



# From spatial orientation to food acquisition in echolocating bats

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**Field research on echolocation behavior in bats has emphasized studies of food acquisition, and the adaptive value of sonar signal design as been considered largely in the context of foraging. However, echolocation tasks related to spatial orientation also differ among bats and are relevant to understanding signal structure. Here, we argue that the evolution of echolocation in bats is characterized by two key innovations: first, the evolution of echolocation for spatial orientation and, second, a later transition for prey acquisition. This conceptual framework calls for a new view on field data from bats orienting and foraging in different types of habitats. According to the ecological constraints in which foraging bats operate, four distinct functional groups or guilds can be defined. Within each group, signal design and echolocation behavior are rather similar.**

The ecological success of microchiropteran bats is based on numerous morphological, physiological and behavioral adaptations of sensory and motor systems for a nocturnal life, especially on the evolution of flight and echolocation. Echolocating bats emit tonal signals produced in the larynx and analyze the returning echoes to detect, localize and characterize the reflecting targets. To date, field studies of echolocation have emphasized its role in food acquisition and many publications deal with the problem of how bats detect, categorize and localize prey. However, bats also use echolocation to localize a perch, to avoid obstacles and to navigate from one place to another. Here, we discuss the recent literature on bat echolocation, not only in the context of foraging, but also in the context of spatial orientation and navigation. We argue that the evolution of echolocation is characterized by two key innovations: first, the evolution of echolocation for spatial orientation and second, the later transition also for prey acquisition. We present a framework for understanding how echolocation signals of bats have been adapted to solve habitat-specific tasks when orienting in space and/or searching for prey.

## Two key innovations in the evolution of echolocation

There are several scenarios to account for how and when echolocation developed during evolution [1–11] reviewed in [8]. Most share the common view that the ancestors of echolocating bats were probably quadrupedal, arboreal

insectivores, but the hypotheses differ in accounts of the timing and the purpose of the development of tonal echolocation signals. Fenton *et al.* [2] and Norberg [3] suggest that a primitive echolocation system with short, low-intensity broadband clicks used for general orientation preceded a sophisticated laryngeal echolocation system that used tonal signals to assess airborne prey. Under this hypothesis, echolocation with strong tonal signals is regarded as the key innovation, primarily evolved for food acquisition rather than for spatial orientation.

In two other scenarios, the initial evolution of a sophisticated form of echolocation for spatial orientation was the prerequisite for the later transition, using echolocation also for prey acquisition [4,7]. Simmons and Geisler [4] postulate that, once flight evolved, bats still used vision for spatial orientation and obstacle detection. Then, a simple echolocation system evolved, using laryngeal signals that enabled the transition from spatial orientation guided by vision to orientation guided by echolocation. In this proposed scenario, echolocation evolved further for perch hunting and later for continuous aerial hawking for flying prey. Schnitzler *et al.* [7] argue that echolocation began with tonal signals when pre-bats evolved to jump, glide and finally fly to distant targets, and that it was used to perform spatial tasks, such as landing control, obstacle avoidance and spatial orientation. The authors propose that, initially, bats listened to prey-generated signals for the detection and localization of sitting prey (passive mode). According to this view, the final step in the evolution of echolocation was the transition to an active mode of prey detection and localization by echolocation, which enabled the bats to forage for aerial prey, first from perches and later in continuous search flights. Comparative studies in recent bat species support the primary role of echolocation for spatial orientation. All microchiropteran bats use echolocation for spatial orientation, whereas prey discrimination by echolocation has been described only in bats that forage either for flying insects or for stationary food, which delivers a food-specific echo signature [12].

## Bat habitats defined by echolocation tasks

When orienting in space, searching for food, and/or approaching a target of interest, microchiropteran bats continuously emit echolocation signals and analyze the returning echoes. The sound complex comprising the

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emitted signal and its echoes is processed in the auditory system to perform the basic perceptual tasks of detection, localization and classification of either a single reflecting target or an auditory scene comprising a combination of targets [12–14]. For detection, bats must determine whether they have received echoes of their own emitted signals. For classification, bats use patterns of echo information to categorize targets. For localization, they measure the time delay between the emitted signal and the returning echo to estimate target distance, and analyze binaural and monaural acoustic cues to determine the horizontal and vertical angles of sonar targets (for a review, see [15]). However, it is unlikely that bats accomplish each of these basic perceptual tasks independently of the others.

Echolocation tasks performed by bats depend on their immediate behavioral goals and vary with the type of habitat in which they are performed (Fig. 1). Bats orienting in space need to solve different problems than do those searching for prey. Bats might also need to solve multiple tasks concurrently (e.g. orienting in relation to background targets and searching for prey). To date, bat habitats have been defined solely according to the echolocation problems to be solved by bats searching for prey. However, in each habitat, bats also have to perform spatial orientation tasks. In narrow space, bats not only have to find prey that is positioned on or near vegetation or the ground, but also have to solve the problem of spatial

orientation close to background targets. In edge space, bats seek prey flying near vegetation edges, in gaps, or above flat water surfaces and also use background targets as landmarks for spatial orientation. In open space, bats hunt for prey far from vegetation or the ground.

When performing sonar tasks, echolocation is hampered if the target of interest is so close to the bat that the emitted signal interferes with the detection of the returning echo (forward masking) (Box 1). Additionally, bats searching for food in the vicinity of background targets can experience interference from echoes of these targets that return shortly after those from the prey item (backward masking). Therefore, in discussions of foraging behavior, vegetation and other non-prey objects are commonly referred to as sources of clutter echoes. In the context of spatial orientation, echoes from background targets are of interest for bats because they enable obstacle avoidance and can be used to characterize landmarks, which bats need for navigation.

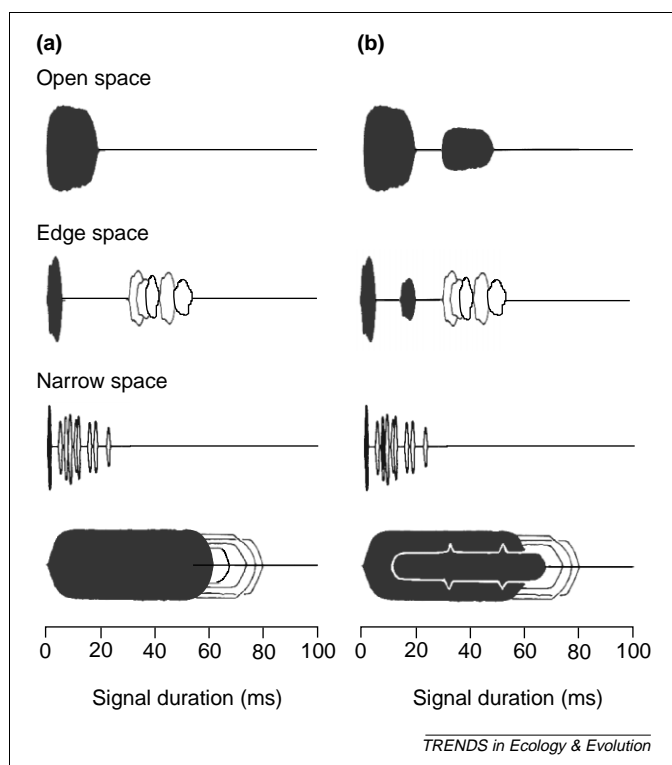
The conditions given by the distance of a bat's flight path to background targets, and particularly the proximity of prey to the background, are the most relevant ecological constraints on the design of sensory and motor systems of bats. These conditions determine the echolocation problems that have to be solved. They also challenge the flight mechanics of bats; for example, near clutter, the maneuverability must be high to intercept insects whilst also avoiding collisions. Clutter conditions for foraging bats have therefore been used for characterizing bat habitats [12,13,16–18] (Box 2).

### Spatial orientation

We postulate that echolocation evolved primarily for orientation in space. According to the orientation situation and the corresponding echolocation tasks, we distinguish three types of navigation: small-, middle- and large-scale navigation. The term navigation is used according to Trullier [19], who defined it as the ability of animals to find, learn and return to specific places. Large-scale navigation, which encompasses long-distance migration and homing, will not be addressed further here, because echolocation plays little or no role in these processes [20].

#### Small-scale navigation

Small-scale navigation includes all tasks in which the target of interest is within the perceptual range of the bat's echolocation system. This includes the localization of landing sites and obstacles, and the classification of background targets as landmarks. It is not yet clear which echo information is used by the bat to identify landmarks such as trees and bushes. Müller and Kuc [21] ensounded the foliage of a yew and a fig tree with simulated bat signals from different directions. These extended targets contain many reflecting facets and generate stochastic sequences of echoes each different from the next. They showed, theoretically, that such random process parameters can be used to discriminate between the two species of plants. Additional information might be encoded in the changes within echoes over time [22]. Theoretical studies suggest that changing echo parameters deliver time-variant echo features (acoustic



**Fig. 1.** Echolocation tasks of bats during spatial orientation (a) and search for prey (b) in different habitats. The emitted pulse and the echo returning from prey (grey) are displayed together with echo trains from background targets (white). Distributed background targets, such as vegetation, comprise many reflecting surfaces and produce trains of overlapping echoes. The information needed for spatial orientation is encoded in the pairs of emitted signal and the train of echoes from background targets; the information needed for prey acquisition is encoded in the pairs of emitted signal and prey echo. Adapted, with permission, from [12,13].

### Box 1. The problem of masking

Auditory masking occurs if the detection of an insect echo is influenced by the preceding emitted sonar vocalization (forward masking) or by following clutter echoes (backward masking). In foraging bats, the detection and evaluation of the prey echo is hampered when the neuronal activity evoked by the signal emitted by the bat or the clutter echoes interferes with the activity evoked by the prey echo; for example, if an insect flies in a forward-masking zone in front of the bat or in a backward-masking zone in front of the background vegetation that give rise to clutter echoes (Fig. 1a). When orienting in space (Fig. 1b), bats experience forward masking only if they fly so close to the background that vegetation echoes fall in the forward-masking zone.

The degree of masking and the width of the masking zones depend on signal structure, the sound pressure level of the masking signals and of the prey echo, and on their temporal relationship. Forward masking is stronger than backward masking [15]. The many variables determining masking make it difficult to judge the width of the masking zone. However, the zone in which the prey echo overlaps with the emitted signal (signal overlap zone) or the clutter echo (clutter overlap zone) is a useful approximation to judge the width of this area [12,13]. The width of the overlap zones depends on signal duration (Fig. 1). For example, with a signal duration of 10 ms, the overlap zone is 1.70 m, given a speed of sound of  $340 \text{ ms}^{-1}$ . Depending on the signal type used by the bat, the masking zone can be smaller than the overlap zone calculated from sound duration. Studies of Natterer's bats *Myotis nattereri* [51], and of Northern bats *Eptesicus nilssonii* [65], indicate that these bats tolerate some overlap between prey and clutter echoes.

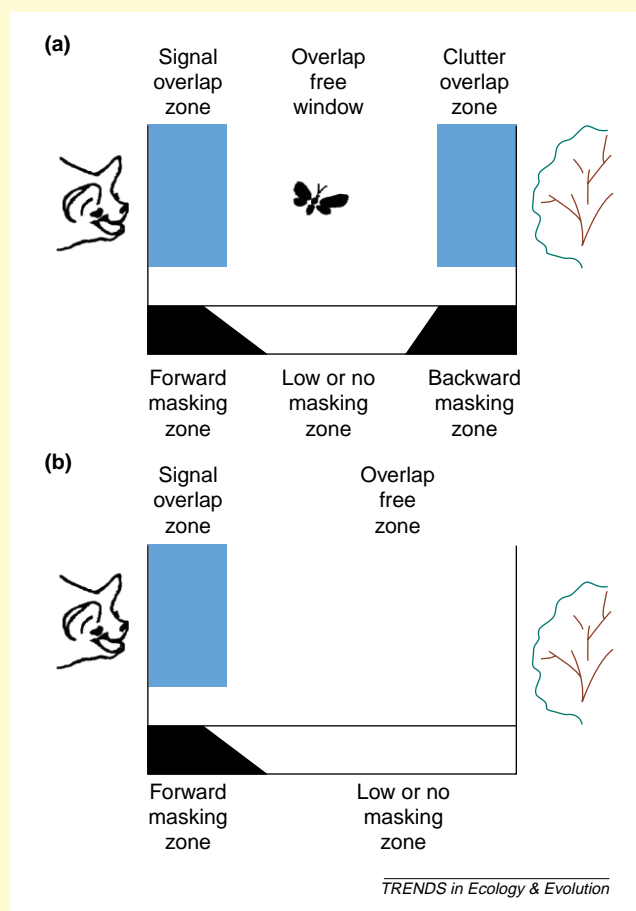


Fig. 1. The masking situation for a bat when foraging (a) or orienting in space (b) near vegetation. Overlap zones are given in blue, masking zones in black. White areas indicate the overlap free window or the zone of low or no masking. Adapted, with permission, from [12,13].

flow), which might contain information about the motion and position of a bat in relation to the passed targets [23,24].

### Middle-scale navigation

Middle-scale navigation comprises the ability of bats to reach goals beyond the operating range of the echolocation system but within their home territory. It also includes a spatial representation of their home territory and the integration of new information into spatial memory. When flying between roosts and feeding grounds, many bats follow more or less distinct routes along linear landscape structures. Individual bats following similar routes travel on a flyway. For some bats flying in narrow space, the spatial constancy of these flyways is very high [22,25]. Bats flying in edge space also follow linear landscape structures [26]. Bats commuting in open space, such as noctule bats *Nyctalus noctula*, are often not bound to background structures and use flight corridors that are much wider (H-U. Schnitzler and A. Denzinger, unpublished).

It is unknown how route knowledge is represented in the spatial memory of a bat. To follow routes, bats must recognize places associated with a decision (e.g. to change the flight direction). These places are characterized by the spatial configuration of landmarks. Thus, the recognition of landmarks is mandatory to being able to follow routes [19,27]. Route knowledge could be stored as a low-level representation of landmark sequences in the bat's central nervous system. Route planning requires a topological representation of the environment and could be achieved by concatenating portions of experienced routes into new routes. Metric information would be required if bats are able to plan shortcuts.

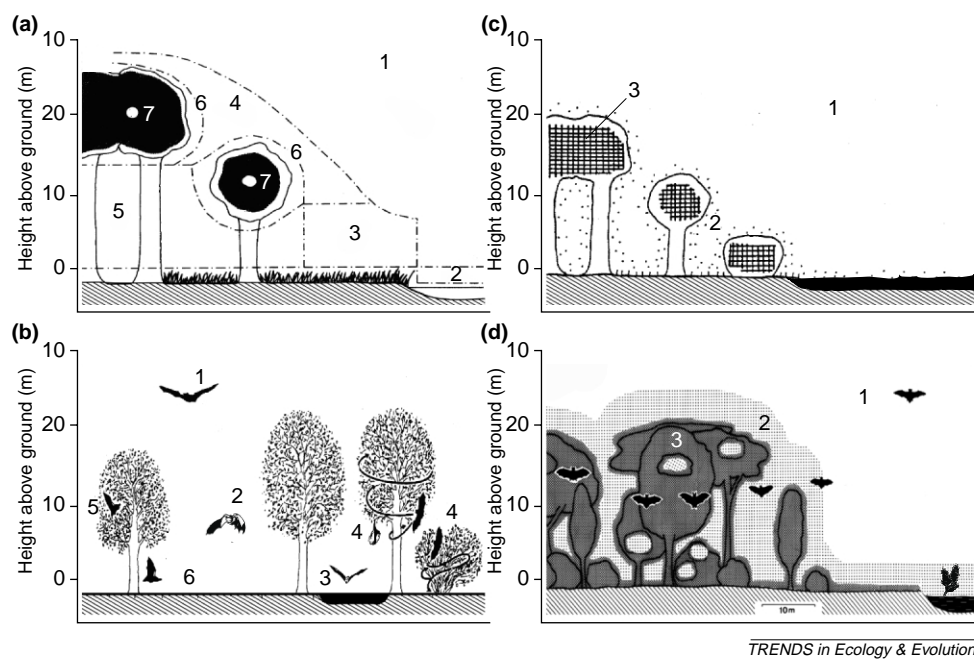
Following background contours with high spatial constancy, a bat must maintain a specific egocentric relationship to landmarks. This navigational behavior is termed guidance and only requires raw sensory information (e.g. the distance between the bat and the background) but not the assessment of an internal spatial representation [19]. Additionally, bats have a detailed spatial representation of their flight routes, as demonstrated in field experiments in which a novel target was introduced in the vicinity of the flight paths of greater horseshoe bats *Rhinolophus ferrumequinum* and mustached bats *Pteronotus parnellii*. This change in the environment elicited an orienting reaction, characterized by a change in the echolocation behavior and, in *R. ferrumequinum*, also by a change in flight behavior [22]. After several passing flights, the bat habituated to the novel object and the orienting response disappeared. Such reactions indicate that the bat noticed a mismatch between incoming and stored information. The orienting response delivers information required to update its internal representation of space.

Our knowledge of how bats establish a spatial representation of profitable foraging areas and roosts is still very limited. Exchange of information among colony members about hunting areas occur in evening bats *Nycticeius humeralis* [28], greater spear-nosed bats *Phyllostomus hastatus* [29], and possibly in species that sometimes hunt in groups [30]. To what extent spatial

## Box 2. Bat habitats

Categorizations of foraging habitats from key publications [12,13,16–18] distinguish three main types of bat hunting environment: in the open; between and along vegetation; and close to and within vegetation and the ground (Fig. 1, Table I). A problem with such categorizations is the definition of the borders between the different habitat types. Schnitzler and Kalko (Fig. 1d; [12,13]) use habitat-specific echolocation conditions for habitat characterization. In open space, bats do not react to the background in their echolocation behavior. In edge space, they react to the background, and prey echoes are not yet masked by clutter. In

narrow space, the echoes of food items are masked by clutter. Because it is difficult to determine the exact extent of the backward-masking zone, use of the clutter-overlap zone has been suggested as a first approximation to describe the backward-masking zone [12]. Fenton (Fig. 1c; [18]) also used overlap to separate open habitats with no overlap between prey echoes and clutter from edge and closed habitats with such an overlap. The categorizations made by all other authors do not explicitly relate the habitat borders with respect to specific echolocation tasks.



**Fig. 1.** Characterization of foraging habitats of bats from key publications.: (a) Aldridge and Rautenbach [16]; (b) Neuweiler [17]; (c) Fenton [18]; and (d) Schnitzler and Kalko [12,13]. The origins of the diagrams [12,13,16–18] and the names of the different habitat types (labeled by numbers) are presented in Table I. Adapted, with permission, from [12,13,16–18].

**Table I. Characterization of the foraging habitats of bats<sup>a</sup>**

(a) Aldridge and Rautenbach [16]	(b) Neuweiler [17]	(c) Fenton [18]	(d) Schnitzler and Kalko [12,13]
1 Open areas	1 Above canopy	1 Open habitat	1 Uncluttered or open space
2 0.5 m above water	2 Open spaces between canopy		2 Background cluttered space or edge space
3 Over pasture	3 Over water surfaces		
4 0.5 m away from canopy	4 Close to and within foliage	2 Edge habitats	3 Highly cluttered or narrow space
5 Between trees	5 Foliage	3 Closed habitats	
6 Surface of vegetation	6 Ground		
7 Within vegetation			

<sup>a</sup>See Fig. 1 for pictorial representation of the different foraging habitats of bats.

information is transferred between mothers and their juveniles is not fully understood. In Bechstein's bats *Myotis bechsteinii* [30], the foraging areas of mothers and daughters overlapped up to 99% and in common vampire bats *Desmodus rotundus*, mother–infant pairs often hunt in the same foraging area [28]. Rossiter *et al.* [31] found the greatest spatial association in *R. ferrumequinum* between females and their adult daughters, both in foraging grounds and night roosts. These results suggest that there could be maternal tutoring of young about foraging areas. One possible behavioral mechanism for the

transfer of spatial information from mother to offspring could be following behavior, but this has yet to be well documented [32].

### Prey acquisition

Bats foraging in a similar habitat with a similar foraging mode for similar food must solve similar tasks. This results in many similarities in their motor and sensory systems, especially in the design of the wings and of the echolocation signals. Therefore, bats foraging under similar conditions have been assigned to functional groups

or guilds (i.e. groups of species that pursue similar behavioral aims under similar ecological conditions [12,13,16,33,34]). Most authors classify bats according to one or more of the following ecological categories in forager groups: hunting site or foraging habitat (e.g. in the open, edge and gap, or narrow space), foraging mode (gleaning, aerial, or trawling) and food (e.g. insectivore, carnivore, piscivore, sanguivore, frugivore, nectarivore, or omnivore). Fenton [34,35] took a different approach and used signal parameters to categorize bat groups (Table 1).

We propose that the guilds defined so far should be assigned to four main forager groups (Table 1) [12]: (1) Open space aerial foragers catch insects in the aerial mode distant from background targets; (2) Edge space aerial/trawling foragers catch insects in the aerial mode at edges, in gaps, or in the trawling mode from smooth water surfaces; (3) Narrow space gleaning foragers take their food from surfaces; and (4) Narrow space flutter-detecting forages use modulations in the echoes of their long signals caused by the beating wings of fluttering insects to categorize prey and to discriminate it from non-fluttering targets.

New data about bats that catch insects in the trawling mode from calm and uncluttered water surfaces [36–38] suggest that the edge space group can be divided into two sub-groups, trawling foragers and aerial foragers [12]. Trawling bats receive echoes from background targets such as the shore but not from the calm water surface, because the water acts like a mirror, reflecting the emitted signal away from the bat. An insect drifting near the shore on the water surface therefore produces a similar echo complex as that of an insect flying in an edge situation near vegetation. Trawling bats might even encounter acoustic situations similar to those of bats hunting in open space, if

the shore is so far away that it does not influence the echolocation behavior.

Many bats vary in their foraging behavior and hunt in more than one habitat [12,13,18]. Some species that mainly glean insects from surfaces in narrow space also catch insects in the aerial mode in less cluttered situations along vegetation edges or even in open spaces. However, bats that are especially adapted to forage in open space are usually restricted to this habitat, and those that are adapted to edge spaces are not known to exploit narrow spaces. Thus, the move of foragers from their specific habitat to a less cluttered habitat is possible, but the reverse is difficult. Schnitzler and Kalko [12] propose to assign species to the forager group where they face the more difficult clutter situation.

### Echolocation behavior

Echolocation tasks exert a strong selective pressure on signal design, thus favoring species-specific signal types that are intimately linked to the ecological conditions encountered by bats that are navigating and/or searching for food. Additionally, within each species, signals vary according to a bat's behavioral aims. The adaptive value of echolocation signals for performing different tasks depends on the information that can be extracted using various echolocation signals or signal elements [12,13,15,18,33,34,39]. In turn, this information depends on the physical structure of the signal elements and on the properties of the bats' auditory systems (Box 3). Some bats alternate between different call types, suggesting a variety of search strategies. However, this behavior is not yet fully understood [40–43].

The four forager groups defined above are assemblies of bats that live under similar ecological conditions and

**Table 1. Characterization of functional groups or guilds by different authors**

Groups defined by foraging site or clutter situation	Groups defined by foraging mode and foraging site	Groups defined by signal parameters	Guilds defined by			Groups defined by habitat and foraging behavior
			Habitat	Foraging mode	Diet	
Open foragers	Open space foragers above vegetation	Low duty-cycle bats, high intensity	Uncluttered space	Aerial	Insectivore	Open space aerial foragers
Woodland/edge/intermediate clutter foragers	Open space foragers between vegetation	Low duty-cycle bats, high intensity	Background-cluttered space	Aerial	Insectivore	Edge space aerial foragers
	Gleaning from water surfaces	Low duty-cycle bats, high intensity	Background-cluttered space	Trawling	Insectivore Piscivore	Edge space trawling foragers
Clutter foragers	Gleaning from leaves and ground	Low duty-cycle bats, low intensity	Highly cluttered space	Gleaning	Insectivore, frugivore, nectarivore, carnivore, sanguivore, omnivore	Narrow space gleaning foragers
Clutter foragers	Foraging close or within vegetation	High duty-cycle bats	Highly cluttered space	Aerial	Insectivore	Narrow space flutter-detecting foragers
Aldridge and Rautenbach [16]	Neuweiler [33]	Fenton [34]	Schnitzler and Kalko [13]			Schnitzler and Kalko [12]

### Box 3. Suitability of signal structure

Generally, echolocation signals comprise frequency-modulated (FM) or constant frequency (CF) components, or a combination of these. The signal elements differ in sound pressure level, duration, absolute frequency, bandwidth and harmonic structure. Short FM signals of large bandwidth are often categorized as broadband steep FM, and longer signals of narrow bandwidth as narrowband shallow FM.

#### Narrowband shallow FM elements (Fig. 1a)

These stay in the response range of the corresponding auditory neurons and evoke neuronal activity, which increases with signal duration, making them well suited for the detection of weak echoes from small insects. Additionally, the longer these echolocation signals are, the better they encode target movements, by carrying characteristic modulations in echo amplitude and frequency. When a signal hits an insect at the favorable instant when its wing is perpendicular to the impinging sound wave, a very short and prominent amplitude peak in the echo, an 'acoustic glint', reveals the fluttering insect (for a review, see [15]). Narrowband sweeps are less suited for accurate localization, because they do not provide a series of time markers for the instant of sound emission and echo reception across a wide frequency band, which the bat requires for precise target range estimation. According to their quasi CF structure, narrowband shallow FM signals are sometimes called QCF signals.

#### Broadband steep FM elements (Fig. 1b)

These elements deliver exact time markers as they sweep rapidly

through the tuning areas of many auditory neurons, making them well suited for accurate target localization, but less so for the detection of small targets. Broadband FM signals also deliver spectral information about the features of the reflecting target. In the laboratory, bats can learn to use such spectral cues for target discrimination [66]. However, to our knowledge, there is no evidence that the spectral signature of prey echoes is so specific that bats gleaning insects in the field can recognize a prey echo within clutter echoes. Another advantage of FM signals could be that they are well suited to classify different types of vegetation, thus enabling the use of plants as landmarks in spatial orientation.

#### Long CF elements (Fig. 1c)

These have all the properties of the narrowband signals. Additionally, in combination with Doppler shift compensation and a specialized hearing system, bats using these signal elements can detect and decode prey-specific modulations (glint patterns) in the echoes, as well as classify fluttering insects in a cluttered environment (for a review, see [15]). Theoretical studies suggest that, because of their long duration and high duty cycles, CF elements deliver flow field information, which might indicate the position of the targets that the bat has traversed [23,24].

Mixed signals (Fig. 1c,d) comprise combinations of the signal elements described above and enable the bat to take advantage of the information carried by different elements within one signal.

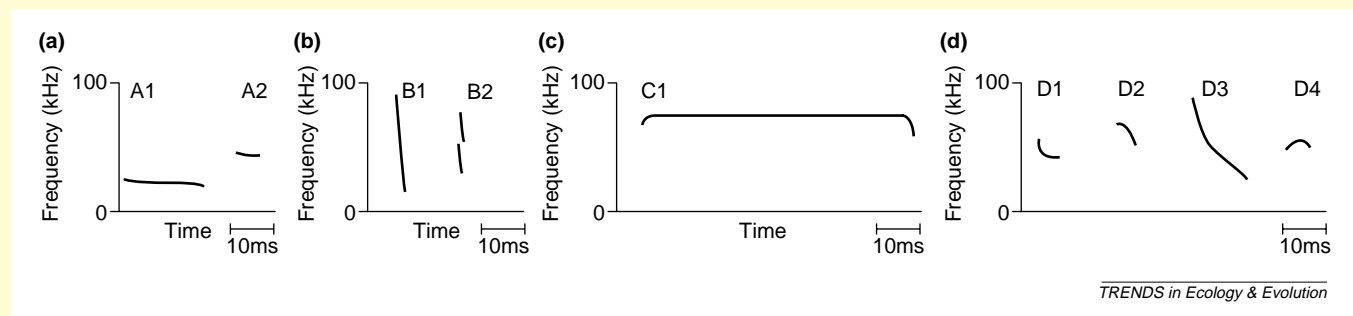


Fig. 1. Signals of a European free-tailed bat, *Tadarida teniotis* (A1), pipistrelle bat, *Pipistrellus pipistrellus* (A2 and D1), greater mouse-eared bat, *Myotis myotis* (B1 and D3), fringe-lipped bat, *Trachops cirrhosus* (B2), greater horseshoe bat, *Rhinolophus ferrumequinum* (C1), MacLeay's moustached bat, *Pteronotus macleayi* (D2), and greater white-lined bat, *Saccopteryx bilineata* (D4). A1–2 were recorded in open space, D1–4 in edge space, and B1–2 and C1 in narrow space. Adapted, with permission, from [13].

perform similar echolocation tasks. Therefore, it is not surprising that the echolocation behavior within each group is rather similar, independent of the phylogenetic relationships of its members (Box 4). Comparative studies support the close linkage between echolocation and ecological conditions [43–54].

Bats switching between habitats adjust their echolocation behavior to habitat-specific tasks. For example, many 'edge space aerial foragers' switch between broadband signals emitted in edge space to more narrowband shallow sweeps emitted in open space. This switch in echolocation behavior provides an index of the border between edge and open space. The width of edge space varies across species. In pipistrelles, edge space ends at ~5 m away from vegetation and/or the ground [13] and, in *E. serotinus*, it ends at ~8 m away [48].

When approaching a specific target (e.g. prey detected by echolocation, or site with prey revealed by other cues), bats switch from search or orienting signals (Box 4, Fig. 1a–f) to groups of several shorter approach signals

emitted in the rhythm of wing beat [55,56]. The number of pulses within a group increases when the bat closes in on a target, and sound duration is reduced. In bats feeding in the aerial mode on moving prey or in the trawling mode on prey drifting on the water surface, the approach sequences end with one (or sometimes more) distinct terminal pulses or buzzes with many short signals and minimal pulse intervals around 5 ms (Box 4, Fig. 1a,b,c). These signals are used by the bat to track the moving prey. Boonman and Jones [57] demonstrated a stereotyped reduction in signal intensity that is not under auditory feedback control in Daubenton's bats *Myotis daubentonii* approaching prey. In bats approaching stationary targets, such as sites with food, the approach sequence does not end with a distinct terminal group or buzz (Box 4, Fig. 1d). Instead, the bats produce a group of not more than 6–8 short, very weak signals emitted at short intervals before contact [13]. In gleaners approaching a food item under the guidance of echolocation (e.g. flowers or fruits [58–60]), the approach behavior is similar (Box 4, Fig. 1e). Very little is known

#### Box 4. Forager groups and their signals

Within each forager group, bats have to perform rather similar echolocation tasks. Under the selective pressure of these tasks, the members of each group have evolved many similarities in signal design and echolocation behavior [12,13].

- Open space aerial foragers searching for insects face the problem that their prey is distributed over a wide area and therefore can be difficult to find. These bats have optimized their echolocation system for the long-range detection of weak echoes from insect prey. They emit narrowband shallow frequency -modulated (FM) signals of rather long duration (8–25 ms), and often make two, three, or even more wing beats without signal emission, resulting in very long pulse intervals. In species predominantly foraging in open space, the terminal frequency of the dominant harmonic is generally <30 kHz. The approach sequence ends with a distinct buzz (Fig. 1a). Because of the limited operating range of echolocation, open space foragers use it predominantly for prey acquisition rather than for spatial orientation.
- Edge space aerial/trawling foragers searching for insects near background targets in the aerial mode (Fig. 1b) or over flat water surfaces in the trawling mode (Fig. 1c) have to find their prey near background targets. Background targets must also be characterized for spatial orientation. Edge space foragers often emit mixed search signals of intermediate duration (3–10 ms). A narrowband component of medium frequency (30–60 kHz) is well suited for detection of insects. A steep FM sweep that precedes or follows the narrowband component is better suited to localize and characterize the background targets. The mixed signals suggest that these bats perform two tasks whilst foraging. They search for insects near clutter and determine their position in space in relation to background targets. In search flight, they generally emit a single signal per wing beat. The approach sequence ends with a distinct buzz comprising many signals emitted at a high repetition rate.

Narrow space foragers either glean their food from substrate or capture prey close to it. However, clutter echoes can mask the prey echo. To overcome this, two behavioral strategies have evolved.

- (1) Narrow space gleaning foragers use prey-generated cues to detect and classify prey and to localize its position. Bats that eat insects and small vertebrates rely on acoustic cues generated by the prey, whereas frugivorous and nectarivorous bats often use olfactory cues in foraging. Whilst flying in narrow space near vegetation or the ground, these gleaners emit sounds in rhythm with their wing beat, either single or in groups with two to three uni- or multiharmonic broadband FM signals of short duration and low sound pressure level (Fig. 1d,e). These signals are used mainly for spatial orientation and should therefore be called orientation rather than search signals. Only if a food target delivers a specific echo (e.g. flowers that act as acoustic reflectors or fruits positioned in wide gaps) can echolocation also be used for recognition of food [58,59]. When approaching a target gleaners increase repetition rate but do not emit a distinct terminal group or buzz.
- (2) Narrow space flutter detecting foragers emit signals comprising a long, constant frequency component followed by a frequency-modulated terminal sweep (CF-FM) (Fig. 1f). With Doppler shift compensation and a specialized hearing system, these bats can recognize echoes from fluttering prey insects modulated in the rhythm of the beating wings between unmodulated background echoes. The flutter information even enables bats using CF-FM signals to categorize prey according to their wing beat pattern (for a review, see [15]). The long CF components of their signals might also help them to commute in narrow flyways along landscape contours. In search flight, they usually emit a single pulse per wing beat and the approach sequence ends with a distinct terminal group.

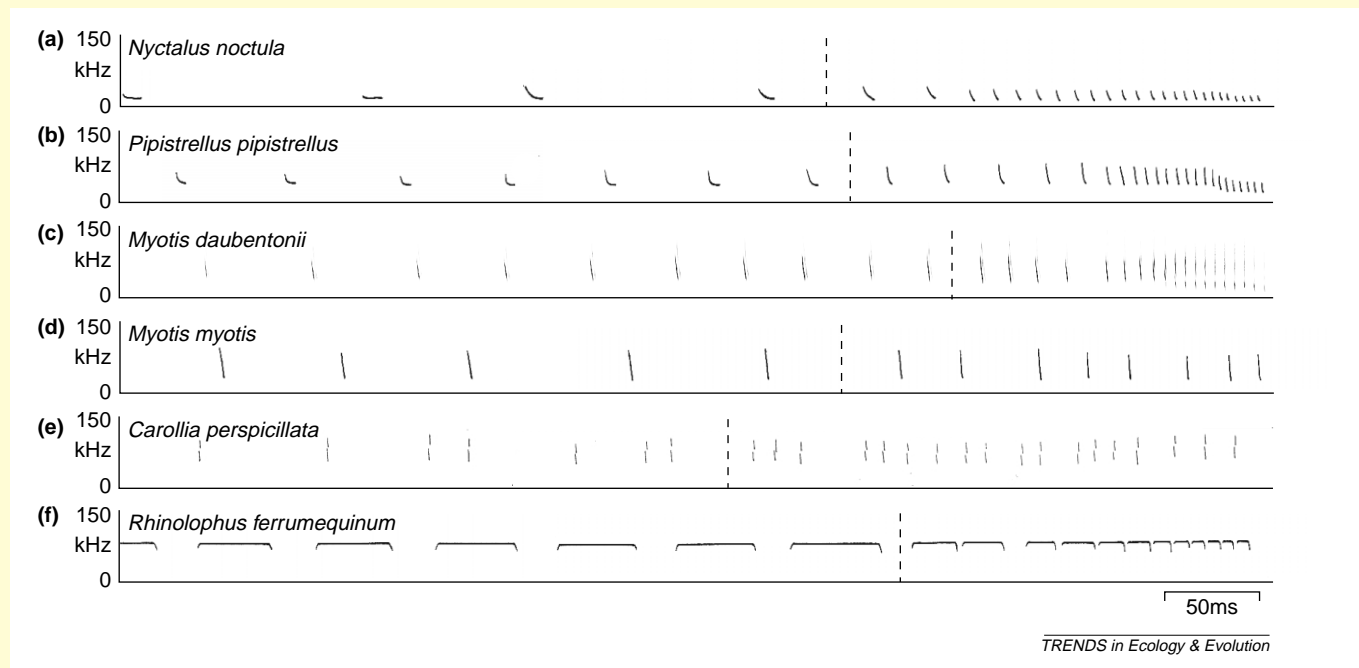


Fig. 1. Search and approach signals of foraging bats from different forager groups. The dashed lines indicate the change from search or orienting signals to approach signals. Adapted, with permission, from [13].

about the echolocation behavior in aerial insectivores when approaching a stationary target. The approach sequence of a northern bat *Eptesicus nilssonii* during landing is similar to that of gleaning bats [61]. By contrast, *R. ferrumequinum* emits a buzz when landing, similar to

the terminal group produced by this species when catching insects [62] (Box 4, Fig. 1f).

Some studies propose that gleaning bats stop echolocation clearly before they contact the prey [63]. However, we suggest that these bats emit very weak sonar

signals, which were not recorded with the available equipment.

When tracking an insect in edge space, bats face a daunting perceptual task, given the acoustic environment in which they must operate. To successfully intercept insect prey and to avoid collisions with background targets, the bat's sonar system must recognize the prey echo in a cascade of returning echoes from multiple background targets (branches, walls, etc.). The bat must therefore perceptually organize the acoustic information collected from multiple sources, arriving from different directions and at different arrival times. Moss and Surlykke [14] suggest for the big brown bat *Eptesicus fuscus*, that its perceptual system organizes acoustic information from a complex and dynamic environment into echo streams, enabling it to track spatially distributed auditory objects (sonar targets) by stream segregation. The bat's vocal production patterns during an approach to an insect are consistent with the notion that it uses information over successive echoes to build a representation of the world that ultimately guides its behavior [14]. The separation between prey and background could be additionally improved by the directional aim and focus of the bat's sonar beam, which might be likened to interest and holds its focus in the presence of distracters [64]. This directional focus of the sonar beam appears important to successful capture of targets in the presence of obstacles.

### Conclusions and future directions

When orienting in space and/or searching for prey, bats perform habitat-specific tasks, which exert a strong selective pressure on the evolution of echolocation behavior. In the context of spatial orientation and foraging behaviors, three types of habitat can be defined; narrow, edge and open space. Spatial orientation tasks differentiate between three types of situations: small-, middle-, and large-scale navigation. Common ecological constraints on prey acquisition in foraging bats yield four functional groups or guilds. In the absence of background targets, open space aerial foragers use echolocation predominately for prey acquisition. Edge space aerial/trawling foragers and narrow space flutter-detecting foragers use echolocation concurrently for prey acquisition and for spatial orientation. Narrow space gleaning foragers use echolocation, with a few exceptions, only for spatial orientation. As echolocation is adapted to context-specific tasks, signal design and echolocation behavior within each group are rather similar.

For a complete understanding of the adaptive value of signal design, more research on the role of echolocation for spatial orientation is required. Research of middle-scale navigation is particularly important for us to understand how bats recognize landmarks, and plan and follow routes within their home ranges. Furthermore, future research should focus on how bats solve multiple tasks concurrently, such as orientation in space and search for prey in and around vegetation.

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