Behav Ecol Sociobiol (1994) 35:327–345

Hans-Ulrich Schnitzler · Elisabeth K.V. Kalko
Ingrid Kaipf · Alan D. Grinnell

Fishing and echolocation behavior of the greater bulldog bat, *Noctilio leporinus*, in the field

Received: 13 October 1993 / Accepted after revision: 11 June 1994

Abstract When hunting for fish *Noctilio leporinus* uses several strategies. In *high search flight* it flies within 20–50 cm of the water surface and emits groups of two to four echolocation signals, always containing at least one pure constant frequency (CF) pulse and one mixed CF-FM pulse consisting of a CF component which is followed by a frequency-modulated (FM) component. The pure CF signals are the longest, with an average duration of 13.3 ms and a maximum of 17 ms. The CF component of the CF-FM signals averages 8.9 ms, the FM sweeps 3.9 ms. The CF components have frequencies of 52.8–56.2 kHz and the FM components have an average bandwidth of 25.9 kHz. A bat in high search flight reacts to jumping fish with "pointed dips" at the spot where a fish has broken the surface. As it descends to the water surface the bat shows the typical approach pattern of all bats with decreasing pulse duration and pulse interval. A jumping fish reveals itself by a typical pattern of temporary echo glints, reflected back to the bat from its body and from the water disturbance. In *low search flight N. leporinus* drops to a height of only 4–10 cm, with body parallel to the water, legs extended straight back and turned slightly downward, and feet cocked somewhat above the line of the legs and poised within 2–4 cm of the water surface. In this situation *N. leporinus* emits long series of short CF-FM pulses with an average duration of 5.6 ms (CF 3.1 and FM 2.6) and an average pulse interval of 20 ms, indicating that it is looking for targets within a short range. *N. leporinus* also makes pointed dips during low search flight by rapidly snapping the feet into the water at the spot where it has localized a jumping fish or disturbance. In the *random rake* mode, *N. leporinus* drops to the water surface, lowers its feet and drags its claws through the water in relatively straight lines for up to 10 m. The echolocation behavior is similar to that of high search flight. This indicates that in this hunting mode *N. leporinus* is not pursuing specific targets, and that raking is a random or statistical search for surface fishes. When raking, the bat uses two strategies. In *directed random rake* it rakes through patches of water where fish jumping activity is high. Our interpretation is that the bat detects this activity by echolocation but prefers not to concentrate on a single jumping fish. In the absence of jumping fish, after flying for several minutes without any dips, *N. leporinus* starts to make very long rakes in areas where it has hunted successfully before (*memory-directed random rake*). Hunting bats caught a fish approximately once in every 50–200 passes through the hunting area.

Key words Bats · Fishing · Echolocation
Hunting behavior

Introduction

Echolocating bats have evolved widely diverse foraging behaviors, echolocation sound designs, and sensory/neural adaptations for the processing of echoes. Various hunting strategies are correlated with particular echolocation sounds and mechanisms of neural analysis (e.g., Fenton 1990; Neuweiler 1989; Schnitzler and Henson 1980). All bats appear to rely on frequency modulated (FM) pulse components for accurate target distance determination, and bats that emit only FM pulses clearly obtain all of the information they need to localize and identify the sources of echoes. There are other bats, however, that emit constant frequency (CF) components, usually preceding the FM sweep. In some well-studied species, the CF component is quite long (10–100 ms), coupled with a terminal sweep of relatively small bandwidth. A major function of the CF signals is detection and recognition of fluttering insects amid

H.-U. Schnitzler (✉) · E.K.V. Kalko · I. Kaipf
Animal Physiology,
University of Tübingen,
Auf der Morgenstelle 28,
D-72076 Tübingen, Germany

A.D. Grinnell
Department of Physiology
and the Ahmanson Laboratory of Neurobiology UCLA
School of Medicine,
Los Angeles, CA 90024, USA

strong background clutter. Echoes from fluttering insects are characterized by a rhythmical pattern of amplitude and frequency modulations produced by the beating wings. The most prominent features are very short and strong peaks in the echos, termed acoustical glints. They are produced in each wingbeat cycle in the brief moment when the insect's wing is approximately perpendicular to the impinging sound wave (Kober and Schnitzler 1990; Neuweiler 1989; Schnitzler 1987; Schnitzler et al. 1983). Rhinolophid and hipposiderid bats and the mormoopid bat, *Pteronotus parnellii*, use the rhythmical glint pattern in the echoes of their CF signals to recognize fluttering insects (von der Emde and Schnitzler 1986, 1990; Schnitzler and Kaipf 1992).

Pulses with short CF components preceding an FM sweep are used by both species of *Noctilio*. They exhibit one of the most interesting behavioral specializations among bats, the capture of fish or insects from the water surface. The greater bulldog bat, *Noctilio leporinus*, (65–75 g) has greatly enlarged feet with laterally compressed claws that can be dragged just below the water surface to catch small fish (Benedict 1926; Bloedel 1955; Goodwin 1928; Griffin 1958; Griffin and Novick 1955; Suthers 1965, 1967). Its smaller relative, the lesser bulldog bat, *N. albiventris* (= *N. labialis*), (30–35 g) is less specialized morphologically and feeds mainly on insects at or near the water surface (Bloedel 1955; Brown et al. 1983; Novick and Dale 1971; Suthers and Fattu 1973). Based on echolocation signal structure it is highly probable that *N. albiventris* uses flutter information to recognize its prey. However, we do not know what information is available to *N. leporinus* when it hunts for fish with CF signals.

Echolocation signals, auditory capabilities, and performance of *N. leporinus* have been thoroughly studied in the laboratory (Altenbach 1989; Hartley et al. 1989; Suthers 1965, 1967; Suthers and Fattu 1973; Wenstrup 1984; Wenstrup and Suthers 1984). Search pulses are often emitted in pairs or triplets, each pulse usually less than 10 ms long, with the first of a pair or middle pulse in a triplet being mostly CF (around 60 kHz), while the second (or first and third) has an abbreviated CF component that terminates in a 2–3 ms FM sweep to about 30 kHz. After target detection, the repetition rate rises, the CF duration decreases, and FM sweeps get steeper, leading to a "terminal buzz" of almost pure FM sweeps at repetition rates up to 165–180 Hz (Hartley et al. 1989).

In *Noctilio albiventris* the signal structure is rather similar to that of *N. leporinus*. Therefore it can be assumed that the signal elements have the same significance for information processing. Range discrimination experiments with the CF-FM bats *N. albiventris* and *Rhinolophus rouxi* (summarized in Roverud 1988) have shown that for the determination of target distance these bats use both the CF and the FM components of their echolocation signals. Furthermore, it has been suggested that the onset of the CF component activates a gating mechanism that establishes a time window during which FM component pulse-echo pairs are processed for distance information. From these data it could be assumed that the only function of the CF components of the echolocation signals of noctilionids is the opening of such a time window. However, the similar results in *N. albiventris* and *Rhinolophus rouxi* suggest that the CF component in *Noctilio*nid bats may have the additional functions which have been found in rhinolophis bats; e.g., it may also be used for flutter detection and evaluation. We will present data which support this assumption.

Laboratory observations have also shown that *N. leporinus* does not detect fish under water, but is extremely sensitive to surface disturbances (Suthers 1965). *N. leporinus* also can evaluate the relative velocity of a target moving along the axis of its flight path (Wenstrup and Suthers 1984), and it can predict the position of a moving target that submerges before the bat reaches it (Campbell and Suthers 1988). For this performance, the bat relies on echolocation. Most observations under natural conditions, on the other hand, have emphasized the long foot-drags of this species and its apparent tendency to hunt randomly through areas that have small fish near the surface, suggesting that in this situation the bat often does not rely on echolocation information for prey detection and localization.

However, with the exception of Bloedel's superb field observations, there have been few published analyses of the behavior of *N. leporinus* in the field. Data on echolocation behavior in the wild are especially sparse, although Suthers (1965) mentioned that the search calls of wild *N. leporinus* are longer than those of captive bats. Since laboratory studies of behavior and echolocation tend to involve learned behavior in confined environments, the resulting observations inevitably provide an incomplete picture of bats' natural behavior and capabilities.

We took advantage of current technology to correlate three-dimensional photographic reconstructions of flight paths during various types of hunting behavior with the echolocation signals used at each point. This provides a more complete picture of how *N. leporinus* obtains the information it needs to capture fish and other prey under natural conditions, and offers some insights into the sources of information and types of neural processing that they employ.

Materials and methods

Field site and animals

The field study was conducted from 20 October to 10 November 1990 at the Tortuga Lodge near Tortuguero National Park, Costa Rica. The observations were made at the boathouse which allowed direct access to the water surface (Fig. 1). Species identification was based on visual and acoustic characteristics. *N. leporinus* can be identified without difficulty in the field by its large size and its characteristic flight over water surfaces. Bats of this species were recorded every night as they foraged along the Tortuguero River.

Photography of hunting bats

We observed foraging bats with 3D night vision goggles. To follow a bat acoustically at the same time, its echolocation signals were picked up by an ultrasound microphone, amplified, and transformed into the audible range by a custom-made bat detector. To document hunting behavior, bats were photographed with a custom-made flash unit (Heinze) consisting of four flash tubes (guide number 50) between two 35 mm cameras (Nikon F301, 35 mm lens) mounted on a bar attached to tripod. Each time a bat appeared in the field of the cameras, or was heard by a bat detector, the observer manually triggered the cameras. The shutters (F-stop 5.6) opened and a custom-made synchronization unit triggered multiple flashes in sequence, following which the shutters closed again. Within a sequence the number of flashes released could be varied. Normally the flash unit was triggered 16 times, which under optimal circumstances gave 16 exposures of an individual bat on one photograph. The flash intervals were set to 100 ms between flashes 1 and 2, and 10 and 11, and to 50 ms between the rest of the flashes. This created a flash pattern that enabled us to define the flash number on photographs, even when the bat was not caught by all flashes in a sequence. The bats appeared not to be disturbed by the flashes as we have occasionally observed in other bats. The *Noctilio* did not show any obvious changes in echolocation and/or flight path in reaction to the flashes.

Sound recordings

Simultaneously with the multiflash pictures we recorded the echolocation signals of foraging bats with ultrasound microphones of two bat detectors (model QMC S100). The signals were amplified and recorded at 76 cm/s on two amplitude-modulated channels of a battery operated high-speed tape recorder (Lennartz 6000/607, 1/4 inch tape). The frequency response of our system was flat within about 10–15 dB between 20–120 kHz. Additionally a voice note and synchronization pulses indicating the flashes were recorded on two frequency-modulated channels of the recorder.

Analysis of photographs

We developed the black-and-white negative films (Kodak TMax 400) the day after each recording session (Microphen, 4–10 min at 20°C). The three-dimensional flight paths of bats and prey were reconstructed with custom-made computer programs. The projected photographs were digitized on a magnetic tablet (Bitpad One; resolution 0.1 mm) and stored in a PC. In the first step the camera positions were reconstructed by iteration and least-square error minimization, referring to a reference system with known coordinates. In the second step the spatial coordinates of the position of bat and/or prey were calculated. Missing data points were estimated by linear interpolation. Afterwards the bat's position in three-dimensional space, flight speed, and distance to targets were calculated and plotted.

Analysis of sound recordings

Sound sequences were analyzed at 1/16 reduced speed with a digital frequency-analyzer MOSIP 3000 (Modular Signal Processor; Medav, Germany) using a fast Fourier transformation (FFT). Parameters such as sound duration, interpulse interval, and starting and terminal frequency were measured with cursors on the sonagrams displayed on the screen in a standardized way. A Hanning Window with 256 lines was chosen for the FFT and the sequences were displayed in consecutive 20-ms segments. This gave the following settings: frequency range 120 kHz, frequency resolution 400 Hz, and time resolution 40 μs. The dynamic range was restricted to 60 dB to eliminate background noise. The measurement points were set 40 dB below maximum.

Correlation of echolocation and hunting behavior

Each flash produced an electronic pulse on the recording tape, allowing the correlation of visual and acoustic information. The three-dimensional analysis of the photographs was merged with the sound recordings using a custom-made software program. Interpolation of the data of the three-dimensional analysis enabled us to define the bat's position in three-dimensional space for each echolocation signal.

Results

Hunting behavior

Every night during a 3-week period we observed the foraging behavior of *N. leporinus* between about 5:30 p.m. and 0:30 a.m. as they flew along the Tortuguero River, Costa Rica. *N. leporinus* first appeared about 0.5 h after dusk, in "passing" flights directly up or down river. In this flight mode the bats fly about 0.5–1.0 m above the water surface, with strong wing beats and without turning, usually appearing from one direction and disappearing in the other without attempting any captures.

Soon thereafter, bats were observed hunting close to shore. The main activity period(s) of *N. leporinus* varied from day to day in unpredictable ways that presumably reflected changes in food availability, wind conditions, and/or moon/tidal cycles. Usually there was a peak of activity between about 6:00 p.m. and 7:00 p.m., followed by a quiet period, and sometimes renewed activity for periods of a few minutes to an hour or more between 9:00 p.m. and midnight. Although two or more bats sometimes flew together in passing flights, and occasionally groups of four or five would fly in close succession during hunting flights, most often the bats hunted alone. Often the bat hunting at our study site was a male (confirmed photographically) whose passages were accompanied by a strong wave of musky odor. This male appeared intolerant of other *N. leporinus* approaching his "territory", and would pause in his own foraging long enough to fly rapidly at other bats in an antagonistic manner, resulting almost invariably in the other bat leaving the area.

This bat and others that foraged near the boat house flew in stereotyped flight paths, the most common of which are reproduced diagrammatically in Fig. 1. Fig. 1a shows the commonest pattern, in which the bat flew back and forth between the edge of the dock and a bush downstream from the boat house, turning widely at each end but hunting within 1–3 m of shore for most of the distance between these points. The analysis of the flight behavior of several bats based on a verbal protocol of about 2 h of continuous observation showed that each loop lasted between 14–22 s. Other patterns were: (1) shorter loops of the same type; (2) still smaller open circles in which hunting near shore occurred only on one side of the circle (Fig. 1c); (3) commonly, a figure-eight pattern with one complete circuit lasting about

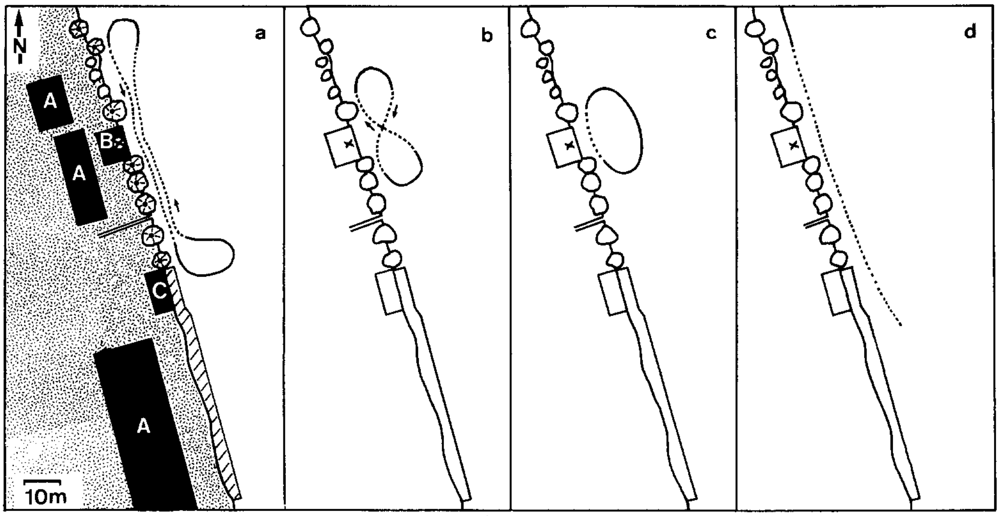


Fig. 1a–d Examples of typical flight paths of *Noctilio leporinus* hunting for fish at the shoreline of the Tortuguero River near Tortuga Lodge (*A*), in front of the boat house (*B*) and the dock house (*C*). The cameras (*X*) were positioned in the boat house about 1 m above the water surface

8–12 s (Fig. 1b); and (4) quite often bats hunted close to the shoreline as they flew up or down stream, without turning to make additional runs (Fig. 1d). During each circuit, the flight behavior of the bats differed in characteristic ways, associated with different stages or types of hunting behavior.

Hunting strategies

High search flight

In high search flight *N. leporinus* flies within 20–50 cm of the water surface, with strong wingbeats at a rate of 4–5 beats/s (Fig. 2a). The three-dimensional reconstruction of eight passes in high search flight revealed flight speeds mostly between 6.6 and 7.4 m/s. During the long straight component of the loop and figure-eight circuits flown by the bats, the animals occasionally approach the water and dip in their feet (see below). At the wide turns of the loops and eights the bats continue to flap their wings strongly and sometimes rise to 1–2 m above the water before descending again.

Near the top of each wingbeat during high search flight, *N. leporinus* emits a group of two to four echolocation signals always containing at least one CF pulse and one CF-FM pulse. In groups with two pulses in the group, usually the first pulse is a pure CF signal and the second a mixed CF-FM signal (Fig. 2b). With more pulses in the group, we found all possible arrangements of the two pulse types, but usually the group of pulses ends with a CF-FM pulse.

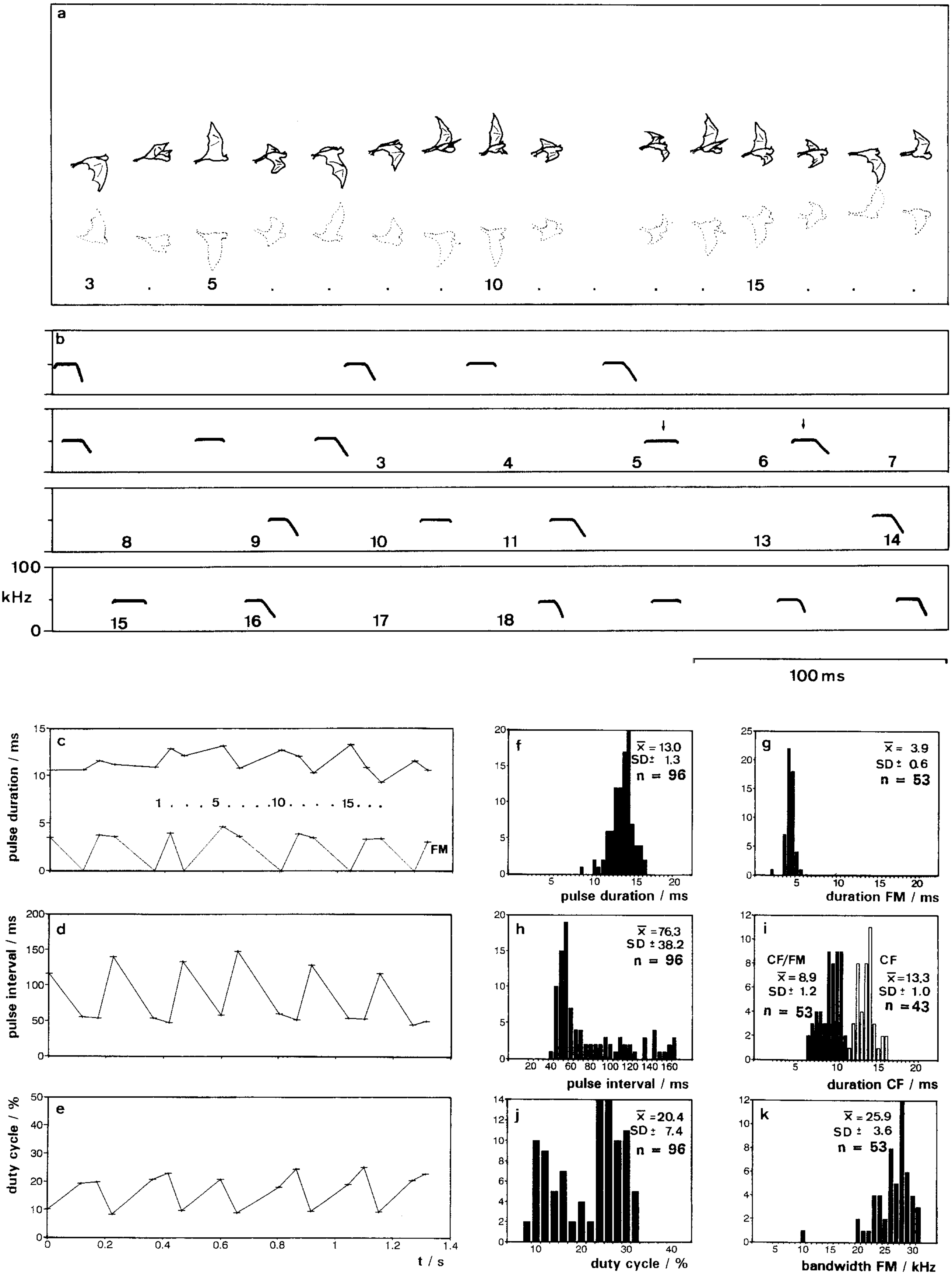
The average sound duration of the signals is 13.0 ms. The pure CF signals are the longest, with an average duration of 13.3 ms and a maximum of 17 ms. The CF component of the CF-FM signals average 8.9 ms, and the FM sweep 3.9 ms. The intervals between the last signal of a group and the first signal of the following group are around 135–165 ms, and the intervals between the signals within a group around 50–55 ms. Within a group of signals the duty cycle is around 24–31%; including the time between groups, around 10–16%.

The FM sweep has an average bandwidth of 25.9 kHz (Fig. 2k). The frequency of the CF pulses changes within a range of 2–4 kHz. A typical signal is characterized by a 1–2 ms initial component in which the frequency sweeps upward by about 0.4–1.0 kHz, a relatively constant middle portion where the frequency stays within a range of 0.4 kHz, and a 2–3 ms terminal component in which the frequency drops by about 2–4 kHz (Fig. 3a–c).

Before the transition into the steeply downward modulated FM portion of a pulse, the frequency structure of the CF portion of the CF-FM signals is similar to that of the pure CF signals. We define the FM portion of the CF-FM signals as beginning when the frequency drops 4 kHz below the highest frequency in the CF portion. The transition period during which the frequency changes from a shallow into a steep sweep lasts about 1.8–2.5 ms (Fig. 3d–f).

The FM portions of the CF-FM signals often show a characteristic pattern of nulls (Figs 3d,e; 4f,g; 7f,g) which is visible in the oscillogram and in the sonagram. These nulls are the result of interference between the signal which travels directly from the bat to the microphone and the delayed signal which is reflected back to

Fig. 2 Flight and echolocation behavior of *N. leporinus* during a typical pass in high search flight. **a** Fifteen images of the same bat (*numbered* 3–18) as it flew past the entrance of the boat house. The faint inverted image (*dotted line*) is the reflection of the bat from the smooth water surface. **b** Sonagrams of the echolocation pulses emitted by the bat during the same flight. *Numbers* correspond to the photographic images. Pulses were either pure CF signals or contained both CF and FM components. Plots **c** of the durations of the signals and of their FM components, **d** of the pulse intervals, and **e** of the duty cycle of the sound sequence emitted by the passing bat. Histograms including means ($\bar{x}$) and standard deviations (SD), for **f** overall pulse duration, **g** duration of FM component, **h** pulse intervals, **i** duration of CF signals or CF components, **j** duty cycle and **k** FM bandwidth for all analyzed pulses of bats in high search flight


a
3 . 5 . . . . 10 . . . . 15 . . .
b
3 4 5 6 7
8 9 10 11 13 14
15 16 17 18
100
kHz
0
100 ms
c
pulse duration / ms
15
10
5
0
1 . . . 5 . . . .10 . . . . 15 . . .
FM
d
pulse interval / ms
200
150
100
50
0
e
duty cycle / %
50
40
30
20
10
0
0 0.2 0.4 0.6 0.8 1 1.2 1.4
t / s
f
x̄ = 13.0
SD± 1.3
n = 96
pulse duration / ms
g
x̄ = 3.9
SD± 0.6
n = 53
duration FM / ms
h
x̄ = 76.3
SD ± 38.2
n = 96
20 40 60 80 100 120 140 160
pulse interval / ms
i
CF/FM
x̄ = 8.9
SD± 1.2
n = 53
CF
x̄ = 13.3
SD± 1.0
n = 43
duration CF / ms
j
x̄ = 20.4
SD± 7.4
n = 96
duty cycle / %
k
x̄ = 25.9
SD ± 3.6
n = 53
bandwidth FM / kHz

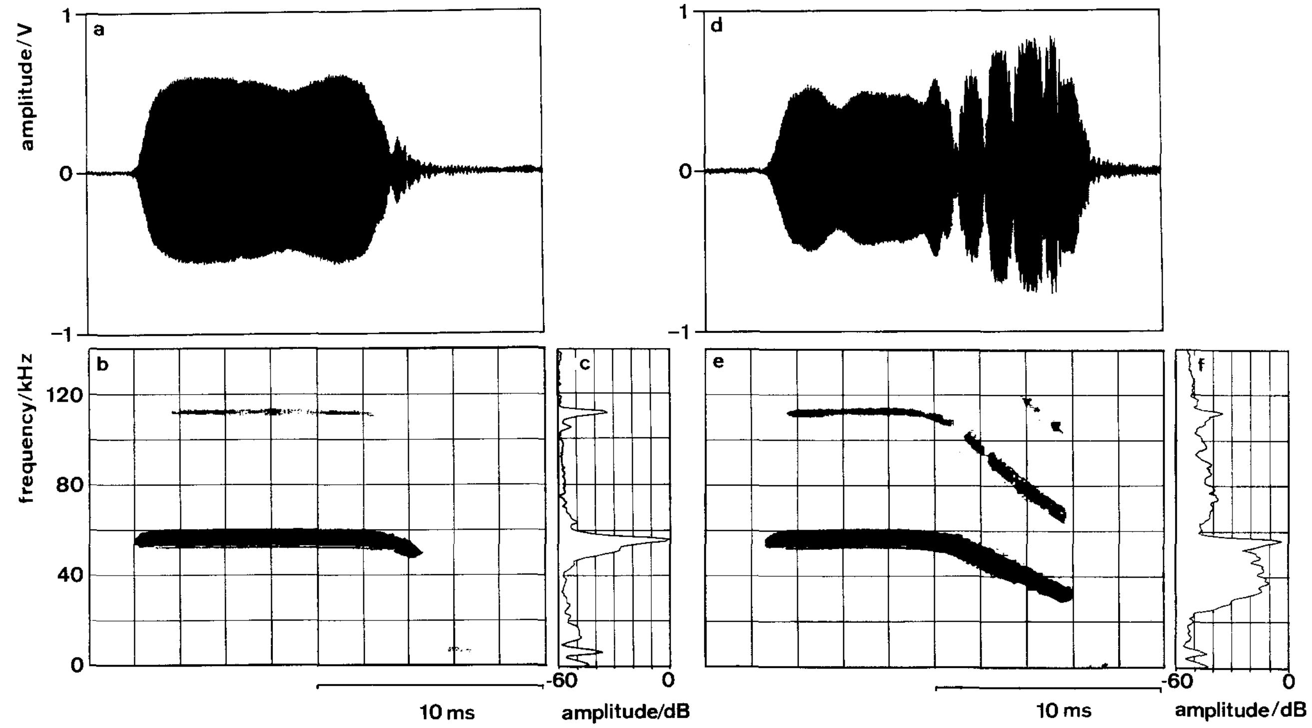


Fig. 3 Typical CF and CF-FM pulses of *N. leporinus* in high search flight (marked with *arrows* in Fig. 2b), with **a,d** oscillograms, **b,e** sonagrams, and **c,f** averaged spectra

the microphone from the water surface (Kalko and Schnitzler 1989a).

The frequency of the signals recorded with a microphone in front of a flying bat is higher than the emitted frequency due to the Doppler shift, which is proportional to the flight speed of the bat and the microphone angle (angle between flight direction and direction to the microphone). To determine the CF frequency of the signals (frequency of the relatively constant middle part of the CF portion) we used only pulses that were recorded with a small microphone angle. Thus, the error due to microphone position was minimal. From such signals, we found that in individual echolocation sequences the CF frequency is similar in the CF and CF-FM signals and is maintained within a range of about 400 Hz. To determine the true emitted frequency it was necessary to correct for Doppler shift caused by the flight speed of the bat. For a measured flight speed of 7 m/s, we calculated an emitted CF frequency of 54.8 kHz in a large male and frequencies between 52.8 and 56.2 kHz in several other bats as they flew towards our microphone. If *N. leporinus* uses Doppler shift compensation, 2.2 kHz must be added to obtain the reference frequency.

The main energy of the signals is concentrated in the first harmonic (Fig. 3c,f). Below about 120 kHz, spectrograms also revealed part of the second harmonic and even the lower frequencies of the FM sweep of the third harmonic. The second harmonic of the CF portion of the signals picked up with the QMC microphone was between 32–40 dB below the first harmonic. As our recording equipment was about 10 dB less sensitive at the second harmonic this degree of attenuation has to be subtracted from the measured value to get the true relationship.

Pointed dip from high search flight

Pointed dips are short dips, often no more than 3–4 cm in length, at a specific spot on the water. Frequently bats were observed to dip at spots an instant after a break in the smooth water surface caused by a jumping fish. Sometimes bats made sharp lateral movements or even reached laterally with one foot to dip somewhat off the immediate line of flight, presumably in response to information about the location of a target.

Pointed dips could be evoked when we simulated a jumping fish by directing a small stream of upwelling water from the surface via a submerged miniature water pump. We photographed several *N. leporinus* which reacted to our "artifish" with a pointed dip developing directly out of high search flight (Fig. 4a). After a descent to the water surface that took 200–500 ms, the bats dipped near the spot where we presented the artifish.

If we assume that the average approach speed is 6 m/s and that the target is detected through the echo of the last pulse before the vocal reaction, we estimate detection distances of 1.2–3.0 m.

Echolocation behavior was similar for naturally occuring pointed dips and dips evoked by the artifish. During the approach phase, the bats produce a continuous series, first of CF-FM pulses and finally of FM-pulses (Fig. 4b,g). During this series, the repetition rate in-

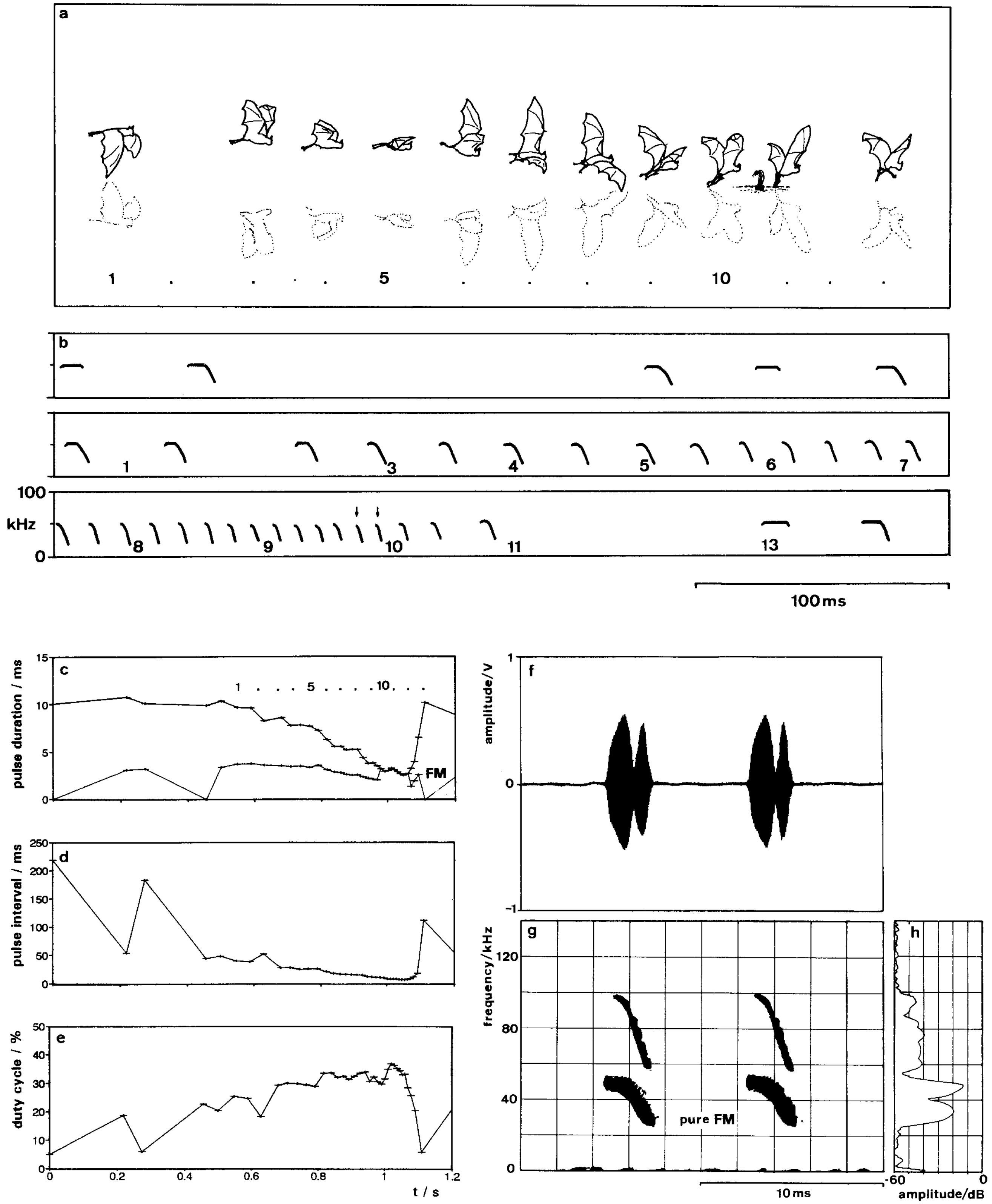


Fig. 4a–e Flight and echolocation behavior during a typical pointed dip of *N. leporinus* to the "artifish" from high search flight, and **f–h** oscillograms, sonagrams and averaged spectra of the two short signals which are marked with arrows in **b**. The "artifish" had been already activated before the photographic sequence started

creases and the sound duration decreases. Shortly before the dip, sound durations and pulse intervals are as short as 2.7 ms and 7.8 ms. During the dip, the signal duration and the pulse interval increases again. After the dip when flying off the bat switches back to the signal pattern typical of high search flight (Fig. 4b–h). In

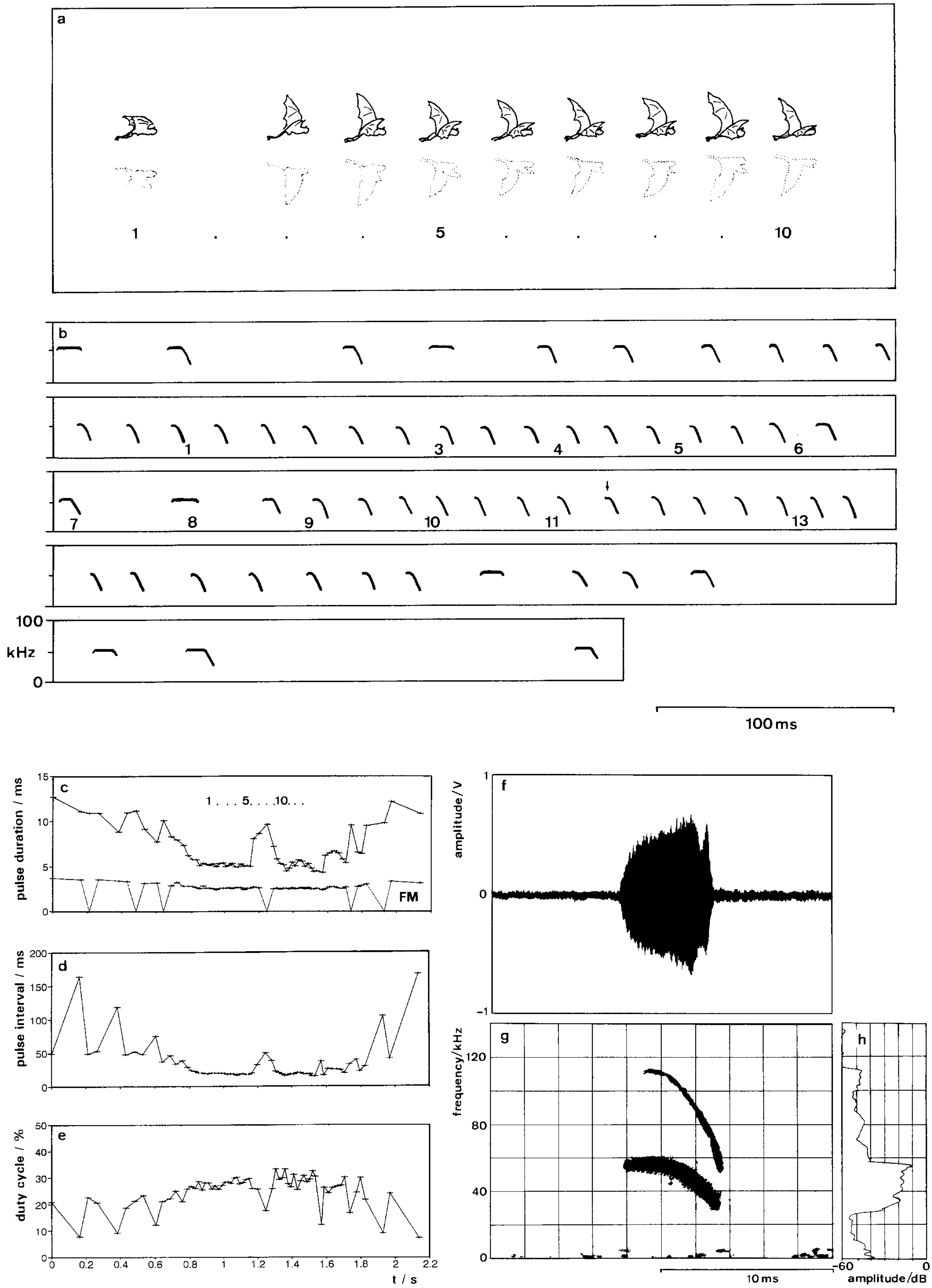


Fig. 5a–e Flight and echolocation behavior of *N. leporinus* during a typical pass in low search flight phase I, and **f–h** oscillogram, sonagram and averaged spectrum of the short signal marked with an arrow in *b*

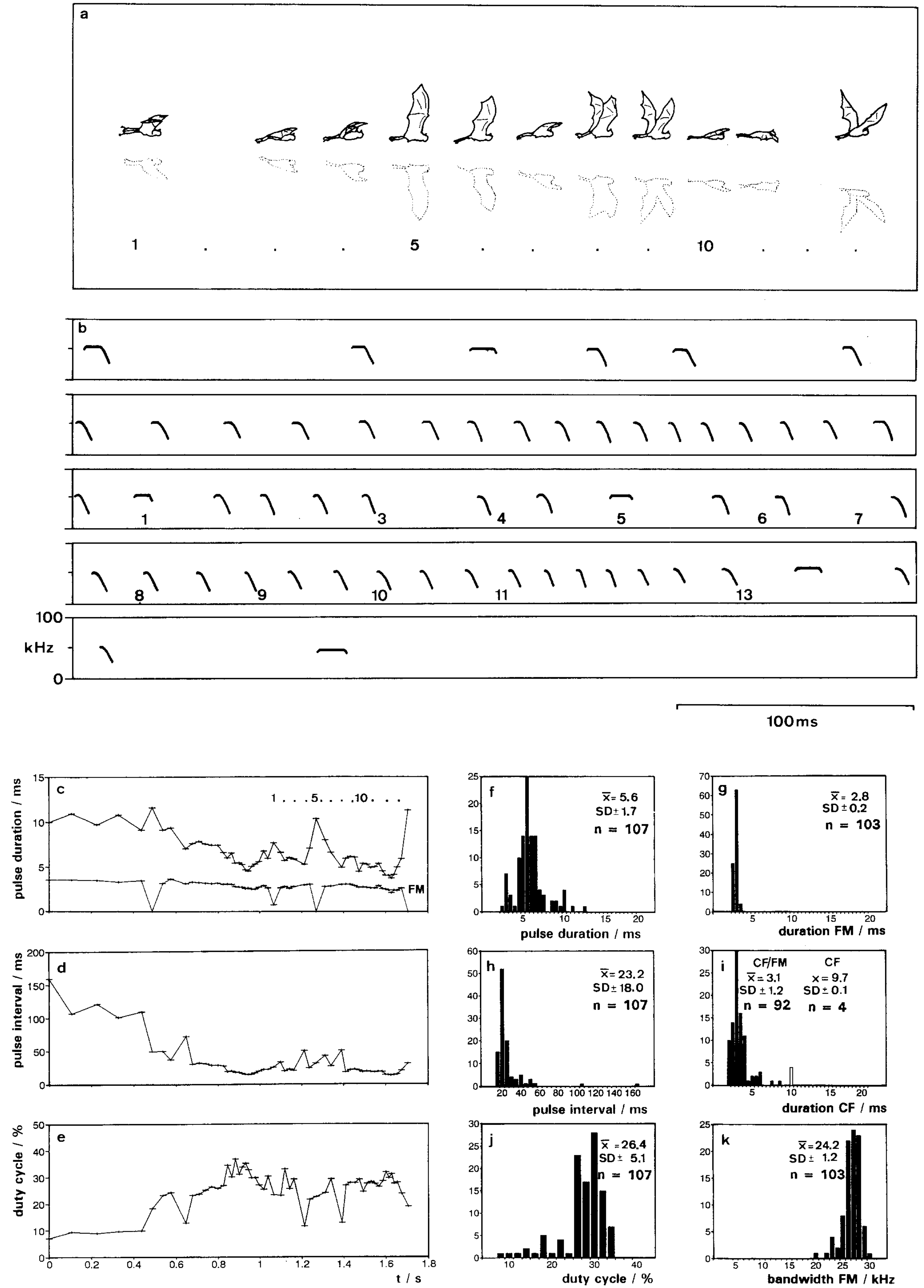


Fig. 6a–e Flight and echolocation behavior of *N. leporinus* during a typical pass in low search flight phase II, with **f–k** histograms and means ($\bar{x}$) and SDs of signal parameters of all analyzed sequences from low search flights

the approach phase the flight speed is about the same as in high search flight. After the dip, the speed is about 0.8–1.0 m/s slower than before dipping.

Low search flight

We found high search flight to be interspersed with segments of low search flight. To enter low search flight a bat decends from high search flight to a height of only 4–10 cm between its belly and water surface, with body parallel to the water, legs extended straight back and slightly downward, and feet cocked somewhat above the line of the legs, poised within 2–3 cm of the water surface (Figs 5a, 6a). Legs are slightly spread. The calcars are directed anteromedially along the legs, folding the interfemoral membrane forward so that it does not touch the surface when the legs are lowered into the water. Bats stay in low search flight for up to 10 m before going back to high search flight. Based on wing movements, we distinguish two phases of low search flight. In phase I the wingbeats are very shallow, around an average wing position about 30° above horizontal (Fig. 5a). In this phase the bats glide over the water. In phase II the bats show distinct wingbeats, with the wings moving between the vertical and horizontal planes (Fig. 6a). Phase I is typical of the first half of a low search flight segment. Somewhere in the second half the bats switch to phase II to stay aloft, and continue it until they ascend again into high search flight.

During the low search flight mode flight speed decreases to 5.8–6.6 m/s at the end of a segment and wing beat frequency increases to 5–6 beats/s ($n = 4$ flights). In low search flight, *N. leporinus* usually emits two (or sometimes more) 450 ms long series of short CF-FM pulses, with an average duration of 5.6 ms (CF 3.1 ms and FM 2.6 ms), an average pulse interval of 23.2 ms, and a duty cycle between 26–34%. These series are separated by one to three longer signals, one of which is always a pure CF pulse lasting about 10 ms (Figs 5b–h, 6b–k).

Pointed dip from low search flight

N. leporinus makes pointed dips during low search flight by very rapidly snapping the feet into the water at the spot where it has detected a fish or disturbance (Fig. 7a). In this case the bat reacts to close targets directly in its flight path. We conclude this from the echolocation behavior, where an additional reduction of pulse duration and pulse interval indicate the bat's reaction as little as 50–70 ms before dipping (Fig. 7b). In the short approach phase the bat continuously reduces sound duration and pulse interval, and switches from short CF-FM pulses to a few pure FM-signals (Fig. 7c–h). In the sequence displayed in Fig. 7b, the last FM signal was 2.2 ms in duration, with a minimal pulse interval of 7.8 ms.

If we assume that the target is detected through the echo of a pulse occurring about 60 ms before the vocal reaction (which means a very short reaction time) and that the bat flies with a flight speed of 6.0 m/s, we estimate detection distances ranging from 66–78 cm.

Random rake

In this hunting mode, *N. leporinus* drops to the water surface, bends its slightly spread legs at an angle of about 120° with respect to the horizontal body axis, immerses the forward pointing claws 1–2 cm, and drags them through the water in relatively straight lines for up to 10 m. As in the other search modes, calcars and interfemoral membrane are folded forward between the legs so that they do not contact the water. While raking, the wings are moved between the vertical and the horizontal plane and the wing beat rate is increased to 6–7 beats/s (Fig. 8a) In the rake segments we analyzed ($n = 8$), flight speed decreases to about 5.2 m/s. With each wingbeat the bat emits a group of two to five sounds containing pure CF and CF-FM signals in most possible combinations (Fig. 8b). The pulse pattern is similar to that of bats in high search flight. The only difference is that pulse groups contain up to five pulses (in high search mode mostly two to three), the average sound duration is 9.3 ms (compared with 13 ms in high search flight), and the average pulse interval is 44 ms (76 ms in high search flight) (Fig. 8c–k). In no case did we observe the pulse pattern typical of a bat that has located a target and that is approaching it as described for pointed dips. This indicates to us that a raking bat does not localize a specific target but surveys the environment much as a bat in high search flight does. We conclude therefore that raking is a random or statistical search for prey.

N. leporinus uses two strategies when it rakes. Often it rakes through limited patches of water where a repeated breaking of the surface indicates a school of fish. The bat lowers its feet specifically at this spot and drags its claws all the way through the school, for distances of one to two meters. As the surface disturbances caused by jumping fish slowly moves along the river, the bat's rakes move with it. This behavior indicates that the bat "knows" that there is prey in the area, at a density high enough for it to be advantageous to hunt randomly without dipping for a specific target. We believe that *N. leporinus* detects the many jumps with search calls emitted before it enters a raking segment, and chooses not to concentrate on a single jumping fish. As the rake is directed to an area with many jumping fish, but catches occur in a random manner, we call this strategy directed random rake.

When there are few or no jumping fish, *N. leporinus* often, after flying for several minutes without any dips, begins to make long rakes (up to 10 m) in areas where it has previously made pointed dips or directed rakes. Such raking probably is based on the bat's memory of a good hunting spot. As bats are unable to use echoloca-

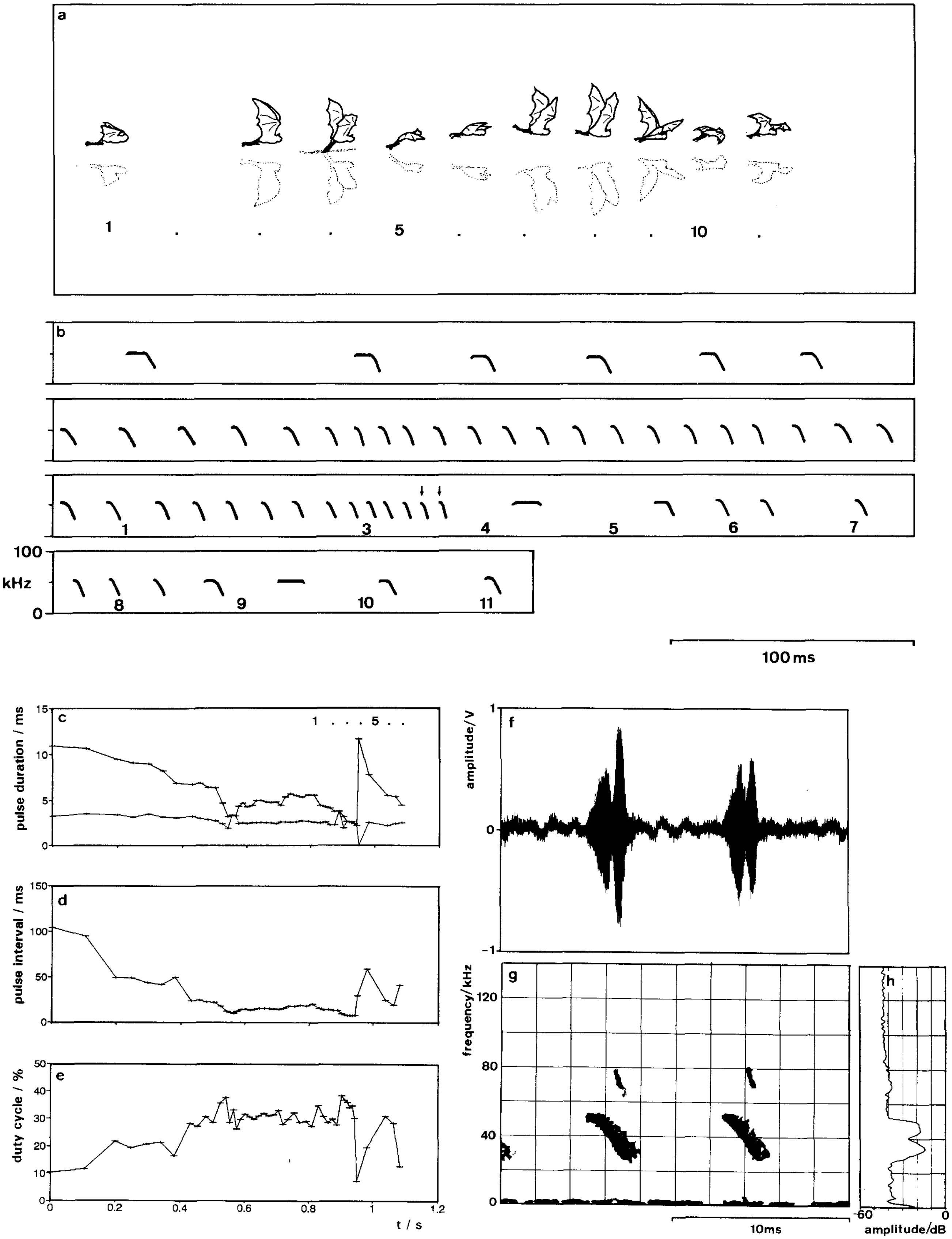


Fig. 7a–e Flight and echolocation behavior of *N. leporinus* during a typical pointed dip from low search flight, with **f–h** oscillograms, sonagrams and averaged spectra of the two short signals which are marked with arrows in *b*. The additional reduction of pulse duration and pulse interval occuring two pulses before photo number 3 probably indicates target detection

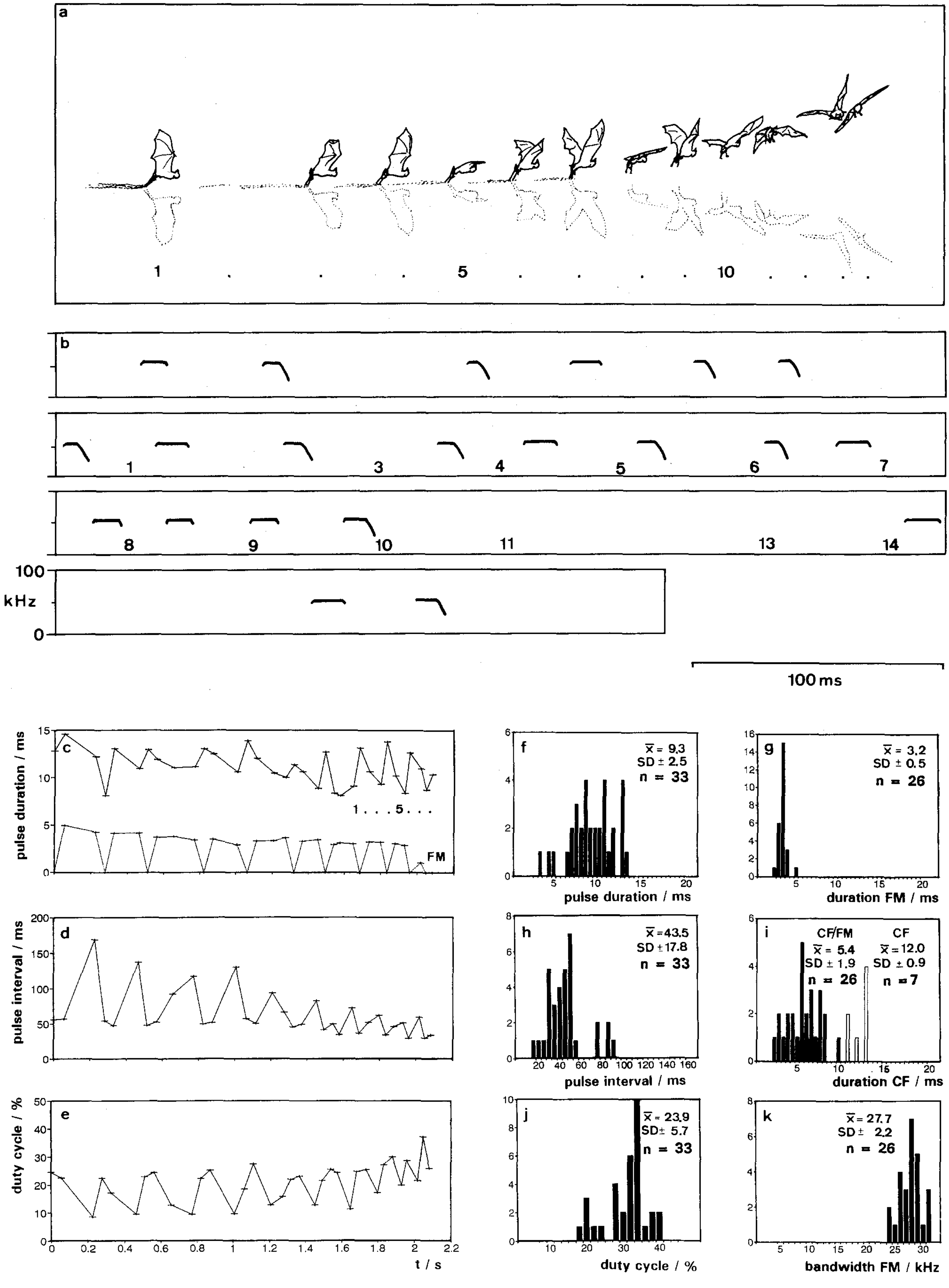


Fig. 8a–e Flight and echolocation behavior of *N. leporinus* during a typical raking pass with **f–k** histograms and means ($\bar{x}$) and SDs of signal parameters of all analysed raking sequences

tion to detect fish below the water surface, we call this strategy a *memory-directed random rake*. We observed memory-directed random rakes rather often just in front of our cameras where *N. leporinus* sometimes flew closer to the boat house to rake its claws through a short stretch (about 1 m) of shallow water that often contained a school of fish.

Prey capture and hunting success

During the three weeks of our observations we had the impression that *N. leporinus*, when searching for prey with echolocation, only attacks jumping fish. In random rakes it sometimes also gets smaller prey, possibly tiny crustaceans like ones we observed regularly in the water close to the shore. Based on about 10 h of continuous observations with night vision goggles of fishing *N. leporinus*, we estimated a capture success rate for fish of 0.5–2% (i.e., in 50–200 passes in front of us, one resulted in the capture of a fish). However, at about 2–3 times this rate there were near captures, when fish were pulled out of the water but subsequently dropped. While these could have been examples of prey rejection by the bats, it seems more likely they were cases of fish being hit but not gaffed or grasped adequately for capture. For other prey items we could not estimate the success rate as we could not see what the bats took out of the water.

When *N. leporinus* snags a fish, it immediately rotates its legs forward and its head downward for transfer of the fish to its jaws. Our observations and photographic documentation suggest the following sequence of events. When a fish is hit, several factors contribute to its capture: The bat's claws partially spear the fish (see Bloedel 1955) and its feet close on the fish, pressing claws deeper into its flesh. When the bat's legs leave the water the calcars are brought backward, unfolding the interfemoral membrane, and forming an interfemoral pouch which prevents the fish from falling free. While the fish is grasped by the bat's feet, it is pressed against the legs. As the legs move forward and up, the bat's head and jaws move down until its jaws can grasp the fish, possibly still held against the legs, as the claws are pulled out. At this moment, the claws are in front of the bat's head. The bat then straightens out with the prey in its mouth. In our observations, following each clear capture of a fish, the bat flew off toward the middle of the river where it remained for 2–5 min, presumably eating the fish on the wing, before returning to the hunt. *N. leporinus* has large cheek pouches. Often it first chews a fish rapidly to fill the pouches, then chews more before swallowing (Murray and Strickler 1975).

In several memory-directed random rakes, the bat brought only one foot forward and appeared to be transfering something from that foot to its mouth ($n = 4$) (Fig. 8a). Since this behavior was seen mainly on nights when small crustaceans ("shrimps") were numerous in the upper level of the water, it is quite possible that these represented captures of single shrimps.

Prey

Although we did not attempt systematically to collect or identify the principal prey of *N. leporinus*, we did collect several sardine-sized fishes near the hunting site. These, which certainly represent only a fraction of the variety of small fishes occurring at this site, belong to the families Clupeidae, Percidae, and Engraulidae. They ranged in weight from 0.5 to 12.8 g. We also collected some of the jumping shrimps which ranged in weight from 0.01 to 0.1 g.

N. leporinus has been reported also to take insects, judged both by stomach contents and the observation that it readily captures grasshoppers and crickets from the surface of the water in the laboratory (Altenbach 1989). Under the natural conditions in Costa Rica, we did not observe any clear-cut insect captures, although bats during the high search phase of flight did, very rarely, make sharp deviations in flight path to briefly approach large flying insects. These deviations did not turn into full pursuit in any observed case, but may indicate a proclivity to pursue flying insects if other prey are not available. In Panamá we twice observed *N. leporinus* capture an insect at about 1 m above the water surface. In general, insects that almost inevitably would have led to a dip by the smaller species, *N. albiventris*, did not cause that behavior in *N. leporinus*.

Discussion

Prey spectrum

N. leporinus is the only bat specialized for fish as a major component of its diet, although a few other bats take fish occasionally, such as myotid bats of the subgenera Pizonyx and Leuconoe (e.g., Brosset 1966; Brosset and Debouteville 1966; Findley 1972; Reeder and Norris 1954; Robson 1984). The greatly elongated feet, enormous, laterally compressed claws, formidable teeth, cheek pouches, and specializations in gastric morphology and biochemistry (e.g., Fish et al. 1991; Hood and Jones 1984; Murray and Strickler 1975; Taboada 1979) of *N. leporinus* are adaptations for this feeding behavior. However, analyzes of feces and stomachs of *N. leporinus* have given evidence that fish are not its exclusive prey. Occasionally stomachs are partly or even entirely filled with insect remains (e.g., Brooke 1994; Fleming et al. 1972; Goodwin 1928; Gudger 1945; Hooper 1968; Howell and Burch 1974; Taboada 1979) including mainly winged ants, flies (Tephritidae), crickets (Gryllidae), molecrickets (Gryllotalpidae), beetles (Carabidae, Cerambycidae, Dytiscidae, Elateridae, Hydrophilidae, Scarabaeidae, and Tenebrionidae), cockroaches (Blattidae), and moths (Lepidoptera). The fish prey include both fresh-water and salt-water species (e.g., Cichlidae, Athernininidae, Clupidae, Exocetidae, Elotridae, Holocentridae, Gerreidae, and Sphyraenidae; Brooke 1994). These findings show that *N. leporinus* retains its ability to feed on insects, supporting the assumption that the piscivory of *N. leporinus* has evolved from insectivorous ancestors (Novick and Dale 1971). In case of reduced availability of fish this behavioral plasticity may enable *N. leporinus* to exploit insect resources. In her longterm study, Brooke (1994) observed pronounced seasonal shifts in the diet of *N. leporinus* on the island of Culebra, Puerto Rico. During the wet season, insect remains (mainly moths and beetles) made up 55–88% and fish remains 12–45% of the dry weight of guano of *N. leporinus* whereas in the wet season, insect remains rose to 84–88% and fish remains made up only 12–16% of the dry weight of guano.

Capture techniques

In the absence of detailed field observations just how *N. leporinus* catches fish has been open to debate. First it was assumed that *N. leporinus* uses its interfemoral membrane alone to scoop fish out of the water (Goodwin 1928). However, several laboratory studies and field observations have made it clear that *N. leporinus* catches fish and other potential prey from water surfaces by piercing them with its gaff-like, laterally compressed claws (e.g., Altenbach 1989; Bloedel 1955; Suthers 1965). Our field studies largely confirm these observations. During long rakes and during capture attempts the strong calcars fold the interfemoral membrane up and forward, preventing its contact with the water. Otherwise increased drag probably would unbalance the bat. The pointed, laterally compressed claws reduce the drag created when the bat immerses its feet into the water (Fish et al. 1991). After a catch *N. leporinus* unfolds its uropatagium and uses it to handle the prey during the transfer from feet to mouth. This agrees with Altenbach's (1989) assignment of an important role to the interfermoral membrane in securing prey after the catch. It is also very likely that *N. leporinus* needs its rather large interfemoral membrane for aerodynamic reasons. We frequently observed that the tail membrane was quickly unfolded as a bat turned after a capture attempt.

Bloedel (1955) noted that *N. leporinus* "may sometimes quickly shoot a foot out to one side". He assumed that this action might imply close range echolocation of a small fish or might be simply a reaction to touching the water with one foot. Our photographs confirm that *N. leporinus* sometimes grasps smaller items with one foot only. We conclude that *N. leporinus* detects potential prey at short range close to its main flight path and tries to catch it with one foot. This capture behavior also occurs sometimes after short raking phases.

N. leporinus usually catches insects either in the air in a manner similar to that of its close relative *N. albiventris* using its tail membrane and/or wing (Brooke 1994; unpublished), or it may gaff the insects from the water surface as observed in the lab (Altenbach 1989). Brooke (1994) frequently observed foraging *N. leporinus* over land, hunting in lighted areas, over open fields, and along roads. However, some of the insects contained in the diet of *N. leporinus*, such as carabid beetles, are unable to fly. In addition, Brooke (1994) also found remains of chewed claws of fiddler crabs, shells of two soldier crabs, one land crab, and tails from scorpions in feeding roosts of *N. leporinus*. These findings suggest that *N. leporinus* is also able to take prey from the ground.

Capture success

Assuming that the bat has a random hunting strategy, Bloedel (1955) calculated the hunting success of *N. leporinus* for various densities of fish. For a density of approximately 10–25 fish/m^2 he estimated a hunting success of 3–4%. His captive bats reached a hunting success of 2% at this prey density, supporting his calculations. If we take the fish density we observed in Costa Rica (20–30 fish/m^2), the documented hunting success of 0.5–2% fits well with Bloedel's results. When we take an average success rate of 0.5–2%, and assume that each pass of a foraging bat is equivalent to a capture attempt, *N. leporinus* would catch a fish about once every 8–60 min. This capture success is much lower than in aerial insectivorous bats (e.g., Fenton 1990). However, the low capture success of *N. leporinus* is compensated by a high nutritional value per prey item.

Prey recognition by *N. leporinus*

During the 3 weeks we observed N. leporinus in Costa Rica, the bats appeared to be hunting almost exclusively for fish. Fish can only be detected by the bats when they break the water surface, as bats cannot echolocate entirely submerged targets. Not only is the attenuation of sound at the air-water interface too large [only 0.1% of the sound energy passes from one medium to the other, in each direction, for an attenuation of 10^{-6} at the optimal angle of 90° perpendicular to the surface (Griffin 1958; Griffin and Novick 1955; Suthers 1965), but the bats show no sign of detecting submerged objects in a pool, even when the objects are good reflectors of underwater sounds (Suthers 1965). In fact, bats will attack the protruding dorsal fin of a fish several times larger than they are and more a danger to the bat than vice versa (A.D. Grinnell and C.R. Slater, unpublished observations, Trinidad 1960). Our observations are entirely consistent with the conclusion that all active echolocation of fish takes place when the fish is partly out of water or causes a disturbance at the water's surface that can reflect a significant echo.

A hunting *N. leporinus* receives a continuously changing mixture of echoes indicating potential prey and other objects in its flight path. *N. leporinus* must recognize and localize the echoes of prey (fish) and separate these from echoes from floating debris, fluttering insects, and jumping shrimp on the water surface. To understand the prey recognition task which has to be solved by hunting *N. leporinus*, it is necessary to consider the types of echoes that come back to a bat while searching for fish and to consider other sensory cues that might indicate the presence of fish.

Glint patterns in echoes

A target that is ensonified with an echolocation signal produces an acoustical image that is different from its optical image. Only the parts of the target that are perpendicular to the impinging sound wave produce strong reflections or acoustical glints. A smooth sphere, for example, produces only one glint. More complex targets produce a glint pattern that reveals something about the target's structure. A stationary complex target that does not change its position relative to the impinging sound produces echoes with a pattern of stationary glints, whereas a moving target reflects echoes with a pattern of temporary glints that change in time.

Echoes from the water surface

A flat water surface acts like an acoustical mirror that reflects a detectable echo without glints only from the spot directly below the bat. Because of the high directionality of sound emission and echo reception and the attenuation of the echo by the middle ear muscles at short echo delays, it can be assumed that this echo is not very loud, even for bats flying low over the water. In front of the bat the echolocation signals are reflected away and produce no intense echo as long as the water surface is flat. On the other hand, surface waves, if they contain frontal parts that are perpendicular to the impinging sound or when they break into droplets, can produce audible echoes with a characteristic pattern of temporary glints. Small and non-breaking waves probably do not reflect enough energy to be detected by a bat, since they have no glint-producing perpendicular surfaces. Small waves can be produced by wind and also by fishes swimming just below the water surface. At our recording site we observed hunting bats predominantly in situations where the water surface was relatively flat, or with waves too small to reflect strong echoes. On those occasions when the breeze was strong enough to produce breaking waves, very few bats were observed, and they were not dipping for prey. Although this may simply have reflected a distaste for flying in a strong wind, it seems probable that the clutter of echoes of glints produced by surface waves would disturb the recognition of prey targets. Also, it cannot be said with certainty whether fish that swim just below the water surface are causing glint-producing surface waves that can be detected by a bat. However, it was our impression that the bats selected fish that clearly broke the surface.

Echoes from jumping fish

The fish for which *N. leporinus* were hunting were present in localized areas at varying density. An average density was approximately 20–30 small fishes/m^2 in the top 10 cm of water. Individuals among these typically jumped out of the water at a frequency of 5–15 jumps per m^2/min. Sometimes in localized areas of a few m^2 fish jumping was at a much higher frequency (up to 5–10 jumps per m^2/s). Previous laboratory observations have established that *N. leporinus* does not detect fish under water, but is extremely sensitive to surface disturbances. Such disturbances are produced by jumping fish. Our photos show that a jumping fish remains in the air up to 50 ms. The body and water disturbances as a fish leaves or enters the water represent good targets for echolocation, each producing a clear pattern of temporary glints that lasts up to 100 ms and is characteristic of jumping fish. Our artifish produced a splash which was rather similar to that of a jumping fish. However, it did not produce the body echo.

Our experiments with the artifish support the hypothesis that *N. leporinus* recognizes specific echo patterns produced by disturbances of the water surface and associates them with potential prey. Naive bats were readily induced to dip at our artifish, even from high search flight, although with repeated trials any given bat appeared to learn that this led to no reward. Similarly, in laboratory experiments, Suthers (1965) evoked pointed dips at an artificial up-welling. Under laboratory conditions, *N. leporinus* readily learns to dip not only at moving targets but also at non-moving targets, such as pieces of fish, mealworms, and bare wires (Altenbach 1989; Campbell and Suthers 1988; Hartley et al. 1989; Suthers 1965; Wenstrup and Suthers 1984), while it seldom if ever attacks passive floating targets in the field. These observations establish that *N. leporinus* can learn quickly to associate a given signal type (even "stationary glints" from non-moving targets) with food, and that normally it dips only at targets returning rapidly changing glints.

Echoes from fluttering insects

On several occasions we also observed insects still fluttering as they floated on the water surface near hunting *N. leporinus*. *N. albiventris*, the smaller relative of *N. leporinus*, almost inevitably attacked such insects and often scooped them out of the water. We never observed this behavior in *N. leporinus*. We conclude that the rhythmical glint pattern produced by a fluttering insect is different from that of a jumping fish and that *N. leporinus* can discriminate between the two targets.

Echoes from clutter targets

Clutter echoes are returned by floating debris such as leaves, twigs, floating coconuts, and large rafts of water plants (mainly water hyacinths), as well as from targets at the shore. These slowly moving or stationary targets produce echoes with rather stationary glints that are different from the echoes with temporary glints from prey or surface waves. Clutter-producing stationary targets were normally not attacked by bats nor did they deter normal hunting. *N. leporinus* seldom dipped at conspicuous stationary targets on the water, e.g., floating debris. These objects were quickly dropped and may only have been attacked as a result of a movement in the water (turning of a leaf to reveal a raised edge, for example) that produced an echo with temporary glints that may have been mistaken for a fish echo.

Other sensory cues indicating prey

Jumping fish also produce low-frequency splashing sounds when they leave and enter the water. These low-frequency sounds could alert the bats to the presence of potential prey. Small pebbles thrown rapidly into the water to the side of the bat can evoke turning and dipping at the site of the splash, when the pebble itself may not have been detected. The silvery body of a jumping fish is also a good reflector of light from moon, stars, or artificial lights, producing optical glints. Although *N. leporinus* can be seen hunting under cloud cover in the absence of artificial light, this does not mean that they cannot take advantage of optical cues when they are present. It seems probable that they use any cues that are available, but we cannot draw additional conclusions from our observations.

In summary it can be stated that echoes from wanted targets such as jumping fish or fluttering insects are characterized by a typical pattern of temporary glints, whereas echoes from unwanted targets such as floating debris have a clearly different pattern of stationary glints. Therefore the bats can recognize their prey even in dense clutter.

Correlation of hunting and echolocation strategies

Our studies show that *N. leporinus* employ a variety of hunting strategies each of which is correlated with a specific echolocation behavior.

High search flight

The long search signals and low repetition rate characteristic of high search flight suggest that during this flight mode the bats are searching for targets over long distances. This assumption is supported by the rather long detection distances of 1.2–3.0 m which can be estimated from our data. Since high search flight leads either to pointed dips or to any of the other specific hunting behaviors (low search flight with dips, and directed or memory-directed random rakes), it is evident that the information the bat received in high search flight determines which of these behaviors it will use. In high search flight the interval between sets of 2–3 pulses is too long to guarantee detection of a given jumping fish. On the other hand, by searching over a wide area and long distance, it can determine where fish are jumping and head toward that area in low search flight. If a fish happens to jump nearby, it will initiate a pointed dip, even though the distance to the water necessitates a long approach phase, which has the disadvantage that the fish is usually back in the water before the bat reaches it. On the other hand, given a long approach phase, a bat can correct its flight path to take advantage of information about the perceived direction and rate of movement of fish, as they have been shown to do in a laboratory situation (Campbell and Suthers 1988).

Information about targets returns to the bat only during a small fraction of the time – when sound pulses are impinging on the environment. This is a relatively minor problem for stationary targets, which will return a certain pattern of glints to every pulse. For a target like a jumping fish, however, which is out of the water only 50–100 ms, it would be possible for the entire jump to occur between sets of pulses and hence not be detected. The shorter the intervals between emissions, the greater the chances of detecting jumping fish. Different search modes with different interpulse intervals suggest different hunting strategies. At least in high search flight, the intervals between the last signal of a group and the first of the following group were as long as 135–165 ms so that it would be possible for a bat to miss a jumping fish.

Low search flight

The long pulse trains of low search flight are characterized by signals with an average duration of 5.6 ms, a pulse interval of about 20 ms, and a duty cycle between 26 and 34%. The relatively short signals and high repetition rate indicate that the bats search for food over much shorter distances than in high search flight. This conclusion is supported by the short approach sequences associated with dips out of low search flight, which reveal that *N. leporinus* reacted to targets at distances between 66 and 78 cm. The distinct approach vocalizations and the short dips also indicate that the bats go for specific targets. The cocked position of the legs a few centimeters above the water suggest that bats in low search flight are searching for jumping fish immediately ahead of them with the strategy of gaffing them when they are still out of water or just resubmerging. In this mode the search range is smaller than in high search flight, and many fish do not disappear before they can be reached. On the other hand, in this short-distance search mode, the bats stand little chance of capturing fish that appear to either side of their flight path, as they do not have time to correct their flight direction. They can, however, extend either leg significantly to the side to reach fish that are not too far off the flight path.

During low search flight close to the water surface, *N. leporinus* may take advantage of the ground effect. The ground effect is an increase in lift and decrease in drag of an aerofoil (wings) close to surfaces. It has been shown for birds and one bat species that the ground effect is responsible for a significant reduction in energy costs of flight (e.g., Withers and Timko 1977; Aldridge 1988).

Directed random rake

The pattern of signals emitted during random rake behavior resembles that of high search flight, suggesting that in this flight mode *N. leporinus* is not trying to echolocate a single target. However, the higher duty cycle during random rake gives *N. leporinus* a better chance to detect jumping fish than in high search flight. We had the impression that the directed random rake mode was chosen when the jumping activity was high whereas high and low search flight were found at lower jumping rates. It may also be that other sensory cues, such as the splashing sounds or optical glint pattern of jumping fish, reveal a fish school to the bat.

Memory-directed random rake

When fish are not breaking the water surface, *N. leporinus* often rake through areas where they have hunted successfully before. In this search mode, the emitted sound pattern indicates that no specific target is being pursued, although the area in front of the bat is being well scanned. As schools of fish often stay at a preferred spot it is likely that the strategy is successful enough that a chance capture is more probable than with a purely statistical search mode. Such behavior has already been described by Bloedel (1955), who reported that *N. leporinus* trained to catch fish out of a small tray would rake the surface of the tray for half an hour or more even when the tray did not contain any fish.

Aerial catches of insects

In Costa Rica, we did not see *N. leporinus* capture insects in air, or even give serious pursuit. However, from faecal analyzis (e.g., Brooke 1994; Hood and Jones 1984), from indirect observations (Goodwin 1928) and observations in Panamá (E.K.V. Kalko), we know that *N. leporinus* does, under some conditions, hunt for flying insects. On two occasions in Panamá the bats clearly soared upwards and caught an insect in the air. Both capture attempts were associated with a typical feeding buzz in echolocation behavior. Presumably, like its smaller relative, *N. albiventris* (unpublished) and other bats that employ CF signals, *N. leporinus* can evaluate the rhythmical pattern of amplitude and frequency modulations produced by the beating wings of the insect to discriminate insect echoes from unmodulated background clutter (Kober and Schnitzler 1990; Schnitzler 1987; Schnitzler et al. 1987).

Insects taken from the water surface

Many insects are able to hear bat cries and escape by evasive movement (e.g., Roeder and Treat 1961). When they are pursued over water, the insects frequently end up, still fluttering, in the water. In this situation, *N. albiventris* often pursue and capture the insect from the water surface (unpublished). Laboratory observations have shown that *N. leporinus* use their feet to pick floating insects off the water surface (Novick and Dale 1971; Altenbach 1989) and they quickly learned to use their feet to "catch" pieces of fish from targets held by forceps about 120 cm above the ground while flying past in a large flight cage (A.D. Grinnell, C.R. Slater, D.R. Griffin, unpublished observations, Trinidad 1960). It is highly probable that *N. leporinus* also use their feet to pick insects off the water surface in the wild. Discrimination of an insect from passive floating objects presumably depends on the pattern of moving glints produced by it. Even the remains of swimming water beetles (Dytiscidae, Hydrophilidae) have been found in *N. leporinus* faeces (Taboada 1979), suggesting that these insects may also produce a typical pattern of changing glints that allows *N. leporinus* to detect and distinguish them.

Prey taken from the ground

Fiddler crab claws found in the roost (Brooke 1994) and remains of ground dwelling carabid beetles in the faeces (Taboada 1979) suggest that *N. leporinus* can also take prey from the ground. This is confirmed by the observation that *N. leporinus* used their feet to catch crickets that climbed out of a pool onto the shore (Novick and Dale 1971). In such a situation the bat has the problem of separating the insect echo from the strong background clutter coming from the ground. We speculate that moving prey would produce patterns of temporary glints whereas background objects are characterized by stationary glints. Further observations are needed to see whether the bats pursue only moving prey.

The extent to which *N. leporinus* uses different hunting strategies varies. During our field studies in Costa Rica we frequently saw *N. leporinus* performing long raking phases. Additional observations in Panamá (1992), gave a different picture. Here the main hunting strategy of *N. leporinus* consisted of dips out of high search flight. Raking was rarely seen. The variable use of hunting strategies might reflect different food availability and density and learned behavior of the bat. Under laboratory conditions Altenbach (1989) could not induce long foot drags by bats accustomed to dipping for prey fixed at specific spots.

Adaptive value of signal design and hearing system

It is generally agreed that a major function of the CF component in CF-FM sounds is fluttering target detection and evaluation. The echoes from fluttering insects are characterized by species-specific patterns of temporary glints, from which bats are able to discriminate prey echoes from background clutter and probably discriminate between different types of prey (e.g., von der Emde and Schnitzler 1986, 1990; Neuweiler 1990; Schnitzler 1987; Schnitzler and Kaipf 1992). We consider it likely that *N. leporinus* use their CF signal components to discriminate between the various targets in the environment and distinguish these from background clutter. Since the longer the CF signal used, the more information can be collected, the most effective target identification would be during high search flight and random rake, when long CF signals and long CF components to CF-FM signals are used.

Bats that employ long CF signal components (rhinolophids, hipposiderids, and the mormoopid bat *Pteronotus parnellii*) show extraordinary specializations both in the vocal behavior of Doppler shift compensation and in the possession of an "auditory fovea" in the cochlea (reviewed in Busnel and Fish 1980; Nachtigall et al. 1988; Neuweiler 1990). Doppler-shift compensation is the lowering of the frequency of emitted sounds by flying bats to compensate for the upward shift of echoes due to bat's flight speed. The echoes of stationary objects directly in the bat's flight path are kept approximately constant at the so-called reference frequency. Echoes from fluttering insects or other moving targets vary just above and below the reference frequency, depending on the targets radial movement toward and away from the bat. The auditory systems of CF-FM bats are highly specialized, with all structures from the cochlea to the auditory cortex showing strong overrepresentation of a narrow band of frequencies around the reference frequency. Thus CF-FM bats establish an analysis window that nicely matches the expectation window generated by moving prey. If *N. leporinus* – as we think – evaluate temporary glint patterns, it would be very helpful if their vocal transmitter and auditory systems were similarly specialized for optimal processing of this information.

With our apparatus we could not decide whether flying *N. leporinus* compensated for Doppler shifts caused by their own flight speed. The observation that the CF frequency of successive pulses is kept constant within about 400 Hz indicates that this frequency is well controlled, perhaps by a feedback mechanism that holds the CF frequency of echoes constant at a reference frequency. This suggestion is supported by the observation of Wenstrup and Suthers (1984) that during the approach phase of *N. leporinus* in the laboratory the emitted frequency is lower than the CF frequency of the CF-FM signals of resting bats. They interpreted the lowering of the emitted frequency as an incomplete compensation of about 50% of the total Doppler shift, assuming that the reference frequency is the same as the resting frequency.

If *N. leporinus* uses Doppler compensation, it would be advantageous for the auditory system to be specialized for the analyzis of a narrow band of frequencies around the reference frequency. Wenstrup (1984), who measured behavioral and auditory brainstem response audiograms in *N. leporinus*, found a distinct dip in threshold near the bats' CF frequency. This may be an indication of a special "analysis window", as in other CF-FM bats. It would be of great interest to know whether neurons tuned to this frequency range are especially adapted for the evaluation of temporary glint patterns.

It is also generally accepted that FM-signals are adapted for the determination of target range and angle. In all search modes the FM portion of the CF-FM signals is relatively uniform, ranging in average duration and bandwidth from 3.9 ms and 24.2 kHz in high search flight to 3.2 ms and 27.7 kHz in random rake and 2.8 ms and 24.2 kHz in low search flight. When a bat approaches a target to make a pointed dip, sound duration and pulse interval are reduced. The reduction in sound duration occurs mainly at the expense of the CF component. Shortly before the dip the CF component disappears altogether and a few brief pure FM-signals are emitted. FM-signals as short as 2.2 ms were measured at a pointed dip out of low search flight. On the other hand, the reduction in FM-duration during pursuit is small compared to that in other bats. A landing greater horseshoe bat reduces the duration of the FM portion of its CF-FM pulses from 2.5–3 ms in search flight to a minimum of about 0.5 ms shortly before landing (Tian 1989) and during insect hunting Daubenton's bat and pipistrelle bats similarly shorten the duration of their FM signals to as little as 0.5–0.3 ms (Kalko 1991; Kalko and Schnitzler 1989b; Schnitzler et al. 1987). For these bats the reduction of FM-duration prevents overlap between outgoing signals and returning echoes. Our observations showed that the FM-signals emitted just before a dip are not short enough to prevent a substantial overlap if there would be returning echoes in this situation. Laboratory experiments where *N. leporinus* learned to scoop pieces of fish or mealworms from the tip of a vertical wire also showed a pulse-echo overlap of FM-signals near the target (Hartley et al. 1989). In other laboratory experiments, Suthers (1965) found that the duration of the FM-pulses emitted near the target were as short as 1 ms, producing a smaller overlap than the 2-ms signals described by Hartley et al. (1989) or those we observed in the field.

Since fishing *N. leporinus* hunt for targets that often are not detectable throughout the approach phase, we suggest that the design of the FM portion of their sounds is optimized for the localization of the target during the brief time when the prey is "visible", and that the approach is directed to this spot much as an owl strikes at the spot where it has localized its prey by passive sounds. With this strategy, the target-induced reduction in signal duration that is conspicuous in bats that pursue permanently visible targets may be of less importance in *N. leporinus*.

Acknowledgements We thank Dr. Richard LaVal for advice and help in the field and also the staff, especially the cook, of Tortuga Lodge, for making our stay at the lodge comfortable. We are most grateful to Charles Handley for his valuable comments on the manuscript and to Anne Brooke for sharing her vast knowledge of *Noctilio* with us. Our research was supported by the Deutsche Forschungsgemeinschaft (SFB 307).

References

Aldridge HDJN (1988) Flight kinematics and energetics in the little brown bat, *Myotis lucifugus* (Chiroptera: Vespertilionidae), with reference to the influence of ground effect. J Zool Lond 216:507–517

Altenbach JS (1989) Prey capture by the fishing bats *Noctilio leporinus* and *Myotis vivesi.* J Mammal 70:421–424

Benedict JE (1926) Notes on the feeding habits of *Noctilio.* J Mammal 7:58–59

Bloedel P (1955) Hunting methods of fish-eating bats, particularly *Noctilio leporinus.* J Mammal 36:390–399

Brooke AP (1994) Diet of the fishing bat, *Noctilio leporinus* (Chiroptera: Noctilionidae). J Mammal 75:212–218

Brosset AP (1966) La biologie des Chiropteres. Masson, Paris

Brosset A, Debouteville CD (1966) Le regime alimentaire du vespertilion de Daubenton *Myotis daubentoni.* Mammalia 30:247–381

Brown PE, Brown TW, Grinnell AD (1983) Echolocation, development, and vocal communication in the lesser bulldog bat, *Noctilio albiventris.* Behav Ecol Sociobiol 13:287–298

Busnel RG, Fish JF (eds) (1980) Animal sonar systems. Plenum, New York

Campbell KA, Suthers RA (1988) Predictive tracking of horizontally moving targets by the fishing bat, *Noctilio leporinus.* In: Nachtigall PE, Moore PWB (eds) Animal sonar processes and performance, Plenum, New York, pp 500–506

Emde G von der, Schnitzler HU (1986) Fluttering target detection in hipposiderid bats. J Comp Physiol A 159:765–772

Emde G von der, Schnitzler HU (1990) Classification of insects by echolocating greater horseshoe bats. J Comp Physiol A 167:423–430

Fenton MB (1990) The foraging behaviour and ecology of animal-eating bats. Can J Zool 86:411–422

Findley JS (1972) Phenetic relationships among bats of the genus *Myotis.* Syst Zool 21:31–52

Fish FE, Blood BR, Clark BD (1991) Hydrodynamics of the feet of fish-catching bats: influence of the water surface on drag and morphological design. J Exp Zool 258:164–173

Fleming TH, Hooper ET, Wilson DE (1972) Three Central American bat communities: structure, reproductive cycles and movement patterns. Ecology 53:555–569

Goodwin GG (1928) Observations on *Noctilio.* J Mammal 9:104–113

Griffin DR (1958). Listening in the dark. Yale University Press, New Haven

Griffin DR, Novick A (1955). Acoustic orientation of neotropical bats. J Exp Zool 130:251–299

Gudger EW (1945) Fisherman bats of the Carribean region. J Mammal 26:1–15

Hartley DJ, Campbell KA, Suther RA (1989) The acoustic behavior of the fish-eating bat, *Noctilio leporinus*, during prey capture. J Acoust Soc Am 86:8–27

Hood CS, Jones JK Jr (1984) *Noctilio leporinus.* Mammal Species 216:1–7

Hooper ET, Brown JH (1968) Foraging and breeding in two sympatric species of neotropical bats, genus *Noctilio.* J Mammal 49:310–312

Howell DJ, Burch D (1974) Food habits of some Costa Rican bats. Rev Biol Trop 21:281–294

Kalko EKV (1991) Das Echoortungs- und Jagdverhalten der drei europäischen Zwergfledermausarten *Pipistrellus pipistrellus* (Schreber, 1774), *Pipistrellus nathusii* (Keyserling et Blasius, 1839) und *Pipistrellus kuhli* (Kuhl, 1819) im Freiland. PhD thesis, Faculty of Biology, University of Tübingen, Germany

Kalko EKV, Schnitzler HU (1989a) Two wavefront interference patterns in frequency-modulated echolocation signals of bats flying low over water. J Acoust Soc Am 85:691–692

Kalko EKV, Schnitzler HU (1989b) The echolocation and hunting behavior of Daubenton's bat, *Myotis daubentoni.* Behav Ecol Sociobiol 24:225–238

Kober R, Schnitzler HU (1990) Information in sonar echoes of fluttering insects available for echolocating bats. J Acoust Soc Am 87:882–896

Murray PF, Strickler T (1975) Notes on the structure and function of cheek pouches within the Chiroptera. J Mammal 56:637–676

Neuweiler G (1989) Foraging ecology and audition in echolocating bats. Trends Ecol Evol 4:160–166

Neuweiler G (1990) Auditory adaptations for prey capture in echolocating bats. Physiol Rev 70:615–641

Nachtigall PE, Moore PWB (eds) (1988) Animal sonar processes and performance, Plenum, New York

Novick A, Dale BA (1971) Foraging behavior in fishing bats and their insectivorous relatives. J Mammal 52:817–818

Reeder WG, Norris KS (1954) Distribution, habits and type localities of the fish-eating bat *Pizonyx vivesi.* J Mammal 35:84–87

Robson SK (1984) *Myotis adversus* (Chiroptera: Vespertilionidae): Australia's fish-eating bat. Aust Mammal 7:51–52

Roeder KD, Treat AE (1961) The detection and evasion of bats by moths. Am Sci 49:135–148

Roverud RC (1988) A time window for distance information processing in the bats, *Noctilio albiventris* and *Rhinolophus rouxi.* In: Nachtigall PE, Moore PWB (eds) Animal sonar processes and performance. Plenum, New York, pp 513–517

Schnitzler HU (1987) Echoes of fluttering insects: information for echolocating bats. In: Fenton B, Racey PA, Rayner JMV (eds) Advances in the study of bats. Cambridge University Press, Cambridge, pp 226–243

Schnitzler HU, Henson OW Jr (1980) Performance of airborne animal sonar systems. I. Microchiroptera. In: Busnel RG, Fish JF (eds) Animal sonar systems. Plenum, New York, pp 109–181

Schnitzler HU, Kaipf I (1992) Classification of insects by echolocation in the moustache bat, *Pteronotus parnellii.* Z Säugetierkde 57 (Supplement):48–49

Schnitzler HU, Menne D, Kober R, Heblich K (1983) The acoustical image of fluttering insects in echolocating bats. In Huber F, Markl H (eds) Neuroethology and behavioral physiology: roots and growing points. Springer, Berlin Heidelberg New York, pp 235–250

Schnitzler HU, Kalko E, Miller L, Surlykke A (1987) The echolocation and hunting behavior of the bat *Pipistrellus kuhli.* J Comp Physiol 161:267–274

Suthers RA (1965) Acoustic orientation by fish-catching bats. J Exp Zool 158:3119–348

Suthers RA (1967) Comparative echolocation by fishing bats. J Mammal 48:79–87

Suthers RA, Fattu JM (1973) Fishing behavior and acoustic orientation by the bat *Noctilio labialis.* Anim Behav 21:661–666

Taboada SG (1979) *Noctilio leporinus.* In: Taboada SG (ed) Las murcielagas de Cuba. Editorial Academia, Cuba

Tian B (1989) Feinanalyse der Ortungslaute der großen Hufeisennase (*Rhinolophus ferrumequinum*) im Flug und bei der Landung. Diplomarbeit. Faculty of Biology, University of Tübingen, Germany

Wenstrup JJ (1984) Auditory sensitivity in the fish-catching bat, *Noctilio leporinus.* J Comp Physiol A 155:91–101

Wenstrup JJ, Suthers RA (1984) Echolocation of moving targets by the fish-catching bat, *Noctilio leporinus.* J Comp Physiol A 155:75–89

Withers PC, Timko P (1977) The significance of ground effect to the aerodynamic cost of flight and energetics of the black skimmer (*Rhynchops nigra*). J Exp Biol 70:13–26