Echolocation behavior of big brown bats, *Eptesicus fuscus*, in the field and the laboratory

Annemarie Surlykke
Center for Sound Communication, Institute of Biology, Odense University, SDU, University of Southern Denmark, DK-5230 Odense M., Denmark

Cynthia F. Moss
Department of Psychology, University of Maryland, College Park, Maryland 20912

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Echolocation signals were recorded from big brown bats, *Eptesicus fuscus*, flying in the field and the laboratory. In open field areas the interpulse intervals (IPI) of search signals were either around 134 ms or twice that value, 270 ms. At long IPI's the signals were of long duration (14 to 18–20 ms), narrow bandwidth, and low frequency, sweeping down to a minimum frequency ($F_{\min}$) of 22–25 kHz. At short IPI's the signals were shorter (6–13 ms), of higher frequency, and broader bandwidth. In wooded areas only short (6–11 ms) relatively broadband search signals were emitted at a higher rate (avg. IPI=122 ms) with higher $F_{\min}$ (27–30 kHz). In the laboratory the IPI was even shorter (88 ms), the duration was 3–5 ms, and the $F_{\min}$ 30–35 kHz, resembling approach phase signals of field recordings. Excluding terminal phase signals, all signals from all areas showed a negative correlation between signal duration and $F_{\min}$, i.e., the shorter the signal, the higher was $F_{\min}$. This correlation was reversed in the terminal phase of insect capture sequences, where $F_{\min}$ decreased with decreasing signal duration. Overall, the signals recorded in the field were longer, with longer IPI's and greater variability in bandwidth than signals recorded in the laboratory. © *2000 Acoustical Society of America.* [S0001-4966(00)03611-0]

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I. INTRODUCTION

Pierce and Griffin, and subsequently Griffin and Galambos, conducted a series of elegant experiments around 1940 that unraveled the mystery of bat orientation in the dark (Griffin, 1958). They demonstrated that microchiropteran bats emit ultrasonic frequency sounds and listen to echoes from objects in the path of the sound beam, allowing them to orient in the dark and exploit the food sources of the night sky. Griffin (1944) called this acoustic orienting behavior ''echolocation.'' This seminal finding triggered a vast amount of research directed at understanding perception by sonar in echolocating bats. Over the past 60 years, research has emphasized the following questions: What are the characteristics of bat echolocation sounds? What adaptations are present in the bat's auditory system to analyze sonar echoes and represent the animal's environment? How does the bat's sonar receiver perform in tasks of ranging, detection, and discrimination? How does sonar signal design influence echo information processing in different bat species hunting in different environments?

Research on echolocation behavior in bats has followed two main avenues. One emphasizes laboratory experiments that introduce careful manipulation of discrete acoustic variables and measurement of behavioral performance in sonar tasks. For example, psychophysical studies determine the bat's detection or discrimination of echoes that differ in amplitude, delay, spectrum, and/or Doppler shift (for review, see Moss and Schnitzler, 1995). Other laboratory studies of echolocation behavior examine obstacle avoidance and insect capture under controlled experimental conditions (Simmons *et al.*, 1995). Neurophysiological experiments examine responses of neurons in the bat's auditory pathway to acoustic parameters relevant to biosonar (for reviews, see Suga, 1988; Popper and Fay, 1995).

The other approach to study echolocation behavior in bats involves field recordings of the signals used by different species foraging in different habitats. There are around 700 species of echolocating bats, and they differ in their sonar signal designs for foraging under different conditions. Bat sonar signals may contain constant frequency (CF) and frequency modulated (FM) components, and these signals range from less than 1 ms to more than 100 ms in duration (Simmons and Stein, 1980; Neuweiler, 1984; Fenton, 1995). Most species that have been studied to date show changes in the parameters of their sonar signals (e.g., duration, bandwidth, and repetition rate) with foraging conditions, such as their proximity to vegetation, water, and buildings (Fenton, 1986; Neuweiler, 1984; Schnitzler and Kalko, 1998). It is widely believed by researchers in the field that sonar signal design reflects the bat's active control over important acoustic information gathered from sonar echoes (Griffin, 1958). Thus one can gain insights to the basics of echolocation by comparing sonar signals produced by different bat species for echolocation under similar and different environmental conditions (Neuweiler, 1984).

Only a small number of the extant bat species have been the subject of extensive field studies. Among the insectivorous species studied, there are some general patterns in acoustic behavior that accompany the pursuit and capture of prey (Simmons *et al.*, 1979). In particular, insectivorous bats produce sonar signals that decrease in duration and increase

in repetition rate as they approach a prey item. The bat's acoustic behavior during insect capture is typically divided into the search, approach, and terminal phases, largely distinguished by the repetition rate of the bat's sonar signals. During the search phase, sonar signals are typically produced at a rate of 2–10 per sec. The repetition rate may increase to about 80 sounds per sec during the approach phase and to as high as 200 sounds per sec during the terminal phase. The terminal phase signals occur at such a high rate that it is often referred to as the terminal buzz (Griffin, 1958).

A common goal of laboratory and field studies of echolocation behavior in bats is to characterize the acoustic signals used to probe the environment and to understand perception by sonar (Simmons *et al.*, 1975). While there are similarities in some broad characteristics of sonar signals produced by different insectivorous species, there are also considerable differences in time-frequency structure, bandwidth, duration, and repetition rate of sonar signals recorded from different species under different foraging conditions. Furthermore, behavioral data on echolocation task performance reveal species-specific differences that appear related to sonar signal features. Thus one cannot simply take information about the natural acoustic behavior of one bat species to interpret the results of laboratory experiments on another bat species. Therefore, it is most striking that almost no field recordings have been published from the big brown bat, *Eptesicus fuscus*, one of the most widely studied bat species in laboratory experiments (Covey and Casseday, 1995; Simmons *et al.*, 1995; Simmons, 1973; Moss and Schnitzler, 1995). Apart from Griffin's thorough, but old, data (Griffin, 1958), the published information on acoustic behavior of *E. fuscus* in the field is limited to bat detector recordings (Betts, 1998, or web sites, e.g., http://talpa.unm.edu/batcall) and cursory data in reviews and papers focusing on other aspects of echolocation (Obrist, 1995; Simmons *et al.*, 1979; Simmons, 1987). The detailed acoustical data on sonar signals produced by *E. fuscus* come from recordings of bats in the lab (Hartley, 1992). However, it has been demonstrated repeatedly that bats do not emit the same signals in the confined environment of a laboratory as they do in their natural habitat (Griffin, 1958).

Thus one purpose of the present study was to provide more detailed reference data on the natural acoustic behavior of *Eptesicus fuscus* in the wild. A second purpose was to compare this species' acoustic behavior in the wild with the echolocation signals it produces while catching tethered insects in a large laboratory flight room.

II. METHODS

A. Field locations

We recorded echolocation sounds from *E. fuscus* at three different sites in Maryland, in areas where we identified *E. fuscus* colonies and/or foraging behavior.

At the first field site, A (Rockville, North of Washington, D.C., recording date: Aug. 3, 1999), we recorded cruising *E. fuscus* as they flew out of their roost on the way to their hunting grounds. The colony roosted in the attic of a townhouse on the shore of an artificial lake. Leaving the roost, the bats flew out from a small opening under the roof, out over the lake, and turned left to fly past the recording microphone (see below) before disappearing over some trees on the opposite brink. Hence, in general our recordings were made with the microphone at $-90°$ with respect to the general flight path of the bats. We started the recordings right after sunset (8:45 pm) when the first bats flew out and stopped at 9:50 pm, before the bats returned. Thus it is highly unlikely that we recorded any single bat more than once, and the risk of pseudoreplication is very small.

The second site, B (Gambrill, 10 km NW of Annapolis, Maryland, recording date: Aug. 8, 1999) was an open hunting area. There was a large grass lawn stretching away from a house. The lawn was lined by large old trees, and an open field extended beyond. The bats flew and hunted at different heights at this site, from 4–5 m above the ground to well above the level of the tree tops ($>$10 m), and our recordings included signals from several bats occupying the area at the same time.

The third site, C (Greenbelt, close to University of Maryland, College Park, recording date: Sept. 14, 1999) was a more confined hunting area, a road (7-m wide), running through a wooded area. We identified this site as ''cluttered,'' in accordance with Kalko and Schnitzler, 1993. Along the road were street lamps, and the bats hunted primarily around the lamps, $\sim$8 m above the ground. Here, as at site B, we have simultaneous recordings of several bats. Thus we know we recorded more than one bat, but we have no control over which bats we recorded, and some of the sequences we chose for analysis might well be from the same bat.

B. Lab recordings

The lab recordings were carried out under long wavelength lighting ($>$650 nm, red filters, Reed Plastics, Rockville, MD) in a $6.4\times7.3\times2.5$ m carpeted flight room, with walls and ceiling lined with acoustic foam (Sonex 1, Illbruck). Two *E. fuscus* were trained to capture tethered mealworms. The worms hung from the ceiling of the flight room by a very thin thread. The position and movement of the worm varied from trial to trial. The bats' flight and capture behavior were recorded on two gen-locked high-speed video recorders (Kodak MotionCorders) at 240 frames/sec. The bat's three-dimensional (3-D) flight path was later reconstructed using commercial motion analysis software (Motus, Peak Performance Technologies).

C. Sound recordings

We used two different recording setups. At sites A and B we used an Ultrasound Advice SM2 microphone and SP2 amplifier (sensitivity is flat up to 40 kHz and decreases gradually by 5 dB from 40 to 100 kHz). The signals were bandpass filtered from 10–100 kHz (filter slope -110 dB at $1.5f_c$) and further amplified using a Stanford Research Systems Model SR 650 digital filter. At site C we used a battery operated system consisting of a 1/4″ G.R.A.S. microphone model 40 BF, amplified (40 dB) and high-pass filtered (13 kHz) through a G.R.A.S. 12AA microphone power supply.

This system is linear (±1 dB from 15–100 kHz). In all cases the microphone was mounted on the end of a ~2-m-long thin rod. The signals recorded by the microphone were continuously A/D converted on-line (12-bit, sampling rate 250 kHz) using a battery operated IoTech Wavebook 512. The signals were stored in a ring-buffer (FirstInFirstOut, FIFO). The Wavebook had 128 Mbytes of random access memory (RAM) and was usually set at 6 sec pretriggering time and 1 sec post-triggering time. The Wavebook was controlled by a laptop computer (AST Ascentia P series or IBM Thinkpad 600). Thus when we picked up strong signals on a bat detector (D240 Pettersson Electronics), we began signal acquisition with the Wavebook, storing the 6 sec preceding and the 1 sec following trigger. At all recordings sites, the data storage system was battery operated. Hence, at site C the entire recording chain, including filtering and amplification of the microphone output, was battery operated, resulting in a lower noise floor than at sites A and B, where we used AC to power the Stanford Research Systems filter/amplifier.

In the lab, a similar system was used. We used two microphones, separated by approximately 3 m, each positioned about 30 cm above the floor. One microphone was supplied by Ultrasound Advice (as at sites A and B) and the other by ACO Pacific (1/4″ microphone, model 7016PM). The signals were bandpass filtered (10–100 kHz) and amplified, using a Stewart Electronics Model VBF 44 filter (−110 dB at $1.5f_c$). The signals were digitized directly on two channels of an IoTech 512 Wavebook (sample rate 240 kHz per channel, over an 8.2-sec period, 7.2-sec pretrigger, and 1-sec post-trigger), and controlled by a Dell Inspiron laptop computer. The channel containing recordings with the best signal-to-noise ratio in the terminal buzz phase of the capture behavior was later chosen for analysis.

D. Sound analysis

We analyzed the sounds using a commercial software program: BATSOUND (Pettersson Electronics). The signals were displayed simultaneously as spectrograms and oscillograms (time traces). The interpulse intervals (IPI) and signal durations (dur) were measured from the oscillograms, while using the spectrograms to distinguish between signals and their echoes. The spectrograms were made of consecutive fast Fourier transforms (FFT's) with a 90% overlap. Usually, a 256-point FFT was chosen as a compromise between good frequency resolution (977 Hz) for the shallow sweep tail of the signals and good time resolution for the steeper FM sweep of short signals and of the initial part of longer signals. For inspection of finer details in either time or frequency, the FFT window was adjusted accordingly.

In order to follow frequency changes correlated with habitat and behavior, we chose to measure the minimum frequency ($F_{\min}$) of all signals, since low frequencies are less subject to excess attenuation than high frequencies. In most cases $F_{\min}$ was measured from the spectrograms as the lowest frequency that clearly had more energy than the background noise. This method was repeatedly checked by producing spectra and measuring $F_{\min}$ from those as the low-frequency limit of $BW_{-15\,\mathrm{dB}}$, the bandwidth of the spectrum at −15 dB relative to the intensity of the peak frequency.

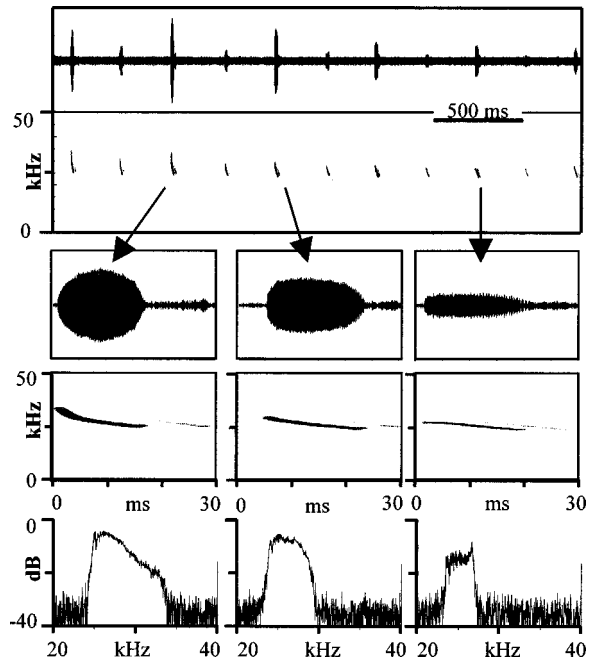

FIG. 1. Signals recorded from cruising *E. fuscus* leaving their roost at area A. The amplitudes alternate. The interpulse intervals (IPI's) are around 270 ms. The signal duration increases through this recording. The spectrograms and spectra of the three signals shown in the zoom below show decreasing frequencies (both Fmin and Fmax) and bandwidth with increasing duration.

Signal bandwidths are often given as the width of the full spectrum above the noise. However, such a bandwidth measure will depend upon the recorded signal level, i.e., the more intense the signal (the closer the bat) the broader the bandwidth. We chose a standard −15-dB bandwidth to try to use a bandwidth measure that is independent of differences in signal levels. For search and approach signals the $F_{\min}$ measured from the spectrogram corresponded very well with the $F_{\min}$ measured from the spectrum of the same signal: the discrepancy was less than 1 kHz. However, at the lowest signal levels (terminal buzz signals recorded from bats at a distance) $F_{\min}$ was often difficult to measure. The variations could be up to 2–3 kHz, and the values should be taken with caution. To examine the relation between the changes in $F_{\min}$ with changes in peak frequency and maximum frequency (and thus in overall bandwidth), we produced spectra of sounds from the best field recordings and from the lab recordings. For those spectra we used a rectangular FFT window that was adapted to the signal duration, e.g., 8192 points (32.8 ms at 250-kHz clock rate) for the longest signals and 512 points (2.13 ms at 240-kHz clock rate) for the shortest signals.

III. RESULTS

A. Cruising bats

When the bats flew out of the roost (site A), they produced long signals. The amplitudes often alternated between high and low, which might be due to the bats scanning up and down or from side to side and changing the direction of their sound beam with respect to the microphone (Fig. 1). For analysis we selected six recordings with only one bat and a good signal-to-noise ratio. The distribution of interpulse

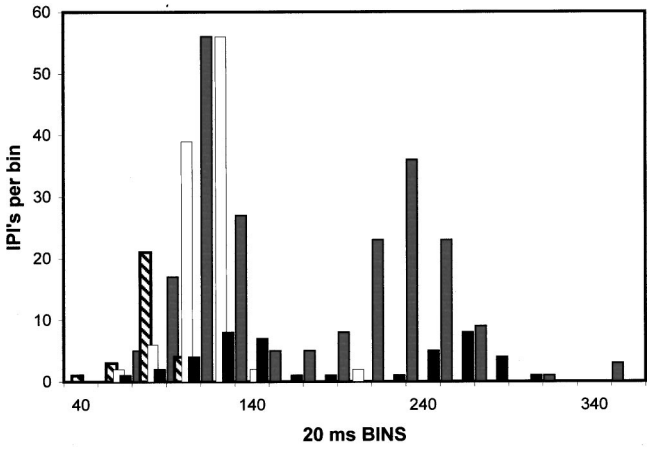

FIG. 2. Interpulse interval histogram. Bin width: 20 ms. The labels give the lower limit of each bin, e.g., 40 is the bin from 40 to 60 ms. The distribution is bimodal for the cruising bats (black bars) and the bats hunting in the open area, B (gray bars), but shows only a single peak for the bats hunting in the cluttered area, C (white bars) and in the lab (diagonally striped bars).

intervals (IPI's) was bimodal (Fig. 2) with a peak at 120–160 ms (avg: 134 ± 27 ms, $N = 24$, where N is the number of intervals) and another peak at approximately twice that value (avg: 270 ± 19 ms, $N = 19$). To calculate these averages we arbitrarily divided the IPI's into two populations, above or below 200 ms, based on the breakpoint in the histogram (Fig. 2). The signal durations changed with the IPI's. At long IPI's the signal durations were between 12 and 19 ms, whereas at IPI's around 120–160 ms, the durations were only between 6 and 13 ms (Fig. 3). The $F_{\min}$ is also correlated with IPI and thus with signal duration, such that when signal duration increase, $F_{\min}$ decreases (Figs. 1 and 3). The correlation between signal duration and $F_{\min}$ is strong [Fig. 3(b)], but does not necessarily imply dependence of one parameter on the other. The bats maintained control over the frequency and could change the frequency without changing the duration (see Fig. 4).

The spectra and spectrograms in Fig. 1 reveal some typical characteristics of the longest signals. The three analyzed signals have durations of 16, 18, and 19 ms, respectively. With increasing signal duration both the $F_{\min}$ and the bandwidth decrease. The initial, steeper sweep rate in the shortest signal is nearly absent in the longer signals. Accordingly, the spectrum changes from having more energy at low frequencies in the shorter signals to a more even distribution of energy across the spectrum in longer signals. Finally, the longest signal starts with an almost constant frequency component, resulting in a small peak at the high-frequency end of the (very narrow) spectrum. However, again the recordings demonstrate how flexible the bats are. For example, comparison with Fig. 5 shows that even the longest signals may start with a short downward sweep.

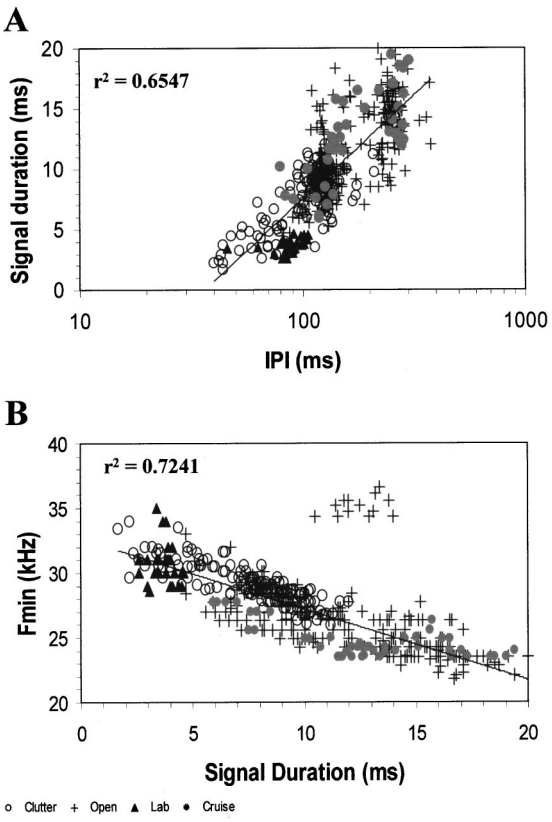

FIG. 3. (a) Correlation of signal duration and IPI. The r^2 of the log-regression line is 0.65 ($y = 7.44 \ln(x) - 26.73$). (b) Negative correlation between signal duration and $F_{\min}$, for all nonbuzz signals. The linear regression line ($r^2 = 0.72, y = -0.55x + 32.66$) is calculated without the 13 high-frequency signals far above the line recorded from a single bat in the open area. Open circles: C, the cluttered, wooded area. Crosses: B, the open area. Closed, gray circles: A, cruising bats. Black triangles: Lab recordings.

Since the water reflected strong echoes at site A, we could get a very rough estimate of the bats' flight elevation by measuring the echo delay, since all bats followed more or less the same route over the water. Our microphone was approximately 3 m over the water surface. Thus for example, the delay of the reflected sound from a bat at a horizontal distance of 15 m would be ~3 ms at a flight elevation of 3 m and 10 ms at a flight elevation of 10 m. We could measure

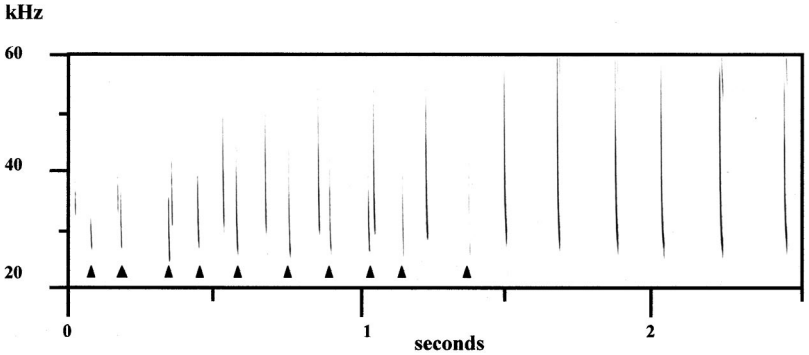

FIG. 4. A simultaneous recording of two bats. At first, their $F_{\min}$'s are separated by 6–8 kHz. Around 1 sec the recorded intensity of the low-frequency bats drops and that of the high-frequency bat increases, while it starts lowering its $F_{\min}$.

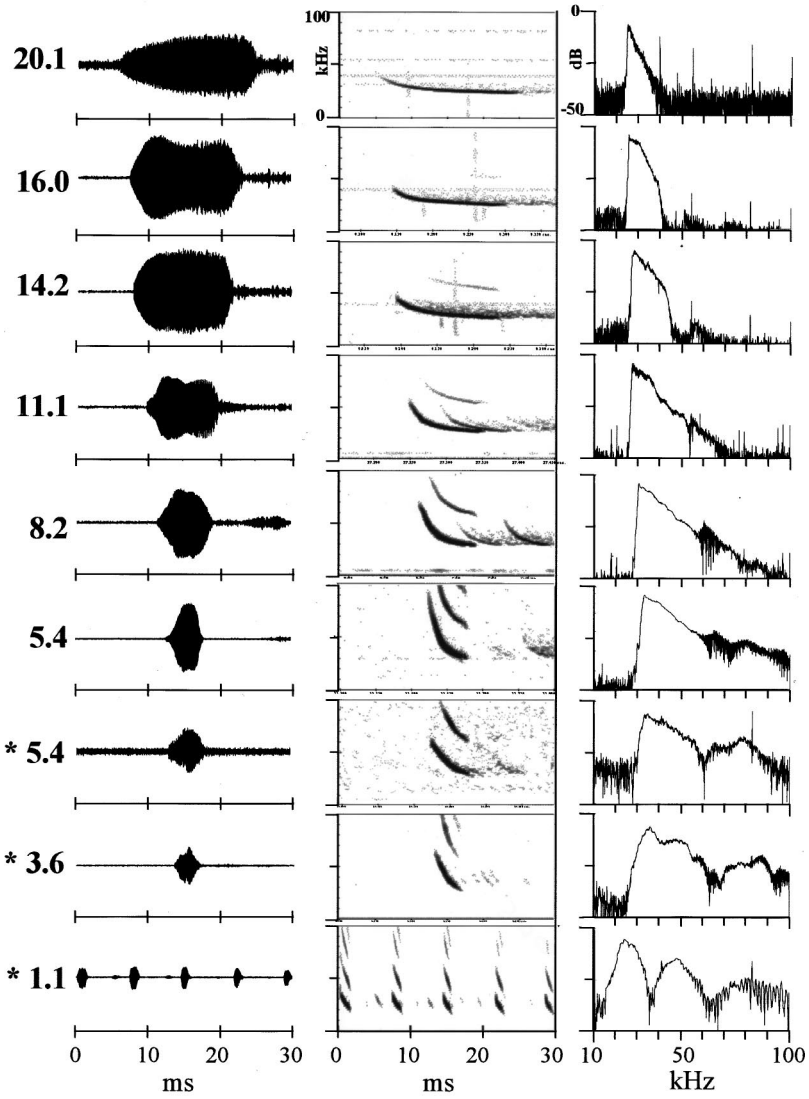

FIG. 5. Typical sounds. Oscillograms, spectrograms, and spectra of sounds with durations from 20.1 to 1.1 ms. Durations in ms are given at the left. Asterisks mark lab recordings. Oscillograms and spectrograms show 30 ms. All spectrograms go from 0 to 100 kHz. All spectra go from 10 to 100 kHz, and show relative dB on a scale from 0 to −50 dB, with the spectra adjusted to a peak value of ~−5 dB. The steep slope on the high-frequency side of the spectrum (especially 16.0 and 14.2 ms) indicate that the lack of high frequencies is a feature of the signals, not a consequence of excess atmospheric attenuation of higher frequencies. In some signals echoes from surroundings are prominent (e.g., 11.1 and 8.2 ms).

the delay directly from the spectrograms (Fig. 1) or indirectly from the interference pattern between direct and reflected sound. The interference creates typical amplitude modulations of the time signals and characteristic notches in the spectra separated by (1/delay ms) kHz, e.g., 3.3 kHz at 3-ms delay between direct and reflected sound (Kalko and Schnitzler, 1989a). Echo delays ranged between 3 and 15 ms and the longer IPI's and longer signals were produced by bats flying at relatively high elevations. In six analyzed recordings only one bat produced short signals (6–8 ms), and this bat was also the only one flying low over the water, indicated by echo delays of 3–3.5 ms. The other five flew higher (echo delays 8–15 ms) and produced longer signals (11–19 ms).

B. Bats hunting in the field

We recorded insect pursuit sequences at sites B and C (Figs. 6 and 7). The signals in the search phase were different in the two habitats. At site B, the open site, the signals (13 sequences analyzed) resembled those of the cruising bats from site A, with IPI's of either around 130–150 ms (avg: 134 ± 15 ms, $N = 100$), twice as long (249 ± 24 ms, $N = 101$), and in a few cases, around three times the basic IPI ($N = 4$: 336,363,376,378 ms) (Fig. 2). At site C, the more cluttered, wooded environment, all the bats' IPI's were short, clustering around 120 ms (avg: 122 ± 19 ms, N 120, 10 sequences analyzed) (Fig. 2). Thus the average IPI at C was shorter than the average of the short IPI's at B ($p \ll 0.01$, two-tailed t-test for equal variances).

IPI, signal duration (dur), and $F_{\min}$ of the search signals recorded at sites B and C were correlated in the same way as measures from signals recorded from the cruising bats at site A. Thus pooling all signals confirmed that signal duration decreases with decreasing IPI. The log regression line [Fig. 3(a)] for the correlation between IPI and dur had a higher $r^2(0.65)$ than the linear regression line ($r^2 = 0.61$), and can be explained by the observation that the increase in signal duration levels off at very high IPI's. The reverse correlation between duration and $F_{\min}$ was also seen for the hunting bats at B and C as well as for the cruising bats at site A [Fig. 3(b)]. Only a single recording gave $F_{\min}$ values that fell outside the main cluster: one (''soprano'') bat recorded at the open site, B, emitted 10–12-ms signals with IPI's of 120–140 ms, thus showing the same correlation between IPI and signal duration, but with unusually high $F_{\min}$, around 35–36 kHz.

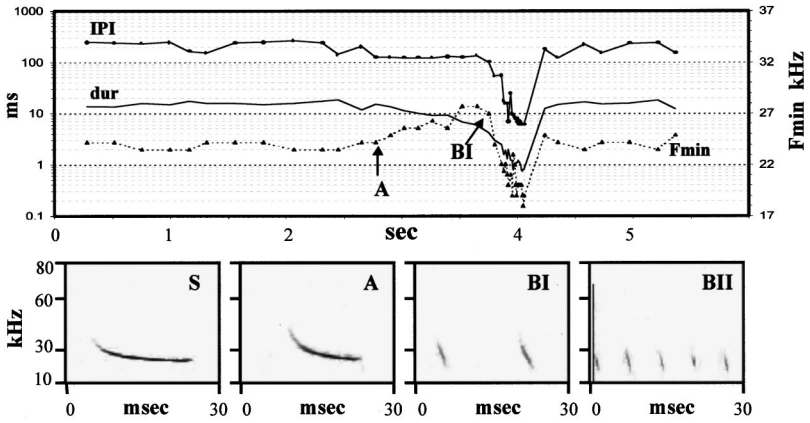

FIG. 6. Pursuit sequence from B, the open area. The upper panel shows the IPI and signal duration (dur) in ms (left *y*-axis, log-scale) and F_{min} (dotted line, triangles) in kHz (right *y*-axis, lin-scale). Below are shown spectrograms of a search signal (dur=18.5 ms), an approach signal (dur=13 ms), two Buzz I (dur=2.4 ms), and five Buzz II (dur=1 ms) signals. Search phase signals had IPI's of ~240 ms and F_{min} around 23 kHz. Note that in this case IPI is kept relatively constant around 120 ms throughout the approach phase.

The start of the approach phase was defined as the first signal in a sequence with monotonic changes in the parameters IPI, dur, and F_{min}, indicating that the bat had reacted to a potential prey (Schnitzler *et al.,* 1987). The dur and IPI decreased and F_{min} increased gradually in all recorded approach phases. The IPI and signal duration in the beginning of the approach phase were highly variable, depending on the signal parameters recorded in the preceding search phase. Therefore it was impossible to define a specific value of any of these parameters that would unequivocally indicate the start of the approach phase. Thus the approach phase can only be defined relative to the preceding search phase of the same sequence. However, the end of the approach phase was more consistent across all recorded sequences, with IPI's around 50 ms (ranging from 43 to 66 ms) and signal durations ranging from 5.5 to 2.9 ms (avg. 3.9 ms, S.DEV.=0.8 ms, $n=9$ sequences, see Fig. 8).

Over the course of the approach F_{min} increased by ~3–4 kHz. The beginning of the buzz was characterized by further decreases in dur and IPI. However, the most characteristic feature of the buzz was the reversal of the correlation between signal duration and F_{min}; at the buzz onset, F_{min} started decreasing with decreasing signal duration, thus allowing for an exact definition of the start of Buzz I based on F_{min}. The start of the Buzz II phase was characterized by an abrupt decrease in IPI. Over just 1–2 cries the IPI reached a minimum of 6 ms (pulse repetition rate of 167 Hz) and remained constant throughout the entire duration of Buzz II. F_{min} also decreased rapidly at the transition from Buzz I to Buzz II [although not as sharply as in, e.g., *Pipistrellus kuhli*

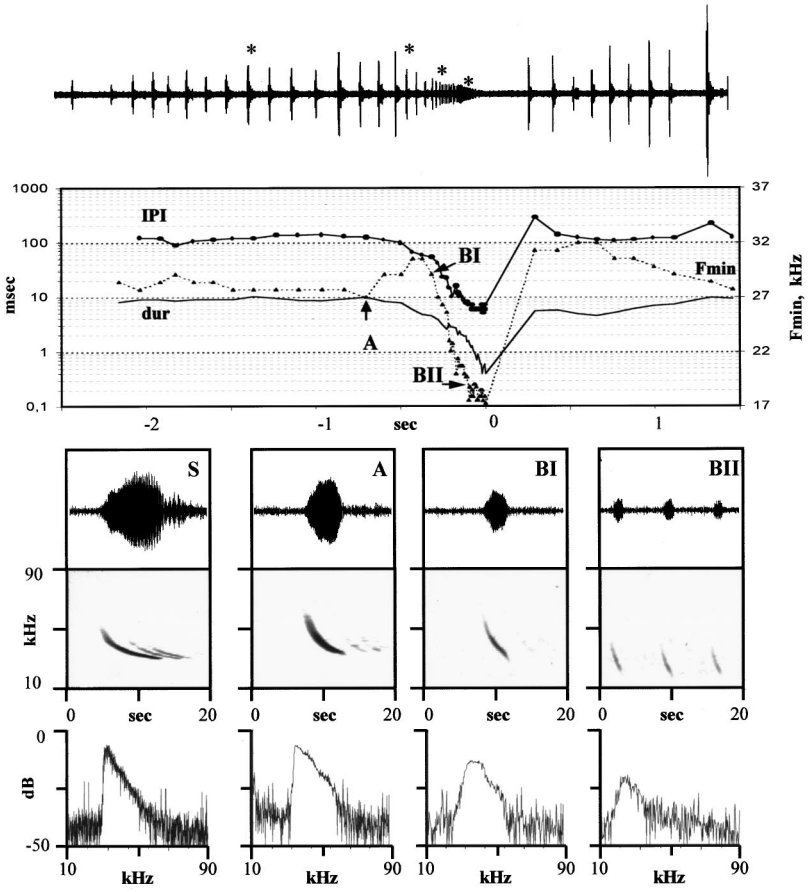

FIG. 7. Pursuit sequence from C, the cluttered area. The upper panel, an oscillogram, clearly shows how the amplitude drops in the buzz. The panel below shows IPI, dur, and F_{min} as in Fig. 6. Below are oscillograms, spectrograms, and spectra of the search, approach, Buzz I, and Buzz II signals marked with asterisks in the oscillogram.

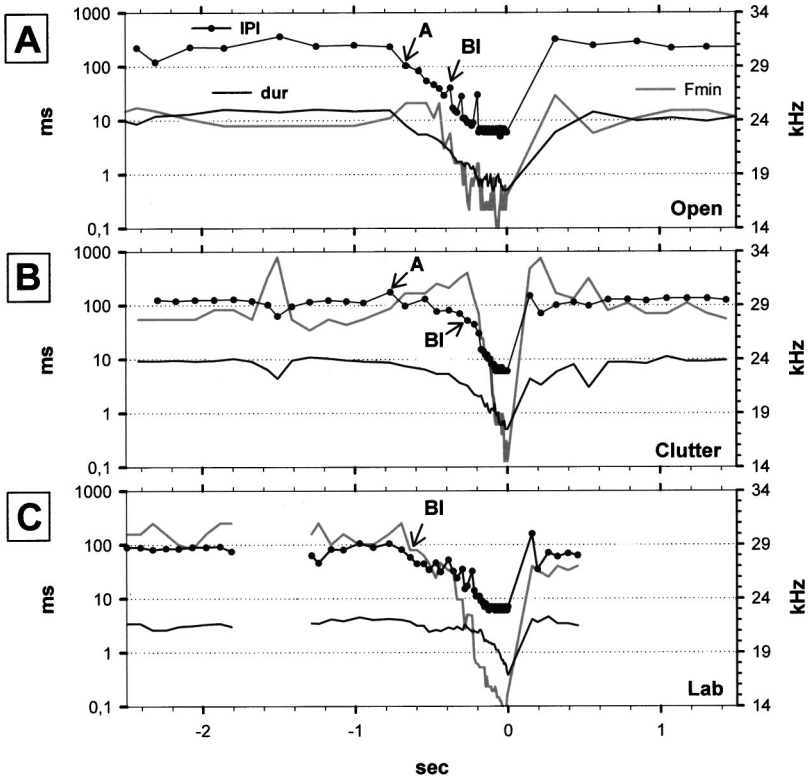

FIG. 8. Pursuit sequences from (a) the open area, (b) the cluttered, wooded area, and (c) the lab. The sequences in (a) and (b) are not the same as in Figs. 6 and 7. The IPI and dur are in ms (left *y*-axis, log-scale). The $F_{\min}$ (gray line) is in kHz (right *y*-axis, lin-scale). The start of approach and Buzz I is marked by arrows and ''A'' and ''BI.'' From upper to lower panel, the signals well before the buzz show a gradual decrease in IPI and dur and an increase in $F_{\min}$. In contrast, the signals in the final Buzz-phase are very similar in all three situations.

(Schnitzler *et al.*, 1987) or *Myotis siligorensis* (Surlykke *et al.*, 1993)]. $F_{\min}$ continued decreasing during Buzz II, but at a slower rate, to end at minimum values of 14–17 kHz (Figs. 6–8). However, there was no sudden change in signal duration at the transition from Buzz I to Buzz II. Instead, signal duration decreased gradually across Buzz phases I and II, starting in Buzz II around 1.2 ms and ending at 0.6–0.8 ms.

The bats' echolocation behavior was flexible, and we recorded variations in all of the above-mentioned parameters. For example, Fig. 6 shows an initial decrease in the bat's IPI from around 260 to 120 ms, and then the IPI remained around 120 ms throughout the approach phase, while $F_{\min}$ rose and signal duration decreased. The duration of the approach and buzz phases varied. The approach phases we recorded lasted between 320 and 620 ms. The buzz phases (Buzz I+Buzz II) lasted between 170 and 660 ms. Also, in other respects the bats demonstrated a great deal of vocal control: We often observed breaks in the buzzes [see, e.g., Figs. 6, 8(a)] and a simultaneous increase in $F_{\min}$, indicating that the breaks were not due to drop-outs in the recordings.

Our recording equipment did not allow us to determine the distance to the bats, and thus we could not determine the emitted intensity. However, the relative amplitude of signals recorded from *E. fuscus* in the present study can be compared within each sound file (6 to 9 sec of continuous recording). The nine pursuit sequences we analyzed show relatively high amplitudes, both before and after the buzz phase, thus suggesting that changes in relative amplitude are not due to changes in distance between the bat and the microphone. These data often show alternating signal amplitudes associated with the search phase similar to the alternating amplitudes for the cruising bats at site A. The recordings also reveal a clear reduction of emitted signal intensity through the terminal buzz phase. In the nine completed pursuit sequences we recorded from sites B and C, the average amplitude in Buzz I was −16 dB and in Buzz II −19 dB relative to the average amplitude of search and approach signals just before and after the terminal buzz (Fig. 7).

C. Bats flying in groups

None of the recordings with vocalizations of more than one bat was included in the data presented above, but we analyzed seven recordings of more than one bat, three from site A, two from B, and two from C. In most cases, the individual bats can be distinguished by a combination of differences in call characteristics, delay of echoes (e.g., from the water surface), and temporal patterning (IPI). The IPI's of bats flying in close proximity were less regular, and both IPI's and signal durations were shorter than those recorded from bats flying alone. Two of the recordings showed overlap in $F_{\min}$ between individual bats. However, in both of these recordings, one of the bats started pursuing an insect, shortening the signals and modifying the $F_{\min}$ up (through approach) and down (through the buzz).

The five remaining recordings of more than one bat only included search/cruise signals. These simultaneous recordings of bats flying in close proximity revealed individual calls that differed in $F_{\min}$ by 2–10 kHz, which was easily distinguished by the human ear in a slowed-down playback. Figure 4 shows an example recorded at site B, where the separation between the $F_{\min}$ of two bats is 6–8 kHz in the beginning of the recording. Here both bats emit short signals (4–7 ms), thus in the case of the low-frequency bat, demonstrating that the bats have sufficient control of all signal pa-

rameters to be able to produce signals with low F_{min} even at short durations. Around 1 sec into the recording, the bats start separating, indicated by the decreasing signal level of the low-frequency bat and the increasing level of the high-frequency bat. As the low-frequency individual disappeared, the former high-frequency bat gradually lowered the F_{min} down to values comparable to those emitted by the other bat in the beginning of the recording.

D. Insect capture in the lab

The sonar signal sequences recorded from bats flying in the lab differed from those in the field, especially in the absence of a true search phase [Fig. 8(c)]. The bats never produced the long narrow-band signals with low repetition rate that characterized search phase signals in the field. Even long before moving in on the prey (the tethered mealworm), the IPI's [avg: 88 ± 12 ms, N (number of IPI's) $= 29$ from two recordings, one from each bat] corresponded to those recorded from bats in the approach phase in the field. The signals were generally shorter (2–4 ms) than those at similar IPI's in the field [Fig. 3(a)].

In the lab, measures of F_{min} corresponded well with F_{min} for signals of similar duration recorded in the field [Fig. 3(b)]. We never observed the increase in F_{min} that accompanied the start of the approach phase in the field, probably because the bats were in constant approach phase. Thus it was difficult to define the approach phase at all using the same criteria as in the field recordings.

The start of the terminal phase was characterized by decreases in signal duration, F_{min}, and IPI, as in the field. There was large variation in the duration of the terminal phase recorded in the lab insect capture sequences, but most often the terminal phase was long compared to field recordings. We analyzed buzzes from 11 recordings of the two bats (5 and 6, respectively). The Buzz (Buzz I + Buzz II) ranged from short (230 ms) up to as much as 1.05 sec. In contrast, the other signal parameters of the lab-buzzes, IPI, duration and F_{min}, resembled those from the field recordings. The good signal-to-noise (S/N) in the lab recordings allowed us to determine the signal parameters at the end of the buzz phase more accurately than in the field recordings. The bandwidth of the signals was broader, with more energy at high frequencies, compared to signals of similar duration from the field recordings. This is probably not due to frequency differences in the emitted signals, but a consequence of the short distance between the bat and microphone.

We used the high-speed video recordings to determine the wing beat rates. The average wing beat period was 83 ms (12 Hz) (S.D. $= 17$ ms, $N = 98$ wing beat periods, from ten video recordings of several bats, not including the two bats above).

E. General signal features

The relations between IPI, duration, and F_{min} were consistent in all the recordings. Thus search signals and cruising signals from all three field locations and the sonar signals (well before the capture) from the lab recordings were pooled to examine the relations between the signal parameters of duration, IPI and F_{min} (Fig. 3). There were clear habitat-dependent differences in distribution of, e.g., IPI and thus signal duration and F_{min}. However, signals of equal duration from the different recording sites were quite similar. Thus in spite of individual and situation-dependent variations, any given signal duration corresponds to a typical signal design with a predictable F_{min} and bandwidth (Fig. 5) for bats flying alone. All recordings showed that the shorter the signal duration and IPI, the broader the signal bandwidth.

IV. DISCUSSION

A. General results

The present study generated three main findings. One, we confirmed preliminary reports that *E. fuscus*, searching for prey in the field, produce signals that are never recorded in the lab. Signal durations of up to 18–20 ms with narrow bandwidth and low minimum frequency are not rare exceptions, but routinely produced in open areas at IPI's of 260 ms or more. Second, we identified a strong correlation between IPI, signal duration, and frequency of search signals. Finally, we found that bats catching tethered insects in the lab do not produce search signals, but only approach and terminal buzz signals. The differences between lab and field recordings we report here are consistent with Griffin's early data and predictions. Modern, more sensitive sound recordings have also enabled us to extend Griffin's work by detailing some characteristics of the bat's acoustic behavior that have not been reported previously (see below).

B. Pulse repetition and wing beat rate

We found statistically reliable correlations among IPI and signal duration and F_{min}. The reliable correlations among these parameters suggest that long IPI measures are not due to missing signals in the recordings. Griffin (1958) described similar long IPI's. Furthermore, Schnitzler *et al.* (1987) and Kalko (1994) also described a similar bimodal distribution of IPI's for pipistrelle bats. Kalko ascribed the long IPI's to the skipping of signals at every second wing beat, or the execution of short gliding flights, but with signals still emitted in phase with the wing strokes. In *E. fuscus* the fundamental periodicity of the IPI histogram is 120–140 ms. This is likely to correspond to the wing beat rate of *E. fuscus* flying in the field. It is energetically most favorable for a bat to emit its signals in phase with the down strokes of the wings (Speakman and Racey, 1991). Our wing beat rates from the lab are in accordance with another more thorough study in the same flight room (Wilson and Moss, 2000). The data suggest that bats flying in the laboratory maintain the phase relation between wing stroke and pulse emission. Hence, the difference between lab and field in bats' sonar signal repetition rate indicates that also the wing beat frequency is higher in the laboratory than in the field.

C. Signal duration and frequency

The maximum signal duration we recorded was 20 ms, but 17–19 ms seems to be the more typical upper limit for duration, even when the IPI was increased to 360 ms. The

fairly long distance to the bats producing the longest signals probably contributes to the absence of a second harmonic, but does not explain the very steep high-frequency roll-off in the spectra (Figs. 1, 5). Thus the narrow bandwidth of the first harmonic is a signal feature. This confirms the data on the European bat, *Eptesicus serotinus*, by Jensen and Miller (1999). They used a microphone mounted on a 15-m-high mast, to show that high-flying bats actually produce long low-frequency signals with narrow bandwidth. The lack of high frequencies in Jensen and Miller's data cannot be attributed to low-pass filtering of the signals by excess attenuation, because their microphone was positioned at an elevation near the high-flying bats. In general, there seems to be a strong similarity between signal characteristics of *E. fuscus* and those reported for the European *E. serotinus. E. serotinus* emits source levels as high as 125 dB SPL [root-mean-square (rms)] at 10 cm (Jensen and Miller, 1999). It would be of interest to compare these signal levels with those of *E. fuscus*. However, none of the methods we employed allowed us to determine the source levels of the emitted signals, and we propose that these measures should be taken in future field studies of *E. fuscus* echolocation cries, ideally combined with photographic documentation of their capture behavior.

There was a statistically reliable correlation between signal duration and $F_{\min}$. Doppler shifts of $F_{\min}$ due to the bat's velocity relative to the microphone are likely to have contributed to some variation of the data. However, even flight speeds of 10 m/s would not change the frequency by more than around 0.7 kHz (at 25 kHz) and the changes in $F_{\min}$ reported here exceeded that value considerably and were correlated with changes in signal duration. The maximum frequency of the signals, $F_{\max}$, decreased when duration and IPI increased. With increasing signal duration, $F_{\max}$ decreased more than $F_{\min}$, producing a decrease in overall signal bandwidth (see Figs. 1 and 5). However, values for $F_{\max}$ in particular should be interpreted with caution, because we had no way of measuring the distance to the bats. Since atmospheric attenuation is more severe at the higher frequencies of the FM sweep produced by *E. fuscus* (Lawrence and Simmons, 1982), it is likely that many of the cries we recorded at long distances contained more energy at high frequencies, in particular more energy in the second harmonic, than our spectra showed. Since the longest signals were emitted by bats flying in the open far away from vegetation and ground, and thus from the microphone, the lack of second harmonic is more pronounced in long signals than in short (compare, e.g., 20.1 and 16 ms with 8.2 and 5.4 ms in Fig. 5). This might also have affected measures of signal duration by filtering out the beginning of the signals. The directionality of *E. fuscus* signals increases with frequency (Hartley and Suthers, 1989), thus also contributing to a high-frequency loss, since in most cases the bats would not consistently direct their vocalizations toward the microphone.

Kalko and Schnitzler (1993) reported a negative correlation between signal duration (or IPI) and signal bandwidth for *Pipistrellus sp.* similar to what we found for *E. fuscus*. The changes in signal duration were mostly due to changes in the tail of the pipistrelle signal. They did not report a lowering of $F_{\min}$ with increasing signal duration. However, the sweep rate at the end of the pipistrelle signal is very low, 0.2 kHz/ms, whereas the sweep rate at the end of *E. fuscus* signals is typically very close to the slope of the regression line in Fig. 3(b), i.e., 0.5 kHz/ms, thus explaining the correlation between $F_{\min}$ and dur in *E. fuscus*. Hence, it is likely, that in the pipistrelle bats, any changes in $F_{\min}$ with signal duration would probably be so small that they would be lost in the overall variation in frequencies emitted by different individuals in different situations.

D. Approach and terminal phase

Our field data showed long duration signals in the approach phase. The duration may exceed 10 ms at the beginning, decreasing gradually to end at 3–4 ms right before the start of the terminal phase. Bats performing in psychophysical experiments usually emit signal with durations of 1–3 ms (Simmons, 1973; Moss and Schnitzler, 1989; Surlykke and Bojesen, 1996). Our data indicate that those signals resemble signals emitted at the transition to or well into the first part of the terminal phase more than they resemble typical approach signals.

The variation in IPI makes it difficult to define the onset of the buzz on the basis of temporal parameters. Long intervals separating the last approach signals from the first buzz signals, as in *P. kuhli* (Schnitzler *et al.*, 1987) did not occur in the *E. fuscus* recordings. However, the change in spectral structure of the signals in these two phases is distinct in all our field recordings. The negative correlation between signal duration and $F_{\min}$ holds all the way through the approach phase, but breaks down when the bats enter the terminal phase. At the transition between the approach and buzz phases of insect pursuit, $F_{\min}$ no longer increases, but instead declines with further decreases in signal duration. Hence, we suggest an exact definition for the onset of the buzz phase: the instance when the correlation between $F_{\min}$ and signal duration becomes positive.

Comparisons of the lab recording with field recordings indicate that neither open-area search phase signals, characterized by relatively long duration ($>$15 ms) shallow FM signals and long IPI, nor search phase signals characteristic of more cluttered areas (call durations around 9–11 ms, IPI's around 120 ms) are produced in the lab. Bats catching insects in the lab operate only in the approach and buzz phases. Our data also indicate that the bats decrease the intensity in the lab, thus corroborating other reports of reduced intensity in confined spaces (Griffin, 1958; Surlykke *et al.*, 1993). Our methods did not allow us to determine the emitted intensities, neither in the field nor in the lab, but an intensity reduction in the lab would explain first that often the signal-to-noise ratio (S/N) of the search/approach signals recorded in the lab was no better than in the field (compare the two 5.4-ms signals in Fig. 5), and second that in spite of the poor S/N the higher frequencies were more prominent in the lab signals.

If we define the start of the terminal buzz using the same criteria as in the field (the first signals where the $F_{\min}$ starts dropping), the duration of the terminal buzz is often surpris-

ingly long in the lab, longer than that recorded in the field. This is somewhat surprising, since the bats have comparatively more knowledge about the position of the prey in the lab (i.e., within the confines of the flight room) than in the field. We do not have a good explanation for this, but it could be that it reflects differences in insect capture strategies in the lab and field. For example, if a bat misses an insect, in the field it may return directly to the search/approach phase in pursuit of a new prey item, but in the lab, the bat may learn that it can turn in flight and catch the same prey item, simply extending the buzz through this adaptive maneuver.

In both the lab and the field, the sound recordings show breaks in signal trains during the approach and buzz phase and a reduction in amplitude during the buzz phase. The high signal-to-noise ratio (S/N) in the lab buzzes helps to confirm the reliability of these two results in the field recordings.

E. Influence of habitat and conspecific bats

The field recordings showed a clear correlation between habitat and search signals, a finding consistent with data reported for other species (Barclay *et al.*, 1999; Kalko and Schnitzler, 1993). We only recorded the long narrow-band search signals in the two open areas (A and B), never in the more cluttered area, C. The mean IPI's decreased according to how open the areas were from A over B and C to the minimum in the lab, probably reflecting how cluttered or confined the bats perceive their surroundings. The very short IPI's and signal durations in the lab indicate that the bats treat the lab flight room as an extremely cluttered habitat.

Our simultaneous recordings of several bats showed greater variation in duration, IPI, and $F_{\min}$ than those of single bats. The directionality of our microphones and of the bat signals makes it likely that bats recorded simultaneously are flying in close proximity. The frequency separation of the signals in the group recordings (for example, those shown in Fig. 4) makes it tempting to speculate that *E. fuscus* exhibits a jamming avoidance response to the signals of other bats in their vicinity (see, e.g., Habersetzer, 1981). However, to directly address the question of jamming avoidance in bats, we need more sophisticated recording methods to track frequency changes in sonar cries with the relative positions and flight directions of two or more individual animals. This could be achieved by mounting lightweight ultrasound microphones with radio transmitters directly on several bats that later forage together, a challenging but not impossible approach. Initial attempts might be taken with established methods, e.g., microphone array recordings (Surlykke *et al.*, 1993) and photographic 3-D reconstruction of flight paths (Kalko and Schnitzler, 1989b).

Fenton (1995) reported geographic variation in *E. fuscus* calls, with bats from eastern North America producing 5–10-ms-long signals and bats from western North America producing 10–15-ms-long signals. However, the variation we have described here from a relatively small geographical area seems to encompass that, and we find it more likely that the reported geographical variation was due to local differences in the habitats where the bats were recorded. Our data indicate that even within the same habitat, bats may change their signals when flying in groups. Our data also indicate that the bats adjust their signals to different flight elevations, in accordance with the results on *E. serotinus* of Jensen and Miller (1999). They found that the higher the bats flew, the longer the duration and the lower the end frequency and bandwidth of the signals. Obrist (1995) reported small, but statistically significant, individual call differences in *E. fuscus*, most often in call frequency. Our data indicate that *E. fuscus* is flexible and adapts its acoustic output (signal duration, repetition rate, and spectral content) to habitat, flight elevation, and/or the presence of other bats. If these parameters are taken into account, it is likely that individual call design differences would become more apparent (see Masters *et al.*, 1995).

V. CONCLUSIONS

Our recordings illustrate echolocation signals produced by *E. fuscus* hunting insects under natural and laboratory conditions. The field recordings show distinct patterns of signals recorded under different hunting conditions and during different phases of insect pursuit. The data also point to potentially important variations in sonar signals not observed in the laboratory, and it is likely that more recordings would reveal even greater flexibility in sonar production patterns in this species. We believe that the acoustic data presented here provide a useful frame of reference for both behavioral and neurophysiological laboratory studies of echolocation in *E. fuscus*.

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