

Echolocation by Insect-Eating Bats

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Bats (order Chiroptera) are ecologically more diverse than any other group of mammals. Numerous morphological, physiological, and behavioral adaptations of sensory and motor systems permit bats access to a wide range of habitats and resources at night. The more than 750 species of the suborder Microchiroptera occupy most terrestrial habitats and climatic zones and exploit a great variety of foods, ranging from insects and other arthropods, small vertebrates, and blood to fruit, leaves, nectar, flowers, and pollen. Echolocation is one of the adaptations that make bats so successful.

Echolocating animals emit signals of high frequency (mostly ultrasonic) and analyze the returning echoes to detect, characterize, and localize the reflected objects. Sophisticated echolocation systems have evolved only in the bat suborder Microchiroptera and in dolphins. Less efficient systems have been reported for a few species of the bat suborder Megachiroptera and for some birds (Henson and Schnitzler 1980). Bats use echolocation for orientation in space, that is, for determining their position relative to the echo-producing environment. In addition, many bats, especially those that hunt for flying insects, use echolocation to detect, identify, and localize prey.

Bats use a wide variety of species-specific signal types differing in frequency structure, duration, and sound pressure level (SPL). In addition, signal structure varies depending on the echolocation task confronting the bat. Search signals that are emitted when bats search for prey differ from approach signals that are emitted when they approach prey.

The echolocation signals and hearing systems of bats are well adapted for gathering behaviorally relevant information (e.g., Schnitzler and Henson 1980, Neuweiler 1989, Fenton 1990, Denzinger et al. forthcoming). In this article we describe the echolocation behavior of insect-eating bats and show how differing circumstances such as habitat type, foraging mode, and diet favor different signal types. To demonstrate relationships between echolocation and ecological conditions, we outline the perceptual tasks that must be performed by foraging bats and discuss the suitability of typical elements of echolocation signals for solving such problems. We then define habitat types according to the problems they impose on bats and relate the observed variability in signal structure to ecological constraints set by habitat type and foraging mode.

WE DEFINE FOUR DISTINCT FUNCTIONAL GROUPS OF BATS AND FIND DIFFERENCES IN SIGNAL STRUCTURE THAT CORRELATE WITH THE TYPICAL ECHOLOCATION TASKS FACED BY EACH GROUP

Perceptual problems for foraging bats

Foraging bats confront a multitude of problems when flying to their hunting grounds and searching for prey. These problems differ depending on where bats hunt, what they eat, and how they acquire their food. For example, bats hunting for insects in the open encounter conditions different from those that search for prey near the edges of vegetation, in vegetation gaps, in dense forest, or near the ground. The problems also differ depending upon whether they capture moving prey in flight (aerial mode) or mostly stationary prey from surfaces such as leaves or ground (gleaning mode) or water (trawling mode).

Foraging bats must detect, classify, and localize an insect and discriminate between echoes of prey and echoes of unwanted targets such as twigs, foliage, or the ground, referred to as *clutter echoes*, or simply “clutter.” For many bats echolocation delivers all of the information they need to catch an insect.

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However, some bats rely partly or entirely on other sensory systems, such as passive hearing, to detect prey-generated signals (e.g., calls and rustling sounds of insects) to find their prey. Independent of specific foraging conditions, all bats must perform the following basic perceptual tasks:

- **Detection.** A bat must decide whether or not it has received an echo of its own echolocation signal or has heard, seen, smelled, or felt something that indicates prey or other targets of interest. However, it is difficult to conceptualize detection independent of classification and localization.
- **Classification.** Bats categorize targets by means of specific echo information (Ostwald et al. 1988) or other features that reveal their nature. Target properties such as size, shape, material, and texture are encoded in the complex temporal and spectral parameters of an echo. Rhythmical amplitude and frequency modulations in the echo reveal movements of prey such as the beating wings characteristic of a fluttering insect (Schnitzler 1987).
- **Localization.** Echolocation reveals the position of a target by its range and by its horizontal and vertical spatial angles. The time delay between emitted signal and returning echo encodes range. Binaural echo cues describe the horizontal angle, and monaural spectral cues the vertical angle. For moving bats, the flow field of reflected sound delivers additional information that may be used for target localization (Lee et al. 1992, Müller and Schnitzler 1999, 2000). Bats using other sensory cues must localize the actual position of the source of a prey-generated sensory signal.

Interfering factors, such as internal and external noise, clutter echoes, and signals from other bats, set limits on the echolocation processes involved in detecting, classifying, and localizing a preferred target. Masking effects between target echo and clutter, and between target echo and emitted signal, notably restrict the processing of relevant information.

The restricted range of echolocation sets spatial limits on where bats can find their prey. The sound pressure level, or SPL, of echoes decreases sharply with increasing target distance because of geometric and atmospheric attenuation of sound traveling in air. Additionally, the echo SPL is reduced because of the target strength, which depends on the size and the form of a target. Bats receive detectable echoes from flying insects only over rather short distances. In an environment with a temperature of 20°C, a relative humidity of 50%, and a realistic detection threshold of about

15 dB, a bat with a signal SPL of 112 dB 40 cm in front of its head, with a signal frequency of 20 kHz, can detect a fluttering insect with a wing length of 2.5 cm at a detection range of not more than 10.5 m. Under similar conditions, a sphere with a diameter of 2.5 cm cannot be detected beyond 7 m. The maximum detection distance decreases still more with increasing signal frequency, humidity, temperature, and decreasing prey size (Kober and Schnitzler 1990). Thus, echolocation is a system that works only over short distances. For long-distance orientation, bats must use other sensory systems, such as vision.

Signals adapted for specific tasks

Ecological constraints exert strong selection pressure on signal structure, leading to species-specific signals that are adapted for specific tasks. To better understand these

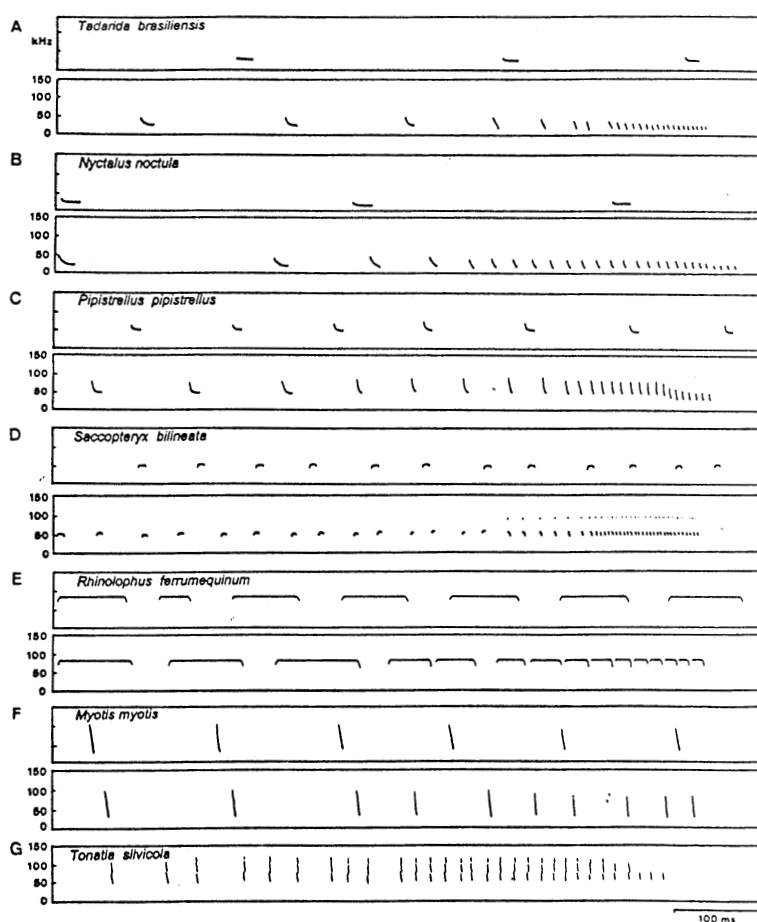


Figure 1. Search and approach signals of foraging bats. (a–e) Signals of bats that captured a flying insect at the end of the sequence. (f, g) Signals of bats that gleaned insects from a surface at the end of the sequence, (f) out of continuous search flight and (g) after the prey has been detected from a perch. In all sequences the increase in repetition rate and the reduction of sound duration indicate the switching from search to approach phase. Note the distinct terminal phase in bats that captured flying insects (a–e).

adaptations, we first discuss the kinds of information that can be carried by individual elements in the echolocation signals of bats.

Most echolocation signals of microchiropterans consist of narrowband or broadband components, or combinations of these (Figure 1). Narrowband components comprise two subtypes: quasi-constant frequency (QCF) elements with frequency changes of a few kHz between the onset and the end of the component (shallow modulation), and long constant frequency (CF) elements with frequency changes of a few hundred Hz within the component. Broadband components normally consist of a downward frequency-modulated (FM) element of large bandwidth (steep modulation). These signal elements differ in absolute frequency, bandwidth, harmonic structure, duration, and SPL, creating the wide variety of signal types found in echolocating bats (reviewed in Pye 1980, Schnitzler and Henson 1980, Simmons and Stein 1980, Neuweiler 1989, Fenton 1990). For the classification of signal components according to their bandwidth, it is necessary to define why a signal is classified as narrowband or broadband. We propose that in narrowband signals the most prominent harmonic sweeps over less than half an octave (starting frequency of the sweep is less than 141% of the terminal frequency), whereas in broadband signals it covers more than half an octave.

The information that can be extracted from the echoes of various elements of a signal depends on their physical structure and on the performance of the bat's auditory system. As a rough approximation, the input stage of the auditory system of most bats (with the exception of bats with long CF signals) can be described as a bank of neuronal filters with similar *Q values* (the best frequency, or the frequency at which neural responses have the lowest threshold, divided by bandwidth). Depending on its absolute frequency, bandwidth, and SPL, a signal element evokes neuronal activity in one or more of the frequency-selective filters. The longer a signal stays within the response range of a filter, the higher the neuronal activity.

Narrowband signals. Signal elements such as CF or shallow-modulated QCF components are well suited for detection of echoes because they activate the neuronal filters tuned to the corresponding frequency band during the entire echo. Narrowband signals, especially those of long duration, also can be used for target classification if bats evaluate the amplitude and frequency modulations in the echoes arising from characteristic target movements. When a signal hits a fluttering insect at the favorable instant when the insect's wings are perpendicular to the impinging sound wave, a short and very prominent amplitude peak in the echo, an acoustic *glint*, reveals the fluttering insect target. This glint, which can be up to 20–30 dB stronger than an echo from the body of the insect, also increases the probability of detection (Kober and Schnitzler 1990, Moss and Zagnesi 1994). The probability of receiving such a glint depends on the *duty cycle* (the percentage of time in which signals are emitted) of the bat and the wing-

beat rate of the insect. For example, a duty cycle of 10% and an insect wingbeat rate of 60 Hz produce an average perceived glint rate of 6 glints/s.

Narrowband signals are less suited for precisely localizing a target when bats must accurately measure range as well as horizontal and vertical angles. Range is encoded in the time delay between an emitted signal and its returning echo. For accurate range determination, bats must determine the exact instant of sound emission and echo reception. Narrowband signals are rather imprecise time markers because they persist within the corresponding neuronal filter for an extended time, thus diminishing range accuracy. The horizontal angle is encoded in binaural echo cues, and the vertical angle in monaural echo cues. Narrowband signals, with their small frequency range, activate only a few channels that deliver such cues, thus reducing a precise angle determination.

Broadband signals. Signals such as steep-modulated FM signals are less suited for the detection of weak echoes. These signals sweep rapidly through the tuning areas of the corresponding neuronal filters so that each detector is activated only for a very short time. Frequency-modulated signals of broad bandwidth are well suited for exact target localization where range and angle must be measured accurately. Steep-modulated broadband FM signals activate each filter for only a very short instant, producing the precise time markers needed for an exact determination of the time delay that encodes the range. Large signal bandwidths activate more neuronal filters, improving the accuracy of range determination if, as is indicated by behavioral experiments, the range information is averaged over all activated channels (Moss and Schnitzler 1995). The activation of many channels also improves the accuracy of angle determination with increasing bandwidth.

Frequency-modulated signals of large bandwidth also deliver spectral cues that can be used for target classification. Target features such as texture (which affects the absorption of sound at different frequencies) and depth structure (which causes an interference pattern due to overlapping multi-wave-front echoes) are somehow reflected in the echo spectrum, thus encoding information about the character of a target (Ostwald et al. 1988). In the laboratory, bats learn to use such spectral differences to discriminate among targets, so it is assumed that broadband FM signals allow spectral characterization of prey (Neuweiler 1989, 1990). However, this is true only if the spectral signature of echoes is so specific that, independent of aspect angle, it is possible for the echo from an insect to be distinguished from clutter echoes.

Long CF signals with Doppler-shift compensation. Long CF signals, like other narrowband signals, are well suited for the detection of weak echoes and less well suited for the exact localization of targets. In combination with Doppler-shift compensation (see below) and a specialized hearing system, the long CF signals facilitate the detection and classification of fluttering insects in a cluttered environment. The beating wings of insects produce a rhythmical pattern of

amplitude and frequency modulations that encode wingbeat rate, wing size, and other species-specific information. The most prominent flutter features are the very short and strong amplitude peaks of acoustic glints, produced when the wings are perpendicular to the impinging sound waves (Kober and Schnitzler 1990). Transmitters and receivers of the echolocation systems of bats emitting CF signals are especially adapted to process this kind of information (Schnitzler and Ostwald 1983, Neuweiler 1990). By lowering emission frequency, these bats compensate for Doppler shifts caused by their own flight movement. Thus, the frequency of the CF component of insect echoes is kept within an “expectation window.” A corresponding “analysis window” is established in the hearing system by a specialized cochlea with a highly expanded frequency representation in the range of the insect echoes. This acoustic fovea leads to an over-representation of sharply tuned neurons with special response characteristics throughout the auditory pathway. With these specific adaptations, bats using CF signals can discriminate the modulated insect echo from overlapping unmodulated clutter echoes and classify insects according to their prey-specific modulation pattern (vd Emde and Schnitzler 1990).

Detection versus localization trade-off. Narrowband signals are good for target detection but less well suited for target localization. Broadband FM signals, however, are good for localization but less well suited for detection. This trade-off between detectability and accuracy of localization is reflected in the structure of search signals in some bats. Bats that have to perform several tasks simultaneously combine suitable signal elements. Typical combinations of broadband and narrowband components are found in FM–QCF, QCF–FM, and CF–FM signals, and also in FM signals with changing steepness. For instance, bats of the genus *Myotis* (Vespertilionidae) flying in the open often produce signals in which the steep initial part of the signal is followed by a shallower part that ends in a steeper segment. The steeper FM components are well suited for localization, and the shallow component improves detection by introducing more signal energy into the corresponding neuronal filters.

The masking problem

The separation of target echo from interfering signals is an important task facing echolocating bats. The evaluation of sonar echoes from a target is hampered when the neuronal activity evoked by clutter echoes and by the bat's own emitted signal interferes with the activity evoked by the target echo. Interfering signals that precede the target echo, such as the emitted signal, produce a *forward-masking effect*. Interfering signals that follow the target echo, such as clutter echoes, produce a *backward-masking effect*. Depending on the signal type, several strategies are used to avoid masking.

Field and laboratory studies indicate that bats (with the exception of those using long CF–FM signals) normally avoid an overlap of the target echo with clutter echoes and also with their own emitted signal (Kalko and Schnitzler 1989, 1993). This avoidance of overlap suggests that all signal types except for CF elements are sensitive to overlap. Due to overlap interference, the ability of bats to evaluate insect echoes depends on the position of an insect relative to the bat and to clutter echo producing background targets. When an insect flies so close to a bat that the returning echo overlaps the emitted signal, forward-masking effects interfere with the evaluation of the insect echo. Therefore forward masking reduces the probability of detection in the zone in front of the bat where overlap occurs. The width of this signal-overlap zone depends on signal duration (Figure 2). For example, with a signal duration of 10 ms the overlap zone is 1.70 m wide at a speed of sound of 340 m/s. If undisturbed detection is only possible beyond this signal-overlap zone, signal duration sets a minimum detection distance. Each ms of signal duration adds 17 cm to this minimum detection distance.

When an insect flies so close to clutter that its echoes overlap the clutter echoes, backward masking reduces the probability of detection in this clutter-overlap zone. The width of this clutter-overlap zone is determined also by signal duration. Only insects flying far away from the bat and from the clut-

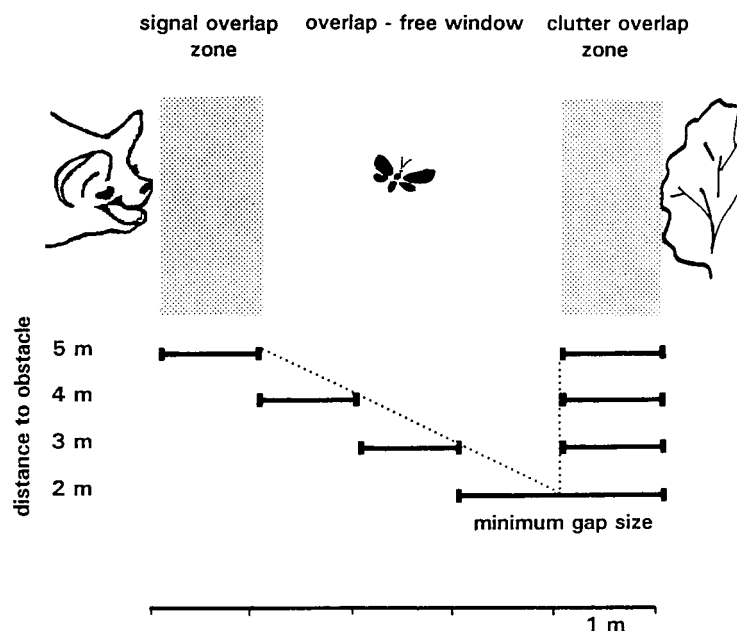


Figure 2. Schematic diagram of the masking situation for a bat foraging near vegetation and emitting signals with a duration of 6 ms. The prey echo overlaps the emitted signal when the insect flies in the signal-overlap zone, and it overlaps the clutter echoes when it flies in the clutter-overlap zone. No overlap occurs when the insect flies in the overlap-free window. At a distance of 2 m the overlap-free window is closed, and for the given signal duration the bat has reached the minimum gap size where overlap-free echolocation is impossible.

ter-producing background where no overlap occurs can be detected without interference. By our definition, these insects fly in an overlap-free window (Figure 2). The forward- and backward-masking effects strongly depend on signal structure, on the SPL of prey echo and masking signals, and on their temporal relationship. Therefore the definition of an overlap zone as an area where masking effects interfere with the evaluation of the echo is only a rough approximation of the effective masking zones. Depending on the signal type used by a bat, the masking zone may be smaller than the overlap zone calculated from sound duration. For example, a study on *Myotis nattereri*, a bat that searches for prey using wide-band FM signals very close to vegetation, indicates that these bats tolerate some overlap between prey and clutter echoes (Siemers and Schnitzler 2000). Nevertheless, the calculation of the overlap zone is a useful tool to judge the danger of masking.

In bats with long CF signals, the CF component of the emitted signal and that of the returning echo often overlap (Figure 3d). This overlap produces no masking effect, because Doppler-shift compensation keeps the target echo in the range of the extremely sharply tuned neurons of the acoustic fovea, whereas the emitted signal is lower in frequency and falls in a range where the auditory threshold is high (Schnitzler and Ostwald 1983, Neuweiler 1990). Therefore, long CF components of Doppler-compensating bats are not vulnerable to overlap.

Foraging habitats defined by clutter conditions

Comparative studies reveal that for foraging bats, clutter conditions are the most important ecological constraints. They can be used to define various foraging habitats (Schnitzler and Kalko 1998, Denzinger et al. forthcoming). Clutter conditions are described by the proximity of the desired prey item to clutter such as vegetation or ground. Such clutter represents perceptual as well as mechanical problems for bats (Fenton 1990). Perceptually, bats are constrained by their sensory capacities (e.g., echolocation, vision, olfaction, passive listening) to detect, classify, and locate prey in the vicinity of clutter-producing background targets. Mechanically, bats are constrained by their motor capacities, such as flight abilities (Norberg and Rayner 1987). For instance, bats that forage near clutter need special maneuverability (e.g., adaptations in wing morphology) to intercept insects while also avoiding collisions. Here we discuss only the perceptual problem, and we define three habitat types according to clutter conditions (Figures 3 and 4).

Uncluttered space. For bats that forage for insects in uncluttered space—in open spaces, high above the ground and far from vegetation—clutter echoes from the background are so far from the emitted signal and target echoes that they play no role in the echolocation process (Figures 3a and 4). In these bats a returning echo generally indicates a flying insect.

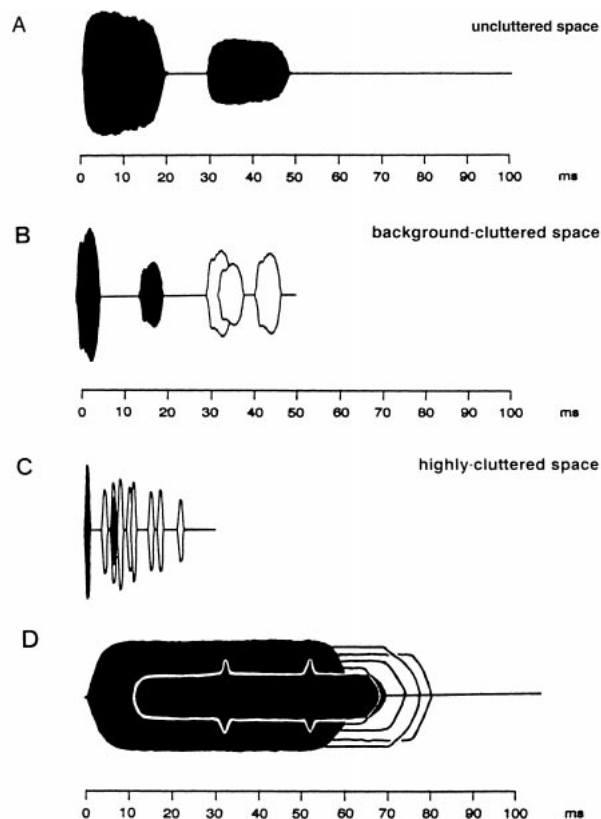


Figure 3. Schematic diagram of the input into the auditory system of bats that forage in different clutter situations. The emitted pulse and the returning insect echo are depicted in black. (a) In uncluttered space, the pulse-echo-pair is far from clutter echoes. (b) In background-cluttered space, the pulse-echo pair is followed by clutter echoes (depicted in white). (c, d) In highly cluttered space, the target echo is buried in overlapping clutter echoes. Sound duration and envelope form correspond to search signals typical for the different spaces: (a) QCF signal of an open-space forager; (b) broadband FM-QCF signal of an edge and gap forager; (c) broadband FM signal of a narrow-space “FM” forager; (d) long CF-FM signal of a narrow-space “CF” forager; the echo shows amplitude modulations, or glints, created by the beating wings of an insect.

Background-cluttered space. For bats that forage for insects in background-cluttered space—near the edges of vegetation, in vegetation gaps, or near ground or water surfaces—the pulse-insect echo pair is followed by clutter echoes from the background (Figures 3b and 4). These bats must solve two problems. First, they must recognize the insect echo and separate it from the echoes of background clutter. Second, they must characterize the clutter-producing background targets to identify landmarks for navigation and to avoid collision.

The border between background-cluttered and uncluttered space is indicated in many species of bats by their echolocation behavior (Kalko and Schnitzler 1993, Schnitzler and Kalko 1998, Jensen and Miller 1999). In uncluttered

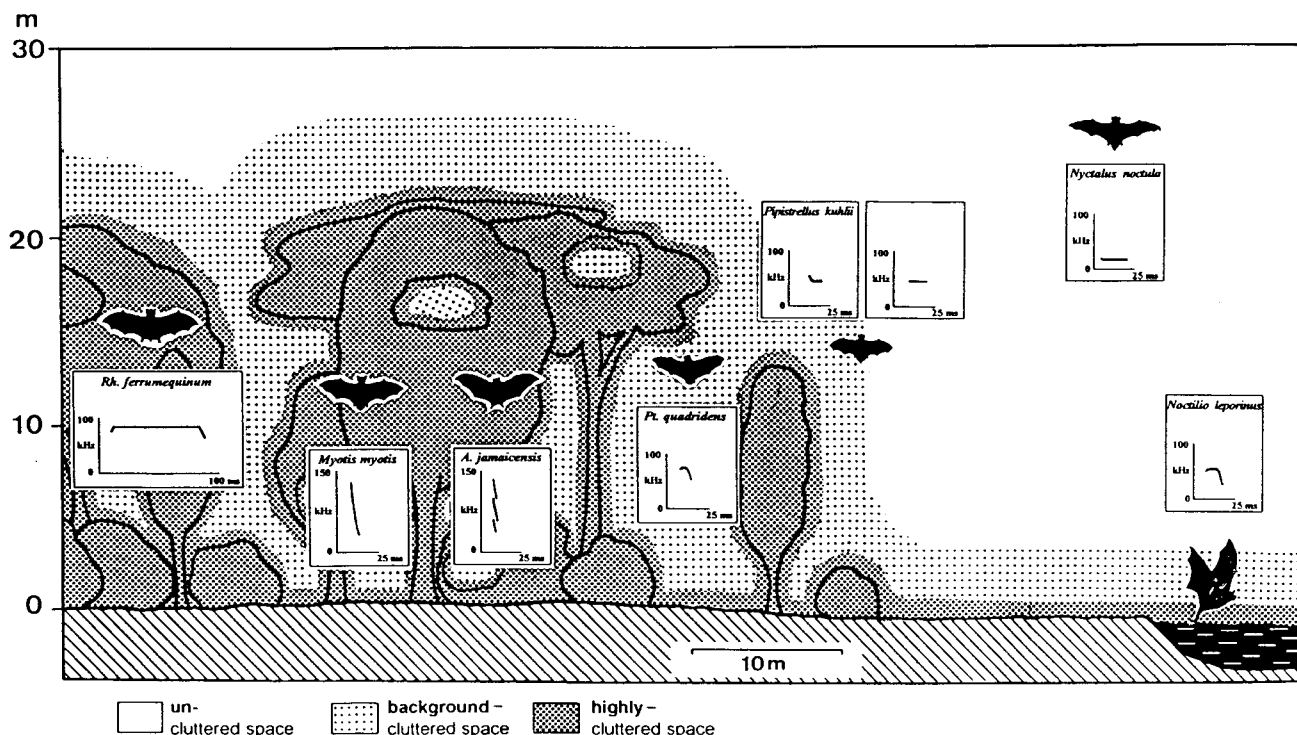


Figure 4. Schematic diagram of the foraging habitats of bats according to the clutter situation, with flight silhouettes and search signals of representative species. In uncluttered space, bats forage for prey far away from vegetation and the ground. In background-cluttered space, bats hunt for insects flying near obstacles (e.g., at edges of vegetation, near the ground or water surfaces, and in gaps between and in vegetation). In highly cluttered space, bats forage for prey flying close to or sitting on vegetation or the ground. The bats depicted are not sympatric. The border between uncluttered and background-cluttered space is defined by the echolocation behavior of bats. When entering the uncluttered space from background-cluttered space, foragers switch from broadband signals to narrowband signals, and vice versa (e.g., *Pipistrellus kuhlii*). In this diagram this border is about 5 m away from vegetation and the ground as described for pipistrelles. The border between background and highly cluttered space is determined by the beginning of the clutter-overlap zone in which insect echoes overlap clutter echoes.

space bats often use relatively long search signals of narrow bandwidth and mostly emit a search signal only every second or third wingbeat. In background-cluttered space most bats emit one search signal of larger bandwidth at every wingbeat, thus indicating that echoes from the clutter-producing background also guide bats' behavior. When crossing the border between the two spaces, bats change their echolocation behavior (see signals of *Pipistrellus* in Figures 4 and 5). The best indicator for the switch between the two spaces is the change in the rhythm of sound emission.

Highly cluttered space. For bats that forage for flying insects in highly cluttered space—very close to surfaces such as leaves or ground—and for bats gleaning stationary food (sitting insects, other animals, fruit, leaves, nectar, blood) from surfaces, two situations occur. For gleaning bats that use short broadband FM signals, echoes from food items are buried in clutter (Figure 3c) so that masking hampers their evaluation. For bats using long CF signals to detect flying insects, the overlapping pulse-echo pair also overlaps clutter echoes (Figure 3d). Bats foraging in highly cluttered space have

the problem of discriminating between echoes from the food item and overlapping clutter echoes. Moreover, they have to navigate along landmarks and to avoid collisions. The relation between insect echoes and masking clutter echoes defines the border between highly cluttered and background-cluttered space. A bat forages in highly cluttered space when the prey is situated in the clutter-overlap zone, where clutter echoes overlap prey echoes. In the few species that tolerate some overlap between prey and clutter, highly cluttered space corresponds more precisely to the zone where the prey echo is masked by the clutter echoes. Furthermore, bats flying parallel to clutter may be able to reduce the masking effect of clutter echoes by spatial clutter rejection. However, to facilitate comparison between species, we propose to define the highly cluttered space as the area where insect echo and clutter echoes overlap as a first approximation to describe the masking problem.

Guild structure of bats

Comparative studies have revealed that bats foraging in similar habitats with similar foraging modes for similar diets

encounter similar ecological constraints and share similar adaptations of sensory and motor systems. In this context, arranging assemblages of species into guilds, that is, groups of species that live under similar ecological conditions (Root 1967), has proven a useful approach toward understanding adaptations of sensory and motor systems. Habitat type, foraging mode, and diet characterize our proposed guilds for bats (Kalko et al. 1996, Schnitzler and Kalko 1998).

To categorize habitats we use the three clutter spaces as defined above. For foraging modes we distinguish bats that capture insects in the air (aerial mode) from those that glean insects and other food from solid surfaces (gleaning mode) or from water (trawling mode). According to their preferred diet we categorize bats as insectivores, carnivores, piscivores, sanguivores, frugivores, nectarivores, or omnivores. These guilds characterize ecological constraints as sets of tasks imposed on sensory as well as on motor systems. The categorization presented here differs somewhat from that in former publications (Schnitzler and Kalko 1998). In light of new data (Boonman et al. 1998, Rydell et al. 1999), we propose an additional foraging mode (trawling) and introduce a new guild “background-cluttered space trawling insectivore/piscivore,” which replaces the former guild “highly cluttered space gleaning piscivore” (Table 1).

Search signals of insect-eating bats

In describing the echolocation behavior of insect-eating bats, we will show that bats belonging to the same guild share many similarities in echolocation behavior, especially in the structure of search signals, which are intimately linked to habitat type and foraging mode. Search signals are emitted when bats are searching for prey, or when they commute from one place to another and do not approach a specific target.

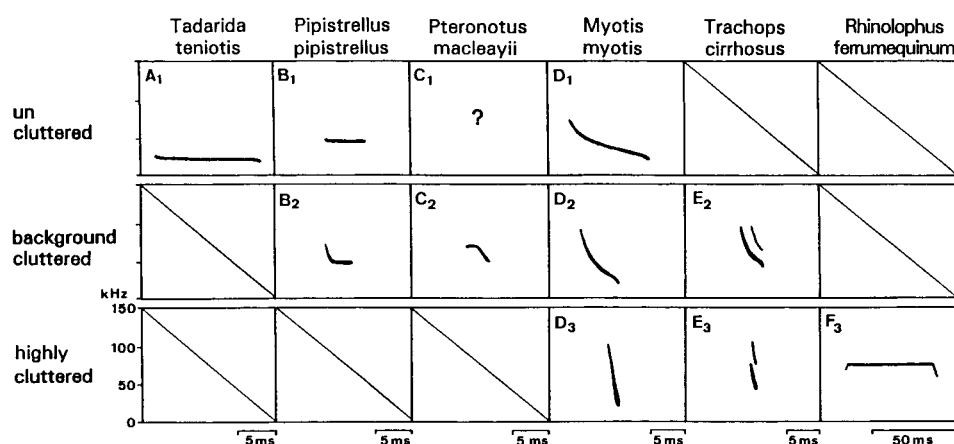


Figure 5. Examples of various search signals and their associated habitat types. Note that bats may leave their preferred space for a less-cluttered space but not the reverse. (a) *Tadarida teniotis*, (b) *Pipistrellus pipistrellus*, (c) *Pteronotus macleayii*, (d) *Myotis myotis*, (e) *Trachops cirrhosus*, (f) *Rhinolophus ferrumequinum*.

Table 1. Guild structure of microchiropteran bats, characterized by habitat type, foraging mode, and diet.

Habitat type	Foraging mode	Diet
Uncluttered space	Aerial	Insectivore
Background-cluttered space	Aerial	Insectivore
Background-cluttered space	Trawling	Insectivore/ piscivore
Highly cluttered space	Aerial	Insectivore
Highly cluttered space	Gleaning	Insectivore
Highly cluttered space	Gleaning	Carnivore
Highly cluttered space	Gleaning	Sanguivore
Highly cluttered space	Gleaning	Frugivore
Highly cluttered space	Gleaning	Nectarivore
Highly cluttered space	Gleaning	Omnivore

Aerial insectivores in uncluttered space. Bats hunting in open, uncluttered space, high above the ground or canopy and far from obstacles, are found mainly in four families: free-tailed bats (Molossidae, e.g., *Molossus*, *Promops*, *Tadarida*), mouse-tailed bats (Rhinopomatidae, *Rhinopoma*), sheath-tailed bats (Emballonuridae, e.g., *Diclidurus*, *Peropteryx*, *Taphozous*), and evening bats (Vespertilionidae, e.g., *Lasiurus*, *Nyctalus*; Figures 1a and 1b, 4, and 5a). When searching for insects, these bats have no masking problem as long as the emitted signal does not overlap the returning insect echo. However, they often have the problem of rather small prey being sparsely distributed in a large space. In that case, a bat must cover a large search area to find an insect. This and the rather low SPL of insect echoes make it difficult to detect potential prey. Thus, echolocation signals should be optimized for detection.

Typically, bats flying in the open emit overlap-sensitive, narrowband search signals of rather long duration (approximately 8–25 ms) with a low frequency (< 30 kHz). The shallow-modulated signals (which can be upward or downward modulated) are emitted at a rather low repetition rate, and signal emission is correlated with the bat's wingbeat. Often these bats make two, three, or more wingbeats without pulse emission, resulting in long pulse intervals of up to 500–1000 ms.

Relatively long narrowband signals are adapted for long-range detection of insects in open space and may also deliver some information based on glints produced by the fluttering wings of an insect. An increase in signal duration improves the chances of detecting an insect, but there seems

to be a limit for such an increase. With increasing signal duration, the signal-overlap zone gets wider, and if undisturbed detection is only possible beyond this zone, the minimum detection distance gets larger (Figure 2). Moreover, signal duration and the corresponding minimum detection distance influence the minimum size of the prey that can be detected. At long signal durations, and therefore large minimum detection distances, only relatively large insects yield echoes strong enough to be detected (Barclay and Brigham 1991). Detection is also influenced by the frequency of a signal. Signals with low frequencies cover a wide search volume because of their low directionality and low atmospheric attenuation. Their long wavelength has the disadvantage of being less suited for the detection of small insects. Signals with higher frequencies cover a smaller search volume because of a higher directionality and higher atmospheric attenuation. Their shorter wavelength makes them better suited for the detection of small targets.

From the detection limits set by signal duration and signal frequency, we propose a size-filtering hypothesis for the narrowband search signals of open-space bats: The minimum size of detectable prey increases as signals become longer and lower in frequency. This suggests that bats with long signals of low frequency are adapted for detection of large insects at long distances, whereas bats with shorter signals and higher frequency can detect insects that are smaller and closer (Schnitzler and Kalko 1998). As the frequency of the narrowband search signals decreases with increasing sizes of bats, the size-filtering hypothesis predicts that prey size should increase with the size of bats. Several field studies confirm this trend (Barclay 1985, 1986, Jones 1994). It has been reported that the typical open-space forager *Nyctalus leisleri* sometimes also hunts for small insects (Waters et al. 1995). We predict that in this case the bats use search signals of shorter duration.

Relatively long pulse intervals are no problem for bats that forage in uncluttered space because their detection range is so large that, even with a large travel distance between consecutive signals, the detection ranges of these signals overlap, thus minimizing the possibility of overlooking an important target. The pulse intervals are far too large to create a situation in which an insect echo returns after the emission of the next consecutive signal. A pulse interval of only 150 ms (which is small in open space) would produce such a situation at a target distance of 25.5 m. This is too large for an echo produced from an insect to be audible to the bat.

Aerial or trawling insectivores in background-cluttered space. Bats hunting for insects in background-cluttered space such as forest edges and gaps mainly include evening bats (Vespertilionidae, e.g., *Eptesicus*, *Myotis*, *Pipistrellus*), leaf-chinned bats (Mormoopidae, e.g., *Mormoops*, *Pteronotus*, except *P. parnellii*), and sheath-tailed bats (Emballonuridae, e.g., *Saccopteryx*; Figures 1c and 1d, 4, 5b and 5c). These bats must perform two tasks simultaneously: They must find insects that fly near clutter-producing back-

ground targets, and they must simultaneously navigate along these targets and avoid collisions. This presents detection and classification problems with rather weak echoes from flying insects, as well as classification and localization problems with much louder clutter echoes from the extended background targets.

Bats of the guilds “background-cluttered space aerial or trawling insectivores” solve these problems by emitting mixed signals. Typically, search signals comprise shallow-modulated narrowband (QCF) and more or less steep-modulated broadband (FM) components. Some bats emit broadband FM signals with a distinct shallow-modulated part in it. Arrangement of components in call types is highly diverse among families and genera. In some bats, such as pipistrelles (Vespertilionidae), the FM component precedes the QCF component (FM–QCF signal); in some leaf-chinned bats (Mormoopidae) the FM follows the QCF component (QCF–FM signal); and in other species, such as the white-lined bat *Saccopteryx bilineata* (Emballonuridae), an upward-modulated QCF component is preceded and followed by two FM elements of moderate bandwidth (FM–QCF–FM signal). Generally, the search signals are overlap-sensitive broadband (bandwidth > half an octave) signals of intermediate duration (approximately 3–10 ms), with a medium frequency narrowband component (approximately 30–60 kHz). Signal emission is usually correlated in a 1:1 ratio with wingbeat. Pulse interval is shorter (approximately 70–150 ms) than that produced by aerial insectivores in uncluttered space.

The narrowband components of the mixed signals greatly facilitate detection of prey, and the broadband FM components are well suited for the localization and characterization of extended background targets necessary for recognizing landmarks and avoiding collisions. Because of the sensitivity to overlap, bats foraging near edges mainly search for and detect prey within the overlap-free window, where the prey echo is not masked by the emitted call (forward-masking effect) and where echoes from the background do not interfere with the prey echo (backward-masking effect). Field studies show that the shorter the signals, the closer to vegetation a bat can hunt (e.g., Kalko and Schnitzler 1993).

Some bats are highly flexible in their foraging and echolocation behavior and switch between uncluttered and background-cluttered space. In uncluttered space the echolocation behavior does not change depending on distance to background targets, whereas in background-cluttered space bats react to the background targets. The border between those spaces is defined by changes in the echolocation behavior of the bats. For instance, pipistrelles hunting for insects in open spaces emit rather long, shallow-modulated, narrowband signals (QCF), whereas those hunting within less than 5 m of clutter-producing background switch to shorter signals and add a steep-modulated, broadband component (FM–QCF). Some preliminary field data from the big brown bat (*Eptesicus fuscus*) and the noctule bat (*Nyctalus noctula*) suggest that the transition distance between spaces is species specific.

A special group within background-cluttered space insectivores consists of bats that catch insects in the trawling mode from calm and uncluttered water surfaces (e.g., *Myotis daubentonii*). They do not receive clutter echoes from the water (but from background targets such as the shore) because a calm surface is like a mirror that reflects the emitted signals away from the bat (Rydell et al. 1999). Therefore these trawling bats can be categorized as “background-cluttered space trawling insectivores” (Table 1). When foraging for insects sitting on or flying close to duckweed or rippled water, bats have difficulty perceiving prey as the prey echo is buried in clutter echoes (Boonman et al. 1998). The two species of bulldog bats (Noctilionidae), one of which, *Noctilio leporinus*, is well known for its fishing habits (Schnitzler et al. 1994, Kalko and Schnitzler 1998), also forage for insects close to or drifting on the water surface while emitting high-intensity CF and CF–FM signals of medium duration that are rather similar to the QCF–FM signals of mormoopid bats.

Aerial insectivores in highly cluttered space. Bats searching for and catching fluttering insects in highly cluttered space close to vegetation or the ground include all horseshoe and Old World leaf-nosed bats (Rhinolophidae, Hipposideridae; Figures 1e, 4, and 5f) and the New World mustached bat, *Pteronotus parnellii* (Mormoopidae). All of these bats must cope with a situation in which insect echoes are buried in background clutter (Figure 3d). Only if the echoes are so unique that they can be distinguished from the clutter echoes can these bats detect, classify, and localize prey by echolocation alone. Moreover, these bats must also know their exact spatial position to navigate and to avoid collision.

Bats in the guild “highly cluttered space aerial insectivores” solve their problems by using long-duration (approximately 10–100 ms), medium to high frequency (> 30 kHz) CF or CF–FM signals. They emit mostly one search signal per wingbeat. The CF component is overlap insensitive, but the FM component is not. Groups of several search signals per wingbeat have also been recorded.

Because of the long duration of signals and the proximity of background targets, bats using CF–FM signals almost exclusively forage for insects flying in the clutter-overlap zone. Special adaptations of the echolocation system, such as Doppler-shift compensation, an auditory fovea in the cochlea, and a highly modified processing area in the auditory cortex, enable bats using CF–FM signals to distinguish insect echoes modulated in the rhythm of the wingbeat from the overlapping, unmodulated emitted signals and clutter echoes. As in other bats, the overlap-sensitive FM component is used for precise localization of targets. With these adaptations, the signals are especially adapted to forage for insects in highly cluttered environments.

The mustached bat (*Pteronotus parnellii*) forages continuously on the wing, whereas others (*Hipposideros*, *Rhinolophus*) sometimes also hunt from perches in a flycatcher style. They capture fluttering insects, mainly in the air, but they sometimes also glean them from surfaces.

Gleaning insectivores in highly cluttered space.

Bats gleaning their prey from surfaces of vegetation or the ground forage in highly cluttered space. They are mainly found among ghost-faced bats (Megadermatidae), slit-faced bats (Nycteridae), New World leaf-nosed bats (Phyllostomidae), and evening bats (Vespertilionidae; Figures 1f and 1g, 4, 5d and 5e). Like bats in the highly cluttered space aerial insectivore guild, they must cope with a situation in which prey echoes are buried in background clutter (Figure 3c). Only if the echoes have a prey-specific signature that can be distinguished from clutter echoes can the bats find their prey by echolocation. Moreover, they also face the problem that they must know their exact spatial position and the position of landmarks for navigation and collision avoidance.

Bats of the “highly cluttered space gleaning insectivores” and all other gleaners use broadband, overlap-sensitive uni- or multiharmonic calls of short duration (approximately 1–3 ms), often at a very low SPL (whispering bats). Depending on the distance from clutter targets, the bats emit either a single signal or groups of two or more signals per wingbeat. The echoes of their mostly stationary insect prey are buried in clutter, making the use of echolocation for detection, localization, and classification difficult if not impossible. In laboratory studies, narrow-space, gleaning, FM-emitting foragers have learned to discriminate various targets according to spectral differences in the echoes (summarized in Ostwald et al. 1988), and it has been suggested that bats can use spectral cues to distinguish stationary prey from clutter (Simmons and Stein 1980, Neuweiler 1990). However, to date no one has been able to demonstrate that spectral cues in echoes from nonflying insects are specific enough for bats to recognize them using broadband FM signals under normal field conditions in a highly cluttered situation.

Many gleaners that emit broadband FM signals use prey-generated acoustic cues (e.g., calls of insects and frogs or rustling noises of insects walking on leaf litter) for detection, classification, and localization of prey (Tuttle and Ryan 1981, Belwood and Morris 1987, Faure and Barclay 1994). Many gleaners are characterized by large ears that facilitate passive acoustic localization of prey. All gleaners always emit echolocation signals in flight to determine the position of the site with food, to navigate, and to avoid collisions. The low SPL of the calls may prevent overloading of the hearing system with loud clutter echoes.

The use of prey-generated acoustic cues for the detection, localization, and classification of prey does not exclude the possibility of a gleaning bat using echolocation to find its prey under favorable conditions. Learning in a context-specific situation may play an important role. For example, if we offer a *Myotis myotis* individual a noisy insect sitting on a screen, it first uses the prey-generated sounds for passive localization, approach, and capture of the insect. After some experience, the bat learns that echolocation cues from a protruding target indicate a sitting insect and thus also approaches silent insects. Bats make such a transfer to echolocation only if, in a

specific place, some kind of echolocation cues can be associated with prey. In other places they do not react to similar echolocation cues.

Other meaningful categorizations of bats

Similar ecological constraints exert similar selective pressures on signal design, resulting in a coherent and distinctive class of characters in the search signals of bats that live under similar conditions. This intimate linkage allows one to classify bats into functional groups such as guilds. The prerequisite for the categorization of bats into meaningful groups is the definition of habitats. Fenton (1990) summarizes such approaches and distinguishes three main habitat types: open, edge, and closed habitat. We use a rather similar classification and define explicit borders between the habitat types (Schnitzler and Kalko 1998). We propose that bats foraging mainly in one of the three defined habitat types, uncluttered space, background-cluttered space, or highly cluttered space, can be categorized as *open-space foragers*, *edge and gap foragers*, and *narrow-space foragers*, respectively. With open-space foragers and with edge and gap foragers, the grouping matches the corresponding guilds “uncluttered aerial or trawling insectivores” and “background-cluttered aerial or trawling insectivores.” The group of narrow-space foragers covers all the guilds of bats that forage in highly cluttered space, gleaned their prey from surfaces or capturing aerial prey close by. In both situations, the prey echo overlaps with the clutter echo from the substratum.

This overlap is likely to mask important information, and to solve this problem two behavioral strategies have evolved. The preferred foraging habitats, behavioral strategies, and the associated signal types are used to categorize two subgroups of narrow-space foragers. To avoid misinterpretation (Fenton 1999) and to make clear that the cited signal types indicate a specific behavioral strategy, the abbreviations of these signal types appear in quotation marks (Schnitzler et al. forthcoming). The group of narrow-space flutter-detecting “CF” foragers corresponds to the guild highly cluttered space aerial insectivores. By Doppler-shift compensation and specialized hearing systems, they separate the long CF–FM emitted signal from the overlapping returning echoes in the frequency domain, and they evaluate flutter information. The group of *narrow-space gleaning* “FM” foragers represents all guilds that include gleaned bats (with the exception of the trawling bats), including the guild highly cluttered space gleaned in-

sectivores described above. It makes sense to categorize all gleaners into one group, as they have to solve rather similar problems when searching for food. While flying in narrow spaces, these bats mainly use prey-generated cues to detect, localize, and classify their prey, and they use their broadband uni- or multiharmonic FM signals of short duration and low SPL mainly for orientation.

Fenton proposes another categorization to describe the echolocation behavior of bats and the approach an animal takes to foraging (summarized in Fenton 1999). He distinguishes between high- and low-duty cycle bats based on the relative amount of time signals are emitted. The high-duty cycle bats correspond to the narrow-space flutter-detecting “CF” foragers, whereas the low-duty cycle bats cover all the remaining foragers and unite groups as different as open-space, edge and gap, and narrow-space gleaned “FM” foragers. Additionally, Fenton differentiates between low- and high-signal intensity bats under the premise that this classification distinguishes aerial insectivores from gleaned bats. We prefer to categorize bats into meaningful groups according to their

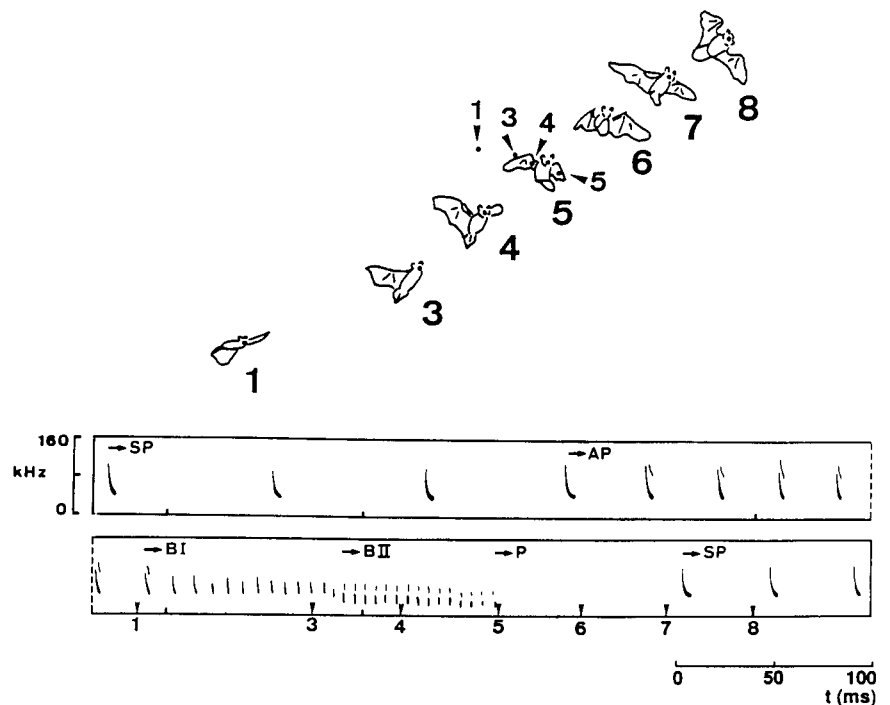


Figure 6. Approach flight and capture maneuver, with the corresponding search and approach signal sequence, of a *Pipistrellus pipistrellus* capturing an insect. The numbers allow a correlation between hunting and echolocation behavior (small numbers indicate the position of the insect). At points 1–4 the bat is in approach flight, at 5 it extends one wing toward the insect and moves its tail into a capture position (tail down), at 6 the bat bends its head into a pouch formed by the tail membrane to retrieve the insect (head down), and at 7 the bat straightens its body and resumes its search flight. In the sequence of echolocation signals, arrows indicate the following phases in echolocation behavior: SP, search phase; AP, approach phase; BI, buzz I; BII, buzz II; P, pause.

main foraging habitat and behavioral strategy, not according to less distinctive signal parameters such as duty cycle and the highly variable signal intensity.

Approach signals of insect-eating bats

After insect-eating bats have detected prey, they approach and capture it (Figure 6). Depending on how these bats forage, they face echolocation problems of varying difficulty. Bats that approach a target or a landing site emit a sequence of approach signals. These signals have the function of guiding the bat to the chosen target or site. The sequence of approach signals is less dominated by the habitat type than by the movement of the chosen target (see Kalko and Schnitzler 1998).

Insectivorous bats that capture prey in the air need to continuously determine the position of prey while closing in on it. Because these bats rely on echolocation to locate and track moving insects, we describe this foraging mode as the *active mode*. By comparison, gleaning bats that take prey from surfaces or the ground mostly evaluate prey-generated acoustic cues to detect, classify, and localize their usually stationary prey. Because gleaners largely do not use echolocation to find their prey, we describe this foraging mode as the *passive mode*.

In a few cases, bats do not use echolocation or other sensory cues directly to find distant prey but screen known or presumed feeding sites based on previous experience. Accordingly, these bats forage in a *random mode* (Schnitzler et al. 1994, Schnitzler and Kalko 1998).

Aerial or trawling insectivores. From photographic sequences of aerial captures by bats in the field and in the laboratory, and from synchronized sound recordings, we found that when aerial or trawling insectivorous bats detect an insect, they immediately switch from search flight to a target-oriented approach flight, with head and ears pointing toward the insect. Simultaneously, the bats change their echolocation behavior from the search phase, with corresponding search signals, to the approach phase or approach sequence, with distinctive approach signals (Figures 1a–e and 6; Griffin et al. 1960).

In the approach phase, bats emit signals in groups correlated with wingbeat and respiratory cycles. The start of the approach is characterized by a change in signal parameters. With a few exceptions, signal duration and pulse interval are reduced throughout the approach phase, which ends in the terminal phase, or *buzz*, prior to capturing an insect. The terminal phase is characterized by a series of short signals at a high repetition rate (up to 180–200 Hz), usually in one but sometimes in two or more groups. Typically, the terminal phase of pipistrelles and some vespertilionids (*Pipistrellus*, *Myotis*) consists of two parts: buzz I (BI) and buzz II (BII; Kalko and Schnitzler 1989). Buzz II signals are reduced in bandwidth and lower in frequency than buzz I signals (Figure 6).

In contrast to the various types of search signals found among insectivorous bats, approach signals are remarkably similar. Evening bats (*Vespertilionidae*) and free-tailed bats

(*Molossidae*) emit broadband FM signals. Narrowband components are eliminated. Similarity in call design reflects a similar challenge: the exact localization and tracking of a moving target in space. Short FM signals are well suited for this task. Moreover, the high repetition rate enhances the information flow needed to control last-instant changes in the insect's position in space.

Sheath-tailed bats (*Emballonuridae*) and mouse-tailed bats (*Rhinopomatidae*) enlarge the bandwidth of the dominant harmonic less strongly than seen in the FM approach signals of vespertilionids and molossids. They maintain the basic structure of their search signals and increase the amplitude of other harmonics (Figure 1d). This change may increase the overall bandwidth of calls of these species.

With the exception of narrow-space flutter-detecting “CF” foragers, aerial insectivorous bats avoid an overlap between approach signals and prey echoes by reducing sound duration and pulse interval to keep the insect in the overlap-free window. It has been shown for pipistrelles that sound emission actually stops several centimeters before the bat reaches the prey (Kalko 1995).

Narrow-space flutter-detecting “CF” foragers reduce the sound duration of the FM portion of their calls but maintain a rather long CF component throughout the approach sequence. As in search phase, the CF component of the echo overlaps with the emitted signal. This has no masking effect, because the emitted CF component does not mask the Doppler-shifted CF component of the echo due to the acoustic fovea and sharply tuned neurons in this frequency range. Presumably, most narrow-space flutter-detecting “CF” foragers need the CF component also during approach to discriminate the fluttering prey from the background. The FM component, however, is reduced and is used for localization.

Gleaning insectivores. Echolocation is used by gleaning insectivorous bats for orientation in space and to guide the bat to the site with prey. After the detection of prey-generated signals, narrow-space gleaning “FM” foragers fly toward the sound source and, nearing the site with food, switch to an approach sequence in which they increase the repetition rate and reduce the signal duration (Figures 1f and g). However, in contrast to aerial insectivores, gleaning bats do not produce a distinct terminal phase when they are close to the site with food. By comparison, the repetition rate remains much lower. This behavioral discrepancy reflects the major difference between gleaners, which approach mostly stationary prey, and aerial insectivores, which track moving prey and constantly need to update the information about an insect's position to successfully intercept it.

Flexibility in foraging and echolocation behavior

Bats are highly variable in their foraging and echolocation behavior (Fenton 1990). Some bats hunt in more than one habitat, or they may use both aerial and gleaning modes. Some species that mainly glean insects from surfaces in highly

cluttered space in the passive mode also catch insects in the aerial mode in background-cluttered space or even in uncluttered space (e.g., *Plecotus*). Increasingly, field studies show that many bats that forage mainly in background-cluttered space also search for insects in uncluttered space (e.g., *Pipistrellus*).

Flexibility in foraging behavior correlates with plasticity in echolocation behavior, such as switching from mixed signals with a broadband FM component in background-cluttered space to narrowband signals in uncluttered space (e.g., *Pipistrellus*). Another strategy is switching from short multiharmonic FM signals of low intensity when gleaning in highly cluttered space to much louder and longer uniharmonic FM signals with a distinct shallow-modulated component when foraging in background-cluttered space (e.g., *Plecotus*). Many gleaners use louder signals when they fly more in the open. Therefore signal intensity is not a good parameter to categorize bats into meaningful groups. However, there are limits to such behavioral plasticity. Bats that are especially adapted for hunting in uncluttered space (e.g., *Tadarida*) are usually restricted to this habitat and cannot search for insects in background-cluttered and highly cluttered space. Bats that are mainly adapted for background-cluttered space do not exploit highly cluttered space. Thus, the access of bats from their specific habitat to a less-cluttered space is possible, but the reverse is not. Fenton (1990) explained this restriction based on perceptual problems (ability to detect prey in clutter) and mechanical problems (ability to fly close to clutter). Limitations of the motor system, particularly flight performance determined by wing shape, largely prevent access to habitats with a more difficult clutter situation. Sensory abilities, or at least the ability to produce the suitable echolocation signals, should be less restrictive, as all bats can produce the short FM signals necessary in cluttered situations.

Flexibility creates exceptions and can make it difficult to clearly define boundaries between guilds and to assign individual species to a particular guild. However, in such cases we would classify bats into guilds according to their dominant sensory and motor adaptation and assign them to the habitat type where they face the more difficult clutter situation. For instance, bats that hunt in background-cluttered and uncluttered space would be assigned to background-cluttered space.

The comparison of the echolocation behavior of insect eating bats reveals that bats foraging in similar habitats with similar foraging modes for similar diets share similar adaptations in their echolocation systems. When moving from one habitat to another, bats change their echolocation behavior and emit the habitat-specific search calls (Figure 5). Therefore, the echolocation behavior of bats and especially the structure of search signals are good indicators of the ecological constraints under which bats search for food.

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