

## The Acoustic Behavior of Four Species of Vespertilionid Bats Studied in the Field

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**Summary.** The acoustic behavior of four species of vespertilionid bats flying in the field was studied using high speed tape recorders and ultrasonic detectors. The bats can be identified solely on the basis of their cries when using a 'divide-by-ten' detector. Three species (*Eptesicus serotinus*, *Nyctalus noctula*, and *Pipistrellus pipistrellus*) show considerable flexibility in their acoustic behavior, while *Myotis daubentonii* has a stereotyped acoustic behavior under our study conditions. Several aspects of the cry repertoire can be correlated with the bats' activities and acoustic environment. During aerial chases and when circling the roost, *E. serotinus*, *N. noctula* and *P. pipistrellus* emit ultrasound that is distinctly different from their orientational cries. Such ultrasound may have a social function.

### Introduction

Field studies provide valuable information for understanding the acoustic behavior of bats. Griffin (1958), in his pioneering work, indicates that certain bats may be more flexible in their cry repertoire than expected from laboratory studies. Recent investigations confirm and expand Griffin's work (Sales and Pye 1974; Simmons and O'Farrell 1977; Simmons et al. 1978a, 1979a; Fenton 1980). For example, when performing target ranging tasks in the laboratory, the Mexican free-tailed bat (*Tadarida brasiliensis*, Molossidæ) emits rather short frequency modulated (FM) cries that contain several harmonics and are quite stereotyped. The same species in the field, however, uses several different types of cries, including nearly constant frequency (CF) cries, appropriate for the acoustic environment and the behavior of the

*Abbreviations:* FM frequency modulation; CF constant frequency

bat (Simmons et al. 1978a, 1979a). Other species of bats also show considerable flexibility in their orientational cries when studied in natural surroundings (Pye 1980).

In this paper we describe the acoustic behavior of four species of vespertilionid bats foraging in the field (*Eptesicus serotinus*, *Nyctalus noctula*, *Pipistrellus pipistrellus* and *Myotis daubentonii*). The acoustic behavior of the first three species varies depending on circumstances, and, therefore, cannot easily be categorized. The foraging behavior of *M. daubentonii* remains constant throughout the season, and it has a stereotyped acoustic behavior. Our results resemble those obtained from similar studies on certain North American species. *E. serotinus* and *N. noctula* can emit characteristic ultrasounds when flying near the roost. *P. pipistrellus* will do the same during aerial chases. To our knowledge this is the first account of 'social ultrasound' used by these species in the field.

### Methods

#### *Apparatus*

Most of our studies were made using 'divide-by-ten' ultrasonic detectors, which are easy to handle and which offer rapid data analysis. These detectors divide the original sound frequency by a factor of 10, and, consequently, translate the ultrasonic frequencies of bat cries to audible frequencies (Andersen and Miller 1977). The device faithfully reproduces cry durations and repetition rates, but harmonics are lost since the most intense frequency component is divided. Information regarding sound pressure level is also lost. The translated sounds can be monitored with headphones and recorded on conventional tape recorders. We used electret microphones (BT 1759 or CA 2832, Knowles Electronics) as ultrasonic transducers. The frequency range of the detector is from 15 kHz to 150 kHz with typical threshold sensitivities of from 60 to 70 dB (sound pressure level re. 20 µPa). Recordings were made on an Uher magnetic tape recorder (Report 4000 IC) at a tape speed of 19 cm/s (–3 dB at 20 kHz) or on a cassette tape recorder (Philips, –3 dB at 10 kHz). Recordings were analyzed using a period

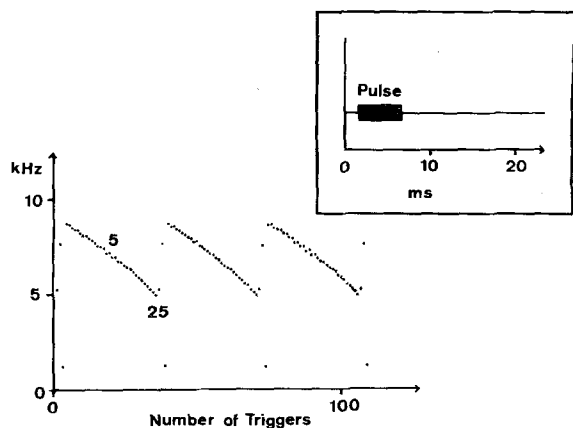


Fig. 1. Computer analysis of an artificial pulsed FM signal. A dot is placed corresponding to the reciprocal of the time between two consecutive triggerings of the computer. The plot shows the change in frequency within each 5 ms pulse. The interval between pulses (25 ms) is represented by a single dot (the lower dots). Insert represents the original signal in real time. The program was used to analyze bat cries recorded via the divide-by-ten detector (see Figs. 3 to 6). In this and in Figs. 3 to 6 the number above the pulse (cry) indicates the duration of the pulse (cry) in ms. The number below and between two consecutive pulses (cries) indicates the interval between pulses (cries) in ms

time histogram program (clock rate=1 MHz, 1024 samples) on a digital computer (PDP 8/e, Digital Equipment Corporation). Figure 1 illustrates the graphic output of the program when synthesized FM pulses like those shown in the insert are analyzed. Each dot represents the reciprocal of the time between two consecutive triggerings of the computer. The change of frequency (periodicity) with time in the 5 ms pulse is displayed with good resolution while the 25 ms interval between pulses is represented as a single dot

(the lower line of dots). Consequently, a rather long recording can be compressed into 'signal only' displays.

High speed tape recordings were made of bat cries using an Analog 7 (Philips) or a Store 7 (Racal) instrumentation tape recorder at 76.2 cm/s. One or two 6.35 mm condenser (free-field) microphones with protective grids removed and appropriate measuring amplifiers (Brüel and Kjær) were connected to two channels of the tape recorder. The frequency range of the recording system extended to at least 100 kHz (-3 dB at normal incidence). A divide-by-ten detector was connected to a third channel. Selected tape recordings were analysed at 1/16 of the real time using a spectrograph (Voiceprint Series 700) and a period meter. For a discussion of apparatus available for research on animal ultrasonic signals see Simmons et al. (1979b).

A comparison of bat cries recorded simultaneously with a divide-by-ten detector and Brüel and Kjær sound recording instruments is shown in Fig. 2. Sound spectrograms of the actual cries appear in Fig. 2B, D and F. The detector signal analyzed with a period meter is shown in Fig. 2A, C and E. Note that the detector signal provides a reasonable duplicate of the first harmonic in the original signal. For each of the four species studied, the first harmonic contains the greatest sound pressure.

#### Location and Animals

The grounds of two estates (Ravnholt and Krengerup 55°15' N; 10°20' E) on Fyn, Denmark, served as study areas. The landscape is varied, consisting of woodlands, parks, ponds and open fields. Most observations and recordings were made from about 1/2 h before sunset to about 2 h after sunset during the spring, summer and fall of 1975 to 1979. In most cases recordings were made from bats that could be seen. Four species of vespertilionid bats foraged regularly, and in large numbers at the study areas. The two larger species (*E. serotinus* and *N. noctula*) were readily identified by their flight patterns and wing morphology. Individuals of the two smaller species were captured for identification. The species studied could be distinguished visually and acoustically. Other vespertilionid species were not observed or recorded at our study areas.

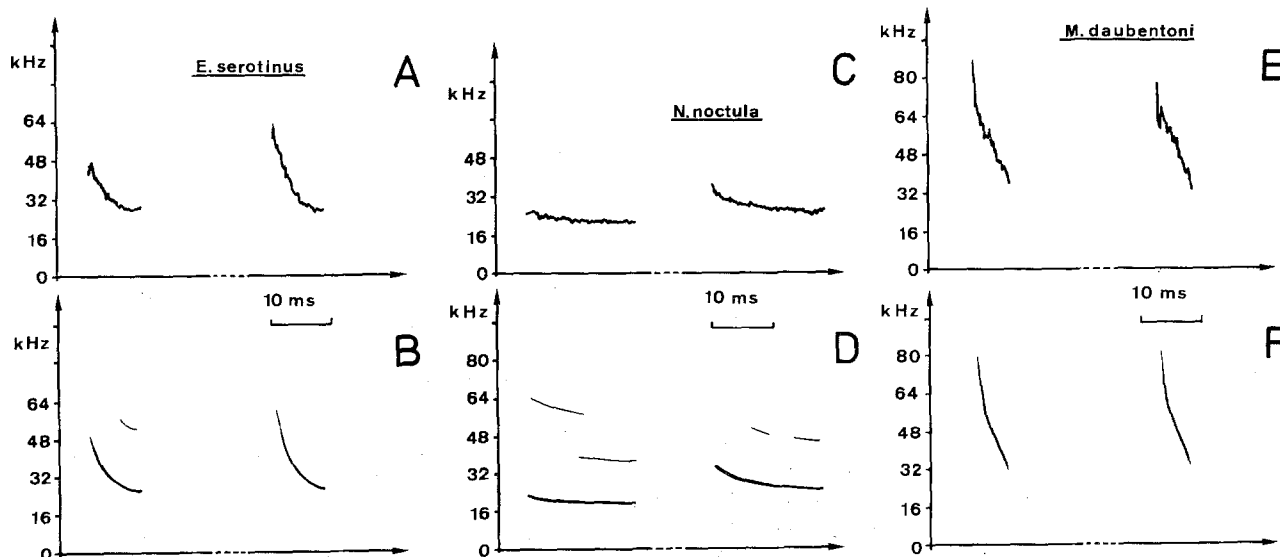


Fig. 2A-F. Bat cries recorded simultaneously using instrumentation equipment and a divide-by-ten detector. A, C, E Time/frequency plots of the detector signal; B, D, F sound spectrograms of the same cries. See Methods for further details. The cries originated from three species. The two cries are sequential. Those shown in A and B are from a bat (*E. serotinus*) hunting at a low altitude (under 5 m). Those shown in C and D were recorded from a bat (*N. noctula*) flying at an altitude greater than 10 m. Those shown in E and F were recorded from a bat (*M. daubentoni*) hunting at the surface of a pond

**Results**

*Occurrence and Foraging Behavior*

*N. noctula* and *P. pipistrellus* first appeared in early to mid April, while *M. daubentoni* and *E. serotinus* first appeared in late April to early May. Heavy foraging activity occurred during May and early June at our study areas, during which time habitats could overlap. By mid to late June and until hibernation the habitats of the four species became more distinct.

*E. serotinus* typically foraged at altitudes of from 5 to 10 m near the edges of woodlots, over open areas, and over ponds. However, they might dip lower than 0.5 m to prey on certain beetles (for example Geotrupidae), and it was not uncommon to see them foraging at altitudes greater than 15 m. We have also heard them foraging well within deciduous woods (beech). *N. noctula* hunted typically at altitudes of from 5 to 20 m, but sometimes they flew higher than 50 m, over open fields, ponds and woods. *P. pipistrellus* foraged typically at altitudes of from 2 to 5 m in larger openings around trees, in parks and over edges of ponds. *M. daubentoni* foraged near the surface of ponds. It rarely flew higher than 0.5 m and we often saw them touch the surface during a ‘buzz’ (cries emitted just before a catch). Presumably these bats were plucking insects off the surface of the water. We observed no seasonal changes in habitat or foraging behavior of *M. daubentoni* at our study areas.

*Acoustic Behavior While Foraging*

Figure 2B shows sound spectrograms of two cries from a sequence emitted by *E. serotinus* while searching for prey at lower altitudes. Most of the sound energy is concentrated in the first harmonic. Under these conditions *E. serotinus* emits rather short (3 to 6 ms) cries starting at frequencies higher than 60 kHz and terminating at about 25 kHz when searching for prey. Cry repetition rates are about 10/s (Fig. 3A). The same species emits longer (10 to 15 ms) cries at lower repetition rates (about 5/s) when flying at high altitudes (15 m or more) (Fig. 3B). (The dots between cries in Fig. 3, and similar Figs. result primarily from echoes.) Such cries are emitted while searching for prey or when in transit. These long cries are produced by extending the duration of lower frequencies, which produces slower sweep rates (the change of frequency with time).

Figure 2D shows sound spectrograms of two consecutive searching cries emitted by *N. noctula* while flying at an altitude of at least 10 m. The cries contain two to three harmonics with the greatest sound energy in the first harmonic. This species often uses cries with durations greater than 10 ms and with slow sweep rates when flying at high altitudes (10 to 20 m) (see also Pye 1980). The terminal frequency of the first cry in Fig. 2D is a few kHz lower than that of the second cry. This sequential alternation in terminal frequency is a regular feature of the searching

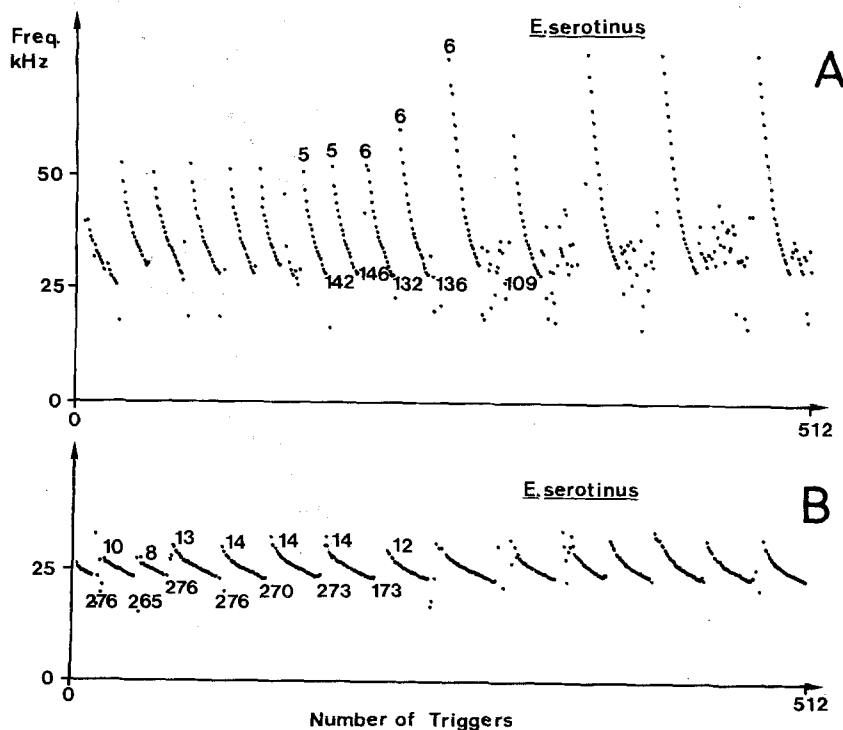


Fig. 3A, B. Recordings of *E. serotinus* flying at different altitudes. The sweep rates and cry rates are high when this bat flies at low altitudes in search of prey (A). At high altitudes, the sweep and cry rates are lower (B). Scattered dots between cries in A caused mostly by echoes

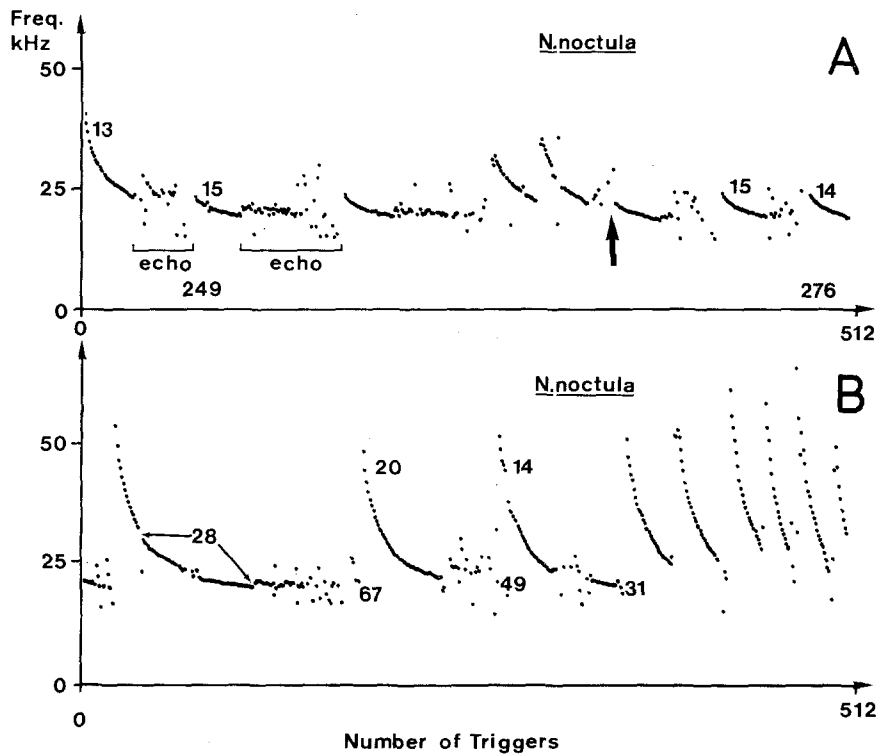


Fig. 4A, B. Recordings of *N. noctula* under different conditions. A Bat flying at an altitude of about 8 m over an open field. The cries to the left of the arrow were made when the bat was flying towards the microphone while cries at the right of the arrow were made when the bat was flying away from the microphone. Notice that the first (13 ms) cry terminates at a higher frequency than the second (15 ms) cry. B Recording made during the pursuit of prey. Note that the lower frequencies are absent during the approach phase (to the right)

cries of *N. noctula*. This species can often be recognized by the alternating higher and lower tonal qualities when heard using a detector (Fig. 2C). Such 'bital' cries are recorded most frequently when *N. noctula* forages at altitudes of from about 10 to 20 m. (Compare also the first two cries in Fig. 4A). Fig. 4B shows three searching cries and the beginning of the approach and capture phase recorded from *N. noctula* at an altitude below 10 m. Searching cries can sweep from about 60 kHz to about 20 kHz, and are more curvilinear than equivalent cries of *E. serotinus* (compare Figs. 3A and 4B). *N. noctula* eliminates the long, slowly sweeping portion of its searching cry when approaching and capturing prey (Fig. 4B).

*P. pipistrellus* shows the most flexible cry repertoire of the four species studied. Searching cries have durations that are usually less than 10 ms. They begin at about 100 kHz and sweep down to about 50 kHz with rather little energy outside the first harmonic. The 50 kHz portion is often held nearly constant for several ms, a characteristic reported earlier by Pye (1973, 1980). We recorded CF and nearly CF cries throughout the season. They can be recorded from single foraging individuals as well as from individuals foraging in groups. When flying in groups, however, bats could separate their CF portions by as much as 14 kHz. Figure 5 shows a record from a group

of bats (three *P. pipistrellus*) flying a circuit in the open, but near trees. Their cries fell into three frequency levels separated by about 3.6 kHz (50 kHz to 57.2 kHz; cry intervals also indicated their origin from three individuals). *P. pipistrellus* drops the CF portion during the approach phase and capture of prey.

Interestingly, lower frequency components of the cries of all three species mentioned thus far can be recorded while bats fly directly away from the microphone. For example, the cries shown in Fig. 4A were recorded from a single *N. noctula* flying an elliptical circuit at an altitude of about 8 m over an open field. The three cries to the right of the arrow were recorded while the bat flew directly away from the microphone at a distance greater than 10 m.

*M. daubentoni* shows the most stereotyped acoustic behavior and has least varied foraging habitat (see above). Figure 2F shows sound spectrograms for two consecutive searching cries. The cries start at around 95 kHz and end at around 35 kHz, with little energy in higher harmonics. These cries are similar to those reported earlier (Sales and Pye 1974). The cries are short (2 to 5 ms) and are emitted at rather high repetition rates (about 15/s) during the searching phase. No deviations from these cry patterns were ever recorded.

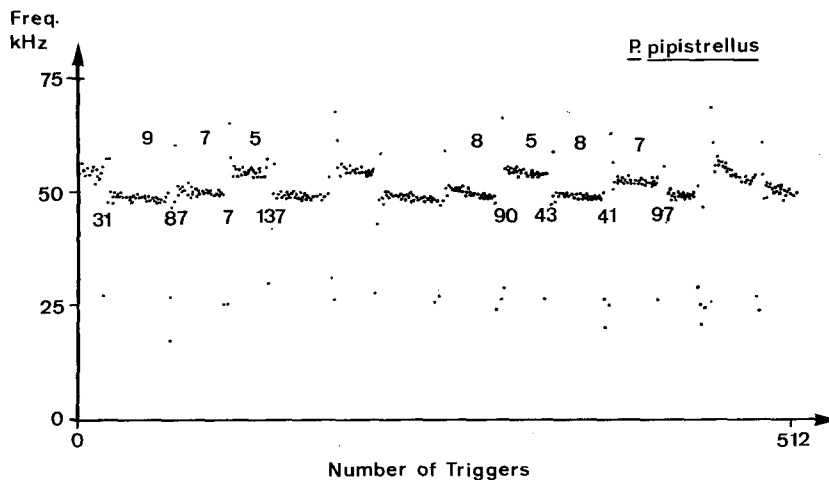


Fig. 5. Recording of three *P. pipistrellus* flying together in a circle 3 to 5 m in diameter. The CF cries are separated by about 3.6 kHz

#### Ultrasonic Vocalizations During Social Activities

*E. serotinus*, *N. noctula* and *P. pipistrellus* sometimes emit characteristic ultrasonic vocalizations during social interactions near the roost or at foraging sites. These vocalizations consist of downward frequency sweeps often followed by upward sweeps producing 'V-shaped' signatures, which frequently occur in a series (the asterisks in Fig. 6). We have recorded V-shaped sounds from *E. serotinus* and *N. noctula* while they circled in front of the roost. This behavior occurred during the mating season. Although the sounds are somewhat similar in shape and time course (7 to 10 ms) in the two species, they occupy different frequency bands. In *E. serotinus* the band ranges from about 28 kHz to about 18 kHz and lies mostly below that used for orientational cries (Fig. 6A). In *N. noctula* the band is from about 40 kHz to about 25 kHz and lies within that used for orientational cries (Fig. 6B). Figure 6B<sub>2</sub> shows a sound spectrogram of a series of V-shaped sounds from *N. noctula*. There are no apparent higher harmonics.

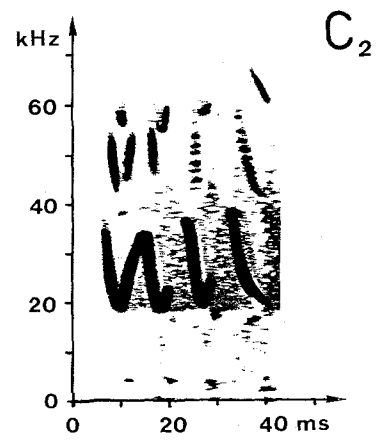
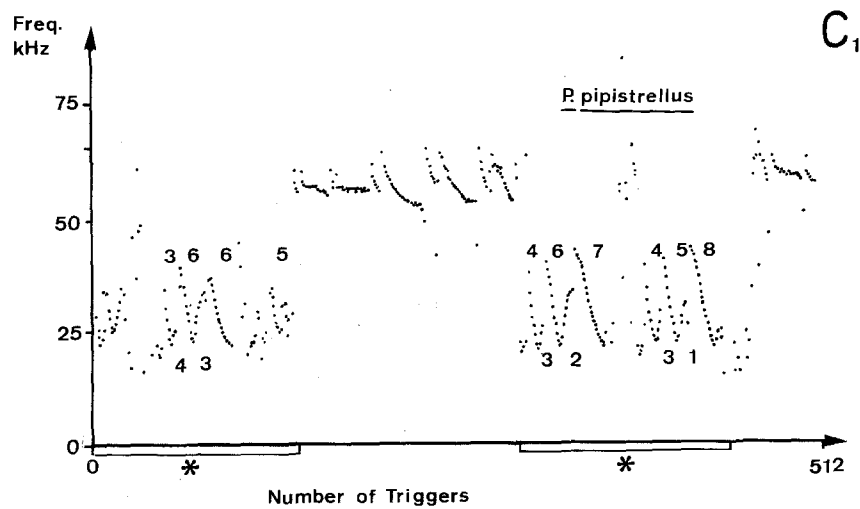
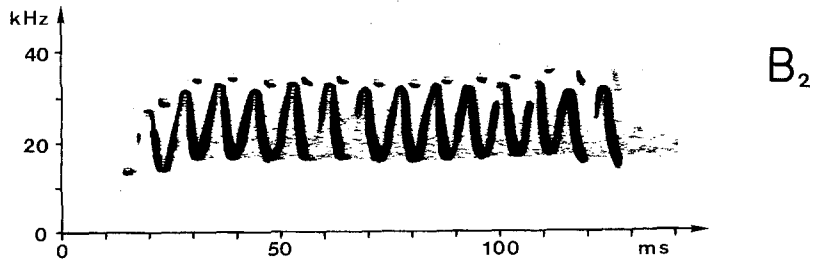
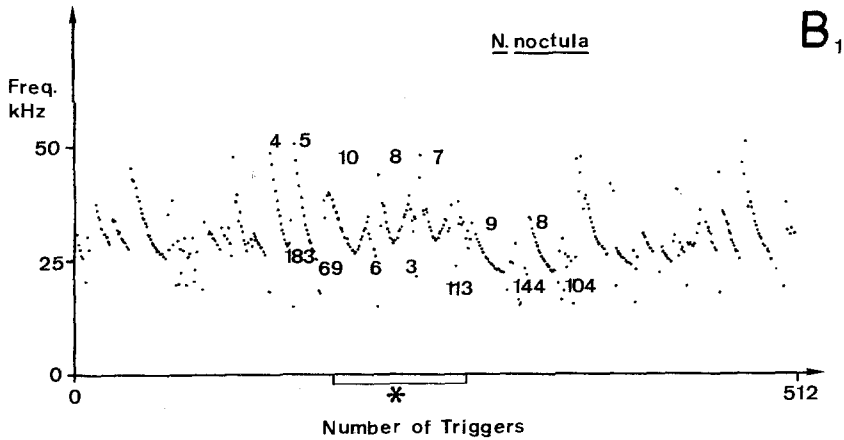
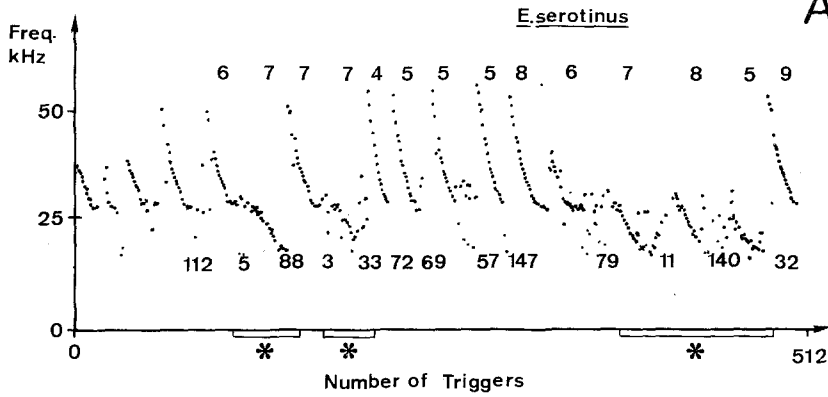
When foraging in groups *P. pipistrellus* commonly emits sounds, which are characteristic when heard in the detector. The sounds are usually emitted when one bat chases another. For example, Fig. 6C<sub>1</sub> (the first asterisk) shows a bout of V-shaped sounds, followed by pairs of orientational cries, which are followed by a second bout of V-shaped sounds. The sounds resemble those of *E. serotinus* in that the upward frequency sweep is sometimes absent or truncated. The V-shaped sounds cover a frequency range of from 50 kHz to about 18 kHz within 3 to 8 ms. The frequency band lies below that used for orientational cries. Figure 6C<sub>2</sub> shows a sound spectrogram of a separate series of V-shaped ultrasounds from *P. pipistrellus*. The major sound energies lie within

the first two harmonics. Aerial chases and vocalizations are not correlated with the lack of prey; many bats continue foraging in the immediate vicinity. Such behavior can be recorded throughout the season. (Aerial chases are seen rarely in *E. serotinus*, and we have never observed them in *N. noctula*. On two occasions we have recorded short (4 to 6 ms) CF (45 to 55 kHz) sounds from *E. serotinus*. These sounds may serve as social signals, but could also be used for detecting large, stationary objects during high speed aerial chases.)

#### Discussion

The acoustic behavior of the four species of bats studied can, in part, be correlated with their foraging activities. All four species use short FM cries (often rich in harmonics) emitted at high repetition rates, when hunting near foliage or near the water surface and when pursuing prey. These conditions can produce an environment with many echoes (acoustical clutter). Precise determination of distance is essential during the pursuit of prey and for distinguishing the target in clutter. FM cries, when correlated with the echoes, are well suited for the accurate determination of distance (Simmons et al. 1979a). Harmonics help reduce ambiguity (in the time/distance domain), which is introduced by the bat's (relative) flight speed (Simmons and Stein 1980).

*E. serotinus*, *N. noctula* and *P. pipistrellus* will also hunt in more open environments (less acoustical clutter) and their orientational cries change accordingly. They apparently extend the lower frequency portion of the cry, producing longer more slowly swept cries with lower repetition rates. Higher fre-



**Fig. 6A-C.** Ultrasonic vocalizations during social activities. Bars with asterisks: 'social' vocalizations. **A, B** Recordings from *E. serotinus* and *N. noctula*, respectively, while they circled the roost. **C** Recording of *P. pipistrellus* during an aerial chase. **B<sub>2</sub>, C<sub>2</sub>** (Non-coincident) sound spectrograms of similar vocalizations. (The spectrograms were kindly provided by Dr. Ingemar Ahlén)

quencies are lacking. However, the radiation pattern of the cry, directionality of the microphone, and atmospheric attenuation all can contribute to the apparent absence of higher frequencies. *P. pipistrellus* uses CF cries extensively during foraging. We cannot correlate altitude, prey density, or seasonal changes with the use of CF cries from this species. This bat will even use CF cries when foraging in groups. The cries sometimes fall into several frequency levels (Fig. 5), which can be separated by as much as 14 kHz. Doppler shifts owing to the bats' flight speed cannot account for these frequency changes. The bats may do this to avoid interference when detecting their own echoes from others in the group. Hipposiderid bats from Kenya will shift the CF portion of their cries when conspecifics are present (Pye 1972, 1980).

It would be advantageous for 'FM' bats to use slowly swept FM cries or CF cries when flying in an open environment or under conditions of low prey density (Simmons et al. 1979a; Schnitzler and Henson 1980). Such cries (when correlated with echoes) can indicate the presence of a target, but will give poor information concerning the distance to the target (Simmons and Stein 1980). These types of cries would also be useful for detecting distant targets. Echoes could be detected at greater distances by increasing the acoustical power of the emitted signal (Simmons et al. 1978b). Lengthening the cry and restricting the bandwidth could improve the chances for neuronal filters to detect faint echoes (Grinnell and Hagiwara 1972). Whether the bats we studied actually employ such strategies is not known.

Some bats, such as *Rhinolophus ferrumequinum*, use the long CF portion of their cry to detect amplitude and frequency (Doppler) modulations in echoes produced by moving prey (Schnitzler 1978; Ostwald 1980). Theoretically, CF cries that exceed 5 to 10 ms in duration can be useful for detecting Doppler shifted echoes (Simmons and Stein 1980). At present, however, we do not know if vespertilionid and other 'FM' bats that are capable of producing slowly sweeping or short CF sounds can detect and use Doppler information.

The terminal frequencies of sequential cries emitted by a single *N. noctula* while foraging in open areas may be separated by several kHz (see the first two cries in Figs. 2D and 4A). Doppler effects owing to changes in flight velocity cannot account for such frequency shifts. At present we have no explanation for this acoustic behavior.

We assume that the predominantly V-shaped ultrasounds of *E. serotinus*, *N. noctula* and *P. pipistrellus* serve as social signals. In the first two species we presumably recorded the vocalizations of individuals circling the roost, but we cannot discount the possibil-

ity that the sounds came from within the roost. We have not yet recorded such sounds from *E. serotinus* and *N. noctula* at the foraging areas. The sounds emitted by *P. pipistrellus* when one individual chases another clearly have a social function. The context and significance of these vocalizations is not known since we do not know the social structure or the individuals of the foraging groups. The most characteristic signature of the 'social ultrasounds' is the upwards frequency sweep in the vocalizations of all three species (Fig. 6). Neurons that are selectively sensitive to upward frequency sweeps are known in myotis bats (Suga 1973).

As yet there are few reports of bats using ultrasound for purposes other than echolocation while in flight. Suthers (1965) recorded 'honks', which extended into the audible range, emitted by fishing bats (*Noctilio leporinus*) when on collision courses. Similar observations are reported for *M. lucifugus*, *M. volans* and *E. fuscus* (Fenton 1980). In an intensive study of *M. lucifugus* Barclay et al. (1979) found 10 call types mostly recorded at or in a nursery colony, night roosts, and mating and hibernation sites. Four types of cries with V-shaped configuration like those in Fig. 6 are classified as mother-young vocalizations. It seems unlikely that the cries reported here can all be of this nature, but field studies are still so few that general conclusions cannot be drawn.

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## References

- Andersen BA, Miller LA (1977) A portable ultrasonic detection system for recording bat cries in the field. *J Mammal* 58:226-229
- Barclay RMR, Fenton MB, Thomas DW (1979) Social behavior of the little brown bat, *Myotis lucifugus*. II. Vocal communication. *Behav Ecol Sociobiol* 6:137-146
- Fenton MB (1980) Adaptiveness and ecology of echolocation in terrestrial (aerial) systems. In: Busnell R-G, Fish JF (eds) *Animal sonar systems*. Plenum Press, New York, pp 427-446
- Griffin DR (1958) *Listening in the dark*. Yale Univ Press, New Haven
- Grinnell AD, Hagiwara S (1972) Adaptations of the auditory nervous system for echolocation. *Studies of New Guinea bats*. *Z Vergl Physiol* 76:41-81
- Ostwald J (1980) The functional organisation of the primary auditory cortex in the CF-FM bat *Rhinolophus ferrumequinum*. In: Busnell R-G, Fish JF (eds) *Animal sonar systems*. Plenum Press, New York, pp 953-955
- Pye JD (1972) Bimodal distribution of constant frequencies in some hipposiderid bats. *J Zool (Lond)* 166:323-335

- Pye JD (1973) Echolocation by constant frequency in bats. *Period Biol* 75:21-26
- Pye JD (1980) Echolocation signals and echoes in air. In: Busnell R-G, Fish JF (eds) *Animal sonar systems*. Plenum Press, New York, pp 309-353
- Sales G, Pye JD (1974) *Ultrasonic communication by animals*. Chapman and Hall, London
- Schnitzler H-U (1978) Die Detektion von Bewegungen durch Echoortung bei Fledermäusen. *Verh Dtsch Zool Ges* 16-33
- Schnitzler H-U, Henson OW (1980) Performance of airborne animal sonar systems: I. Microchiroptera. In: Busnell R-G, Fish JF (eds) *Animal sonar systems*. Plenum Press, New York, pp 109-181
- Simmons JA, O'Farrell MJ (1977) Echolocation by the long-eared bat, *Plecotus phyllotis*. *J Comp Physiol* 122:201-214
- Simmons JA, Lavender WA, Lavender BA, Childs JE, Hulebak K, Rigden MR, Sherman J, Woolman B, O'Farrell MJ (1978a) Echolocation by free-tailed bats (*Tadarida*). *J Comp Physiol* 125:291-299
- Simmons JA, Lavender WA, Lavender BA (1978b) Adaptation of echolocation to environmental noise by the bat *Eptesicus fuscus*. *Kenya Nat Acad* 97-104
- Simmons JA, Fenton MB, O'Farrell MJ (1979a) Echolocation and pursuit of prey by bats. *Science* 203:16-21
- Simmons JA, Fenton MB, Ferguson WR, Jutting M, Palin J (1979b) Apparatus for research on animal ultrasonic signals. *R Ont Mus Life Sci Misc Publ*
- Simmons JA, Stein RA (1980) Acoustic imaging in bat sonar: Echolocation signals and the evolution of echolocation. *J Comp Physiol* 135:61-84
- Suga N (1973) Feature extraction in the auditory system of bats. In: Møller AR (ed) *Basic mechanisms in hearing*. Academic Press, New York, pp 675-744
- Suthers RA (1965) Acoustic orientation by fish-catching bats. *J Exp Zool* 158:319-347