

Z. Säugetierkunde 53 (1988) 281–293
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ISSN 0044-3468

Search calls of echolocating *Nyctalus leisleri* and *Pipistrellus savii* (Mammalia: Chiroptera) recorded in Switzerland

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Receipt of Ms. 06. 04. 1987

Abstract

Studied the search calls of hunting *Nyctalus leisleri* and *Pipistrellus savii* north and south to the Swiss Alps.

The ultrasounds were converted to audio frequencies by a 8:1 dividing detector and subsequently analysed in the laboratory on a dual channel digital oscilloscope using a period meter.

In both species single harmonic pulses with shallow frequency modulation and pulses of constant frequency were recorded.

Search pulses of *N. leisleri* (median values of 204 signals): pulse duration 9.2 ms; start frequency 25.1 kHz; center frequency 24.3 kHz; end frequency 23.7 kHz; sweep bandwidth 1.6 kHz. The intervals ($N = 2153$) between search pulses followed a bimodal distribution with a higher mode at 243 ms and a weaker one at 350 ms.

Search pulses of *P. savii* (median values of 236 signals): pulse duration 12.1 ms; start frequency 34.2 kHz; center frequency 32.8 kHz; end frequency 32.0 kHz; sweep bandwidth 2.2 kHz. The intervals ($N = 1341$) between search pulses followed a bimodal distribution with a higher mode at 192 ms and a weaker one at 294 ms.

In both species various signal variables were significantly correlated. In addition to echolocation signals two types of social calls of *N. leisleri* were recorded. The first type consisted of a group of 4 pulses ranging from 38–16 kHz. The second type was a single, linear period modulated pulse of 20–27 ms duration, ranging from 21–10 kHz.

Introduction

In the course of a study about the acoustic identification of certain bat species in Switzerland, tape recordings of the acoustic behaviour of *Nyctalus leisleri* and *Pipistrellus savii* were made. Until now only little information on the echolocation sounds of both species had been available. HOOPER (1969) described the approximate frequency range and pulse repetition rate of captive *N. leisleri*. KONSTANTINOV and MAKAROV (1973), and PATLJAKEVITSCH (1980) studied echolocation pulses of captive *P. savii*. The present paper describes search calls of free flying individuals of both species as well as cries of *N. leisleri* which are assumed to be social calls.

Material and methods

Search pulses of free flying *N. leisleri* were recorded in the southern Alps ($N = 38$ analysed signals) and northern alps ($N = 140$) of Switzerland. One *N. leisleri*, marked with reflective tape on a ring, was recognized some weeks after release in the northern Alps. Search pulses were recorded, when this bat was hunting above a road with street lights. A further batch of signals ($N = 26$) of a single individual in the plane near Berne has been analysed. For statistical analysis all the recordings were pooled ($N = 204$ analysed signals).

Search pulses of free flying *P. savii* were recorded in northern ($N = 73$ analysed signals), central ($N = 90$) and southern ($N = 73$) parts of the Swiss Alps. For statistical analysis all the recordings were again pooled ($N = 236$ analysed signals).

"The distinction between search and approach calls is arbitrary as they are part of a continuum. . ." (FENTON and BELL 1981). For this study only pulses being part of more or less regular

sequences were analysed. Pulses whose BW/T-factor (kHz/ms) exceeded a value of 1.0 were not considered as search pulses and excluded from calculations.

In addition to the above signal sample obtained from free flying bats, echolocation pulses of several individuals of *P. savii* and *N. leisleri* were collected, when the bats were released after net trapping. The aim was to get reference signals from known individuals in order to facilitate the acoustic recognition of free flying bats.

All ultrasounds were picked up with a modified QMC S100 ultrasound detector connected to a frequency divider, developed and built by K. ZBINDEN, University of Berne. The frequency divider produces a sinusoidal waveform at one eighth of the original frequency and retains the envelope of the original signal. Further specifications are: Frequency range 10–220 kHz (+/-2 dB), S/N-ratio 55 dB (lin. 10–220 kHz), switchable HP-filter (20 kHz, 24 dB/octave). The transformed ultrasounds were recorded with a SONY TC-D 5M on metal cassettes (-3 dB at 15 kHz).

The recordings were analysed on a Nicolet type 3091 dual channel digital oscilloscope (2x4K words) using a period meter (zero crossing detector, developed by D. HARTLEY, Queen Mary College, London and K. ZBINDEN, University of Berne, who also built the instrument). Of each pulse the following signal variables were measured: The start frequency (f_s), the instantaneous frequency at maximum signal amplitude (f_{max}), the center frequency (f_c) at half the pulse duration and the end frequency (f_e). The frequency variables were estimated to an accuracy of +/-0.4 kHz in realtime. The sweep bandwidth was calculated as $BW = f_s - f_e$. The pulse durations were estimated to an accuracy of approx. 0.2 ms and intervals between pulses (from pulse center to pulse center) to an accuracy of +/-2 ms.

Averaged power spectra were obtained on an FFT-analyser type 2033 of B & K, Denmark (400 lines, flat weighting, linear average mode, RMS spectrum).

Computations of quartiles and modes were made according to SACHS (1978). Preceding the computations all the measurements were classified using class widths of 10 ms for interval durations, 1 ms for pulse durations and 0.8 kHz for frequencies (real time). Goodness-of-fit tests for normal distribution, correlation coefficients and arithmetic means were computed on a HP-71B calculator, using its AMPI statistics library.

In those cases where the distribution did not conform to the standard probability models, the median instead of the arithmetic mean was taken as a representative measure of location (or of central tendency).

The interquartile-range $Q_{(0.75)} - Q_{(0.25)}$, which contains 50% of a sample, was used as a measure of dispersion. To allow a comparison with the data obtained by other authors, both the parametric and nonparametric statistics were calculated.

Results

Nyctalus leisleri

Intervals between search pulses showed a bimodal distribution and varied considerably (Fig. 1A). A first prominent mode was at 243 ms and a second weaker mode at 350 ms (both modes were estimated using the original class width of 10 ms).

The pulse durations were normally distributed ($\chi^2=9.5$, $df=10$) with a median of 9.2 ms (Fig. 1B).

The distributions of the four frequency variables are shown in Figure 2, their statistical parameters in Table 1. A goodness-of-fit test was consistent with normal distribution in the case of the center frequency ($\chi^2=12.3$, $df=9$), the maximum frequency ($\chi^2=12.2$, $df=8$) and the end frequency ($\chi^2=2.8$, $df=7$), but not the bandwidth ($\chi^2=351$, $df=8$) and the start frequency ($\chi^2=71.3$, $df=14$), which skewed towards the higher frequencies.

In this sample the end frequency had the smallest statistical dispersion. The averaged power spectrum of 50 search pulses showed a dominant frequency at 23.8 kHz and a -6 dB spectrum bandwidth of 2.9 kHz (Fig. 3).

Most search pulses of *N. leisleri* were frequency modulated by a small amount only. Nine of 204 pulses ($T=3.7$ –12.2 ms) were of constant frequency (CF) in the range of 22.4–27.2 kHz. In the distribution of bandwidth (BW) the modal class and both classes on each side of it (range 0.8 to 2.4 kHz) contained 76% of the analysed pulses (see Fig. 1C). Pulses emitted during the approach phase however, frequently had a very steep frequency modulation and a bandwidth of more than 30 kHz.

Search pulses of *N. leisleri* often increased rapidly to a high amplitude level at their beginning (Fig. 4). When listening to the bats by means of a broadband detector this

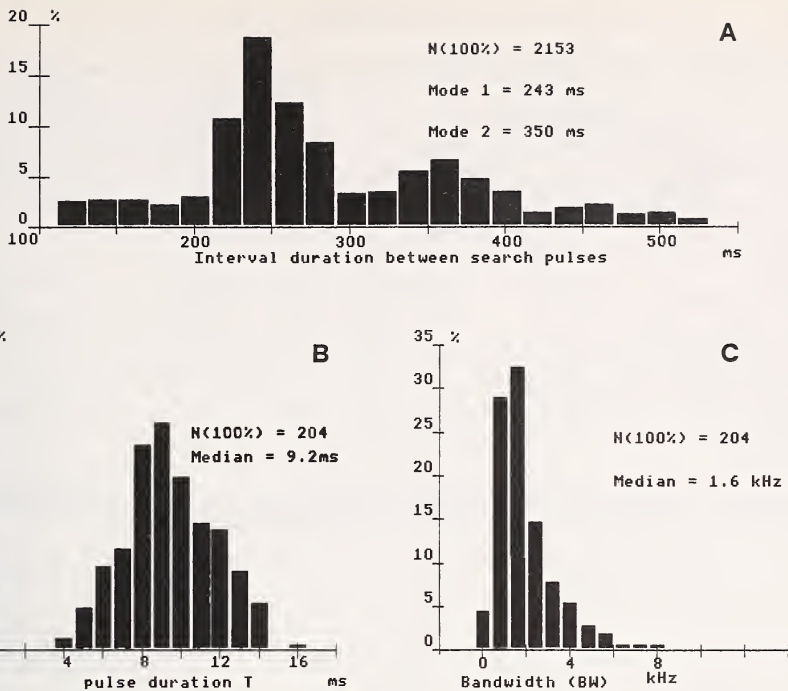


Fig. 1. *Nyctalus leisleri*. A: Interval duration between search pulses (from pulse center to pulse center). Width of classes is 20 ms. B: Duration of search pulses. Width of classes is 1 ms. C: Sweep bandwidth (BW) of search pulses. Width of classes is 0.8 kHz

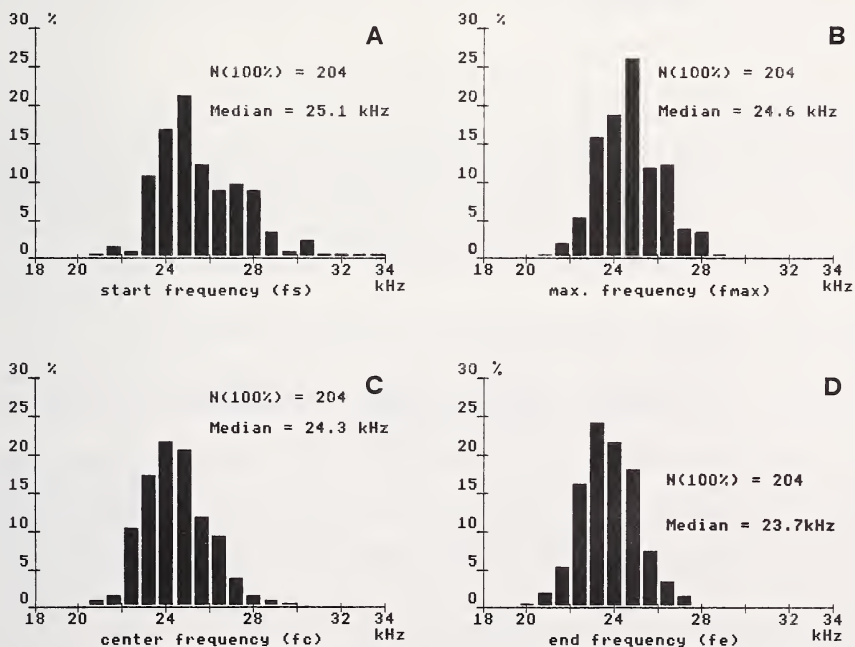


Fig. 2. Frequency variables of search pulses of *Nyctalus leisleri*. Width of classes is 0.8 kHz. A: Start frequency at the beginning of a pulse. B: Instantaneous frequency at maximum signal amplitude. C: Center frequency at half the pulse duration. D: End frequency

Table 1. Parameter values of search pulses (N = 204) of *Nyctalus leisleri*, as shown in Figs. 1 and 2

	Q1	Median	Q3	Q3-Q1	95 % confidence interval of \bar{x}
Pulse duration					
T (ms)	7.8	9.2	11.1	3.3	9.1–9.7
Start frequency					
fs (kHz)	24.1	25.1	27.0	2.9	25.3–25.9
Maximum frequency					
fmax (kHz)	23.7	24.6	25.7	2.0	24.5–24.9
Center frequency					
fc (kHz)	23.4	24.3	25.4	2.0	24.2–24.7
End frequency					
fe (kHz)	22.8	23.7	24.6	1.8	23.5–23.9
Bandwidth					
BW (kHz)	1.0	1.6	2.5	1.5	–

Q1 and Q3 are the quartiles $Q_{0.25}$ and $Q_{0.75}$ of the distributions. Q3-Q1 is the interval that contains 50 % of the whole sample (or 50 % of the frequency distribution area).

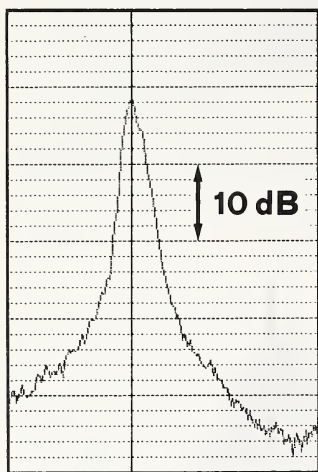


Fig. 3. *Nyctalus leisleri*. Averaged power spectrum of 50 search pulses (400 lines, RMS-spectrum type, flat weighting, linear averaging). Frequency span: 8–48 kHz. The vertical cursor is at the dominant frequency of 23.8 kHz. The -6 dB spectrum bandwidth is 2.9 kHz

resulted in an explosive sound, a phenomenon not found to the same extent in other bat species of Switzerland.

Due to the recording system used, the presence of harmonics could not be checked systematically. In a few search pulses 'steps' in the period plot seemed to indicate the eventual presence of a strong second harmonic, however.

It is known that there may exist relationships e.g. between pulse duration and bandwidth, depending on the function of a pulse (TUPINIER et al. 1980; HARTLEY 1985). Correlation coefficients were computed (Tab. 2) to check interesting relations between the measured variables of search pulses. Negative correlations between pulse duration T and the four frequency variables were found. This indicates that shorter search pulses tended to have higher values in all the frequency variables. There was no significant correlation between bandwidth and search pulse duration. This and the positive correlation between the end and the start frequency means that short pulses as a whole were situated higher in the frequency scale.

Fig. 4. Characteristic search pulse of *Nyctalus leisleri*. Oscillogram with superimposed frequency plot. $T=8.2$ ms, $f_s=23.2$ kHz, $f_{\max}=22.4$ kHz, $f_c=22.4$ kHz, $f_e=22.4$ kHz. The vertical cursor indicates the pulse center (half duration). The horizontal cursor is at 30 kHz in the frequency plot

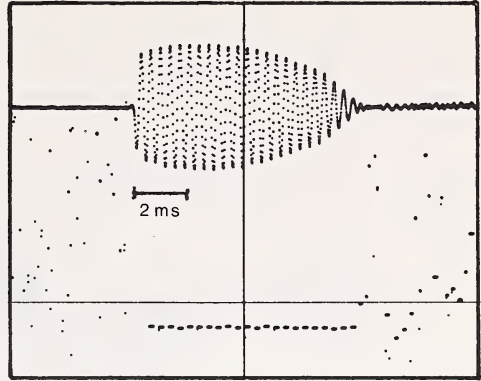


Table 2. Correlation coefficients (arranged from highest to lowest) of selected variables of a random subsample of 49 search pulses of *Nyctalus leisleri*

$r(f_e, f_s) = +0.777$	$r(f_c, T) = -0.653$	$r(BW, T) = +0.001$
$r(f_e, T) = -0.739$	$r(f_s, T) = -0.554$	
$r(f_{\max}, T) = -0.667$	$r(BW, f_e) = +0.037$	

A goodness-of-fit test was consistent with normal distribution for all the variables. T : $\chi^2=8.8$ ($df=8$). f_s : $\chi^2=2.5$ ($df=5$). f_{\max} : $\chi^2=2.4$ ($df=6$). f_c : $\chi^2=3.8$ ($df=4$). f_e : $\chi^2=3.8$ ($df=5$). BW : $\chi^2=7.4$ ($df=3$). The null hypothesis, $H_0: p=0$, can be rejected at $P<0.001$, for all the r -values, except $r(BW, f_e)$ and $r(BW, T)$, where $P>0.1$

Social calls of *N. leisleri*

On 4 July 1986 at 2:30 MEZ, two *N. leisleri* were hunting insects above the street lights at Meiringen (Northern Alps). In addition to echolocation signals, complex patterns of cries, probably of social function, were recorded. It is not known whether the calls were emitted by both animals. Two types of social calls will subsequently be described.

The first type of social call consisted of a group of four pulses (Fig. 5). Four of these calls were emitted in short sequence separated by intervals of 195–485 ms, containing a number of echolocation pulses.

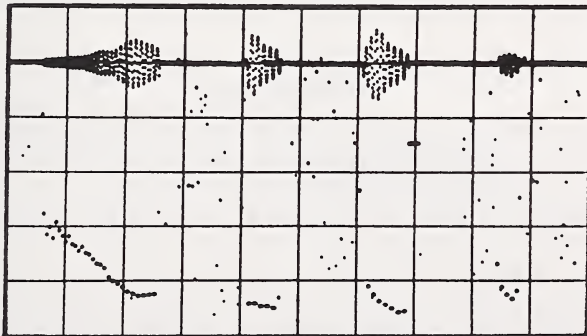


Fig. 5. *Nyctalus leisleri*. Social call type 1. Oscillogram with superimposed frequency plots (horizontal axis 4.0 ms/div). Cf. text for further details

With about 9 ms the first cry of a group had the longest duration. It used to start at 38 kHz with a short, shallow frequency modulation, followed by a long, steeper part and ended at 22 kHz with shallow modulation again. In one group the change in the modulation rate of the first pulse occurred abruptly and resulted in an "elbow"-shaped frequency plot (Fig. 5).

The following three pulses in the groups were all different from the first one. Their pulse duration was shorter and varied from 1.6 to 4.8 ms. In each group the last pulse was the shortest. The second, third and fourth pulse started at 20–27 kHz with a maximum amplitude at approx. 21 kHz and ended at 16–20 kHz. They, and especially the fourth pulse in each group, appeared to include higher harmonics of varying strength. The intervals between pulses were in the range of 4.7–11.5 ms.

In late August 1986 similar social calls were recorded in southern Switzerland. They were emitted by two or three unknown bats which stayed in a group of chestnut trees (*Castanea sativa*). The calls consisted of three to five pulses. The first pulses had a duration of 9–14 ms. They started with shallow frequency modulation at 25–28 kHz. The modulation rate became steeper in the second half of the pulse which ended at a frequency of 18–20 kHz. The plot of the instantaneous frequency showed a convex curve. The following pulses in a group always had a shorter duration (1–5 ms). Their lowest frequency varied from 14 to 21 kHz.

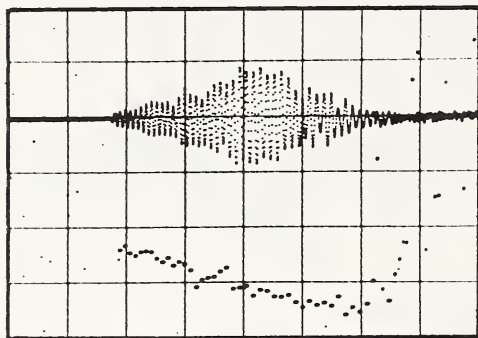


Fig. 6. *Nyctalus leisleri*. Social call type 2. Oscillogram with superimposed frequency plot (horizontal axis 5.4 ms/div.). T=24 ms, fs=17 kHz, fmax=fc=13 kHz, fe=10 kHz

At Meiringen a second type of social call of *N. leisleri* was recorded three times, when a pipistrelle bat (*P. pipistrellus*) passed (Fig. 6). The pulse duration varied from 24 to 27 ms. All pulses were more or less linear period modulated, started at 18–17 kHz and ended at 11–10 kHz. The FFT power spectrum of the pulse shown in Figure 6 had a peak at 12.6 kHz and a -6 dB spectrum bandwidth of 1.4 kHz.

The same type of social call was recorded in southern Switzerland from the same two or three unidentified bats as described above.

Mean values \pm standard deviation of 22 analysed signals from southern Switzerland were: T=22.1 \pm 2.17 ms, fs=19.2 \pm 0.78 kHz, fmax=12.5 \pm 0.57 kHz, fc=13.7 \pm 0.57 kHz, fe=11.2 \pm 0.39 kHz and BW=8.0 \pm 0.63 kHz. These parameter values are close to those of the calls recorded in northern Switzerland.

Pipistrellus savii

The distribution of intervals between search pulses (Fig. 7A) was again multimodal and had a prominent peak at about 190 ms. There was a second much smaller mode at 294 ms (both modes were computed using the original class width of 10 ms).

For all the variables T, fs, fmax, fc, fe and BW the hypothesis of normal distribution could not be maintained (Chi-square goodness-of-fit test). Thus the median and the quartiles are better suited to characterize the distributions.

In the distribution of pulse durations (median: 12.1 ms) 50% of the sample were between 10.9 ms ($Q_{0.25}$) and 13.8 ms ($Q_{0.75}$) (Fig. 7B and Tab. 3). Two pulses in the sample were considerably longer (20 and 21 ms).

Although their BW/T is not higher than 1.0, five pulses of the sample may be classified

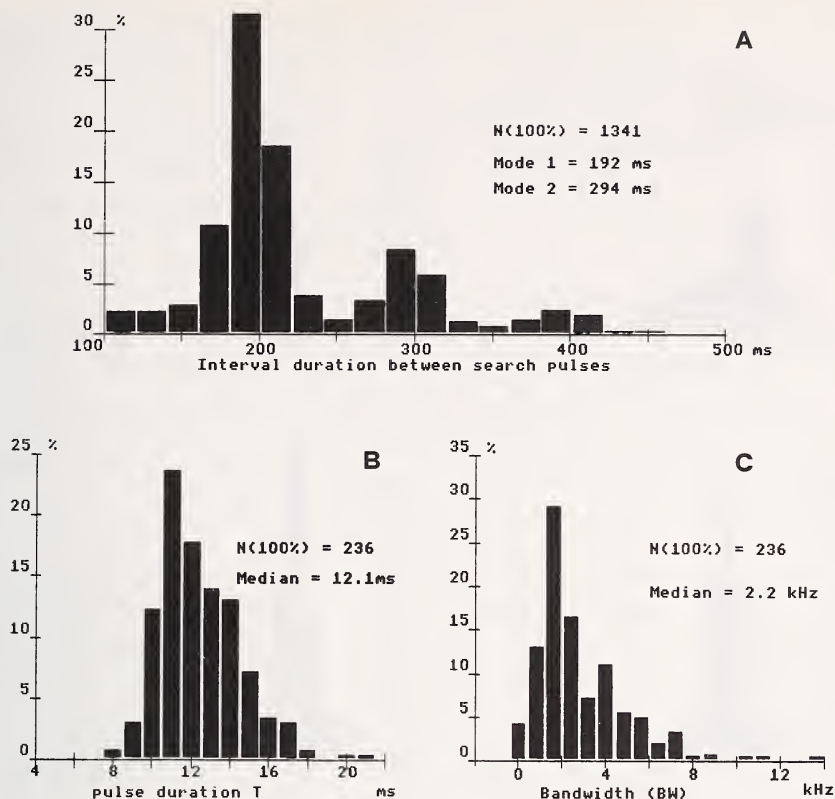


Fig. 7. *Pipistrellus savii*. A: Interval duration between search pulses (from pulse center to pulse center). Width of classes is 20 ms. B: Duration of search pulses. Width of classes is 1 ms. C: Sweep bandwidth (BW) of search pulses. Width of classes is 0.8 kHz

as approach pulses when their high start frequencies and bandwidths are considered (Figs. 8A and 7C). Parameter estimation excluding these five outliers does not shift the obtained results substantially, however.

The end frequency had a very prominent peak at 32 kHz and the smallest dispersion (Fig. 8D). The center frequency (Fig. 8C) and the maximum frequency (Fig. 8B) also had a rather small dispersion. Again the distribution of the start frequency (Fig. 8A) was platycurtic, skewed towards higher frequencies and was most dispersed. The averaged power spectrum of 50 search pulses had a dominant frequency of 33.2 kHz and a -6 dB spectrum bandwidth of 1.6 kHz (Fig. 9).

The bandwidth of the search pulses (Fig. 7C) varied more than in *Nyctalus leisleri* but, with 1.6 kHz, had the same peak value. The modal class and both classes on each side of it (range 0.8 to 2.4 kHz) contained only about 59% of the sample.

Nine search pulses ($T=11-18$ ms) of the whole sample were of constant frequency, in the range of 32.0–33.6 kHz.

Table 4 shows the correlation coefficients of selected variables of a random subsample of 49 search pulses of *P. savii*.

The three strongest correlations indicate that shorter search pulses tended to have a higher start frequency and a larger sweep bandwidth.

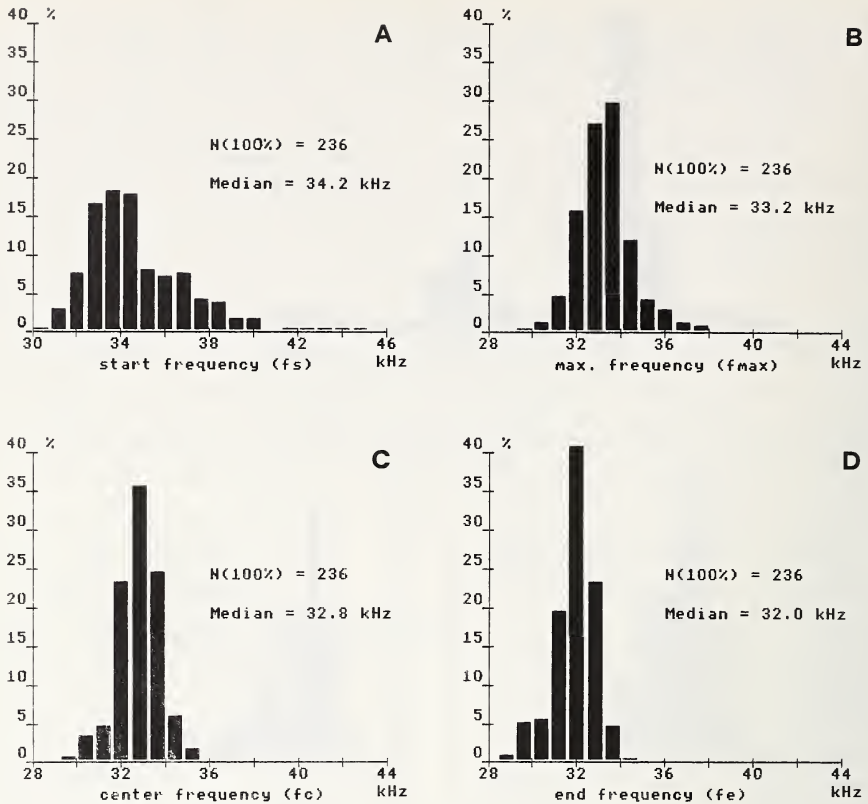


Fig. 8. Frequency variables of search pulses of *Pipistrellus savii*. Width of classes is 0.8 kHz. A: Start frequency at the beginning of a pulse. B: Instantaneous frequency at maximum signal amplitude. C: Center frequency at half the pulse duration. D: End frequency

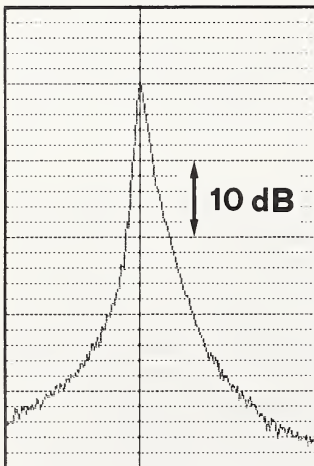


Fig. 9. *Pipistrellus savii*. Averaged power spectrum of 50 search pulses (settings cf. Fig. 3). Frequency span: 16–56 kHz. The vertical cursor is at the dominant frequency: 33.2 kHz. The -6 dB spectrum bandwidth is 1.6 kHz

Fig. 10. Characteristic search pulse of *Pipistrellus savii*. Oscillogram with superimposed frequency plot. T=10.9 ms, fs=33.6 kHz, fmax=32.8 kHz, fc=32.8 kHz, fe=32.0 kHz. The vertical cursor indicates the pulse center. The horizontal cursor is at 30 kHz in the frequency plot

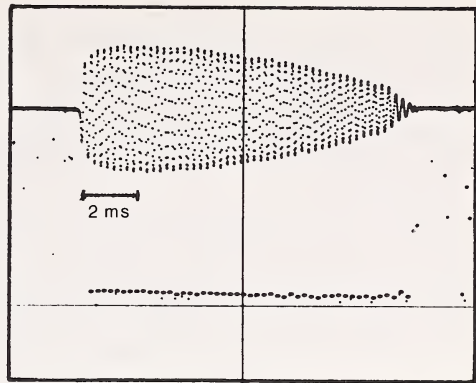


Table 3. Parameter values of search pulses (N=236) of *Pipistrellus savii*, as shown in Figs. 7 and 8

	Q1	Median	Q3	Q3-Q1	95 % confidence interval of \bar{x}
Pulse duration					
T (ms)	10.9	12.1	13.8	2.9	12.1–12.7
Start frequency					
fs (kHz)	33.1	34.2	36.0	2.9	34.4–35.0
Maximum frequency					
fmax (kHz)	32.5	33.2	33.7	1.2	33.1–33.4
Center frequency					
fc (kHz)	32.2	32.8	33.4	1.2	32.6–32.9
End frequency					
fe (kHz)	31.4	32.0	32.5	1.1	31.8–32.0
Bandwidth					
BW (kHz)	1.4	2.2	3.9	2.5	–

Q1 and Q3 are the quartiles $Q_{0.25}$ and $Q_{0.75}$ of the distributions. Q3-Q1 is the interval that contains 50 % of the whole sample (or 50 % of the frequency distribution area)

Table 4. Correlation coefficients (arranged from highest to lowest) of a selected variables of a random subsample of 49 search pulses of *Pipistrellus savii*

$r(fs, T) = -0.607^{***}$	$r(fmax, T) = -0.411^{**}$	$r(BW, fe) = +0.047$
$r(BW, T) = -0.514^{***}$	$r(fc, T) = -0.357^*$	
$r(fe, fs) = +0.451^{**}$	$r(fe, T) = -.300^*$	

A goodness-of-fit test was consistent with normal distribution for all the variables. T: $\chi^2=4.8$ (df=8). fs: $\chi^2=3.9$ (df=6). fmax: $\chi^2=5.3$ (df=6). fc: $\chi^2=1.3$ (df=4). fe: $\chi^2=2.3$ (df=3). BW: $\chi^2=11.2$ (df=6). Significance levels to reject the null hypothesis, $H_0: p=0$, are: $^{***}P < 0.001$, $^{**}P < 0.01$ and $^*P < 0.05$. But $P > 0.1$ für $r(BW, fe)$

Discussion

During the field work I realized that bats did show a different acoustic behaviour, depending on how they were released. If they were allowed to decide themselves when to fly away from the hand of the observer, most bats emitted short FM pulses with a steep frequency modulation.

But when the bats were thrown upwards in the air, there was a good chance that they changed from the initial steep FM pulses to shallow modulated search pulses still within the range of the recording microphone.

Generally pipistrelle bats (*P. pipistrellus*, *P. nathusii*, *P. kuhli* and *P. savii*) used to change quickly from approach pulses to search pulses and to turn round close to the place where they had been released. Sometimes they even started to hunt insects in the proximity of the observer.

Noctule bats (*N. noctula* and *N. leisleri*) on the other hand often used to fly straight away from the observer in fast flight and it was difficult to record search calls in this way. For this reason tape recordings of released and in their behaviour probably disturbed bats were not taken into account for the analysis so far.

To allow a comparison, parameter values of a pooled sample of 44 pulses recorded from 12 *N. leisleri* when they were thrown in the air, is shown in Table 5.

Table 5. Parameter values of echolocation pulses (N=44) of 12 *Nyctalus leisleri*, recorded shortly after the bats had been released

	Q1	Median	Q3	Q3-Q1	Minimum value	Maximum value
Pulse duration T (ms)	9.8	11.7	12.4	2.6	7.2	15.9
Start frequency fs (kHz)	25.0	27.0	32.1	7.1	21.6	48.8
Maximum frequency fmax (kHz)	23.9	24.8	26.8	2.9	21.6	31.2
Center frequency fc (kHz)	23.7	24.6	26.2	2.5	21.6	30.4
End frequency fe (kHz)	23.0	23.9	25.1	2.1	20.8	27.2
Bandwidth BW (kHz)	1.5	3.3	7.3	5.8	0	21.6

Q1 and Q3 are the quartiles $Q_{(0.25)}$ and $Q_{(0.75)}$ of the distributions. Q3-Q1 contains 50 % of the whole sample (or 50 % of the frequency distribution area)

The parameter values of the pulse sample of released bats were generally similar to the parameter values of the search pulses of undisturbed, free flying *N. leisleri* (compare with Tab. 1). The end frequency and the center frequency showed the least divergence.

The extreme upper values of the start frequency and the bandwidth in Table 5 indicate that the sample contained a few pulses similar to those emitted in the approach phase.

In general terms the variables of search pulses analysed in this study varied less in *P. savii* than in *N. leisleri*. This points to a more regular flight behaviour in *P. savii*. I could not see Savi's pipistrelles when they were hunting along the streets, since they used to fly higher than the bright streetlights at approximately 10 m above ground.

The flight height of the Lesser noctules varied considerably. On average the bats were hunting at the level of the street lights, but I observed Lesser noctules pursuing moths down to the ground or searching much higher than the street lights. This flexible flight behaviour may be the reason for the large dispersion of pulse interval durations.

Search calls of *P. savii* had the lowest end- and center frequency of the four *Pipistrellus* species (*P. pipistrellus*, *P. nathusii*, *P. kuhli*, *P. savii*) that occur in Switzerland (unpubl. data). The search calls of Savi's pipistrelle appear to be closer to those of *Eptesicus nilssonii* than to those of the other three *Pipistrellus* species. This similarity between *E. nilssonii* and *P. savii* can be affirmed by their resembling appearance (e.g. colour of the skin, shape of

the ear, projecting tail-tip), a fact already mentioned by MILLER (1912, p. 224). HORACEK and HANAK (1986) now propose to place *P. savii* in a separate genus *Hypsugo*.

The correlations showed that in *N. leisleri* shorter pulses were generally of higher frequency, but without an increase of the bandwidth of the fundamental harmonic. It is conceivable that in fact a higher sweep bandwidth was realized by introducing additional harmonics, which of course were not detectable by the system used in this study. In general terms the values of the correlation coefficients are smaller in *P. savii* than in *N. leisleri*. The relations between bandwidth BW and pulse duration T were markedly different in the two species. In *N. leisleri* there was no significant correlation between these two variables in the case of search pulses. In *P. savii* on the other hand a significant negative correlation existed between the bandwidth and the pulse duration: When the search pulse duration decreased, their bandwidth increased. Since the end frequency showed only little variability, the higher bandwidth of short pulses was due to an increased start frequency. This is affirmed by its negative correlation to the pulse duration.

HOOPER (1969) and WATSON (1970) evaluated the frequency range of *N. leisleri* by means of a heterodyning detector (Holgate Ultrasonic Receiver) only. HOOPER (1969) determined 80 and 25 kHz as "upper and lower limits of the detected range of frequency sweep" and measured a pulse repetition rate of 8–10 pulses per sec (i.e. 125–100 ms interval duration) under indoor conditions (crawling). Only the lower frequency limit resembles the end frequencies of search calls presented in this paper.

WATSON (1970) gave an "approximate frequency range for field work" of 15–70 kHz, which should be valid for both noctule species (*N. noctula* and *N. leisleri*). This frequency range is far wider than the range of search calls of *N. leisleri* (20–34 kHz) reported here.

KONSTANTINOV and MAKAROV (1973) analysed 44 signals of one *P. savii*. The short pulse durations (0.8–2.3 ms) as well as the high start frequencies (90–100 kHz) and end frequencies (40–45 kHz) are consistent with indoor conditions. The authors mentioned a second harmonic and a near linear frequency modulation in the first part of the signal.

PATLJAKEVITSCH (1980) measured a mean start frequency of 71.3 kHz and a mean end frequency of 35.7 kHz from handheld *P. savii*. This is still above the highest end frequency I have found in search pulses. The pulse duration of his handheld bats ranged between 0.4 and 36 ms. When the bats were flying away from the wall of an aviary he measured pulse durations up to 5 ms. In our recordings the pulse durations were in the range of 8 to 21 ms.

The evidence of constant frequency (CF) pulses in *N. leisleri* and *P. savii* is not surprising. Pure CF-pulses have formerly been reported of *N. noctula* (PYE 1978, 1980; VÖGLER and NEUWEILER 1983) and *P. pipistrellus* (PYE 1978, 1980; AHLEN 1981; MILLER and DEGN 1981).

A sequential alternation of the end frequency on a pulse to pulse basis, as known from *N. noctula* (AHLEN 1981; MILLER and DEGN 1981; HARTLEY 1985), was rarely observed in *N. leisleri*. On the contrary, pulse sequences with end frequencies varying less than 1 kHz seem to be characteristic for this species.

It is interesting to compare the positions of the modes of intervals between search pulses. In *P. savii* I got the equation 'mode 2 = $1.53 \times$ mode 1' and in *N. leisleri* 'mode 2 = $1.44 \times$ mode 1'. A comparable relation between modes can be established from the interval distribution of search pulses of *Nyctalus noctula* (high flight) in AHLEN (1981).

For *N. noctula* HARTLEY (1985) measured a wing beat rate of 9/sec (= 111 ms interval duration) in pursuit flight, corresponding to one pulse per wing beat. In cruising flight he found two wing beats per pulse. The interpulse intervals (cruising flight) presented in this paper might be consistent with the hypothesis of two wing beats per pulse (first mode) and three wing beats per pulse (second mode).

Due to lacking behavioural data, the social calls described in this paper should be interpreted with caution. The first type of social call, recorded in July 1986 at Meiringen, appeared to be an interaction between two individuals of *N. leisleri*. The first and the

second type of social calls were also recorded when a *P. pipistrellus* passed the Lesser noctules. At the same time sequences of short pulses (3–4 ms, probably multiharmonic) with end frequencies of about 10 kHz (interpulse duration ca. 6 ms) were recorded. Figure 11 shows part of such a sequence enclosing an echolocation pulse.

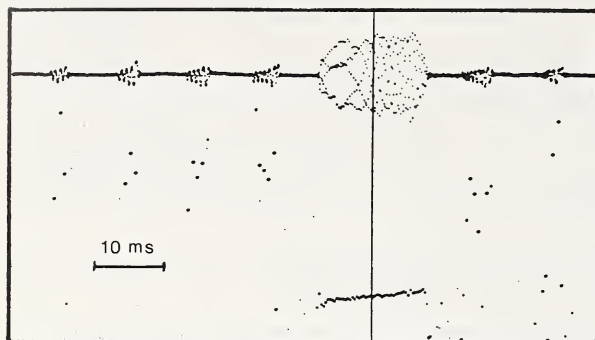


Fig. 11. *Nyctalus leisleri*. Oscillogram and superimposed period plot showing a search pulse ($T=14.9$ ms, $f_s=28.0$ kHz, $f_c=24.8$ kHz, $f_{max}=f_e=24.0$ kHz) and part of a sequence of ten short pulses of social context ($T=2.7$ – 4.2 ms, f_e =ca. 10 kHz, interpulse duration = 4.6–8 ms). The vertical cursor indicates the pulse center of the search pulse. The total time from the start of the first short pulse to the end of the tenth short pulse was 113 ms

In southern Switzerland the social calls resembling type 1 and 2 of Meiringen were recorded during the mating season (August 86) and there was no indication that interactions with other species occurred. On the basis of the similar structure and the combined occurrence of call type 1 and 2 at Meiringen as well as in Southern Switzerland, I assume that these two types of social calls were actually emitted by individuals of *Nyctalus leisleri* at both recording sites.

In the field, the social call of type 2 could be confused with echolocation pulses of *Tadarida teniotis* (ZBINDEN and ZINGG 1986). But signal analysis shows that search calls of *T. teniotis* have not such a high start frequency and are not normally of linear period modulation.

Acknowledgements

I wish to thank ELISABETH BUCHER and RAPHAËL ARLETTAZ for their precious help in the fieldwork. Prof. V. AELLEN kindly supplied me with Russian literature, parts of which were translated by Mrs. V. SCHNELL and R. HODEL. I thank Dr. O. BERNATH, Departement of Audiology of the Berne University Hospital, for permitting the use of the FFT-analyser. I am greatly indebted to Dr. KARL ZBINDEN for critically reading the manuscript, making important suggestions for its improvement and correcting the text. This study was supported by the Swiss National Science Foundation (grant no. 3.177-0.85).

Zusammenfassung

Suchflugortungslaute von Nyctalus leisleri und Pipistrellus savii (Mammalia: Chiroptera) in der Schweiz

Suchflugortungslaute jagender *Nyctalus leisleri* und *Pipistrellus savii* wurden mittels QMC S100 Detektor und 8:1 Frequenzteiler auf der schweizerischen Alpennord- und Alpensüdseite registriert. Bei beiden Arten wurden sowohl schwach frequenzmodulierte als auch konstantfrequente Suchfluglaute festgestellt.

Für 204 analysierte Suchfluglaute von *N. leisleri* waren folgende Medianwerte charakteristisch: Signaldauer 9.2 ms, Anfangsfrequenz 25.1 kHz, Zentrumsfrequenz 24.3 kHz, Endfrequenz 23.7 kHz, Signal-Bandbreite 1.6 kHz. Die Intervalldauer ($N=2153$) zwischen den Signalen zeigte eine bimodale Verteilung, mit einem starken Modus bei 243 ms und einem zweiten, schwächeren bei 350 ms.

Für 236 Suchfluglaute von *P. savii* waren folgende Medianwerte typisch: Signaldauer 12.1 ms, Anfangsfrequenz 34.2 kHz, Zentrumsfrequenz 32.8 kHz, Endfrequenz 32.0 kHz, Signal-Bandbreite 2.2 kHz. Die Intervalldauer ($N=1341$) zwischen den Signalen war bimodal verteilt, mit einem starken Modus bei 192 ms und einem zweiten, schwächeren bei 294 ms. Bei beiden Spezies wurden zwischen verschiedenen Variablen der Suchfluglaute signifikante Korrelationen ermittelt.

Zusätzlich werden als Soziallaute interpretierte Ruftypen von *N. leisleri* beschrieben. Der erste Typ bestand aus einer Gruppe von vier Lauten im Frequenzbereich von 38–16 kHz. Der zweite Typ, ein linear periodenmodulierter Einzellaut ($T=20\text{--}27\text{ ms}$), überstreicht ein Frequenzband von 21–10 kHz und kann im Felde mit Ortungsrufen von *Tadarida teniotis* verwechselt werden.

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Zeitschrift/Journal: [Mammalian Biology \(früher Zeitschrift für Säugetierkunde\)](#)

Jahr/Year: 1988

Band/Volume: [53](#)

Autor(en)/Author(s): Zingg Peter E.

Artikel/Article: [Search calls of echolocating Nyctalus leiston and Pipistrellus savii \(Mammalia: Chiroptera\) recorded in Switzerland 281-293](#)