Identification of Scandinavian Bats by their sounds
Fältbestämning av skandinaviska fladdermöss med hjälp av läten

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Summary

Sounds from flying bats were studied, recorded and analyzed using portable ultrasonic detectors, an instrumentation tape recorder and various instruments in a bioacoustic laboratory. The material collected gave data on pulse design, rhythm and other features of the flight sounds from the 13 species known to inhabit the Nordic countries today. The possibilities to identify species by their sounds under field conditions were evaluated with special attention to observed variation due to hunting situations, differences outdoors and indoors, the use of social calls, etc.

Seven species (Nyctalus noctula, Pipistrellus pipistrellus, Epotesicus nilssonii, E. serotinus, Barbastella barbastellus, Plecotus auritus, Vespertilio murinus) are easily characterized, primarily by specific frequencies in pure CF-pulses, shallow parts of FM-sweeps, alternation of two pulse types and pulse rhythm (statistical distribution of pulse intervals). The remaining six species belong to the genus Myotis. They are more difficult to identify, requiring a lot of experience and training. Myotis myotacinus and M. brandtii, which are described as sibling species, seem to be impossible to separate from each other on sounds. With this exception it is possible to identify M. myotacinus/brandtii, M. nattereri, M. daubentoni and M. daubentoni on pulse rhythm, amplitude and some other peculiarities, but it is difficult and requires favourable conditions. Thus, checking recorded sounds afterwards in the laboratory is sometimes necessary. Combined aural and visual observations facilitate species identification and is therefore recommended. Myotis bechsteini is only recorded from an indoor situation so far, but results suggest that differences from other Myotis species could be expected in the field.

On the basis of results from three years of survey work, some methods are discussed as to their possible application.

Mapping species occurrence. For investigating bat fauna of larger areas, distribution of species, comparing abundance of a species in selected habitats.

Line transects using cars with roof hatch. For securing large amounts of data on abundant species for comparing areas or monitoring population trends.

Sammanfattning

Ljud från flygande fladdermöss undersöktes, spelades in och analyserades med hjälp av ultraljudsdetektorer, en måtbandspelare, samt olika instrument i ett bioakustiskt laboratorium. Det insamlade materialet gav data om pulsernas utseende, rytmen och andra egenskaper hos flyg-lättena hos 13 arter i den skandinaviska fladdermusfaunans. Möjliggörer att identifiera arterna med hjälp av deras lätten under fältförhållanden utvärderades med hänsyn till variationen på grund av flyktsätt, skillnad utomhus och inomhus, användning av sociala lätten etc.


Bechsteins fladdermus M. bechsteini har ännu endast spelats in inomhus, men resultat tyder på att man kan vänta sig skillnader gentemot andra Myotis-arter i fält.

Med ledning av erfarenheterna från tre års inventeringarbetes förelås och diskuteras några metoder för faunaomventering och populationstudier.

Kartläggning av artförekomster. För undersökning av fladdermusfaunan i större områden, arters geografiska utbredning, jämförelse av abundansen för någon art i skilda biotoper.

Linjefotografering med lyssning i tidsläckurs. för att insamla stora mängder av data från vanliga arter, för att jämföra olika områden eller för monitoring av populationers förändring i tiden.

1. Introduction

Flying bats produce sounds for orientation and also for social communication. The acoustic behaviour of bats and the function of the sound signals have been dealt with in an extensive literature. Portable ultrasonic detectors (McCue & Bertolini 1964, Sales & Pye 1974, Andersen & Miller 1977) have made it possible to study bat sounds in the field. However, very few field ecological investigations based on this technique have been published. Problems of species identification based on sounds have received even less attention in the literature. Today it is generally accepted that detectors can be used in the field for separating at least some species in a bat fauna (e.g., Yalden & Morris 1975) but the problems involved are in need of serious examination. Hooper (1969) made a pioneering attempt to classify British bats on their sounds heard in a portable detector. The approximate frequency range, pulse repetition rate and some other notations were given for each species. He was unable to describe distinctions between all species and some data are only based on indoor situations. Therefore some of the most typical sonar sounds used outdoors were not mentioned in Hooper's paper. With regard to this and the fact that 6 of the 14 species in the Scandinavian fauna are not dealt with in any publication on sounds, I found it necessary to study bat sounds and evaluate the identification possibilities.

This publication summarizes the results of three years' work (1978-1980) on the problems of identification in the field. It was mainly carried out in Sweden but some observations and recordings were also made in Denmark and Finland. In 1979 and 1980 I was skilfully assisted by Mats Forslund in parts of the field work. When making recordings in southernmost Sweden I have had a valuable cooperation with Rune Gerell, Lund University, and in Denmark with Hans Baagøe, Zoological Museum, Copenhagen and Hans Jørgen Degen, Odense University. Lee A. Miller, Odense University and Birger Jensen, Århus University have kindly contributed by giving aid and suggestions during the work.

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2. Methods and material

Bat sounds were studied and recorded with the aid of the English QMC S 100 bat detector (heterodyne system) described by Pye in Sales & Pye (1974:17-22) and a modified version of the Danish divider (decade-counter system) described by Andersen & Miller (1977) (available as Bat Monitor by Westec, California), various cassette recorders and a Nagra IV tape recorder. The work that started in 1978 was extended in 1979 to include the recording of original sounds by an instrumentation tape recorder (Brüel & Kjaer 7004 F) with a sound level meter (Brüel & Kjaer 2209) used as preamplifier. Most recordings were made with the microphone of the QMC detector but in some cases also with the Brüel & Kjaer 4135 microphone. In most cases the detector signal was recorded in channel 1 simultaneously with the original signal in channel 2.

This recording system has some limitations. Only frequencies up to approximately 83 kHz are recorded and there is no linearity allowing exact measurements of relative sound pressure levels above 50 kHz. Nevertheless, this system was chosen because of its advantages over potentially competing systems. The most significant diagnostic qualities of Scandinavian bat sounds are found below 50 kHz and are not absolutely dependent on measures of relative sound pressure levels above 50 kHz. Furthermore the extremely good signal to noise ratio, as compared to other instrumentation tape recorders, is of importance when, for example, documenting weak portions of otherwise strong signals. Finally, the equipment is portable and can be carried in the field without difficulty.

The two detector systems were used and compared as to their qualities in identification of bat sounds. Both systems transform ultrasounds into audible signals. The QMC S 100 was found to have the best range (highly sensitive microphone) and my personal experience is that it is easier to learn to recognize different types of sounds when listening to the QMC than to the divider. However, when signals from the QMC detector have been documented on a cassette recorder, no information on frequency is available apart from the user's recollection of how the tuning knob was adjusted. When listening to the divider, signals are heard at one-tenth of their true frequencies and the signals documented on a cassette recorder can be analysed for frequencies by using a period counter.

A quite good, but simple documentation of bat sounds can be achieved with the two detector systems combined. I did this by taking out the high frequency signal from the
QMC S 100 and running it through the divider. The signals from the two detector systems were simultaneously recorded on the two channels of a small portable stereo cassette recorder, Sony TC-D5. Then the QMC-signal was used for listening and searching the tape as well as for pulse rhythm analyses, while the divider signal was used for frequency studies with a period counter.

The small and inexpensive detector version called QMC mini bat detector was also used and examined. It has roughly the same properties as the QMC S 100 but the quality (range, frequency resolution) is not sufficient for the more difficult identifications in the field. In some cases it is necessary, for example, to separate 30 from 25 kHz and this is difficult with the mini detector.

A Myotis nattereri hunting among tree tops cannot be heard in the mini detector.

The field recordings were carried out primarily in connection with a survey of the bat fauna of the Swedish province of Uppland (13 000 km²) but also when making comparative investigations in other areas, mainly on the island of Gotland (3100 km²). Material from this survey comprise results from more than 600 investigated localities, some of them visited repeatedly during the three years (1978–1980), more than 1300 km line transects and finally 35 randomly selected investigation areas. A very large number of the observations were documented on tape, resulting in a reel archive of several thousand recordings of bats sounds. This enabled analyses of many sounds from each species to be carried out, e.g., for the study of variation according to season, habitat, flight type, hunting behaviour and geographical locality. Species identification was checked, primarily by catching the recorded bats with nets, but bat colonies found by searching buildings, hollow trees, old mines, etc., were also used for reference recordings.

Recordings were also made on the archipelago of Aland in Finland, in the provinces of Halland, Skåne and Uland in southernmost Sweden and on Funen and Jutland in Denmark.

The problem of who is who among the unknown bats heard was great in the beginning in 1978 and it was not until 1980 that most of the identification problems were definitely solved. With the gradual progress in the work to disclose the source of different bat sounds, it was in most cases possible to carry out retroactive species determinations. As a result, almost all recorded bats could be identified sooner or later, provided the recordings were of good quality. However, the work is by no means complete with the presentation of this publication, but I consider it impossible to predict the
further time and effort required to solve the remaining identification problems (difference between *Pipistrellus pipistrellus* and *P. nathusii*, and outdoor sounds from *Myotis bechsteinii*).

Analyses of the recorded sounds were carried out at the acoustic laboratory of the Department of Wildlife Ecology in Uppsala. The main instruments used were a Voiceprint 700 making sonagrams and a Nicolet digital memory oscilloscope 2090 C with floppy disks and a Nicolet frequency analyzer 446A. Recordings made on the instrumentation tape recorder were played at one-tenth of original speed for analyses. The various types of diagrams and examinations of sounds are explained in the next section.

A selection of more complicated bat signals were also analyzed at the Department of Speech Communication at the Royal Institute of Technology in Stockholm. The signals were examined by a programme developed from the Interactive Laboratory System on the computer Eclipse S-200.

Finally, an additional possibility to document and analyze certain bat sounds was utilized. People without detectors who helped me to check the occurrence of *Vespertilio murinua*, recorded the display call (maximum energy 14-15 kHz and heard in October) with one of the cheapest and simplest cassette recorders in the market. It has a built in electret microphone and when playing back, nothing was heard. However, after copying the recording to a high quality tape recorder and slowing down the speed, the typical sounds of *Vespertilio* could easily be heard and the rhythm be checked.

The technical systems for recording and analyzing bat sounds can be designed according to other principles. Simmons et al. (1979), for example, gave a comprehensive review of the techniques used by a number of American scientists working with ultrasonic signals.
3. Explanation of the sound descriptions

In the following section the results are presented as diagrams of the original sounds. These were selected from the material to illustrate pulses which are the most common, typical for special situations, or to show examples of the great variation. The diagrams are accompanied by comments on the circumstances under which the various sounds can be heard. Finally, remarks on the sounds as they are heard from the detector are characterized by verbal descriptions.

The diagrams used are of five different types. First, oscillograms, where sound pressure is a function of time, give either the most exact information on the waveform, or the so-called envelope of the pulse (Fig. 1 A) or the rhythm of many pulses (Fig. 11 A), all depending on the time resolution. Second, the frequency/time relation or the so-called sonagram shows the signal with frequency as a function of time where degree of blackness represents sound pressure level (Fig. 1 B). Third, the frequency spectra are derived from the oscillograms by fast fourier transform, where the curve represents relative sound pressure level as a function of frequency (Fig. 1 C). Fourth, some signals are shown as time-frequency structures or so-called landscapes. These figures are made by rows of densely packed frequency spectra each covering a short time segment of the signal. The diagrams can be regarded as three-dimensional but where each frequency curve has been folded down to the right (scale: 20 dB relative sound pressure level between lines)(Fig. 11 K). Fifth, the pulse repetition rate of the pulse trains, has been measured as the time length of intervals. The rhythm is displayed as number of measured intervals (in percentage) that fall into time classes (often 10 ms) (Fig. 1 H). When analyzing the pulse rhythm, the type of flight must be known and specified. The slowest and most regular rhythm comes from bats flying straight at constant speed or in the so-called search phase (Griffin 1958), while the rate is faster and more irregular when making turns, catching insects (approach and terminal phase) as well as flying indoors. In some species different rhythms are linked to the use of different pulse types but the comparison still refers to straight flight (or search phase).

In the literature, pulse types are often classified into groups. Two main groups of bat sounds are frequency modulated sweeps (FM-sweeps) and constant frequency (CF) sounds. Both types occur in the following descriptions but pulses combining FM-sweeps with CF components also occur. Shallow sweeps with almost, but not exact, constant
frequency occur in several species. Such sounds or parts of sounds are sometimes called CF (Simmons et al. 1975) and sometimes shallow FM-sweep (Fye 1980). Nevertheless, such sounds are interesting in species diagnosis because of the possibility to tune the frequency of them with the detector and their species-specific design, e.g., as a sonagram.

For reviews of pulse types and their possible functions see, inter alia, Bullock (1977), Busnel & Fish (1980) and Novick (1977).
4. Sounds recorded from Scandinavian bats

Before going into the sound descriptions a few remarks on the Scandinavian bat fauna will be made.

The bat fauna in Scandinavia includes the following 14 species: *Myotis mystacinus*, *M. brandti*, *M. nattereri*, *M. beechsteinii*, *M. daubentoni*, *M. daubentoni*, *Nyctalus noctula*, *Pipistrellus pipistrellus*, *P. nathusii*, *Eptesicus nilsoni*, *E. serotinus*, *Vespertilio murinus*, *Barbastella barbastellus* and *Plecotus auritus* (Baagøe 1973, Curry-Lindahl 1975, Gerell & Frykhammar 1980, Jensen 1969, Ryberg 1947, Siivonen 1976). However only 13 of these are certainly known to inhabit the area today.

Some of the bat species are rare and confined to limited geographical areas. However, knowledge of their distribution is still scanty. In Scandinavia, *M. beechsteinii* is never found outside the province of Skåne and in recent years only a few single specimens have been observed hibernating in old mines. *Barbastella barbastellus* has been reported from various places in Denmark, south Sweden and Norway but no nursery has been found. *Pipistrellus nathusii* has been found in four places in the southwestern part of Skåne, Sweden and in a limited number of localities in Jutland, Zealand, Lolland and Falster. However, no observations confirming the regular occurrence of this species have been reported during the last few years.

As to the remaining species, there are well-established populations but the exact distribution in Scandinavia is still unknown. Only smaller areas covering the Swedish provinces of Skåne, Öland, Gotland and Uppland have been thoroughly investigated in recent years.
4.1. *Myotis mystacinus* (Kuhl, 1819) and *Myotis brandti* (Eversmann, 1845). Whiskered Bat and Brandt's Bat.

*M. mystacinus* and *M. brandti* have recently been separated as two species. A taxonomic examination of Scandinavian material made by Baagøe (1973) supported the suggestion that they really are two species, both with extensive and overlapping distribution.

Comparing the sounds of these two species appeared to be a difficult task. As to the sounds heard with detector, there was no grouping that supposedly could be referred to the two species. In connection with my recording work in Uppland many bats were caught with nets. So far, all of these were found to be *M. mystacinus* and none of them *M. brandti* (criteria used were relative height of the premolars P₂/P₃ and size of penis in males). On Jutland in Denmark, where only *M. brandti* occurs, active animals from a hibernation locality were used for laboratory recording of the sounds. This was then compared with similarly arranged laboratory recordings of *M. mystacinus* in Sweden. The best basis for comparison, sounds from straight or cruising flight in search phase documented outdoors, still remains to be carried out.

The common echolocation sound emitted by *M. mystacinus* in search phase outdoors is an FM-sweep 2.5 to 3 ms long in duration. It usually sweeps down to 30 kHz and has one maximum of sound pressure in the middle of the second half of the pulse (Fig. 1 A, B). The frequency spectrum (Fig. 1 C) shows a marked peak of energy between 40 and 45 kHz. When flying indoors *M. mystacinus* like most other species, modifies the pulses to be weaker, shorter in time (ca 1 ms) and with peak of energy at higher frequencies (approx. at 50 kHz) (Fig. 1 E, F).

Sounds from *M. brandti* have only been recorded from indoor situations (old mines, laboratory) so far. The pulses were found to be quite similar to those of *M. mystacinus* emitted under corresponding conditions (Fig. 1 D). Frequency spectra were made by averaging 32 sound samples from each species recorded indoors (Fig. 1 F, G). With respect to slight differences in the acoustics of the two laboratories used, there should not be any basis to believe that there are any important differences in the sounds emitted. The problem will be the subject of further studies. The pulse repetition rate of *M. mystacinus* varies, as in all other species, with the type of flight. Repetition in straight cruising flight is, however, often fairly regular. Measured pulse intervals from such a sequence gave a rhythm diagram with an extremely marked peak for the interval 90-100 ms (Fig. 1 H) which is quite typical for the species. The diagram shows that more than 70 % of all measured
Fig. 1. *Myotis mystacinus* recorded in the field (A, B, C, H) and in the laboratory (E, F). *M. brandti* recorded in the laboratory (D, G). Intervals between pulses in sample of straight flight by *M. mystacinus* (H). Comparison between laboratory recordings of *M. mystacinus* (F) and *M. brandti* (G) where each frequency spectrum is averaged on 32 sampled pulses.
intervals between pulses were between 90 and 100 ms long in time, which corresponds to a repetition rate of 10-11 pulses per second. The pulse rhythm is, however, more variable and more difficult to recognize under other flight situations, for instance, when circling around in a small opening or along the wall of a barn.

Pulse repetition rate was analyzed from field recordings of a large number of _M. mystacinus/brandti_ at different localities in Sweden but without the possibility to check the species identity. In the analyses I failed to find any separation into the two groups that could be expected if the rhythm differs between _M. mystacinus_ and _M. brandti_. The negative result might also be explained by the possible absence of _M. brandti_ in the material. Despite its wide distribution it is still unknown whether this species is common or not in Sweden.

The sonar from _M. mystacinus/brandti_ heard in the QMC S 100 bat detector sounds like a rattle of 'dry' atonal clicks best heard when the tuning knob is turned to approx. 45 kHz. The fairly regular repetition rate that sometimes occurs in straight flight is suggestive of the rhythmic sound of a train or a machine.

In many situations it is difficult to distinguish _M. mystacinus/brandti_ from _M. daubentoni_ (see section 4.4.) and in fact both species sometimes hunt in the same habitats. The best way to learn the differences is to gather experience by combined aural and visual observations at localities with only one of the species present, which is quite possible. Recording the detector sounds on a cassette recorder for subsequent examination of the sounds is also a good help in order to acquire identification routines.

The echolocation pulses used outdoors are FM-sweeps only about 2 ms long, usually sweeping down to 35 or 40 kHz. The sweep has a sound pressure maximum in the second half of the pulse, and a peak of energy somewhere close to 50 kHz (Fig. 2 A, B, C). Flying indoors the pulses are shortened to about 1 ms long (D) and the frequency range of the sweep can be shorter (E, F). The sounds are weaker than in *M. mystacinus*. When *M. nattereri* was observed hunting among tree tops, 15-25 m above ground, the sounds were barely heard in a QMC S 100 detector. Pulse repetition rate is higher than in *M. mystacinus*. Data from outdoor flight, search phase, (Fig. 2 G) show a peak for intervals 70-90 ms in length corresponding to 11-14 pulses per second. From recordings made indoors (cellar vaults), data show a peak at 60-70 ms corresponding to 14-17 pulses per second (H).

Especially near the nurseries, e.g., in vaults, ruins and old mines, a very loud pulse is often emitted, singly or repeatedly. It consists of an FM-sweep running from 60 to 13 kHz in about 10 ms (Fig. 2 I, J). According to a detailed analysis made on an Eclipse S-200 as threedimensional frequency-time 'landscapes' (not shown here), the pulse has a maximum sound pressure around 35 kHz. At least in some pulses the sweep levels out to CF at 13 kHz during the last two ms. This sweep is sometimes accompanied by weak second and third harmonics. The pulse is most often heard in spaces with very strong echoes which made it extremely difficult to obtain a pure pulse recording good enough for analysis. In Fig. 2 I the echoes have been deleted so as to enable the fundamental sweep to be distinguished.

The long pulse just described might be of some social significance but I have no observation that really confirms this. It is rather similar to the loud long-sweep of *Plecotus auritus* (see section 4.12.).

The possibility to identify the species *M. nattereri* with the aid of an ultrasonic detector is quite good but not without problems. Once identified, it is quite easy to realize that the very distinct but faint clicks caused by the short pulses and the special rhythm really differ from, e.g., *M. daubentoni*. However, after practical experience obtained when discovering a number of new localities for this species in Uppland and Västmanland, I realised that in almost all cases the awareness that I had encountered *M. nattereri* arose when aural impressions from the detector were combined with visual observations of the flying bat. Two factors were important then. First, the weak clicks can only be accurately interpreted when the distance to
Fig. 2. A-H Nycticeinomys nattereri recorded in the field (A, B, C) and in the laboratory (D, E, F). Pulse rhythm outdoors (G) and in cellar vaults (H).
Fig. 2. I-J. *Myotis nattereri*. Loud long-sweep recorded in cellar vault. Fundamental of pulse with echoes deleted (I), pulse with second and third harmonics as well as echoes (J).

the bat is known (by seeing it) and related to a solid experience of loudness-bat distances for different species. Second, the special flight can be recognized with some training. *M. nattereri* is a master of flying around within small spaces. When the researcher approaches the site of a nursery at dawn, e.g., the opening of a vault, a cellar, or a stone bridge, the bats often meet and inspect the visitor by circling around in front of him and then returning to the vault. This can be repeated a number of times and allows for visual observation, listening and recording. It is also quite easy to catch the bats with nets under such circumstances. The skilful flight in limited spaces was also seen when *M. nattereri* was recorded in the laboratory. The bats inspected all narrow spaces, landed frequently on the floor where it ran like a rodent and easily took to wing again.

Sometimes the identification of *M. nattereri* is confirmed when the loud long-sweeps are heard. In the detector these pulses are suddenly heard as very sharp smacks (which are painful to the ears if the detector sensitivity is adjusted to the weak sonar). Compared to the softer long-sweeps of *Plecotus auritus* these pulses sound harder but there are obvious risks of confusion.
Fig. 3. *Myotis bechsteinii* recorded indoors (A, B, C). Pulse rhythm in straight flight indoors (D).


Because of the rarity of this species the data on its acoustic behaviour is very limited. It has not been heard or recorded in outdoor situations so far. My only material is a recording of a female flying in a large room. To judge from experiences of other species, the sounds may lose their most characteristic and species-specific features when bats are flying indoors. Therefore it is uncertain whether the following description of its sound is of any help to identify the species in the field. However, the results suggest some differences from other *Myotis* species.

The pulses from the flying bat were FM-sweeps from 80-30 kHz 1.2-1.3 ms long. In most cases, after 1 ms, the pulses were followed by a second, slightly weaker pulse (Fig. 3 A, B, C). Such double notes have been recorded in the laboratory from other *Myotis* species but never so regularly occurring as in this case. The time distance between the two pulses was almost exactly constant (2.2 ms between the start of each pulse) throughout the whole recording. The repetition rate from selected straight flight sequences was slow with respect to the indoor situation (Fig. 3 D). The flight appeared to be relatively slow with shallow wing-beats (according to my subjective impression).

The echolocation pulse emitted by *M. daubentoni* flying outdoors (in search phase) is an FM-sweep which goes down to 30 or 25 kHz with a duration of 3-4 ms, sometimes up to near 6 ms. The sweep has almost always a sinusoidal amplitude modulation with approximately 10 maxima throughout the pulse (Fig. 4 A, B). As a result, the frequency spectrum shows a series of peaks with the highest sound pressure levels usually around 45 kHz (Fig. 4 C).

Pulses analyzed from recordings of flight indoors are often somewhat shorter, the sweeps cover a shorter and lower range, e.g., 60-25 kHz (Fig. 4 D, E, F). The pulses are still usually amplitude modulated in the same way as documented outdoors.

Pulse shape being fairly constant in this species, the pulse repetition rate, in contrast, is very variable due to the flying behaviour. Sometimes sequences of slow and regular pulses can be heard (Fig. 4 G) but more often, as in typical hunting flight, a more rapid and variable rate is heard (H). The loudness also varies. The loudest pulses can be heard up to a distance of 40 or 50 m when using a QMC S 100.

Probably all Scandinavian bat species hunt over water at least on some occasions. *M. daubentoni*, however, seems to be more linked to water, and its close vicinities, than most other species. The special hunting technique, close to the water surface, now and then circling around in small areas, is typical. Combined visual and aural observations is therefore the best method for identifying this species. When *M. daubentoni* hunts over land the sounds can be similar and indistinguishable from those used over water. During short periods, probably with special meteorological conditions, almost all *M. daubentoni* in my observation areas moved away from the water and hunted in small clearings in the forest. Apart from this, the species hunted over water surfaces throughout the season (cf. different behaviour described by Nyholm (1965)). Miller & Degn (1981) also found this species hunting over water from spring to autumn.

As to problems separating *M. daubentoni* from *M. dasycneme* see following section.
Fig. 4. *Myotis daubentoni* recorded in the field (A,B,C) and in the laboratory (D,E,F). Pulse rhythm in sequence of straight flight (G) and when flying about (H).

The echolocation pulses of this species are rather similar to those of the preceding species. However, some differences were discovered in connection with an observation of *M. daubentoni* in the province of Uppland in Sweden, 1978 (Ahlén 1979). The slower pulse repetition rate and the different shape of the pulses (slightly bent in sonagrams) were pointed out. Since then, further studies confirmed these statements and gave more details of interest for identification.

The echolocation pulses used outdoors are FM-sweeps usually going down to 25 kHz with a duration of 5-8 ms (Fig. 5 A, B). The pulses often have a sinusoidal amplitude modulation with a varying number (often about 10) of maxima throughout the pulse. According to subjective impressions, the sounds may be louder than those from *M. daubentoni*.

In my report on *M. daubentoni* found in Uppland, I mentioned that Hans Jørgen Degn in Denmark thought he had heard CF signals, possibly social calls from this species. However, when we cooperated in September 1979 in an attempt to confirm this, we failed. Nevertheless, when we were making further studies and recordings there in August 1980 I discovered that the pulses from passing *M. daubentoni* often had a smacking sound when the detector was tuned at approximately 35 kHz. I have never heard anything similar in any of the other *Myotis* species. The smacking (instead of dry clicks) at 35 kHz indicated the presence of either a CF-component or a time-extended, shallow sweep portion there. Subsequent analyses of the recordings revealed that most sweeps were slightly curved somewhere at 30–40 kHz, as known before. In some pulses there was also a levelling out to almost constant frequency followed by a steep sloping sweep. The level portion of the sweep had usually a second harmonic. The sweeps before and after the level portion had sinusoidal amplitude modulations.

Some pulse examples are shown in Fig. 5 E-E where E shows the most extended levelling out I found in the recorded material. Detailed analysis of this signal made on the Eclipse S-200 gave the following data. The duration of the pulse totals 18 ms. It starts sweeping from 45 kHz but levels out after about 4 ms at 35 kHz. From there it slowly slides down in frequency to 32 kHz during 12.5 ms, the last 2 or 3 ms of which with pure CF level. Finally, the last 1.5 ms of the pulse is a continued sweep down to 23 kHz. The frequency spectrum of a segment of the level portion of the pulse in E is shown in F, where the peak of energy at about 34 kHz is prominent and a second harmonic at 68 kHz is seen. The signal is disturbed by the sound of
Fig. 5 A–K. *Myotis dasyclada* recorded in the field (A–F) and in the laboratory (G–I). Pulse rhythm in sequence with straigh flight (J) and when flying about (K).
Fig. 5 L. Myotis dasyoneme. The same pulse as in 5 B in longer time scale.

A waterfall.

The pulse repetition rate is slower than in *M. daubentoni* but varies widely according to flight situations (Fig. 5 J, K). Data from straight flight gave an average length of intervals between pulses of about 115 ms, corresponding to slightly less than 9 pulses per second (Fig. 5 J).

Recorded sounds from *M. dasyoneme* flying indoors show pulses approximately 3 ms long, sweeping from 80 to 30 kHz (Fig. 5 G, H). Like the outdoor pulses, there is also a sinusoidal amplitude modulation, giving a number of peaks in the frequency spectrum (Fig. 5 I). The highest sound pressure level in that spectrum is at 42 kHz.

In addition to the description of the sounds it should be mentioned that the flying behaviour of *M. dasyoneme* seems to differ slightly from *M. daubentoni* and the size difference is possible to see at least under very favourable conditions (Ahlén 1979). Here again, combined aural and visual observations should facilitate identification.

This species regularly uses different pulse types for echolocation. Two principal types will be described. One is a steep FM-sweep ending with a short levelling out (Fig. 6 A, B, C). The other is a long shallow sweep sliding down a few kHz (Fig. 6 D, E, F). In addition there are intermediate forms.

The steep FM-sweep goes down to about 25 kHz were it ends with a levelling out. The pulse shown in Fig. 6 A, B, C is approximately 6 ms long and has a peak of energy at 27 kHz.

The long shallow sweep is usually about 25 ms long, sliding down only 3-4 kHz around 20 kHz, sometimes down to 18 kHz. It usually has weak second and third harmonics. This pulse is audible to young people.

The first pulse type is used when the bat hunts at low height above ground, e.g., in clearings of a wood, among trees in a park. When it hunts at higher height, above the forest canopy or in completely open landscape, it uses both the first and the second pulse type, often alternating regularly. This is the reason why *Nyctalus noctula* sometimes sounds as 'plip-plop' in the detector, because the shorter pulse gives a plip and the longer a plop. I have never heard it only use the second type of pulse.

Further details on vocalization and flight in *Nyctalus* are given by Miller & Degn (1981).

The sounds are quite loud and, according to one observation, when it was possible to measure the distance to the bat, it could be heard with a QMC detector from at least 150 m. However, there are indications that one bat heard really was at a distance of 200 m from the detector. In the Scandinavian bat fauna only *Vespertilio murinus* can compete with that loudness.

The repetition rate varies with the type of flight. The high hunting with alternating pulses is associated with a very slow and irregular pulse rhythm (Fig. 6 G). Data from such flights show peaks for intervals between pulses at 300 and 450 ms corresponding to a repetition rate of 1-3 per second with frequent longer gaps. Data from bats hunting at low heights and only using the short pulses (Fig. 6 H) show a peak at about 100 ms corresponding to 7-8 per second.

*Nyctalus noctula* using alternating pulses is quite easy to identify with detector. When it is only using the short FM
Fig. 6 A-H. Nyctalus noctula. Two types of echolocation pulses (A, B, C and D, E, F). Pulse rhythm in high flight (above forest canopy) (G) and in low flight (opening in forest) (H).
sweeps it may be confused with *Eptesicus serotinus*, *Vespertilio murinus* and possibly *E. nilssonii* (for details see sections about these species). Inexperienced detector listeners should also ensure that they are familiar with the social call of *Pipistrellus pipistrellus* in order to avoid confusion with *Nyctalus noctula*.

When several specimens fly in the vicinity of the nursery at dawn some social calls can be heard. In the evening of 31 May 1979 I recorded the long call shown in Fig. 6 I. It consisted of a whistle starting at 13 kHz and then undulating up and down between 17 and 32 kHz 14 times in 110 ms. It has a prominent second and weak third harmonic belonging to the lower frequencies of the fundamental. In Fig. 6 J, K the first 38 ms of the call is shown in detail.
Fig. 6 J-K. Nyctalus noctula. First 38 ms of the social call shown in Fig. 6 I.
4.7. *Pipistrellus pipistrellus* (Schreber, 1774) & *P. nathusi* (Keyserling & Blasius, 1839). Pipistrelle and Nathusius' Pipistrelle.

The most common echolocation pulse of *Pipistrellus pipistrellus* in my recordings from various places in Sweden is a short (often 4-6 ms) FM-sweep (Fig. 7 A, B, C, D) that ends with a short level out (B) or a short pure CF-component (C). Sometimes the pulse is like a hook, the sweep goes down, levels out and then the very end sweeps upwards again. According to my recordings from the province of Upland, the most frequent position of the level or CF portion of the pulse in the frequency scale is at 58 kHz but varies normally between 63 and 50 kHz. Miller & Degn (1981) have shown that CF portions can separate as much as 14 kHz between individuals when flying in groups.

Another echolocation pulse type is a pure CF-signal about 10 ms long (Fig. 7 E, F, G). In my recorded material from the province of Upland this pulse has almost invariably had a frequency of 51 kHz.

The two pulse types are not used alternately as in *Nyctalus noctula* or *Barbastella barbastellus*. On some occasions single bats only using the 51 kHz CF pulse are heard. Despite a number of observations I have not observed any difference in flight or hunting technique between the use of the two pulse types.

Pulse repetition rate differs according to the pulse type used. When pure CF pulses are used the intervals between pulses (Fig. 7 I) are on average 10 ms longer than when FM sweeps are used (H).

It is most likely that the two pulse types are used for different purposes but I must also point out that specimens using the pure CF-signals have never been caught for species examination.

The sounds heard in the detector are a rapid series of clicks and if the level portion, CF portion or the pure CF signal are tuned in accurately, the pulses are heard as smacks (chirrups) or droplike sounds making it impossible to confuse *Pipistrellus* with any other Scandinavian bat.

When recording bats on Jutland in Denmark, in the provinces of Skåne and Gotland in Sweden, I documented other sounds from *Pipistrellus* that have never been heard or recorded earlier in the province of Upland. These consisted of short FM-sweeps with short CF ending at 40-45 kHz (Fig. 7 J, K). The repetition rate was slightly slower (Fig. 7 L) (on average 5 ms longer intervals) than is...
typical for the use of the corresponding pulse type by *Pipistrellus pipistrellus* (Fig. 7 H). In addition a pure CF signal at about 40 kHz was also documented in these areas.

It is hard to explain why the latter sounds from *Pipistrellus* have never been heard in the province of Uppland, despite the fact that my recorded material from there covers all seasons, hunting in various habitats, social behaviour such as swarming prior to hibernation, etc. The possibility that *Pipistrellus nathusii* is involved cannot be excluded but at the moment I have to leave it as an open question.

Social calls from *Pipistrellus pipistrellus* are quite frequent and can be heard in all seasons when the bats are active. The most common call is an undulating sweep that in about 35 ms goes down and up about 4 times, often between 35 and 18 kHz (Fig. 7 M). It is quite loud and audible to young persons. There are relatively strong second and third harmonics. In the detector this is heard as a sharp smack and when repeated regularly it can cause confusion with sounds from *Myotis myotis*.

In the areas where possibly both *P. pipistrellus* and *P. nathusii* occur a somewhat different version of this social call has been documented. It consists of the similar undulating sweeps down and up 4 times but ranging between 28 and 15 kHz and after a pause of 80 ms a series of 3-4 V-shaped frequency variations at 35 kHz follows (Fig. 7 N, O, P).

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**Fig. 7 A-L. Pipistrellus pipistrellus.** The most common echolocation pulse type (A,B,D), another example of pulse (C). Pure CF-signal used as echolocation pulse (E,F,G). Pulse rhythm when using the first pulse type (H), when using the CF-signal (I). *Pipistrellus* sp. pulse (J,K) and rhythm (L), see text.

**Fig. 7 M. Pipistrellus pipistrellus.** Social call used in flight.
Fig. 7 N-P. *Pipistrellus* sp. Social calls.
Northern Bat.

The sounds heard from this species have been described by the author (Ahlén 1980). In Sweden it is the most common bat and the echolocation sounds are quite easy to identify. The echolocation pulses in the search phase are 10-12 ms long FM sweeps that level out to almost CP or a very short CF portion often at 30 kHz (Fig. 8 A, B, C). This sound is quite loud, could be heard with detector at least 50 m away, probably more, and is repeated in fairly typical rhythm (Fig. 8 D). The intervals between pulses show a large peak at 200 ms (corresponding to 5 pulses per second) and a smaller peak at 300 ms.

When the detector is tuned at 30 kHz these pulses sound like powerful smacks. They resemble the sonar of *Vespertilio murinus* and the low-hunting *Nyctalus noctula* although these two give smacks when the detector is tuned at approximately 25 kHz. They are also similar to *Eptesicus serotinus* but this species also smacks at 25 kHz and has a faster repetition rate. The sound can also be confused with the sonar of *Barbastella barbastellus* which, however, can be separated by the alternating pulses, faster rhythm and more compact and energetic-sounding pulses. There should be no particular problems of identification once a certain degree of experience of the species has been obtained.

When *E. nilssonii* flies indoors it emits FM-sweeps about 3 ms long and with a strong second harmonic (Fig. 8 E, F, G).

Social calls from *E. nilssonii* have mostly been heard in autumn when the bats swarm outside the old mines where they are going to hibernate. When groups of bats are chasing around they frequently emit long-sweeps with powerful second and third harmonics. These sweeps usually level out or sometimes have a CP component up to 10 ms long (Fig. 8 H, I, J, K, L).
Fig. 8 A-G. *Eptesicus nilssonii* recorded in the field (A,B,C) and in the laboratory (E,F,G). Pulse rhythm outdoors in search phase (D).
Fig. 8 H-L. *Eptesicus nilssonii*. Social calls.
Fig. 9. Eptesicus serotinus recorded in the field (A,B,C).


My material on this species consists only of two recordings, one from Funen and one from Jutland, both in Denmark. However, Miller & Degn (1981) who studied this species thoroughly, give a detailed description of the acoustic behaviour and the variation of the sounds.

The echolocation pulses in search phase which I recorded from hunting specimens are FM-sweeps that level out at approximately 25–26 kHz. The pulse shown in Fig. 9 A, B has a duration of 13.5 ms and has second and third harmonics. According to Miller & Degn (1981), this is the longer of two common pulse types used by this species.

Miller & Degn (1981) report that the repetition rate differs according to which pulse is used. The shorter pulses are repeated 10 times per second and the longer about 5 per s. The pulse rhythm in my recordings is much faster than in E. nilssonii, with the highest peak of measured intervals at 150 ms, which corresponds almost to 7 pulses per second (Fig. 8 C). The diagram also shows that longer gaps between pulses are quite common.

In the detector the pulses sound like smacks and the species identification must be based on the rhythm, frequency and of course, if possible, visual impressions of the very special flight. Under good circumstances there should be no real problems of recognition.

The common echolocation pulse of this species is an FM-sweep that often has a slight curve or small level portion at about 25 kHz, sometimes a little higher up. The whole sweep goes from 50 to 20 kHz but with a peak of energy at 25 kHz and sometimes with a relatively strong second harmonic (Fig. 10 A, B, C).

The pulse repetition rate in search phase (Fig. 10 G) is only slightly slower than in Eptesicus nilssonii and makes it necessary to tune the detector for the peak of energy. However, V. murinus often produce sequences of very regular rate and as illustrated by the diagram, the frequent longer gaps typical of both Eptesicus species may be lacking.

In addition to the pulse described, I have recorded a 20 ms long, shallow sweep, almost CF in the end. The fundamental usually slides down about two kHz, e.g., from 26 to 24 kHz, and has prominent second and third harmonics (Fig. 10 D, E, F).

In the autumn V. murinus has a flight display. The bat produces a song when it is flying high up in the air. In the province of Uppland this song has been regularly heard in the month of October, but in mild weather also throughout November. This display call, or song, was described by Wallin (1963) who presented a sound spectrogram showing parts of the song below 16 kHz. I have recorded this song from a number of localities and in order to document the weaker parts of it, I took the opportunity to make recordings from roofs of houses and a church. The best conditions for observation and recordings, however, was found on the upper edge of a 100 m high precipice above an old mine where singing bats passed just in front of me.

The whole song is about 150 ms long. The first part consists of a dozen rapidly repeated FM-sweeps followed by an upward sweep which then turns down from 50 to 14 kHz where it levels out to a 10 ms long CF signal, followed by a continued sweep down to 10 kHz. The final part of the song has strong second and weak third harmonics (Fig. 10 I, J, K).

Time-frequency structures of the terminal part of the song are shown (Fig. 10 K) where it can be seen that the highest levels of sound pressure are found at 14 kHz. This part of the song is audible to the unaided human ear.
Fig. 10 A-H. *Vespertilio marinus*. Common type of echolocation pulse (A,B,C) and shallow sweep (D,E,F). Pulse rhythm in search phase (G) and rhythm of display flight song (H).
Fig. 10 I-K. *Vespertilio murinus*. Display flight song. The whole song (I, J) and the terminal part (K).
The song is usually repeated quite regularly. Measured intervals form a peak at 230-240 ms, corresponding to a rate of a little more than 4 times per second (Fig. 10 H).

Apparently, in a state of excitement, bats who chase each other can emit undulating sweeps that go up and down two or three times without any gap. As seen in Fig. 10 L, this call can undulate for instance between 15 and 28 or between 13 and 26 kHz and has a second harmonic to the bottom parts.

A recording of a flying *V. murinus* made in the laboratory shows 1.5 ms long pulses with strong second harmonics (Fig. 10 M, N).

The song and the other social calls are easily recognized in the detector. Even if these sounds are audible, the detector extends the range for detecting the sounds. For surveys of bat fauna and for collecting population data, listening for the song has proved to be the most efficient method to find and observe *V. murinus*.
4.11. *Barbastella barbastellus* (Schreber, 1774).

*Barbastelle.*

My material on this species is limited to one laboratory and one field recording. The echolocation sounds used outdoors consisted of two different pulses used alternately. One is very loud and the other rather weak (Fig. 11 A, B).

The loud pulse is approximately 4 ms long. In Fig. 11 C it starts with a CF portion 1 ms long at 35 kHz and then it slides down to 28 kHz. It has a distinct second harmonic. The weak pulse is longer, in Fig. 11 D 5.2 ms. Like the other pulse, it starts with a CF portion 1.5 ms long at 43 kHz and then it slides down to 33 kHz. No second harmonic is seen.

The repetition rate or pulse rhythm in the search phase, as seen in Fig. 11 H, shows a peak for intervals of 110-120 ms, which corresponds to 8-9 pulses per second.

The echolocation sounds documented from *Barbastella barbastellus* were very characteristic when heard through the detector. The pulses gave very hard and compact smacks suggestive of castanets. The alternating loud and weak pulses make this sound different from anything else. The loud smacks resemble those of *Eptesicus nilssonii* but the repetition rate is much faster in *Barbastella* and the smacks reveal more tonal quality of the pulses.

Flying indoors, this species emits FM sweeps without any CF or levelling out (Fig. 11 E, F, G). Pulses often come as double notes.
Fig. 11. *Barbastella barbastellus*. Alternating loud and weak pulses (A,B). The loud pulse (C) and the weak pulse (D). Pulse rhythm outdoors in search phase (E). Laboratory recording (E,F,G).

The most common echolocation pulse used by this bat is a faint and short FM-sweep (Fig. 12 A, B, C). The pulse is often about 2 ms long and has prominent second harmonics. The pulse analyzed in Fig. 12 C shows a number of peaks in the frequency spectrum, the highest at 26, 42 and 59 kHz. However, there is a great deal of variation from pulse to pulse, the diagrams just serve as typical examples. The repetition rate is usually high, often exceeding 20 pulses per second (Fig. 12 C).

This echolocation sound is so weak that it is only heard in the detector when the bat is flying less than 5 m away. In combined visual and aural observations this fact can be used for identification. A bat seen at a distance of 10 m but not giving any sounds in the detector is bound to be a *Plecotus* (if the observation is made in Scandinavia).

However, *Plecotus auritus* is not always a silent or whispering bat. Sometimes it uses quite a loud pulse that can be heard at a distance of at least 40 m (probably more) with a QMC S 100 detector (Fig. 12 E, F). A detailed analysis of such a pulse presented in Fig. 12 H, I, J shows that the fundamental sweep, 7.1 ms long, starts from 42 kHz and slides down to 12 kHz, the last portion being constant in frequency for about 1 ms but ends with a very short downward sweep. There is a prominent second harmonic and weaker third and fourth harmonics.

This loud long-sweep is sometimes heard at an irregular rate, e.g., indoors when flying around in old mines. Under such circumstances short but rapid series of these pulses are sometimes emitted. However, when the pulse is used in flight outdoors there is a more regular rate. According to recorded data, intervals between pulses have a peak at 170-200 ms which corresponds to about 5.4 pulses per second (Fig. 12 G).

The loud long-sweep is heard in the detector as a powerful but soft smack. The rapid series of these pulses, which can be heard at times, form trills in the detector.

The special hunting behaviour performed in this species is also an aid in species identification, a fact that again suggests combined visual and aural observations. Observing a relatively large bat hovering or circling slowly in front of leaves, tree trunks or walls at the same time as nothing is heard in the detector is the most typical encounter with this species in the field.

The echolocation sounds used by the American species
Fig. 12 A-H. Plecotus auritus. The most common echolocation pulse (A,B, C) with rhythm (D). The loud long-sweep (E,F,H) with rhythm (G).
Fig. 12 I–J. Plecotus auritus. Loud long-sweep.
Plecotus phylloste was described by Simmons & O'Farrell (1977). It has a long-CF/PM sound in addition to the ordinary FM sonar. The CF component occurs at 27 kHz while the FM sweeps down from 24 to 12 kHz. This sweep has some similarities with the loud long-sweep of Plecotus auritus but is apparently shorter. The CF component does not seem to have any corresponding sound in P. auritus.
5. Summarizing remarks on the sounds

In the preceding section I described sounds used in flight by the following Scandinavian species: *Myotis myotacinus & brandti* (1), *M. nattereri* (2), *M. bechsteinii* (3), *M. daubentoni* (4), *M. dasycneme* (5), *Nyctalus noctula* (6), *Pipistrellus pipistrellus* (7), *Eptesicus nilssonii* (8), *E. aerotinus* (9), *Vesperilio murinus* (10), *Barbastella barbastellus* (11) and *Plecotus auritus* (12). In addition, some sounds recorded from *Pipistrellus* sp. in Denmark (Jutland) and south Sweden (Skåne, Gotland) were presented and ascribed to either a greater variation in vocalization in *P. pipistrellus* than in central Sweden, or the possible involvement of *P. nathusii*.

From all species except one (3), sounds were recorded in the field. Ten of the species were recorded flying in laboratory or other indoor situations.

The principal types of sounds used in flight are summarized in Table 1. Echolocation sounds were documented from all species. Probably social flight calls were recorded from at least 6 species (2, 6, 7, 8, 10, 12).

FM-sweeps occur in all the species investigated. Linear or almost linear FM-sweeps are the main echolocation sounds in 7 species (1-5, 12). FM-sweep can also at least occasionally be used (in search phase) by most of the remaining species. FM-sweeps that regularly have sinusoidal amplitude modulation are typical for two species (4, 5). An FM-sweep with a short level portion somewhere in the middle of the sweep is characteristic of two species (5, 9). An FM-sweep that ends with a levelling out to a shallow portion occurs in 8 species (2, 6, 7, 8, 9, 12). Shallow sweeps, not far from CF, were found in 3 species (6, 10, 11). In one case these are initiated by a CF-part (11). Pure CF signals or CF portions of pulses were found in 7 species (2, 5, 7, 8, 10, 11, 12). Undulating sweeps occurred in the social calls of 3 species (6, 7, 10).

In 8 species two or more pulse types are regularly used (5, 6, 7, 8, 9, 10, 11, 12). In two species two types can be used by repeated alternation between the two pulses (6, 11). In the other cases special pulse types are often linked to special hunting situations or are just used on special occasions.

The length (time duration) of the pulses varies from 2 ms in the shortest FM-sweeps recorded outdoors (2, 12) to about 20 ms in the longest shallow sweeps (10), probably used for echolocation. Among the (probably) social flight calls, continuous sounds up to a length of 110 ms (6) were found and in one species (10) the display flight song consists of a number of discrete parts which together
total 150 ms.

The repetition rate is variable according to type of flight, accelerates through approach to terminal phase with its buzz. When turning or circling around, the rate is also increased. However, in straight flight or in sequences of search phase each species seems to attain a special rhythm that probably depends on at least some correlation between vocalization, respiration and wing-beat rate as observed in some bats (Novick 1977, Yalden & Morris 1975). If body size, wingshape and other anatomical features result in a convenient average wing-beat rate in straight cruising flight, a specific length of intervals between pulses should be expected. Pulse rhythm diagrams were made by putting a number of measured intervals into classes of length in time. These diagrams gave peaks (not averages) that were species-specific, thus confirming the wing-beat/pulse correlation. In some species (e.g. 7, 8, 9) there is one main peak and one smaller peak corresponding to a specific length of longer gaps between pulses that occurs now and then in the pulse sequence.

In general, larger species have slower repetition rate than the smaller ones. The largest species (in high flight) (6) has an interval peak at 300 ms while the smallest species (7) has its normal peak at 85 ms. However, two species, apparently well adapted for hunting in caves, old mines, along walls, etc. (2, 12), may at times have very high repetition rate probably due to the special flying behaviour. Of two related species (8, 9) the larger one (9) has the highest repetition rate with a peak at 150 ms, while the smaller has a peak at 200 ms. The reason for this could be that bats can choose different multiples of pulses per wing-beat or, of course, that there is no wing-beat/pulse correlation.

The frequencies used by the investigated Scandinavian bats in flight cover the ultrasonic range from about 100 kHz down to 10 kHz in the audible range. Of the pulses that probably only have an echolocation function there are only two that extend down into the audible range, to 18 kHz (6) and to 12 kHz (12). Of the (probably) social calls there are generally parts down in the range between 20 and 10 kHz (2, 6, 7, 8, 9, 10, 12). The frequency position of CF sounds are found at many different values, from 63 (7) to 12 (12).
Table 1. Principal types of sounds recorded from Scandinavian bats in flight.

<table>
<thead>
<tr>
<th>Species</th>
<th>Pulse type FM=frequency modulation in search, AM=amplitude modulation phase or CF=constant frequency in social calls</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. <em>Nyctis mystacinus</em> Å brandt</td>
<td>FM</td>
</tr>
</tbody>
</table>
| 2. *Nyctis nattereri*        | 1) FM  
2) FM/short CF (probably social)                                                                           |
| 3. *Nyctis bechsteinii*      | (FM indoors)                                                                                                 |
| 4. *Nyctis daubentonii*      | FM (with sinusoidal AM)                                                                                        |
| 5. *Nyctis dasycneme*        | FM/short level out or CF/FM (FM with sinusoidal AM)                                                            |
| 6. *Nyctalus noctula*        | 1) FM/level out  
2) Long shallow FM (1 & 2 alternating in high flight, only 1 in low)  
3) Undulating sweeps (probably social)                                                                             |
| 7. *Pipistrellus pipistrellus* | 1) FM/short CF  
2) CF  
3) Undulating sweeps (probably social)                                                                               |
| 8. *Eptesicus nilssonii*     | 1) FM/level out or short CF  
2) FM  
3) FM/CF or level out (probably social)                                                                              |
| 9. *Eptesicus serotinus*     | FM/level out  
FM  
V-shaped sweeps                                                                                                      |
| 10. *Vespertilio murinus*    | 1) FM/short level out/FM  
2) Long shallow FM, almost CF  
3) Undulating sweeps (probably social)  
4) Song: FM series, sweep up and down/CF/FM                                                                         |
| 11. *Barbastella barbastellus* | 1) Loud short CF/FM  
2) Weak short CF/FM  
(1 & 2 alternating)                                                                                                  |
| 12. *Plecotus auritus*       | 1) Weak FM  
2) Loud long FM/short CF  
3) Trill of 2 rapidly repeated (probably social)                                                                     |
<table>
<thead>
<tr>
<th>Approximate duration, ms</th>
<th>Peak of energy in frequency spectrum, kHz (Range in V-shaped and undulating sounds)</th>
<th>Example of repetition rate in search phase, Peak of interval lengths, ms (rate, s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.5-3</td>
<td>40-45</td>
<td>95 (10.5)</td>
</tr>
<tr>
<td>2</td>
<td>50</td>
<td>80 (12.5)</td>
</tr>
<tr>
<td>10</td>
<td>35</td>
<td>-</td>
</tr>
<tr>
<td>(1.2 indoors)</td>
<td>(50 indoors)</td>
<td>(85 (11.8) indoors)</td>
</tr>
<tr>
<td>3-4</td>
<td>45</td>
<td>75 (13.3)</td>
</tr>
<tr>
<td>5-8</td>
<td>35-40</td>
<td>110 (9.1)</td>
</tr>
<tr>
<td>6</td>
<td>25</td>
<td>125 (8.0) (low flight)</td>
</tr>
<tr>
<td>25</td>
<td>20</td>
<td>300 (3.3) (high flight)</td>
</tr>
<tr>
<td>110</td>
<td>17-32</td>
<td></td>
</tr>
<tr>
<td>4-6</td>
<td>58 (50-63)</td>
<td>85 (11.8)</td>
</tr>
<tr>
<td>10</td>
<td>e.g. 51</td>
<td>95 (10.5)</td>
</tr>
<tr>
<td>35</td>
<td>20-40</td>
<td></td>
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<tr>
<td>10-12</td>
<td>30</td>
<td>200 (5.0)</td>
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<tr>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10-25</td>
<td></td>
<td></td>
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<tr>
<td>13</td>
<td>25</td>
<td>150 (6.7)</td>
</tr>
<tr>
<td>3-6</td>
<td>18-28</td>
<td></td>
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<tr>
<td>6</td>
<td>25</td>
<td>210 (4.8)</td>
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<tr>
<td>20</td>
<td>25 (25-30)</td>
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<td>40</td>
<td>12-28</td>
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<tr>
<td>150</td>
<td>14</td>
<td>235 (4.3)</td>
</tr>
<tr>
<td>4</td>
<td>35-30</td>
<td>115 (8.7)</td>
</tr>
<tr>
<td>5.2</td>
<td>43</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>e.g. 26, 42, 59</td>
<td>45 (22.2)</td>
</tr>
<tr>
<td>7</td>
<td>12</td>
<td>190 (5.3)</td>
</tr>
</tbody>
</table>
6. Evaluation of identification possibilities

When bats are observed in ideal conditions and the sounds are recorded with an instrumentation tape recorder for later analyses, there are good possibilities to identify the Scandinavian species. An exception seems to be the two sibling species *Myotis mystacinus* and *M. brandti*, which were not found to differ in their sounds. It is also uncertain whether *M. beechtteini* has easily recognizable sounds outdoors. In all other cases, species-specific pulse shapes, frequency peaks or ranges, amplitude and pulse rhythm make identification possible.

However, when bat detectors are used, a lot of information on the sounds gets lost. First of all, knowledge of the exact shape of the pulse as seen in a waveform oscillogram or in a sonogram is not secured, although some indications of the type can be interpreted from the detectors. The two detector systems that are in use at present (see section 2) differ as to the information content of the transformed signals. The heterodyne system allows fairly exact tuning of the frequency, the relative amplitudes are heard and the difference between clicks and smacks indicates either FM-sweep or CF-signals/shallow sweeps to be present. The divider system loses the amplitude information but retains the frequency (at least of the fundamental). Frequencies of different values can be heard but otherwise I find it more difficult to recognize different types of signals just by listening to the divider. As mentioned in section 2, a good documentation of bat sounds is achieved by a combination of the two systems.

With the limitation of the present-day detector systems there are still quite good possibilities to identify the species. Identification requires a lot of training and it is advisable to document sounds on a cassette recorder for subsequent checking. Information on pulse rhythm and data on frequencies are then often the most valuable.

Checking recorded sounds can be done by listening and comparing with a bat sound cassette prepared for identification training. In a bioacoustic laboratory there are better possibilities to check the recorded sounds. It should always be done when, for example, supposedly rare species have been recorded in new geographical areas.

In Table 2 I have tried to present a brief review of the diagnostic characters for the bats as they are encountered when using a QMC S 100 detector. However, it should be kept in mind that all figures on frequencies and repetition rate are subject to a great deal of variation, not fully indicated by this key. The descriptions in section 4 should be used and this key can serve as a summary or an aid to
Table 2. Key for identification of Scandinavian bat sounds with the aid of ultrasonic detector.

<table>
<thead>
<tr>
<th>Sounds from detector characterised as</th>
<th>Relatively slow rate, 10.5 s⁻¹, sequences with quite regular rhythm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry clicks when tuned at 40-50 kHz</td>
<td>Weak, rate 12.5 s⁻¹, but very high in typical flight, circling around, *</td>
</tr>
<tr>
<td></td>
<td>Sounds in the field unknown. Probably slow rate</td>
</tr>
<tr>
<td></td>
<td>Variable rate, e.g. 13.3 s⁻¹ faster than (1) and (5), *</td>
</tr>
<tr>
<td></td>
<td>Louder and slower than (4), rate 9.1 s⁻¹,</td>
</tr>
<tr>
<td></td>
<td>Sometimes smacks when tuned at 35 kHz, *</td>
</tr>
<tr>
<td></td>
<td>Extremely weak, very high rate, 22.2 s⁻¹, *</td>
</tr>
<tr>
<td></td>
<td>All other species if not tuned at CF component or level portion of sweep,</td>
</tr>
<tr>
<td></td>
<td>58 (50-63) kHz, rate 11.8 s⁻¹</td>
</tr>
<tr>
<td></td>
<td>51 kHz, rate 10.5 s⁻¹</td>
</tr>
<tr>
<td></td>
<td>40 kHz, rate 10.5 s⁻¹</td>
</tr>
<tr>
<td></td>
<td>30-35 (and 43) kHz, rate 8.7 s⁻¹, loud and weak pulses alternating, like castanets</td>
</tr>
<tr>
<td></td>
<td>30 kHz, rate 5 s⁻¹ with frequent longer gaps</td>
</tr>
<tr>
<td></td>
<td>slow rate, 4.8 s⁻¹ with quite regular sequences</td>
</tr>
<tr>
<td></td>
<td>25 kHz, rate 6.7 s⁻¹, sometimes faster with frequent longer gaps, *</td>
</tr>
<tr>
<td></td>
<td>rate 8.0 s⁻¹ when hunting low, *</td>
</tr>
<tr>
<td></td>
<td>'plip-plop', rate 3.3 s⁻¹ when hunting high</td>
</tr>
<tr>
<td></td>
<td>20 kHz, hard smacks, sounding alike</td>
</tr>
<tr>
<td></td>
<td>14 kHz, loud smash preceded by a trill, heard in autumn, rate 4.3 s⁻¹, very regular</td>
</tr>
<tr>
<td></td>
<td>down to 12 kHz, loud and hard smash, not regularly repeated, *</td>
</tr>
<tr>
<td></td>
<td>20-10 kHz, various other social calls from</td>
</tr>
</tbody>
</table>

* combined visual and aural observations make identification easier.
memory.

It should be repeated that the most difficult identification is to separate the Myotis species, especially *M. daubentoni* and *M. mystacinus*. However, there is at least some risk of confusion between the three smacking species that are best heard at 25 kHz, namely *Vespertilio murinus*, *Eptesicus serotinus* and *Nyctalus noctula* (in low flight). If the detector has a poor frequency resolution (as in QMC mini) *Eptesicus nilssoni*, best heard at 30 kHz, can be included in the group for possible confusion. Hard smacks (social calls) at 20 kHz from *Pipistrellus pipistrellus* can be confused with pulses from *Nyctalus noctula* by inexperienced listeners. Finally, the loud long-sweeps used by *Myotis nattereri* and *Plecotus auritus* are quite similar.

It should again be stressed that combined visual and aural observation makes it easier to identify a number of species.

The ability to identify bats on their sounds seems to be dependent on the observer's musical ear and sound memory. It should not be denied that it is difficult and requires long training. It is recommended to spend one season on intensive bat listening and observing before going into serious survey work or ecological research based on detector technique.
6. Applications for surveys of bat fauna and population studies

The procedure to investigate the bat fauna with ultrasonic detectors as the main method was tested on a practical scale for three years 1978-1980 in the province of Uppland (13 000 km²) and with some comparisons in other areas, especially on the island of Gotland (3100 km²). The work gave good opportunities to examine the reliability of species determination and gave data on the efficiency of detecting the different species at a locality. These results will be published elsewhere but the main problems with regard to identification were presented in the descriptions in section 4.

On basis of the results, some methods to gather data on bat fauna and bat populations with detectors as the main method will be presented and discussed as to the possible application.

Mapping species occurrence

Purpose: Collecting data on bat fauna of larger areas, distribution of species, comparing abundance of a species in selected habitats.

Procedure: Regions to be investigated are subdivided in areas covered by topographical maps, e.g., 25x25 km. Within these, 25-50 localities are selected for investigation with detector listening (according to specified rules as to minimum requirements on weather, hours during night, etc.) and searching in buildings, caves, old mines, hollow-trees etc. Localities are selected in order to cover the best bat habitats, habitats of specialized species if such habitats occur, and finally the total habitat variation. At each locality all potential bat habitats within c. 0.8 km² (circle with a radius of 500 m) are investigated at least three times (within specified seasonal limits). Potential habitats for Vespertilio murinus must be investigated in October when the display flight song can be heard. The total number of localities must be adapted to the type of landscape, e.g., its heterogeneity, and must be based on a certain amount of experience. The species mapping method should result in a complete knowledge of the number of species present in the map area and some rough data on species richness in the best habitats. Furthermore, the abundance of a species could be compared between different habitats.

Application: This method is recommended for faunal work in larger regions, surveys in order to locate areas of
interest for nature conservation, and in other cases when an initial survey of the bat fauna is wanted.

**Line transects using car roof hatch**

Purpose: Securing large amounts of data on abundant species for comparing areas or measuring population trends.

Procedure: Bat sound data are collected by placing the ultrasonic microphone in the opening of a car roof hatch. The microphone is directed backwards and owing to the velocity of the car, 50-60 km per hour, individual separation is quite easy. The method has proved to be highly efficient as to the large number of bat observations per time unit. Of course, data are biased because of the possible concentration of bats along roads (roosts and nurseries in houses and hunting over roads). Nevertheless, data can be used for comparing different areas and it should be possible to measure population changes in time by repeated line transects. The number of observations needed, the optimal system for choice of roads, etc. require further studies.

Application: The method is recommended for monitoring bat fauna and for comparing the relative abundance of common bat species in different areas.

**Bat counts in random sample areas**

In order to estimate population density or estimate number of flying bats per area it is necessary to use random sample areas. However, this requires a standardized procedure for counting to be developed. Because of the uneven distribution of bats in the landscape, the random sample areas give a very low number of bat observations per time unit. The rarest species are not likely to be observed at all.
8. References


Publikationer i vittekoologi i en tidigare serie "Rapporter och Uppsatser" från institutionen för skogszoologi, Stockholm (övriga nummer i skogsentomologi).

Publications in wildlife ecology in an earlier series "Research notes" from Institute of Forest Zoology, Stockholm (remaining issues in forest entomology).


20. Hansson,L. 1975. Smådagsdjurs frökonsumtion i skogsmark och skydds möjligheter mot skadegörelse. (Forestry problems with seed-eating small mammals)

21. Larsson,T.-B. 1975. Laboratoriefsöök med angrepp på träplanter av åkersock, Micrurus aegrestis (L.) och skogssock, Clothroncynys glareolus (Schreb.). (Damage to forest seedlings caused by the Voles Micrurus aegrestis (L.) and Clothroncynys glareolus (Schreb.) under laboratory conditions)

22. Hansson,L. & Larsson,T.-B. 1975. Försök med avskräckande medel mot smågngarsangrepp på planter och frön inom skogsbruket. (Examinations of repellents against small rodent attacks on seedlings and seeds in forestry)

23. Lavsund,S. 1975. Undersökningar av spillningshögar. (Investigations on pellet groups)

24. Larsson,T.-B. 1975. Skogliga markbearbetningsmetoders inflytande på bestånd och skadegörelse av smågngare. (The influence of forest regeneration measures on the abundance and damage caused by small rodents)

25. Lavsund,S. 1976. Kronhjortens, Cervus elaphus L., ekologi i områden med nyetablerade populationer i Syd- och Mellansverige. (The ecology of red deer, Cervus elaphus L., in areas in southern and central Sweden with recently established populations)

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Tidigare utgivning

Earlier publications


3. Hansson, L. 1980. Överskottsområden för sork på skogliga förnyingsytor och deras betydelse för sorkskadornas omfattning. (Surplus areas for voles on forest regenerations and their importance for the voles damage)


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