Sensory Ecology: Echolocation Calls Are Used for Communication

Noctule bats locate tree roosts faster by eavesdropping on the echolocation calls of conspecifics. Increasing evidence suggests that echolocation is important not only for orientation and finding prey, but also for communication.

Gareth Jones

We are often aware of bats only when they fly briskly past us at night. Although bats find their food during darkness, for the remainder of the day they need protection from extremes of weather and from predators by occupying roost sites. Bats often roost in large groups, and behaviours such as mating, hibernation and rearing young are conducted in roosts. Finding suitable roosts is therefore of fundamental importance in the lives of bats [1].

Bats' roosts include caves, buildings, modified leaves and trees [1]. Tree-dwelling bats move roost every 1–3 days, perhaps to disrupt ectoparasite lifecycles or to reduce the risks of being detected by predators [2]. Recurrent patterns of roost switching result in the formation of fission–fusion societies, where society members coalesce to form groups, although the individuals comprising any group may vary over time [3]. Social dynamics at roosts can therefore be complex, and there is experimental evidence that bats may share information about the location of these valuable resources with other colony members: naïve Bechstein's bats, *Myotis bechsteinii*, are more likely to be recruited to suitable roosts than to unsuitable ones where the entrance to interior chambers is blocked. Recruitment of conspecifics may be beneficial because it brings thermoregulatory benefits to individuals by reducing heat losses when roosting in a group [4]. Roosts are crucial resources for bats, although finding new tree roosts with suitable cavities can be difficult, especially in large forests. Such challenges may be especially severe for migratory species that encounter unfamiliar tracts of forest on a regular basis.

Finding a roost rapidly could therefore confer major fitness advantages to tree-dwelling bats. A new study [5] has explored the sensory mechanisms used in roost location by a migratory tree-roosting bat — the noctule *Nyctalus noctula* — under controlled laboratory conditions (Figure 1). Noctules were trained to find the entrance to artificial tree cavities in a flight room. Sensory cues available to the bats were manipulated, and the time taken for the bats to find a roost cavity was recorded.

In the control condition the bats could use only echolocation to find cavities — they flew in darkness. In other treatments bats were provided with additional cues that were visual, temperature-related, olfactory or acoustic in nature. To determine if the bats found roosts faster when visual cues were available, experiments were conducted under light levels that mimicked those experienced by noctules hunting in the early evening. Tree cavities used by noctules are typically about 7°C warmer than ambient temperature, and so cavities were artificially heated to determine whether the bats used temperature cues to locate roosts. The researchers presented olfactory cues by placing cloth exposed to the bat's odour together with a small number of bat faeces in roost cavities. The final treatment involved playing back echolocation calls from a speaker positioned to mimic a noctule calling from within a cavity, to determine whether bats find cavities faster when presented with passive acoustic cues (the speaker was left in position during all other treatments, except no sound was transmitted through it).

There were no significant differences in the search time taken to locate roost cavities compared with the control situation, except for when passive acoustic cues were also provided: the search time was then reduced by half. Acoustic cues were beneficial to the bats both at relatively long range (when they were flying) and at short range (crawling). Although echolocation can be used by bats to determine the texture of targets [6], detecting and localizing cavities against complex backgrounds such as bark and overlapping branches may not be straightforward. Listening to the calls of other bats facilitates the task of roost location, and may explain why tree-dwelling bats, including noctules [7] 'swarm' in flight around roosting trees at dawn.

Echolocation is sometimes viewed as 'autocommunication', with the bat operating as both signaller and receiver [8]. But bats often communicate with conspecifics by using 'social calls'; these are less stereotyped than echolocation signals [9], because

Figure 1. A noctule calling from an experimental tree cavity attracts eavesdropping conspecifics.
Photograph by Ireneusz Ruczyński.

the latter are constrained to solve specific perceptual tasks from a sonar perspective. Social calls are often lower in frequency than echolocation calls, and can therefore be transmitted over long distances, and their utility in communication has been proven in playback experiments [10,11]. Many bats have elaborate repertoires of social calls, with particular calls used in specific behavioural contexts [12]. Little brown bats (*Myotis lucifugus*), however, are attracted to playbacks of echolocation calls at feeding sites, and they are also attracted to the echolocation calls of other species [13]. Eavesdropping at foraging sites makes good sense in the light of what is known about target detection ranges and echolocation call intensities in bats. Bats must send out intense calls to receive detectable echoes from insect prey. For example, little brown bats may be able to detect insects only over a range of less than 5 metres, whereas the echolocation calls of other foraging bats may be heard more than 50 metres distant, greatly increasing the chances of a bat finding a swarm of insects [13]. Similar long range detection benefits will apply to eavesdropping bats searching for roosting sites.

The finding that bats may regularly eavesdrop on calls from other bats supports the hypothesis that echolocation is important in communication as well as in biosonar. The importance of echolocation in communication is also supported by studies of the frequency bandwidths utilised in bat communities. Densely packed communities of bats with similar echolocation call designs comprise species that utilise species-specific bandwidths that rarely overlap with the frequencies used by other, often closely related species [14]. Initially, this frequency partitioning was believed to minimize interspecific competition for food: call wavelength needs to be smaller than or equal to the wing length of an insect to return echoes that are not weakened by Rayleigh scattering effects [15]. Bats calling at different frequencies could therefore be specialised to detect different sizes of insect prey, with higher frequency echolocators (emitting shorter wavelength calls) specialising on smaller prey. However, echo strengths from insects differ by negligible amounts even with a 10 kHz difference at the mid-range of frequencies used by bats [16]. The 'prey size detection hypothesis' is therefore unlikely to explain why many bats avoid overlapping call frequencies, especially at higher frequencies where wavelength differences are smaller [17].

A more likely hypothesis for frequency partitioning is that each species utilises a 'private bandwidth' for acoustic communication. Echolocation signals are emitted continuously and frequently by flying bats, and will function as simple and effective badges of species identity. This 'acoustic communication hypothesis' is supported by a recent finding of apparent acoustic character displacement [18]. A bat species present on Sardinia but absent in areas of peninsular Italy appears to force two closely related species into emitting higher and lower bandwidths than typically used on the peninsula so that each species occupies its own acoustic space for effective communication on the island [18].

The performance of bat echolocation for the detection, localization and classification of targets [19,20] never ceases to amaze. It is now increasingly apparent that bats are listening in the dark not only for echoes from food items and obstacles, but also for the calls of other bats that may lead them to valuable feeding and roosting sites.

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School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK.
E-mail: Gareth.Jones@bristol.ac.uk

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