 13.5 g). It is likely that larger, heavier fruit bats cannot find leaves to modify that are strong enough to shelter entire groups. Similarly, hanging bird nests cannot support large groups of heavy bats, and the social insect nests that bats excavate are not big enough to accommodate groups of large bats. Small size also allows for increased manoeuvrability, and the ability to navigate the tropical and subtropical forest understories where the majority of bat-constructed roosts are found.

Roost lifespan and social systems

Many social animals make their own shelters, and it is believed that the creation of long-lasting structures that are maintained across generations, such as the burrows of naked mole rats or the nests of many social insects, have contributed to the evolution of eusociality. Roosts likewise play a critical role in the evolution of bat social systems. A large portion of bat social interactions take place at the roost, including territorial displays, courtship, mating, rearing of the young, and information transfer. It has been suggested that the combination of the unusual longevity of bats with female philopatry promotes social stability and cooperation. However, in contrast to most bat roosts, such as caves or tree cavities, bat-made roosts are ephemeral, usually lasting a few months to a few years.

Many bat species are known to switch roosts frequently, likely to avoid an accumulation of parasites or to evade detection by predators. A review on the relationship between group stability and roost lifespan in tent-making bats found that almost all species that use roosts with comparably long lifespans had unstable and often seasonal female groups, while social groups in shorter-lived tents were more stable and lasted year-round. One explanation is that suitable leaves for making more short-lived tents, such as certain *Heliconia* spp. leaves, are actually quite rare. In fact, it was found that the requirements for making leaves suitable as roosts are very specific, resulting in very limited roost availability. In contrast, bats making tents from longer-lasting materials, kitul or coconut palm fronds, for example, often have several tents within a small area, with group members flexibly switching between them. It seems that roost longevity and the social system of tent-making bats did not evolve independently, and both roost-making behaviour and roost longevity should be considered when trying to understand the evolution of bat social systems.

Females making leaf-tents

One of the most important influences on the social system of roost-making bats is likely the identity of the bats involved in construction behaviour. Although observations are only available for few bat species, it is assumed that in most cases it is single males that construct roosts. But there is evidence that this is not always true, adding strength to the realization that female groups are important in bats and often the core of species' social systems. In fact, female cooperative behaviour such as babysitting, allonursing or allogrooming is often linked to particularly stable social groups, for example in greater spear-nosed bats (*Phyllostomus hastatus*), which do not make roosts but form closed small groups of unrelated females that last their entire lifetimes in caves in Trinidad.

One of the few bat species in which tent-making has been observed is *E. alba*. In this species, the first record was of a female modifying a leaf. This raised great interest and the speculation that females may cooperate with other females when making leaf-tents. However, roost making was later observed on several other occasions showing both males and females contributing to tent making. Why this is the case remains an open question and is especially interesting because roost fidelity is low in this species. Females likely have a great interest in having suitable roosts close to their foraging areas especially during lactation, when they must return to the roost frequently to nurse their young, and for this reason may shift roost locations frequently.

Roosts as extended phenotypes

In species in which roosts are constructed by males, it is likely that roosts serve as an extended phenotype (*sensu* Dawkins) to attract females. Roost making has only been directly observed in six species of bats, and in five of these species, construction and modification were conducted exclusively by males (*A. lituratus*, *B. maculata*, *C. brachyotis*, *C. sphinx*, *L. silvicolum*). If and how roost making helps males attract females remains an open question. Most bats — and as far as it is known, all roost-making bats — live in harems (single male, multi-female groups). As the male defends the roost, he also defends the females within the roost in resource defence polygyny. Interestingly, this investment is not necessarily directly reflected in the relatedness with the offspring currently roosting with him.

Females of many bat species enter oestrus soon after giving birth and a roost-making male may thus be joined by females pregnant from another male. Yet he may shelter them in his roost even so in order to mate with them postpartum and sire their next pup. In *L. silvicolum*, and also in Old World fruit bats, the paternity of harem males in the roosts they construct is around 50%, which apparently is high enough to justify investing daily effort into creating and maintaining the roost. Interestingly, male infanticide has been observed in *L. silvicolum*. Even though female oestrus is seasonal and synchronized in this species, reducing the effort invested in another male's offspring may improve investment into the next offspring and thus the harem male's own genes, similar to examples from langurs, lions, and other taxa.

As in most mammals, female choice is probably vastly underestimated in bats and females aggregating in the roosts of harem males are a good example. The roost-making male, and in fact harem males in all bat species observed to date, can only defend the roosting site and the females currently in it. Females usually forage without the harem male and are free to visit and mate with other males. When the roost they are occupying is disturbed, female *L. silvicolum* immediately switch to the roost of another harem male, indicating prior knowledge of additional male's cavities in termite nests. In observations of Old and New World tent-making bats, the composition of the females in a given tent can vary from day to day, suggesting that they, too, are aware of and use other males' tents.

Female roost fidelity is generally lower than that of males. Males therefore are under selective pressure to create and maintain high quality roosts in terms of microclimate, location, and protection. In *L. silvicolum*, for example, it is likely that not only traits of the harem male himself, but also the shape, size, location and temperature of the cavity he creates — his extended phenotype — affect female choice. The temperatures in the termite nests male *L. silvicolum* excavate are more stable and warmer than the tree cavities occupied by closely related species and even higher than maximum ambient temperatures. This likely also explains why these roosts are abandoned by the bats when the termite colony dies. Even though the nests maintain the same excavated shape for a long time after the termites leave, without the presence and activity of the termites, the cavity temperatures fluctuate with outside temperatures.

Roost density is also important. A study on the four species of short-nosed fruit bats (*Cynopterus* spp.) known to make roosts found that the percentage of paternity of a harem male in his roost is greatly affected by the number of roosts in the area. Fidelity of females to males and thus to roosts in these species is mostly low, but lower roost density results in harems with more females, increasing the harem male's paternity. This also results in stronger skew in paternity between different harem males within a species. In this same genus another interesting behaviour has been observed. Clearly it is advantageous for a male to make his roost in an area where suitable roosts are rare; however, young males sometimes trigger the formation of new harems by occupying tents that were abandoned by an established harem male and then actively recruiting females to this roost. In this case, the young, upcoming male profits from the proximity of the older male and his harem, as well as this male's previous roost construction work.

While the benefit of roost making for harem males — increased paternity — is obvious, the costs are manifold. Roost-making male bats experience physical costs such as increased tooth wear compared to females. Harem males also must spend as much time as possible in their roosts to defend them from other males. This, together with the time required for roost construction and maintenance, results in significantly shorter foraging times in *L. silvicolum*. Only males in good physical condition can afford to attract females and maintain harems. This reflects a widespread mammalian pattern in which a small number of males gain access to a disproportionate amount of reproductive success, while older, younger, and physically inferior males live as bachelors.

Roosts and species distribution ranges

Bat species vary in their degree of roost specialization. Many bats are opportunistic and use a wide variety of structures as roosts, while others are highly specialized. The latter is true for many roost-making bats. Roost specialization can limit a species' distribution range, while roost flexibility can expand it. The Jamaican fruit-eating bat (*Artibeus jamaicensis*), for example, commonly roosts in caves when available, but can also roost in tree cavities or leaf-tents. Like most bats living in leaf-tents, this species has never been observed making tents. It is possible that *A. jamaicensis*, and other large bat species, use tents abandoned by other bats, or even usurp occupied tents, evicting the roost-making tenants, as they are larger than most tent-roosting bats in the Neotropics. *Artibeus jamaicensis* is one of the most common bats in Neotropical rainforests with a large distribution range, which may be due in part to their flexibility in roosting behaviour. Interestingly, this species' social system varies with roost type, from large aggregations in caves to male resource defence polygyny in tree cavities and tents, corroborating the importance of the roost type in the evolution and maintenance of social systems. The degree to which this pattern holds across species is an intriguing question that warrants further study.

The interconnected importance of roost availability for mating and social systems, as well as for shaping population sizes and distribution ranges, becomes most evident when

Figure 3. Optical camouflage in bats roosting in leaf-tents.
(A) White markings on Peter's tent-making bats (*Uroderma bilobatum*) in Panama and (B) greater short-nosed fruit bats (*Cynopterus sphinx*) in Hong Kong serve as optical camouflage, minimizing detection by visual predators. Photos by Kamran Safi and John Allcock, respectively. Two photographs of the same group of roosting Honduran white bats (*Ectophylla alba*) in their leaf-tent roost in Costa Rica (C) with flash and (D) with natural lighting. Under natural lighting, the green light passing through the leaf-tent partially camouflages the light-coloured bats inside. Photos by Marco Tschapka.

roosting behaviour is shifted in human-modified landscapes. Roosts can become highly clumped when preferred roost plants are artificially common, for example in gardens or through agriculture. Artificially high roost density can have effects on harem sizes and stability, often resulting in a larger 'colony' made up of multiple harems, with females switching between males in the colony. When anthropogenic structures are available, tent-making bats have been documented to switch to using them as alternative roosts. For example, *U. bilobatum* constructs tents in forests, but commonly roosts under the eaves of houses where available. This shift can result in large local population sizes, especially in disturbed areas where figs, the staple diet of many tent-making bats, are abundant.

In *U. bilobatum*, the introduction of stable, long-term human-constructed roosting sites has led to a fission-fusion system with a larger 'meta-colony' using several roosts, and individual bats moving freely between them. Whether this social system also occurs in areas where houses are absent is unknown, but may vary depending on whether tents are made in longer-lasting palm fronds or shorter-lasting boat-shaped leaves as outlined above. As most of the plants bats use for tent making are part of secondary vegetation that naturally occurs in forest gaps and along forest edges, anthropogenic disturbance can profoundly influence population sizes as well as the local mating and social systems of tent-making bats.

Bat roosts and predation

In general, the ability to fly allows bats to roost in protected sites that are difficult for predators to access. Several roost-associated adaptations have evolved to deter predator detection. Many foliage roosting bats, including nearly all tent-making bats, have white or mottled markings, likely serving as a form of crypsis. The tent-roosting genera *Artibeus*, *Vampyressa* and *Uroderma*, for example, all have white stripes on their faces (often the only part of the bat visible from below; Figure 3A), while several tent-roosting species, for example, great stripe-faced bats, *Vampyrodes caraccioli*, also have white lines down their backs. These stripes likely serve as optical disruptors, decreasing detection by visual predators. Similarly, short-nosed bats in the genus *Cynopterus* (Figure 3B), and *B. maculata*, as its Latin species name ('spotted') implies, have light coloured wing joints and often appear otherwise mottled, also increasing disruptive camouflage in their vegetation tents.

Other tent-making species have full bodies that are light in colour, for example, MacConnell's bat, *Mesophylla macconnelli*, or even white, for example, *E. alba* (Figure 3C,D). The green light passing through the leaf-tents in which these bats roost results in remarkable camouflage, especially because these species, unlike other tent-roosting bats, hide their more noticeable faces while roosting (Figure 3C,D).

How effective cryptic colouration is in protecting tent-roosting bats from predation remains largely unknown. Reports of monkeys, snakes and birds catching bats from leaf-tents are common, and it has been speculated that predators may even develop search images for the distinctive modifications bats make to construct their tents. Whether the rates of leaf-tent predation are higher than predation in more common roost types, especially in roosts occupied by much larger groups of bats, has not been quantified. Many bat predators, including hawks, falcons, hornbills, raccoons, foxes, and snakes, wait at the exits of large bat roosts such as caves for bats to emerge in the early evening, resulting in high levels of regular nightly predation.

Predation on large, conspicuous aggregations of bats in permanent roosts may have played a role in the evolution of roost-making in bats. The vegetation and hanging bird nests in which bats construct roosts likely transmit vibrations of approaching predators better than more fixed, concrete structures such as tree cavities or caves, giving the bats a head start in escape through their basal exits. The small, transitory groups of bats that roost in ephemeral tents and in modified bird or social insect nests also accumulate less guano, and thus are associated with fewer conspicuous chemical cues potentially attracting predator notice, compared with larger, more permanent bat roosts.

Outlook

Of the over 1400 extant species of bats worldwide, only a small subset has been studied in detail. As volant, nocturnal taxa, bats are challenging to observe, and across all behavioural contexts, roosting included, more investigation is needed. With increasing availability of miniaturized, field-resistant technology, doors are opening in bat research. To date, roost modification has only been reported in a handful of bat species, but increased observation across a greater range of taxa will likely reveal that this behaviour is more common than previously reported. Future work should not just broaden taxonomic representation across a broad geographic range, but delve deeper into understanding the factors that select for and maintain this fascinating behaviour.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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