

# Acoustic Ecology of European Bats

Michel Barataud

Species Identification, Study of their Habitats and Foraging Behaviour

---

## Comments of the × 10 time-expanded sequences Folder “3\_x 10 time-expanded sequences” of the Sound File

Sound File provided with the book *Acoustic Ecology of European Bats. Species Identification, Study of their Habitats and Foraging Behaviour*, Inventaires & biodiversité series. Biotope éditions, Mèze; Muséum national d'Histoire naturelle, Paris, 2020, 368 pages.

In the following commentaries, click on the name of the desired sequence (for example “3.3”) to listen to the corresponding audio recording (a warning will pop up, click on “allow”). The sequence opens with your web browser. Should you prefer to open the file with another software application, go directly to the .wav file on the Sound File without using the links below.

- **Sound File 3.1:** Sound File 3.1: Signal with a long CF element and with a clearly audible final FM sweep; bat hanging in its roost; the first harmonic is visible (**Figure 51**) and audible, giving a lower-pitched tonality to the sound, except in the last 6 signals, in which it is less intense. The second harmonic (the dominant one) has its FME at 81 kHz (and therefore gives a × 10 time-expanded output at 8.1 kHz). *Rhinolophus ferrumequinum*.
- **Sound File 3.2:** Sound File 3.2: Signal with a long CF element and a clearly audible final FM sweep (**Figure 52**); bat in flight in its foraging area. The second harmonic (the most intense) has its FME at 107.8 kHz (and therefore the time-expanded sound is at 10.8 kHz). *Rhinolophus hipposideros*.
- **Sound File 3.3:** Long QCF signals (20 ms); bandwidth is 1.5 kHz and mean FME is at 26.5 kHz (**Figure 54**).
- **Sound File 3.4:** Short QCF signals (8 ms); bandwidth is 0,8 kHz and mean FME is at 46,5 kHz (**Figure 55**).
- **Sound File 3.5:** Long flat-ended FM signals (18 ms); bandwidth of approximately 20 kHz, mean FME at 26 kHz (**Figure 56**).
- **Sound File 3.6:** Short flat-ended FM signals (6.5 ms); bandwidth of 19 kHz, mean FME at 39 kHz (**Figure 57**).
- **Sound File 3.7:** Long steep FM sweeps (9 ms); bandwidth of 37 kHz and mean FME at 26 kHz (**Figure 58**).
- **Sound File 3.8:** Short steep FM sweeps (3.3 ms); bandwidth of 65 kHz and mean FME at 51 kHz (**Figure 59**).
- **Sound File 3.9:** QCF/FM sweeps signals of *M. daubentonii* (recording by P. Favre).
- **Sound File 3.10:** Short QCF signals (8 ms) of *Nyctalus leisleri*.

- **Sound File 3.11:** Long QCF signals (21 ms) of *Vespertilio murinus*.
- **Sound File 3.12:** Signals with a whistled sonority (*Myotis* type).
- **Sound File 3.13:** Signals with a nasal sonority (*Plecotus* type).
- **Sound File 3.14:** QCF signals with explosive start.
- **Sound File 3.15:** Brief flat-ended FM signals with explosive start.
- **Sound File 3.16:** Steep FME signals with explosive start.
- **Sound File 3.17:** Saturated signals giving a false impression of explosive start. At the beginning and at the end of the sequence, the flat-ended FM signals exhibit true explosive starts, but in the middle of the sequence there are two successive phases during which the bat comes too close to the microphone and the recording of the signals is saturated. The saturation produces a multi-frequency sound that should not be confused with an explosive start on signals with no energy peak.
- **Sound File 3.18:** Low-frequency steep FM signals with final whack.
- **Sound File 3.19:** High-frequency steep FM signals with final whack.
- **Sound File 3.20:** Steep FM signals with both explosive starts and final whacks together.
- **Sound File 3.21:** This long sequence includes the signals of two bats of different species: a *Plecotus macrobullaris* (narrowband FM sweep with nasal sonority and explosive start) and a *Myotis nattereri* (very broadband low-frequency FM sweep, whistled sonority and final whack). Both are flying inside their night-time roost. This sequence is a useful exercise for learning to perceive simultaneously all these different criteria.
- **Sound File 3.22:** Signals with a pumping effect (recording artefact) giving the false impression of a final whack.
- **Sound File 3.23:** Narrowband FM signals with no energy peak.
- **Sound File 3.24:** Steep FM signals with an even energy distribution and no energy peak.
- **Sound File 3.25:** Steep FM signals with the energy concentrated in the second half of the signal and no energy peak.
- **Sound File 3.26:** Steep FM signals with sine-like amplitude modulations.
- **Sound File 3.27:** Intervals < 40 ms: distance to obstacles < 0.5 m.
- **Sound File 3.28:** Intervals 40-50 ms: distance to obstacles 0.5-1 m.
- **DVE 3.29:** Intervals 50-80 ms: distance to obstacles 1-3 m.
- **Sound File 3.30:** Intervals 80-100 ms: distance to obstacles 3-5 m.
- **Sound File 3.31:** Intervals 100-250 ms: distance to obstacles > 5 m.
- **Sound File 3.32:** *B. barbastellus*: sequence of signals of alternating FMEs and intensities, followed by a short series of QCF-FMd signals triggered by the meeting of a conspecific.
- **Sound File 3.33:** *B. barbastellus*: long series of QCF-FMd signals produced when two bats meet on the wing.
- **Sound File 3.34:** Flat-ended FM signals in the first part of the sequence, then long QCF signals (mean duration: 16.5 ms); EF at 27.5 kHz, BW of 4 kHz and FME at 28 kHz; the long duration of the signals, given the EF, points especially to *Vespertilio murinus* and *Eptesicus nilssonii*; when FME is combined with BW, we are left with *E. nilssonii* only; level of confidence: certain.
- **Sound File 3.35:** Long sequence recorded in a lighted urban environment in which can be heard long QCF signals (16 ms) with an FME at 28 kHz and flat-ended FM signals of varying bandwidths depending on the bats' behaviour but at generally higher frequencies; cruising phases with a slow repetition rate only contain QCF signals with no variation in frequency (but sometimes variations in intensity according to the direction of emission in relation to the microphone); the FM signals appear when the repetition rate increases (in the second part of the sequence, two bats are flying side by side then fly into the distance while resuming their QCF signals); the auditory analysis rules out genus *Nyctalus* and the measurement of the QCF signals points to *Eptesicus nilssonii*; level of confidence: certain.
- **Sound File 3.36:** Long sequence, recorded along a forest border, containing both long QCF signals (20 to 24 ms) with FME at 23 kHz and flat-ended FM signals higher in frequency, with a bandwidth that varies depending on the bats' behaviour; slow repetition rate cruising phases only contain QCF signals with no variation in frequency (but sometimes variations in intensity according to the direction of emission in relation to the microphone); the transitions from QCF to FM signals are progressive and coincide with an acceleration of the repetition rate (when closing in on obstacles or prey items); the auditory analysis rules out genus *Nyctalus* and the measurement of the QCF signals points to *Vespertilio murinus*; level of confidence: certain.

- **Sound File 3.36a:** The sequence starts with medium-bandwidth QCF signals and later changes to narrow-bandwidth flat-ended FM signals on 26-27 kHz. Irregularly alternating FMEs can be heard, but only slightly different (generally < 1 kHz; it is useful to listen to the sequence in heterodyne, with the virtual bat detector of BatSound, in order to distinguish this from *N. leisleri* alternating sequences for example). The emission of a low QCF signal just before the approach phase is intriguing (a similar phenomenon was also recorded in *N. lasiopterus*, see Sound File 3.48) and could reveal a need to detect some more distant element ahead or, alternatively, a strategy designed to confuse a tympanate prey. The fast rhythm of the end sequence of non-alternating QCF signals does not conform to a *N. leisleri*'s passive-transit sequence with non-alternating signals, and, moreover, the signals are longer than 20 ms. *Vespertilio murinus*; level of confidence: probable to certain (recording by Jean-François Desmet).
- **Sound File 3.37:** The signals vary from broadband QCF pulses (with a BW of 3 to 5 kHz) to narrowband flat-ended FM sweeps (with a BW of 5 to 16 kHz), but the FME remains pretty much the same throughout (between 21.5 and 23.5 kHz); slow repetition rate (mean interval duration of 350 ms), which rules out genus *Nyctalus* (which, at this rate of repetition, would include at least some flat QCF signals with a BW < 1 kHz alternating with higher flat-ended FM signals); the absence of explosive start and the measurement of the signals (especially the EF between 20 and 22 kHz) point to *Eptesicus serotinus*; level of confidence: certain.
- **Sound File 3.37a:** Long QCF signals (18 to 21.5 ms, which is too long for a *Nyctalus leisleri* in transit flight) with an FME at approximately 22 kHz; explosive start; slight acceleration of the repetition rate in the first part of the sequence, indicating too much inquisitiveness for a passive transit flight (which rules out *Eptesicus serotinus*); sequence recorded in Extremadura (Spain), which makes *Vespertilio murinus* pretty unlikely, and moreover some EF are below 21 kHz; sequence characteristic of *Eptesicus isabellinus* when it is engaged in its typical (at least at dusk) high aerial foraging, with frequent long QCF signals; in contrast, when it approaches obstacles, the characteristics of the flat-ended FM signals emitted overlap those of other species, especially *E. serotinus*. *Eptesicus isabellinus*; level of confidence: certain.
- **Sound File 3.38:** With the exception of the final approach phase, flat-ended FM signals with slow repetition rate (intervals of approximately 300 ms), with some shorter intervals of approximately 140 ms indicating a slow and irregular cruising rhythm; in such conditions, the absence of QCF signals (BW of approximately 15 kHz) rules out genus *Nyctalus* and the absence of explosive start rules out *Eptesicus nilssonii* and *Vespertilio murinus* (which could not have been ruled out if the recorded sequence had only included the final approach); *Eptesicus serotinus*; level of confidence: certain.
- **Sound File 3.39:** One bat hunting with QCF signals; short QCF signals (11 to 13 ms) showing some variation in FME and BW but no obvious correlation with an approach behaviour (approach behaviour: progressive acceleration of repetition rate, increase of FME and widening of BW over several successive signals), which is characteristic of genus *Nyctalus*; the FME of the QCF signals at 23 kHz points to *Nyctalus leisleri*; level of confidence: certain.
- **Sound File 3.40:** Medium band FM signals (BW of 20 kHz) with just a trace of final QCF component (shortened flat-ended FM signal) with an FME at 29 kHz; fast and regular rhythm indicating it is nearing an obstacle; no possibility of identification in the first part of the recorded sequence as all the species emitting QCF and flat-ended FM signals with an FME between 20 and 30 kHz could be concerned (even though the narrow bandwidth makes *Eptesicus serotinus* rather unlikely); however, in the second part of the sequence, as soon as the obstacle is cleared (a broadleaved hedge tree skirted by the bat), the signals immediately revert to a short QCF structure (7 ms long) with the FME at 24 kHz; *Nyctalus leisleri*; level of confidence: certain.
- **Sound File 3.41:** Series of sequences typical of the behaviour of *Nyctalus leisleri*: short QCF signals at 23 kHz followed by broader flat-ended FM signals suggesting approach attempts, captures or simply probings for more precise information about the distance to various objects in the vicinity.
- **Sound File 3.42:** Sequence with alternating long QCF signals (>20 ms) at 18-19 kHz and QCF or flat-ended FM signals at 20-21 kHz; alternation present, although somewhat irregular, in cruising phase; no approach rhythm can be heard that would explain the more broadband signals: genus *Nyctalus*; measurements carried out on the signals leave us with *Nyctalus noctula* as the sole possibility; level of confidence: certain.
- **Sound File 3.43:** Sequence with alternating FM signals; the noctule is here flying close to obstacles (around a street light) and has stopped emitting QCF signals although it continues alternating FMEs, thereby indicating its genus; the lowest FME signal is at 23 kHz with a BW of approximately 9 kHz; the only species of the genus that can exhibit such values is *Nyctalus noctula*; level of confidence: certain.
- **Sound File 3.44:** Long, regularly alternating signals with slightly different FMEs (16 versus 17.5 kHz) and BWs (5 versus 10 kHz); *Nyctalus lasiopterus*; level of confidence: certain.
- **Sound File 3.45:** Same type of sequence as Sound File 3.44, but the signals alternate more irregularly: the bat is probably much more inquisitive about its surroundings; the higher-frequency and more modulated signals provide more precise information in terms of distance and direction; *Nyctalus lasiopterus*; level of confidence: certain.
- **Sound File 3.46:** Signals with an FME at 19-20 kHz (therefore in the range of *Nyctalus noctula* QCF signals), but with a BW of about 15 kHz: the bat needs to locate nearby obstacles, and the FME is accordingly higher

than if the bat were cruising in open space (the bat is here flying about 10 m from a vegetation border); a prey item is also spotted at a certain distance, as demonstrated by the capture phase at the end of the sequence; another bat, further away from the vegetation border, is emitting signals that are a little lower in frequency and less modulated; *Nyctalus lasiopterus*; level of confidence: certain.

- **Sound File 3.47:** In this sequence, several *Nyctalus lasiopterus* are foraging high above a street-lit village; the lower signals are mostly flat QCF signals, indicating open space, far from any obstacle.
- **Sound File 3.48:** Low QCF signal isolated amidst a capture sequence; cruise signals thereafter, with alternating FMEs and structures pointing to *Nyctalus lasiopterus*; level of confidence: certain.
- **Sound File 3.49:** Flat QCF signals (BW < 1 kHz) at a low frequency (FME at 10-11 kHz), long duration (20 ms), slow repetition rate (intervals of approximately 600 ms); no signal with different frequency or structure (the frequency varies between 10 and 11 kHz according to the flight conditions, but each series of signals is homogeneous); the conjunction of BW and FME rules out *Nyctalus lasiopterus*; *Tadarida teniotis*; level of confidence: certain.
- **Sound File 3.50:** Flat-ended FM signals (duration: 17 ms, EF: 12.5 kHz, BW: 15 kHz, FME: 14.5 kHz) gradually turning into QCF signals (BW: 3 kHz) at 13 kHz; in both cases, the set of values measured rules out *Nyctalus lasiopterus*; the bat is a *Tadarida teniotis* flying along a cliff face and then gradually veering off to fly into the open; level of confidence: certain.
- **Sound File 3.51:** Soundscape including 1) low QCF signals at 11 kHz (*Tadarida teniotis*), 2) a sequence of irregularly alternating short QCF signals at 26.5 kHz and flat-ended FM signals at 29-35 kHz (*Nyctalus leisleri*), and 3) shortened flat-ended FM signals with abridged QCF component at 40-42 kHz (*Pipistrellus kuhlii*).
- **Sound File 3.52:** FM-QCF signals with an FME at 56 kHz and a BW of 30-40 kHz; the measurements of EF and duration also fail to provide any diagnostic information; in the scatter diagrams, we are in the area where *Miniopterus schreibersii* and *Pipistrellus pygmaeus* overlap (even though some of the more broadband signals with BW > 45 kHz are slightly out of *P. pygmaeus*' data point cloud); when the spectrogram window is configured to 100 ms horizontally and 150 kHz vertically, the signals' curvature varies from generally fairly open and even at the beginning of the sequence to mostly less evenly rounded and even angular in the second half of the sequence; *Pipistrellus pygmaeus*; level of confidence: certain.
- **Sound File 3.53:** Sequence including the QCF and FM-QCF signals of three individuals; the FME of the QCF signals is at 55 kHz, which rules out *Miniopterus schreibersii*; the FME/BW values of the FM-QCF signals vary from 56/15 kHz to 60/40 kHz; all the figures are in the reference measurement range of *Pipistrellus pygmaeus*; level of confidence: certain.
- **Sound File 3.54:** Approach and capture sequence of high-frequency FM signals (FME at 60-70 kHz), some of which exhibit a terminal 'heel' typical of an abbreviated FM-QCF signal; the subsequent signals confirm that the emitting species belongs to the flat-ended FM group, then quickly take on a QCF structure (some ending with a brief ascending FM segment over 1.5 kHz); none of the signals has measurements permitting us to decide between *Miniopterus schreibersii* and *Pipistrellus pygmaeus*, but all exhibit a 'break' in the bend joining the two components – a characteristic of the latter species; *Pipistrellus pygmaeus*; level of confidence: certain.
- **Sound File 3.55:** The sequence contains two series of FM-QCF signals; one with an FME above 55 kHz, at 57 kHz, clearly angular signals and a BW of about 20 kHz: *Pipistrellus pygmaeus*; level of confidence: certain; the other series varies in BW between 5 and 35 kHz but has a stable FME at 41.5 kHz (an area where *P. kuhlii* and *P. nathusii* overlap), some highly modulated signals descend to an EF of 32 kHz, which is far too low for *P. nathusii*, and the co-occurrence of typical social calls (see "Identification through social calls", page 254) confirm *Pipistrellus kuhlii*; level of confidence: certain.
- **Sound File 3.56:** Short sequence of FM-QCF signals with an FME varying between 51 and 53 kHz while BW varies from 14 to 46 kHz; the broadband signals are long (12 ms), with an open and evenly rounded bend; fast repetition rate (intervals of 60 to 70 ms), even at the beginning of the sequence, when the BW is only 11 to 15 kHz wide; all the criteria, whether measured (long broadband signals) or estimated, converge on *Miniopterus schreibersii*; level of confidence: certain.
- **Sound File 3.57:** Long sequence including several hunting bats emitting FM-QCF signals of varying BW, FME, duration and EF depending on the individual context; all the signals are in the range of both *Miniopterus schreibersii* and *Pipistrellus pygmaeus*; signal curvature is mostly typical of the former species, as well as some signal durations, between 9 and 10 ms (this being also discernible by ear); *Miniopterus schreibersii*; level of confidence: certain.
- **Sound File 3.58:** Sequence displaying many characteristic features of *Miniopterus schreibersii*. By ear, many signals exhibit a progressive start, especially the longer ones (in contrast to the systematically explosive start of pipistrelles' signals); the signals often appear and disappear suddenly throughout the sequence, indicating high flight speed; two capture sequences, both long to very long and at very high repetition rates, with no preceding obvious approach phase (probably reflecting attempts to catch tympanate moths, which involve longer pursuits). The analysis on computer reveals signals with characteristic measurements as well as regularly rounded and open bends; level of confidence: certain.

- **Sound File 3.59:** Sequence involving one *Miniopterus schreibersii* flying first along a forest border then across a clearing (narrower BW and slower repetition rate) to reach the opposite edge; a characteristic feature of the species can be noted: successive signals vary considerably in intensity, giving the impression that several individuals are flying at various distances from the microphone (this is also perfectly audible on the heterodyne output, see Sound File 2.38).
- **Sound File 3.60:** Sequence in which signals with different bandwidths can be heard, with some, towards the end of the sequence, fluctuating around 5 kHz; these long (11-12 ms) broadband QCF signals are typical of *Miniopterus schreibersii* foraging in an open environment where prey is scarce; level of confidence: certain.
- **Sound File 3.61:** Sequence of FM-QCF signals typical of a bat actively probing a semi-open environment: BW of 10 to 40 kHz depending on the distance to obstacles, relatively stable FME at about 45-46 kHz; *Pipistrellus pipistrellus*; level of confidence: certain.
- **Sound File 3.62:** Sequence of FM-QCF signals typical of a hunting bat, including a capture phase; the FME is at about 48 kHz, and the BW is of approximately 30 to 50 kHz; *Pipistrellus pipistrellus*; level of confidence: certain.
- **Sound File 3.63:** Sequence of FM-QCF signals; although repetition rate is slow and the rhythm irregular, the FME is rather high: at 50-51 kHz for the most broadband signals (BW of 30 kHz), then later lowering to 49 kHz when the BW narrows to 12 kHz; the duration and curvature of the signals seem typical of *Pipistrellus pygmaeus* and *P. pipistrellus*, but the EF (49-50 kHz) and the combination of BW and FME values position the data points outside the range of the former species; *Pipistrellus pipistrellus*; level of confidence: certain.
- **Sound File 3.64:** Sequence recorded at the entrance of a forest track tunnelling through the understorey to a clearing; the first signals are steep FM signals similar to those of a *Myotis* of the 'explosive start and high-frequencies' category (see "Identification of FM sweeps" p.192), but very quickly one notices a heel at the bottom of the signal indicating a truncated QCF component: the emitting bat is an FM-QCF specialist, but the obstacle-strewn environment forces it to use high frequency FM signals; this is confirmed by the last signals of the sequence, when the bat comes out in the open and reverts to its usual emissions. Three species are possible here: *Pipistrellus pygmaeus*, *P. pipistrellus* and *Miniopterus schreibersii*; this last species is rather unlikely since some of the shortened broadband flat-ended FM signals exhibit a 'break' in the curvature that is typical of the pipistrelles; the last signals of the sequence are the ones that will offer the best chances of discriminating between the two pipistrelles because they are the most species-specific; the EF (50.5 kHz) and the conjunction of BW and FME all point to *Pipistrellus pipistrellus*; level of confidence: probable.
- **Sound File 3.65:** Sequence typical of *Pipistrellus pipistrellus*, FM-QCF signals with FME at 49 kHz and one social call; twice, the bat emits a pair of high-frequency signals with an FME at 65 kHz, maybe related to the presence of a conspecific, perceived in the background at 47 kHz.
- **Sound File 3.66:** Hunting sequence (capture phase) including two types of structure: first, QCF signals with FME at 43-44 kHz and BW of 3-5 kHz, then FM-QCF signals during the approach phase (and resource phase after the capture). The frequencies spanned are the same as for *Pipistrellus nathusii* and *P. pipistrellus*, but the latter does not emit QCF signals when hunting actively, and moreover, at this bandwidth, its FME value is usually higher; *Pipistrellus nathusii*; level of confidence: probable.
- **Sound File 3.67:** The majority of the signals from this sequence are QCF signals; bandwidth varies a great deal, from 0.5 to 8 kHz, and FME varies from 39.5 to 42 kHz; all these values are diagnostic; some typical social calls can also be heard in the background, emitted by conspecifics (see the section "Identification through social calls", page 254); *Pipistrellus nathusii*; level of confidence: certain.
- **Sound File 3.68:** Sequence of QCF signals, ending with a capture phase; the bandwidth starts to broaden only during the approach phase; the FME between 39 and 41 kHz when the bat is hunting with QCF signals is characteristic of *Pipistrellus nathusii*; level of confidence: certain.
- **Sound File 3.69:** Long sequence in which several bats are foraging with different degrees of activity; two different frequency bands: 1) FME at 50-51 kHz with a BW up to 30 kHz and an angular signal shape: *Pipistrellus pipistrellus*; level of confidence: certain; 2) FME at between 35 and 40 kHz depending on the individual (one is at 35.5-36 kHz and another at 37.5-38.5 kHz), both varying in structure between QCF and narrowband FM-QCF signals (they are further away from the forest border than the common pipistrelles); all this places the sequence in the monospecific cloud of data points of *Pipistrellus kuhlii*; level of confidence: certain.
- **Sound File 3.70:** The sequence starts with approach signals: a broad BW (50 to 65 kHz) with a heel at the end of the signal indicating the beginning of a shortened QCF component, the emitting bat is therefore an FM-QCF specialist; the conjunction of the FME at 42 kHz and the BW places the data points in the area of overlap of *Pipistrellus kuhlii* and *P. nathusii*, but the EF is too low for the latter; another bat appears in the sequence with an FME at 38 kHz and a BW of about 20 kHz, the conjunction of these values points to *Pipistrellus kuhlii*; level of confidence: certain.
- **Sound File 3.71:** Sequence including the FM-QCF emissions of two bats, one at 36.5 kHz, with a BW < 15 kHz, and the other at 40 kHz with a wider BW (up to 40 kHz); in both cases, these values place the data points in the exclusive domain of *Pipistrellus kuhlii*; these two bats underline the structural variability of this species; level of confidence: certain.



- **Sound File 3.72:** One bat is flying between a rock face and some vegetation; the sequence starts with a series of high-frequency pulses with an FME varying between 45 and 80 kHz; the beginnings of a heel observed at the end of some signals indicates that this bat is an FM-QCF specialist; the bat flies progressively away from the rock face and the FME decreases to about 39-40 kHz with a BW of 25-30 kHz; these values place the data points in the zone of contact between *Pipistrellus kuhlii* and *P. nathusii*; however, the abbreviated flat-ended FM structure of the signals shows that the bat is still close to obstacles, suggesting that in a more open environment the FME would drop still further – something that pitches the scales more in favour of *Pipistrellus kuhlii*; level of confidence: probable.
- **Sound File 3.73:** Flat QCF signals at 33.7 kHz; the only species concerned by this type of structure in this frequency range is *Hypsugo savii*; level of confidence: certain.
- **Sound File 3.74:** Broadband QCF signals with a BW varying between 32.4 and 33.7 kHz, recalling the alternating FMEs often produced by noctules at lower frequencies, but with no change of structure; great variations in intensity, probably due to movements of the bat's head probing in different directions to widen its angle of perception; the capture phase at the end of the sequence shows that this species emits QCF signals when hunting actively in open space; *Hypsugo savii*; level of confidence: certain.
- **Sound File 3.75:** Flat-ended FM signals with an FME at 34-35 kHz and a BW between 12 and 20 kHz; this places the data points in the domain of *Hypsugo savii*, but in an area overlapping with a more occasional acoustic behaviour of *Pipistrellus kuhlii*; signal duration is close to 10 ms and the EF is at 33.7 kHz: these values tend to support the former without ruling out the latter; however, a QCF signal at 33.7 kHz just before the approach phase suggests that the emitter belongs to a QCF specialist, which rules out *P. kuhlii*; *Hypsugo savii*, level of confidence: probable.
- **Sound File 3.76:** One bat is hunting between the branches of a patchy larch grove; most of the FM-QCF signals have an FME at 36-37 kHz, but the FME drops to 35.4 kHz as soon as the BW narrows to under 25 kHz; no QCF signal due to the cluttered nature of the foraging area, but the tendency towards lower FME values and the number of signals concerned vote clearly in favour of *Hypsugo savii* over *Pipistrellus kuhlii*.
- **Sound File 3.77:** Long QCF signals (> 20 ms) with an FME at 34-35 kHz inserted between two short descending FM components; the only species capable of producing such signals is *Myotis dasycneme*; level of confidence: certain (recording by M. Van de Sijpe).
- **Sound File 3.77a:** *Eptesicus serotinus* in a forest understorey, emitting short-duration FME signals with a slightly nasal sonority; in a short and homogeneous sequence such as this one, it is possible to mistake these signals for those of a *Plecotus*, and especially of a *Barbastella* (since the start is progressive and not explosive); however, this acoustic behaviour is uncommon and generally transient in *E. serotinus*, and is mostly preceded and/or followed by more typical signals (such as the ones heard at the end of the sequence, which mark the beginning of a transition).
- **Sound File 3.77b:** *Eptesicus serotinus* in a forest understorey, emitting short-duration FME signals with a slightly nasal sonority; capture phase followed by a resource phase near dense vegetation, which together make up a long phase at a fast repetition rate; the last signals of the sequence become typical of the species.
- **Sound File 3.78:** The sequence begins with a quick series of nasal signals with a progressive start; when examined on the computer, the signals reveal two clear energy peaks on the slightly convex first harmonic; after some hesitation (due to the presence of a few remaining obstacles along the flight path), the signals then begin to alternate in frequency and intensity, with a regular rhythm; this leaves no doubt as to the emitting species (see "FME < 35 kHz", page 207); *Barbastella barbastellus*; level of confidence: certain.
- **Sound File 3.79:** This long sequence begins with a phase of signals alternating in FME and intensity in the background; it is followed by a first phase of approach signals with a nasal sonority, then again by a series of alternating signals (another bat in the background emits successively alternating signals then approach signals); the bat comes gradually closer to the observer then dodges suddenly to avoid him or her (saturated approach signals), recedes with alternating signals, turns round and comes back towards the observer with an approach phase starting much earlier than the previous one since the obstacle is now located and identified; all the approach signals have a nasal sonority and a progressive start – characteristics that, together with the alternating signals, point to *Barbastella barbastellus*; level of confidence: certain.
- **Sound File 3.80:** All the signals of the sequence have a nasal sonority; no alternating signals typical of the barbastelle; progressive start (the 'cracks' produced by two saturated signals should not be mistaken for energy peaks); the energy maximum is on the second harmonic; convex signal shape; all these traits are characteristic of *Barbastella barbastellus*; level of confidence: certain.
- **Sound File 3.81:** The sequence includes two types of signals at slightly different frequencies, but not alternating regularly; by listening attentively, one understands that there are two individuals and avoids the pitfall of a possible confusion with the barbastelle's alternating signals; the higher-pitched one is emitting flat-ended FM signals at approximately 45 kHz (*Pipistrellus pipistrellus*); the lower-pitched one has a nasal sonority; the concave shape of the signals closely resembles those of long-eared bats, but the assessment of the energy distribution by ear reveals a progressive start (do not mistake the 'cracks' produced by the four saturated signals for energy peaks); this bat is a barbastelle in approach phase, flying in dense forest

understorey – hence the long duration of the sequence, the regular rhythm and medium repetition rate; level of confidence: certain.

- **Sound File 3.82:** In this sequence, one barbastelle is hunting along a flight path through a forest, strewn with low branches; it repeatedly switches between typical hunting signals (with alternating FME and intensity) and approach signals (nasal sonority and progressive start, with a linear or slightly convex shape); level of confidence: certain.
- **Sound File 3.83:** Weak signals amid a noisy background; the bat is 'whispering' in the foliage, hence the high repetition rate, nasal sonority and explosive start: genus *Plecotus*; The signals are very brief (1.6 ms on average); the pairs of variables SF/EF (51/28 kHz) and FME(H1)/FME(H2) (42/65 kHz) place the signals, in the scatter diagrams, in the cloud of data points corresponding to *Plecotus auritus* with no risk of overlap; level of confidence: certain.
- **Sound File 3.84:** Long *Plecotus* sequence in a fairly open forest understorey (nasal sonority and explosive start); signal duration between 3 and 4 ms; the pairs of variables SF/EF (54/26 kHz) and FME(H1)/FME(H2) (44/62 kHz) place the signals, in the scatter diagrams, in the cloud of data points corresponding to *Plecotus auritus* with no risk of overlap; level of confidence: certain.
- **Sound File 3.85:** Sequence of *Plecotus* signals along a forest border, as attested by the nasal sonority and the explosive start; signal duration between 3 and 4 ms; the pairs of variables SF/EF (56/25 kHz) and FME(H1)/FME(H2) (44/64 kHz) place the signals, in the scatter diagrams, in the cloud of data points corresponding to *Plecotus auritus* with no risk of overlap; level of confidence: certain.
- **Sound File 3.86:** Sequence in a semi-open environment (scattered trees); nasal sonority for the first signals only (shorter and higher-pitched), then the sonority becomes whistled and the signals start to closely resemble those of *Eptesicus serotinus*, for example, albeit with a slightly explosive start; genus *Plecotus* can only be identified by analysis of the signals on computer: the sigmoid shape (in particular the second harmonic), the short terminal FM 'tail', and the transfer in maximum energy from the beginning of the first harmonic to the tail of the second in some signals (see box 99) are all characteristic of the genus; signal duration above 6 ms; the pairs of variables SF/EF (51/18 kHz) and FME(H1)/FME(H2) (27/51 kHz) place the signals, in the scatter diagrams, more or less in an area common to all three species; however, the SF value is more characteristic of *P. auritus* without entirely ruling out *P. austriacus*; *P. macrobullaris* is not considered plausible in the geographical area; *Plecotus auritus*; level of confidence: probable.
- **Sound File 3.87:** Sequence in which the fast repetition rate of the signals indicates that the bat is flying in a cluttered environment (foliage); nasal sonority and explosive start: genus *Plecotus*; the signals are very brief (1.5 ms on average); the pairs of variables SF/EF (44/26 kHz) and FME(H1)/FME(H2) (34/62 kHz) place the signals, in the scatter diagrams, in an area where *P. austriacus* and *P. macrobullaris* overlap, but the latter is believed not to occur in the geographical area where the recording was made; *Plecotus austriacus*; level of confidence: probable.
- **Sound File 3.88:** A bat is flying along a forest border, close to foliage; nasal sonority and explosive start: genus *Plecotus*; medium repetition rate but short signals, mostly just over 2 ms in duration, a few 2 ms long; the pairs of variables SF/EF (42/23 kHz) and FME(H1)/FME(H2) (35/60 kHz) place the signals, in the '2-3 ms' scatter diagrams, in a reference data point cloud that includes all three species; if the two or three signals very close to the upper limit of the '<2 ms' class are taken into account and placed on the '< 2ms' scatter diagram, then we are left with *P. austriacus* and *P. macrobullaris*; however, the latter is believed not to occur in the geographical area where the recording was made; *Plecotus austriacus*; level of confidence: possible.
- **Sound File 3.89:** One bat is flying above a road through a forest; explosive start and nasal sonority although the signals are fairly long (4 to 5 ms) and at low frequencies; the spectrogram shows that the intensity maximum jumps from H1 to H2 in the course of the signal: genus *Plecotus*; the pairs of variables SF/EF (42/20 kHz) and FME(H1)/FME(H2) (26/45 kHz) place the signals, in the scatter diagrams, in a zone where *P. austriacus* and *P. macrobullaris* overlap, but the latter is believed not to occur in the geographical area where the recording was made; *Plecotus austriacus*; level of confidence: probable.
- **Sound File 3.90:** Forest border; nasal sonority and explosive start: genus *Plecotus*; signal duration is 2-3 ms in the central part of the sequence; the pairs of variables SF/EF (44/22 kHz) and FME(H1)/FME(H2) (32/60 kHz) place the signals, in the scatter diagrams, in a zone common to the three species; however, when the longer signals (3-4 ms) are examined, some measurements rule out successively *P. auritus* and *P. austriacus* (moreover, the latter is not known to occur in the area where the recording was made, at an elevation of 1500 m in the Alps); *Plecotus macrobullaris*; level of confidence: probable (recording by P. Favre).
- **Sound File 3.91:** Forest border; nasal sonority and explosive start: genus *Plecotus*; signal duration is 3-4 ms in the central part of the sequence; the pair of variables FME(H1)/FME(H2) (30/50 kHz) places the signals, in the corresponding scatter diagram, in a zone common to the three species; however, the pair of variables SF/EF (46/17 kHz) places the signals in a monospecific *Plecotus macrobullaris* data point cloud; level of confidence: certain (recording by P. Favre).
- **Sound File 3.92:** A bat is flying along a road in a forest; explosive start and slightly nasal sonority (undoubtedly different from a typical whistled sonority, such as that of a serotine, for example) in spite of the long

duration of some of the signals (> 7 ms), at low frequencies: genus *Plecotus*; the pairs of variables SF/EF (46/14 kHz) and FME(H1)/FME(H2) (21/38 kHz) place the signals, in the scatter diagrams, in monospecific *Plecotus macrobullaris* data point clouds; level of confidence: certain (recording by P. Favre).

- **Sound File 3.93:** Sequence in which two types of signals co-occur; flat QCF signals at 43-44 kHz fall in the monospecific data point cloud of *Pipistrellus pipistrellus* (level of confidence: certain); the other signals, at low frequencies, are more unusual: their sonority is more nasal than whistled and, on the computer screen, they display a sigmoid shape and a shift in the intensity maximum from H1 to H2 during the signal: genus *Plecotus*; the pairs of variables SF/EF (40/7 kHz) and FME(H1)/FME(H2) (14 and 24/33 kHz) are puzzling, especially the end frequency; such signals strongly recall the features of a social call and closely resemble the social calls of *Plecotus* species (see "Identification through social calls", page 254 however, in this case, the pulses are emitted on the wing with a repetition rate consistent with the environment and the flight speed of the individual (the bat was not marked but was dimly visible in the twilight), and this is more in keeping with sonar emissions... Such observations are not rare with long-eared bats transiting through open areas; the signals were very intense and audible over 50 m away with the heterodyne system. Unfortunately, we have never been able to identify reliably to species level the bats responsible for this type of emission, but *Plecotus auritus* is probable in many cases and *P. austriacus* fairly unlikely given the scatter diagram of **Figure 120**.
- **Sound File 3.94:** Sequence of medium-duration FM sweeps (6 ms) with a bandwidth of 35 kHz and an FME at 30 kHz: these three criteria are evaluated together during the auditory analysis, and reveal marked differences with Sound File 3.8 and 3.24; however, confusion is possible with Sound File 3.7; *Eptesicus serotinus* hunting in a canopy gap.
- **Sound File 3.95:** Regularly alternating signals of *Barbastella barbastellus*. In this sequence, recorded from the ground, the type A signal is picked up more strongly than type B. The criteria taken together allow the unambiguous identification of the emitting bat (except special cases such as Sound File 3.99).
- **Sound File 3.95a:** Alternating sequence of a *B. barbastellus* flying in forest understorey recorded by a microphone placed at 25 m above the ground, in the canopy: type B signals appear the most intense, in contrast with sequences recorded from ground level (see "Example 1: the sonar of the barbastelle", page 312).
- **Sound File 3.96:** Alternating signals of *Barbastella barbastellus*. The regular alternation rhythm is interrupted once as two B signals are produced in succession, maybe because the bat was inquisitive about an element of its environment, which in the end did not call for a full-blown approach phase.
- **Sound File 3.97:** Alternating signals of *Barbastella barbastellus* with typical variation in intensity between the two signal types. In the beginning, the A signal is less intense, then the normal pattern prevails as the B signal becomes weaker than the A signal, to the point of disappearing altogether when the bat recedes into the distance.
- **Sound File 3.98:** The sequence begins with an approach phase (nasal sonority, progressive start: *Barbastella barbastellus*) and continues with typical alternating signals often interrupted by approach signals: the bat is flying along a forest track with branches that droop into its flight path and hamper the continuous emission of alternating signals at a regular rhythm.
- **Sound File 3.99:** Authentic 'catch sequence': two species are flying close to one another and emitting flat-ended FM sweeps at different frequencies (38 and 45 kHz). The overall rhythm of the sequence could well evoke the specific rhythm of a barbastelle emitting alternating signals. The FMEs, structures and durations, although slightly different, could easily mislead an inattentive or inexperienced observer; *Pipistrellus kuhlii* and *P. pipistrellus*.
- **Sound File 3.100:** Sequence of alternating signals of *Barbastella barbastellus* ending suddenly with a capture phase although no approach phase precedes it (recording by P. Jourde).
- **Sound File 3.101:** The sequence begins in the midst of a capture phase lasting at least 1.5 s (its beginning is not recorded and therefore not timed) and including at least five pursuit phases separated by resource phases (time to breathe?); this is followed by a few transition signals (derived from type B signals) and then by typical alternating signals.
- **Sound File 3.102:** Sequence of typical ES high signals; the five most saturated signals also produce a false impression of final whack: when, like here, this is only heard in the most intense signals of a sequence with no change in rhythm to indicate a change in flight conditions, it is important to check whether the signals concerned are saturated (the oscillogram display of the signals should be examined to see whether the maxima and minima of the envelope are clipped – i.e. cut off along a horizontal straight line at a certain height); in this sequence, all the signals should be considered as ES high.
- **Sound File 3.103:** Brief high-frequency signals in which the ES sensation is rather faint and unequal; in most signals, the intensity is at its maximum level right from the start, including towards the end of the sequence, when the end frequency decreases; the start of the signal is therefore abrupt rather than truly explosive, but not progressive; this sequence should be categorized as a ES high sequence.



- **Sound File 3.104:** The sequence contains signals with a weak, almost imperceptible, explosive start (e.g. signals 1 and 3) as well as typical abs high signals (see Sound File 3.2, 3.7, 3.9 and those following); the bat worker should classify this sequence as abs high, but also take into account the fact that the emitting bat is capable of producing ES high signals (and therefore exclude *Myotis daubentonii* from the list of possible species).
- **Sound File 3.105:** Only the signals from the middle of the sequence give the sensation of a marked explosive start (select and listen to the first three and last four signals for comparison); however, the oscillogram display shows that they are saturated (clipped maxima and minima of the envelope) and the auditory sensation differs from that of true explosive starts; if you are still hesitating between explosive start and absence of peak for the other signals, consider 1) that as the bat is close to the microphone the signals are intense (and the high frequencies fairly unattenuated), and 2) that the repetition rate is fast, indicating that the bat is actively probing its environment and spending more energy in the high frequencies; no explosive sensation is audible at the very start of the signals (whereas it would be unmistakable in such conditions); absence of peak.
- **Sound File 3.106:** The first signals are of the abs med type, but the following signals in the middle of the sequence, more intense and with an accelerating repetition rate, give a clear sensation of explosive start; however, although they show no evidence of saturation on the oscillogram, they cannot be considered as ES signals since the auditory sensation produced is more like the sound of an electric spark than a true 'biological' explosive start: the bat was too close to the microphone and the excessive intensity of these few signals produced this recording artefact; the signals recorded immediately afterwards, as the bat was receding while maintaining a fast repetition rate, produce a clear explosive start with no risk of saturation; the signals are indeed of the ES med acoustic type and the sequence therefore includes a transition from abs med to ES med.
- **Sound File 3.107:** The signals of this sequence produce an unusual auditory sensation; the 'final whack' sounds more like a final 'crack': it is in fact made up of a rapid series of peaks. This false whack is due to several factors: the first is the sine-like amplitude modulations resulting from the reflection of the signals on the water surface, which produces a 'rasping' effect (due to the succession of intensity peaks, visible on the spectrogram, oscillogram and power spectrum); second, this amplitude modulation is amplified by the echo that follows each signal and is responsible for the time-lapse between the signal and the 'crack' sound, making it resemble a final whack; third, the saturation amplifies all these effects and interferes with the auditory analysis. Only a few signals, including the last three, are unsaturated and allow the listener to classify them confidently as abs med signals with amplitude modulations (the bat is flying just above the surface of still water).
- **Sound File 3.108:** Sequence with brief, typical ES high signals; these are the signals for which the evaluation of the energy peaks and their position is most difficult (brief duration, high frequencies); the energy peak occurs at the start of the signals, on all signals; the last, weak signals of the sequence, as the bat is receding, generate an echo at lower frequencies that must not be interpreted as a final whack: not only does it sound different, but it would also have been audible in the previous signals since there is no change of rhythm to justify a switch of acoustic type (one signal is practically inaudible, highly attenuated by the distance).
- **Sound File 3.109:** Sequence in which all the signals should be classified in the absence of peak category: this is obvious for the weaker signals at the beginning and end of the sequence; the middle signals are more intense because the bat is closer to the microphone and the entire spectrum of the frequencies swept is picked up, including the highest frequencies at the very beginning of each signal (the frequencies most attenuated by distance); no explosive start is audible.
- **Sound File 3.110:** This *Myotis bechsteinii* sequence begins with abs med signals; the bat is flying in a clearing then approaches a low branch and quickly switches to FW high signals, skirts a mass of foliage a mere 20 cm away, then flies away and switches back to abs med signals (last signal). The final whack is not audible on the weakest signals: overall, it is not very explosive, but the signals do end very abruptly.
- **Sound File 3.111:** Short sequence in which two *Myotis bechsteinii* meet when flying among the loose foliage of a rather open forest understorey; both are emitting FW high signals.
- **Sound File 3.112:** Sequence in which a *Myotis brandtii* emerges from the forest undergrowth (first FW high signals), then skirts the forest edge close to the vegetation using typical FW med signals with a slow repetition rate, and eventually locates a prey (capture phase).
- **Sound File 3.113:** Sequence in which a *Myotis emarginatus* flies along an ivy-covered wall and actively explores its surface; the FW high are emitted at a fast and regular rhythm.
- **Sound File 3.114:** Sequence in which two *Myotis emarginatus* are flying along a forest track strewn with obstacles; the FW high signals vary in frequency and repetition rate depending on the distance of the nearby masses of foliage.
- **Sound File 3.115:** Typical sequence of *Myotis mystacinus* in cruising flight (ES high), approaching a tree and flying round it: the final whack becomes clearer in the middle of the sequence, when the explosive start

disappears and the frequency drops (on the weaker approach signals, it is necessary to increase the density of the spectrogram display by lowering the threshold in order to measure the EF); the approach signals of the end of the sequence are of the FW med type but they are weak and must be listened to attentively.

- **Sound File 3.116:** Typical sequence of two *Myotis daubentonii* flying side by side in an open understorey; the signals are first of the abs med type (at times close to abs high), switch to FW med in the middle of the sequence (somewhat subdued, and not all signals), and eventually revert to abs med when the two bats start to separate.
- **Sound File 3.117:** Two *Myotis daubentonii* foraging together in the sparse foliage of a walnut-tree crown; all the signals belong to the FW med type.
- **Sound File 3.118:** Two *Myotis myotis* flying in succession along a narrow forest track strewn with branches; EF is medium, repetition rate high and there is a slight final whack; some FW high signals of *Myotis emarginatus* can be heard in the background.
- **Sound File 3.119:** Just after emerging from its roost, a *Myotis oxygnathus* flies through some forest undergrowth; the first three signals are of the abs med type, but then the bat switches to FW med signals; the last two signals are very close to the FW low type (recording by R. Toffoli).
- **Sound File 3.120:** A *Myotis oxygnathus* is flying through dense vegetation (a few FW med signals) before reaching open space (ES high) (recording by R. Toffoli).
- **Sound File 3.121:** Typical *Myotis bechsteinii* abs med sequence of broadband signals with an FME at around 40 kHz; the last four signals are emitted as the bat flies through denser forest understorey; since the flight speed remains slow, the repetition rate is barely faster, but the acoustic type changes: a slight final whack becomes audible at a medium EF, this being especially true of the last two signals of the sequence.
- **Sound File 3.122:** Two *Myotis bechsteinii* are flying together in forest understorey; the more distant one is emitting abs med signals while the other one, closer to the foliage mass, is emitting FW med signals.
- **Sound File 3.123:** Two *Myotis brandtii* are flying together along a vegetation border, close to the foliage; both are emitting FW med signals at a fast repetition rate.
- **Sound File 3.124:** Typical FW med sequence of *Myotis brandtii*; slow and fairly regular rhythm; the final whack is perfectly audible, even on weaker signals; the bat is flying along a vegetation border.
- **Sound File 3.125:** Sequence of a *Myotis myotis* picking its way through dense undergrowth; the signals of the beginning of the sequence are of the abs low type (towards the upper end of the spectrum due to the flight context), then the bat switches to FW low for three signals during a brief approach phase; after two resource signals with a higher FME, the bat emerges from the vegetation and gradually reverts to a typical abs low acoustic type.
- **Sound File 3.126:** Long sequence of FW low signals emitted by several *M. oxygnathus* near the entrance of their roost (the sequences tend to be shorter when the bats are out foraging); EF and duration values are comparable to those of *M. nattereri* but the BW is narrower and the FME lower; the final whack is very strong (recording by R. Toffoli).
- **Sound File 3.127:** Brief FW low signals with a very wide bandwidth emitted by a group of *Myotis escaleraei* emerging from their roost; no difference noted with *M. nattereri* signals in similar circumstances (recording by M.-O. Durand).
- **Sound File 3.128:** Series of weak, rapidly repeated FW low signals typical of a *Myotis nattereri* hunting in forest undergrowth, close to foliage or the ground; the bandwidth is much broader in reality than what is perceptible or visible here due to the weakness of the signals; the final whack dominates the overall auditory impression and remains the only audible element when the bat departs; a *Hypsugo savii* in approach flight can be heard in the background.
- **Sound File 3.129:** Typical FW low sequence emitted by a *Myotis nattereri* in open understorey; variations in rhythm and bandwidth, some signals span 130 kHz from 140 kHz down to 10 kHz; note the convex shape of the upper part of the signal, which is characteristic of this type of signal in this species.
- **Sound File 3.130:** Typical FW low sequence emitted by a *Myotis nattereri* in a forest understorey, including the capture of a prey item followed by a resource phase with slow repetition rate.
- **Sound File 3.131:** The first signals of this *Myotis nattereri* sequence are of the abs high type, with a very high FME and intervals > 100 ms; the bat then comes closer to the vegetation and quickly switches to the FW low acoustic type, with a rhythm that varies depending on the distance to foliage; the sequence ends with a capture phase.
- **Sound File 3.132:** Sequence emitted by a *Myotis nattereri* flying along a widely cleared forest road; repetition rate is very slow (intervals of 150 ms), the bandwidth spans 120 kHz (from 130 to 10 kHz) and signal duration is long (5 ms); the final whack is strong, even in this context.
- **Sound File 3.133:** Long sequence of a *Myotis brandtii* in passive search in its foraging area in woodland; all the signals are of the ES&FW type; the two energy peaks are both audible in all signals,

whatever the distance to the microphone (hence the intensity of the recorded signal); the capacity of *M. brandtii* to employ the explosive start, the final whack or both regardless of its behaviour (i.e. regardless of repetition rate, signal duration or FME...) is highly characteristic.

- **Sound File 3.134:** Same type of sequence as Sound File 3.133: *Myotis brandtii* foraging in woodland; the great diversity in energy distribution patterns is more obvious here: some of the first signals are of the ES high type, the most intense ones in the middle of the sequence are closer to FW med signals, and all the other signals of the sequence are of the ES&FW type.
- **Sound File 3.135:** One *Myotis bechsteinii* is flying in circles above the entrance to its roost after emergence, at dusk, in an open forest understorey; other individuals (not audible here) are flying in the vicinity and many others yet are still inside the roost; very slow repetition rate (intervals often over 100 ms) and broad bandwidth (one signal reaches 100 kHz in BW); this acoustic behaviour lasts only for a brief moment: after a few seconds, the bats revert to their usual acoustic types.
- **Sound File 3.136:** One *Myotis oxygnathus* is flying close to a vegetation border; its behaviour is not wholly natural since it has just been released after being mist-netted and handled; however, these signals were not emitted in the first seconds after the release; the sequence shows that the species is capable of producing ES high signals but does not shed much light on what behavioural and environmental contexts could trigger such emissions in natural situations; variables as measured are close to those of *Myotis capaccinii* (recording by R. Toffoli).
- **Sound File 3.137:** Typical sequence of *Myotis capaccinii* emitting ES high signals, at a slow rhythm; some of the signals from the end of the sequence exceed the 30 kHz threshold for EF, which is very unusual: the targeted individual (another one can be heard in the background) is flying between the bushes of a sparse *maquis*, narrowly skirting the upper branches.
- **Sound File 3.138:** Sequence of *Myotis capaccinii* emitting ES high signals at a fast rhythm; the bat is flying above a denser sector of a sparse *maquis*; the signals are shorter, with a higher EF and a narrower BW than in Sound File 3.137.
- **Sound File 3.139:** Soon after its release, this *Myotis brandtii* emits a short series of ES high signals and then switches to ES&FW signals when nearing an obstacle; this pattern has been observed several times in natural flight and seems to be common in this species, in which the ES high type is only used during a brief transition phase prior to approach, when the FW feature (as FW med, FW high or ES&FW) appears (recording by P. Favre).
- **Sound File 3.140:** One *Myotis emarginatus* is transiting along a forest track; the first five signals show no trace of energy peak: abs high type; then the bat notices an obstacle to be avoided and switches to ES high (from the sixth to the 16<sup>th</sup> signal); the remainder of the sequence is made up of FW high signals; such a transition is unique to this species.
- **Sound File 3.141:** Typical *Myotis emarginatus* sequence: the bat flies through forest undergrowth (ES high signals), locates an obstacle and avoids it (FW high signals) and continues in more open understorey (ES high signals); attention should be focused on the position of the energy peaks: explosive starts and final whacks are never on the same signal; in similar circumstances, *Myotis brandtii* would certainly have used ES&FW signals.
- **Sound File 3.142:** Long sequence of a *Myotis alcathoe* hunting in an open forest understorey; all the signals belong to the ES high type regardless of repetition rate; the explosive start is audible even on the very weak signals of the middle of the sequence.
- **Sound File 3.143:** *Myotis alcathoe* transiting in the open (flying 2 m high above a meadow, more than 50 m from the nearest vegetation border); the explosive start is less strong, but the beginning of the signals is still 'abrupt'; the EF remains high.
- **Sound File 3.144:** *Myotis alcathoe* in transit above a forest road, between two foraging bouts in the canopy; mean EF remains high and the explosive start is clearly audible.
- **Sound File 3.145:** Typical sequence of *Myotis mystacinus* flying in an open forest understorey; according to the mean EF value the signals are of the ES high type, but most of the signals that are sufficiently intense for measurement end very near 30 kHz.
- **Sound File 3.146:** Another typical ES high sequence of *Myotis mystacinus* flying along a forest track; the approach phase does not involve any substantial elevation of the EF.
- **Sound File 3.147:** ES med sequence of *Myotis mystacinus* in transit close to a forest border; at first the bat is closely skirting the foliage (the first two signals are of the ES high type) then it comes a little more into the open and decreases both repetition rate and EF.
- **Sound File 3.148:** The reverse of what was happening in Sound File 3.147: a *Myotis mystacinus* is flying in semi-open environment (ES med signals) then comes closer to foliage and changes over to ES high signals.
- **Sound File 3.149:** ES med sequence of a *Myotis daubentonii* hunting along a narrow footpath through forest undergrowth.

- **Sound File 3.150:** Abs high sequence of *Myotis capaccinii* in transit flight; the smooth sonority and the duration of the signals are characteristic.
- **Sound File 3.151:** Abs high sequence of *M. capaccinii* hunting (recording by T. Disca).
- **Sound File 3.152:** Abs high sequence typical of *Myotis daubentonii*; with the exception of three saturated signals, the sonority is smooth; signal duration is shorter and the EF lower than in *Myotis capaccinii*.
- **Sound File 3.153:** Abs high sequence of *Myotis emarginatus*; these signals during transit through open habitats have a sonority that is not quite as smooth as in the other species; three signals from the middle of the sequence display hints of an explosive start.
- **Sound File 3.154:** This *Myotis nattereri* sequence of abs high signals was recorded amidst heavy background noise and had to be filtered to improve signal clarity; note the very high FME as well as two FW low signals typical of this species.
- **Sound File 3.154a:** Long sequence recorded in fairly open forest understorey. A first series of abs high signals is heard (with a very faint final whack maybe due to an echo; the start is clearly progressive). This is followed by a series of FW low signals from another bat: the curve at the end of the signal is sharply concave and announces a QCF component, which is clearly visible at 24,850 ms and confirms the auditory sensation (narrow BW, faint explosive start) that the emitting bat is a *P. pipistrellus* producing abridged flat-ended FM sweeps; this bat leaves the area suddenly at 32,850 ms. At 48,000 ms appears a new series of high frequency *M. nattereri* signals; duration, EF, BW and FME values are very similar in the two species and the curvature is here also hyperbola-like (but not concentrated at the extreme end of the signal, as in *P. pipistrellus*). Confirmation is possible when these signals progressively shift to the FW low type. A new phase follows after 63,000 ms, in which the bat seems to 'hesitate' between the abs high and FW low types. After 83,700 ms, there is a series of long abs high signals (sometimes the EF descends to 25 kHz) with a sigmoid shape - a rare acoustic behaviour in *M. nattereri*. At 121,600 ms, another series of FW low signals is heard as the bat is approaching obstacles. This sequence is remarkable for the diversity of the abs high signals it contains, showing the acoustic plasticity of *M. nattereri* in spite of its strong specialization in the FW low type.
- **Sound File 3.155:** Abs high sequence of *Myotis daubentonii* hunting on a lake.
- **Sound File 3.156:** A *Myotis dasycneme* flies along a forest border and then leaves it in the second part of the sequence; all the signals are of the abs med type but there are marked variations in signal duration.
- **Sound File 3.157:** *Myotis dasycneme* hunting over still water; the signals are of the abs med type but clearly longer, and with a narrower BW, than in Sound File 3.156.
- **Sound File 3.158:** *Myotis capaccinii* in transit along a forest border; abs med signals less than 5 ms long; high repetition rate.
- **Sound File 3.159:** *Myotis capaccinii* hunting over still water, in wide circles at 0.5 to 1.5 m above the surface (not skimming); abs med signals more than 5 ms long; the EF is lower than in Sound File 3.158; BW is often less than 50 kHz.
- **Sound File 3.160:** *Myotis daubentonii* hunting along a forest border; abs med signals of approximately 3.5 ms in duration; FME at about 50 kHz.
- **Sound File 3.161:** *Myotis daubentonii* hunting actively over still water, skimming the surface; abs med signals 6-7 ms long; FME under 45 kHz.
- **Sound File 3.162:** The same *Myotis daubentonii* as in Sound File 3.161 a few minutes later, this time in passive search for prey above still water (skimming the surface); abs med signals about 7 ms long, with an FME under 40 kHz; the first part of the signal, at higher frequencies, is less intense (probably due to attenuation by the bat itself), giving the auditory impression of a narrower BW than in Sound File 3.161.
- **Sound File 3.163:** *Myotis brandtii* foraging in open forest understorey; the first signals are of the FW med type (the final whack is not heavily marked, but present) with an EF at around 25 kHz, then the energy peaks disappear altogether and the bat changes over to abs med signals with a slightly stepped-up EF, at about 29 kHz (highly variable in this species when it emits this acoustic type).
- **Sound File 3.164:** *Myotis brandtii* hunting along a forest border at a varying distance from the foliage; all the signals are of the abs med type: repetition rate varies according to distance from obstacles, but otherwise signal measurements remain fairly constant; broad BW (about 80 kHz); EF at around 25 kHz.
- **Sound File 3.165:** *Myotis mystacinus* flying across a meadow about 20 m from the nearest vegetation border; a very faint explosive start can be sensed in the first signals but is absent later on; this species only uses this type of signal when in transit along an uncluttered flight path, sometimes for very brief periods of a few seconds only.
- **Sound File 3.166:** Another *Myotis mystacinus* sequence; the bat is in transit above a meadow, about 20 m from the nearest vegetation border; the artefact due to sound saturation, audible in some signals, must not be taken for an energy peak produced by the emitting bat: no explosive start is audible on any of the unsaturated signals.



- **Sound File 3.166a:** A *Myotis mystacinus* flying in a small clearing, not very far from the forest border; apart from a few ES med phases (e.g. between 8000 and 10,000 ms), most signals are of the abs med type (no explosive start can be heard between 5000 and 7000 ms; the saturation artefact audible on a few signals should not be mistaken for an energy peak). On many signals, a very faint explosive start can be discerned, something between an abs med and an ES med signal: one feels that the bat 'hesitates' between the two acoustic types. The capture phase around 12,000 ms shows that the acoustic behaviour of passive search in a semi-open habitat does not prevent the bat from making the most of a passing opportunity.
- **Sound File 3.167:** *Myotis bechsteinii* foraging in dense forest undergrowth; high repetition rate; all the abs med signals are alike.
- **Sound File 3.168:** Two *Myotis bechsteinii* meet in a forest understorey; the abs med signals at the beginning of the sequence are brief, with an EF at 24 kHz on average; one of the two bats reaches an opening and immediately emits a few longer abs low signals before reverting to the abs med type: this pattern is typical of the species.
- **Sound File 3.169:** A *Myotis bechsteinii* flying in open forest understorey and emitting abs med signals; the phases during which repetition rate and EF change correspond to the bat avoiding individual trees.
- **Sound File 3.170:** *Myotis bechsteinii* hunting in the canopy; the repetition rate remains slow because the bat is flying at low speed; there are, however, many variations in signal structure, depending on the density of the foliage masses; the signals are of the abs med type, but there are remarkable changes of FME and SF from one signal to the next; the most high-pitched signals are intense right from the start, a trait that reinforces the impression of high frequencies.
- **Sound File 3.171:** A *Myotis bechsteinii* flying across an orchard with scattered trees more than 20 m apart; the sequence illustrates perfectly how this species is able to adjust its abs med and abs low signals in real time: as soon as it has a few metres of open space ahead of it, it produces one or more longer and lower-pitched signals.
- **Sound File 3.172:** A *Myotis punicus* hunting in an abandoned meadow with scattered shrubs; due to the weakness of the signals, there is some doubt as to their start frequency (and hence duration and bandwidth); BW seems fairly narrow to the ear; the EF is well marked, at about 23 kHz; the slow repetition rate indicates that the bat is passively seeking prey and that obstacles are few and fairly distant; the medium EF is remarkable for a large *Myotis* species in this type of context.
- **Sound File 3.173:** A *Myotis myotis* hunting in dense forest undergrowth, winding in and out of the shrubs and emitting abs med signals whose EF is adjusted according to the proximity of the obstacles; in tighter passages between branches, the bat switches to a series of abs low signals before changing back to abs med signals.
- **Sound File 3.173a:** A *Myotis myotis* hunting in a forest; a few abs high signals quickly followed by typical abs med signals; medium repetition rate with intervals between 70 and 90 ms (but the repetition rate is often much slower); the phases with an end frequency > 30 kHz are fairly rare and always very brief (4 or 5 signals only); their rhythmic layout recalls that of the abs high signals of *Myotis nattereri*, but with a higher FME.
- **Sound File 3.173b:** The sequence starts with QCF-FM signals with an FME of approximately 38 kHz. The signals progressively and irregularly increase in bandwidth by a rising start frequency, taking on a sigmoid FM structure. The auditory analysis could suggest steep FM sweeps of a *Myotis* in abs med, but the variations of structure and bandwidth (sometimes from one signal to the next) suggest otherwise. Moreover, in this recording, two individuals are present, and one of them produces trilled social calls at around 30 kHz. A one-off social behaviour in *P. kuhlii* (recording by Julien Vittier).
- **Sound File 3.173c:** A sequence in which two *P. kuhlii* are present. The typical flat-ended FM signals of the beginning progressively change shape to take on the sigmoid FM structure of the social behaviour described in the 3.173b recording. Trills can also be heard (recording by Loïc Bellion).
- **Sound File 3.174:** Abs low sequence of *Myotis nattereri* illustrative of the short signal duration and fleeting nature of this acoustic type in this species: the FW low type takes over rapidly with a lower EF.
- **Sound File 3.174a:** Sequence including a transition between the FW low and abs low acoustic types in *Myotis nattereri*; the FW low signals display the entirely convex shape typical of the species; the abs low signals appear as the bat is crossing an open area; the duration of the signal increases and the shape becomes sigmoid. A very faint impression of final whack can sometimes be heard on such signals (this is not a true final whack, but a sudden drop in intensity at the end of the signal), probably linked to the systematically concurrent behaviour of flying along a horizontal vegetation surface: the same feature is found in the larger *Myotis* species when they probe passively the ground or the vegetation. In the case of such sigmoid abs low signals with subdued 'final whack', distinguishing between *M. myotis/oxynathus* and *M. nattereri* is very difficult; the only additional element that can settle the matter is the presence of associated FW low signals (curvature and intensity criteria). On the other hand, this faint final whack is never heard in *M. bechsteinii* signals.

- **Sound File 3.175:** *Myotis brandtii* sequence of abs low signals recorded from a bat crossing a meadow; the EF is stable at around 20 kHz; the evenly distributed energy gives a smooth sonority to the signals.
- **Sound File 3.176:** All the signals in this sequence end at 23 kHz or lower and show no audible energy peak, but the auditory sensation is close to that of abs med signals because the energy is nonetheless concentrated in the middle of each signal; the fifth and seventh signals are the only ones to display the typical smooth sonority; such disparity from one signal to the next is characteristic of *Myotis bechsteinii* (as seen earlier in the section on abs med signals); without this characteristic behavioural trait, it would be impossible to distinguish these signals from those of *M. brandtii* (on the sole basis of signal measurements).
- **Sound File 3.177:** Typical abs low sequence of *Myotis bechsteinii* in transit across a meadow more than 10 m away from the nearest vegetation border; the smooth sonority (except for a few saturated signals) and the signal duration of longer than 10 ms are highly characteristic; the FME above 40 kHz rules out *Myotis myotis*.
- **Sound File 3.178:** A *Myotis oxygnathus* hunting in *garrigue* scrub with small scattered trees; although the bat is flying at less than 2 m above the ground, it emits abs low signals with low FME and narrow BW: two important characteristics of the species.
- **Sound File 3.179:** A *Myotis myotis* hunting in a forest; the first eight signals of the sequence are of the abs med type with an EF at between 23 and 25 kHz; the bat then avoids a bush with a few FW med signals and reverts to abs low signals as the undergrowth opens up a little.
- **Sound File 3.180:** A *Myotis myotis* hunting along a forest track; the energy maximum is distributed over the second half of the signal and the upper end of the frequency band is faded; the EF lies between 20 and 23 kHz, with a few rare signals ending at 24 kHz.
- **Sound File 3.181:** A *Myotis myotis* in transit flight along a wide forest track between two high forest edges; the features of the signals are the same as in the previous sequence (Sound File 3.180) except that the repetition rate is slower and more regular.
- **Sound File 3.182:** An *Eptesicus serotinus* in transit flight along a wide forest track between two high forest edges (context identical to that of the *Myotis myotis* sequence of Sound File 3.181); signal duration is a little longer and the FME a little lower: these slight differences are, however, perceptible to the ear; since such differences are not always clearly audible, it is often necessary to analyse the signals on the computer, measuring them and gauging their shape, in order to reach a confident decision.
- **Sound File 3.183:** A *Myotis myotis* foraging in a recently cut hay meadow; the abs low signals are similar to those of the transit flight; attenuation due to the distance thins out the higher frequencies first.
- **Sound File 3.184:** A *Myotis myotis* in transit above very open grassland, about 4 m above the ground; the sonority of the signals is smooth and recalls those of *Myotis bechsteinii* because the energy is distributed over the full extent of the signal; however, the FME is at 31 kHz, which is too low for *M. bechsteinii*.
- **Sound File 3.185:** Transition from FW high or med signals to abs med signals, followed by a series of abs med signals containing an isolated abs low singleton: in this case, the identification is certain: *M. bechsteinii*; the bat afterward flies across a screen of foliage again (FW high signals) and emerges into a clearing with a series of abs low signals.
- **Sound File 3.186:** Very long sequence recorded by Marc Van de Sijpe in a forest in Belgium, in which several *M. brandtii* are followed from their maternity roost to a foraging spot close by; a typical detail can be heard: many signals that one would be tempted to consider as abs med (given their duration and end frequency) exhibit faint explosive starts and final whacks, while the typical short and high-frequency ES&FW signals are mostly produced during approach phases (especially before capture phases); one *P. pipistrellus* is also heard now and then in the background (sonar signals and social calls).
- **Sound File 3.187:** *M. capaccinii* emitting mixed signals of the ES high and abs high types in the same sequence; the decisive criterion is the duration, longer than in other species.
- **Sound File 3.188:** *M. dasycneme*. This species hunts mostly above quiet water bodies, using two types of foraging behaviour; one consists in flying at a constant height close to the water surface, not far from the banks in the manner of *M. daubentonii* but a little higher (0.43 m above the water on average, as against 0.24 m); the other foraging behaviour consists in flying at high speed along the central axis of large canals in order to catch tympanate moths located above the bat's flight path; the signals emitted are of the abs med type in both cases, but in the latter they are also long-duration flat-ended FM signals, highly characteristic of the species (recording by Marc Van de Sijpe).
- **Sound File 3.189:** Long sequence of *M. daubentonii* hunting above a small lake, including different phases of activity marked by changes of signal type; the bat arrives in the area by flying over an abrupt forest border: signals are of the abs med type with a smooth sonority (energy evenly distributed over the entire duration of the signal); it immediately begins to hunt above the water surface: the signals are still of the abs med type, but the second part of the signal concentrates more energy and the sonority takes on a 'rasped' quality due to amplitude modulations; as a conspecific joins in, a few FW med signals are heard when the two bats are close to each other in approach phase (also when in pre-approach of prey); the bat then crosses the lake

about one metre above the water: the repetition rate becomes clearly slower, but the acoustic type remains the same – in such conditions, *M. bechsteinii* would have produced one or more abs low signals.

- **Sound File 3.190:** *M. emarginatus*; sequence showing how a bat hunting in forest understorey changes over between ES high and FW high signals depending on the repetition rate.
- **Sound File 3.191:** *M. emarginatus*; illustration of the unique capacity of this species to produce FW high signals over long sequences.
- **Sound File 3.192:** Sequence in which several *M. myotis* are coming out of a forest understorey on to a forest track about 50 m from their roost, from which they have just emerged: the first signals, in the forest undergrowth, are of the FW med type, but the bats switch to FW low as they burst through the leafy screen bordering the track; the final whacks continue a little since the two bats arrived at the forest border very close to one another; the one further away crosses the track to plunge into the undergrowth on the other side while the nearest one rises to about four metres above the ground and flies between the two parallel forest edges, quickly changing its acoustic type to abs low; it then swerves round, brushing the foliage (FW med signals), and passes by the microphone a second time, in high, direct flight, emitting abs low signals, many of them over 8 ms long.
- **Sound File 3.192a:** Sequence showing a number of characteristic traits of the emissions of *M. myotis* foraging in forest understorey. The first signals are of the abs med type, with an FME between 40 and 44 kHz; the particularly slow rhythm (intervals of 110 to 300 ms) makes unlikely both *M. bechsteinii* (which would be emitting abs low signals in such a context) and *M. mystacinus* (whose intervals, even in open environments, average less than 100 ms); another characteristic is the difference in intensity from one signal to the next. After 1.5 s, the signals' FME increases abruptly by about 30 kHz and the rhythm, slow at first, accelerates; the EF is at approximately 30 kHz. Between 7 and 7.5 s, one of the signals stands out as particularly intense. All these criteria (low repetition rate in abs med mode, and variations in rhythm, intensity and FME) confirm the identity of the emitting bat and are typical of this species' behaviour in the understorey.
- **Sound File 3.193:** One *M. nattereri* hunting in forest understorey, with variations in rhythm and frequency although all the signals are of the FW low type; the final whack is so audible that it is the last thing heard when the bat recedes into the distance; the phases of high repetition rate (approximately 30 pulses per second) when the bat is moving through foliage are remarkable.
- **Sound File 3.194:** Sequence of high-frequency sonar signals produced by adult *Myotis bechsteinii* bats flying in the foliage surrounding their roost tree; a single, isolated call, very like an abs low sonar signal, is taken to be a social call because the flight context does not justify the use of such low-frequencies in a sonar signal; according to our current knowledge, these emissions are characteristic of the species.
- **Sound File 3.195:** Trilled social call of *Pipistrellus pygmaeus*; each trill often includes more than three elements; note that the last one is more high-pitched than the others.
- **Sound File 3.196:** Social call of *Pipistrellus pygmaeus*, varied, with rich modulations, somewhat resembling the social calls of *Hypsugo savii*.
- **Sound File 3.197:** Trilled social calls of *Pipistrellus pipistrellus*; the trills comprise a variable number of elements, but often two or three; in general, the individual components are all at the same frequency.
- **Sound File 3.198:** Trilled social calls of *Pipistrellus pipistrellus*; here the trills comprise more than three elements and the intervals are very short.
- **Sound File 3.199:** A more uncommon type of social call of *Pipistrellus pipistrellus*: descending FM sweeps of various lengths, sometimes prolonged by an ascending FM sweep.
- **Sound File 3.200:** Double-trill social calls of *Pipistrellus nathusii*.
- **Sound File 3.201:** Trilled social call of *Pipistrellus nathusii*; here, the second trill is sometimes repeated (recording by T. Pottier).
- **Sound File 3.202:** Trilled social call of *Pipistrellus nathusii*. Note the single, simple call inserted between the two trills (it is almost always present, but in this case it is very obvious and sometimes reiterated); such a call is occasionally emitted on its own (Pottier, pers. com.); confusion is possible with sonar signals of another species (especially *Plecotus* spp, due to the rich timbre of the sonority – but these social calls, unlike the sonar signals of long-eared bats, do not display the transfer in maximum energy from the beginning of the first harmonic to the tail of the second). In this sequence, the sonar signals are highly modulated and high-pitched: the two bats involved are probably flying very close to one another (recording by T. Disca).
- **Sound File 3.203:** Trilled social calls of *Pipistrellus kuhlii*; note that, compared with the other species, the frequency is lower and the intervals are longer (slow trill).
- **Sound File 3.204:** Trilled social calls of *Pipistrellus kuhlii*; although the frequency is higher than in the previous recording and the intervals are shorter, the difference from *P. pipistrellus* trills is still clear.
- **Sound File 3.205:** A more uncommon type of social call of *Pipistrellus kuhlii*, consisting of an FM-QCF pulse with an FME at 27 kHz.

- **Sound File 3.206:** Sequence in which two *Hypsugo savii* are flying along a forest border; one or both is emitting characteristically undulated social calls.
- **Sound File 3.207:** Song of *Vespertilio murinus* in Norway; some of the calls are reverberating against building walls (recording by L. Gjerde).
- **Sound File 3.208:** Simple song of a male *Nyctalus leisleri*; this element may be repeated for several hours at a rhythm of approximately one per second.
- **Sound File 3.209:** Compound vocalizations of a *Nyctalus leisleri*, comprising both trills and long QCF calls.
- **Sound File 3.210:** Long, convex QCF social calls of *Nyctalus noctula*.
- **Sound File 3.211:** Complex vocalization of a *Nyctalus noctula* perched on a tree trunk; combination of trills and long QCF calls (the second QCF call similar in structure to the long QCF calls of *N. leisleri*, with an initial constant frequency component with an FME at 14 kHz).
- **Sound File 3.212:** A *Plecotus* sp. is flying along a road in a forest; sonar signals, weaker and higher-pitched, can be heard along with social calls whose FMEs vary between 14 and 18 kHz and whose pattern of emission is not compatible with acoustic navigation.



