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Echolocation and foraging behavior of the lesser bulldog bat, *Noctilio albiventris*: preadaptations for piscivory?

Abstract We studied variability in foraging behavior of *Noctilio albiventris* (Chiroptera: Noctilionidae) in Costa Rica and Panamá and related it to properties of its echolocation behavior. *N. albiventris* searches for prey in high (> 20 cm) or low (< 20 cm) search flight, mostly over water. It captures insects in mid-air (aerial captures) and from the water surface (pointed dip). We once observed an individual dragging its feet through the water (directed random rake). In search flight, *N. albiventris* emits groups of echolocation signals (duration 10–11 ms) containing mixed signals with constant-frequency (CF) and frequency-modulated (FM) components, or pure CF signals. Sometimes, mostly over land, it produces long FM signals (duration 15–21 ms). When *N. albiventris* approaches prey in a pointed dip or in aerial captures, pulse duration and pulse interval are reduced, the CF component is eliminated, and a terminal phase with short FM signals (duration 2 ms) at high repetition rates (150–170 Hz) is emitted. Except for the last pulses in the terminal phase *N. albiventris* avoids overlap between emitted signals and echoes returning from prey. During rakes, echolocation behavior is similar to that in high search flight. We compare *N. albiventris* with its larger congener, *N. leporinus*, and discuss behavioral and morphological specializations that can be interpreted as preadaptations favoring the evolution of piscivory as seen in *N. leporinus*. Prominent among these specializations are the CF components of the echolocation signals which allow detection and evaluation of fluttering prey amidst clutter-echoes, high variability in foraging strategy and the associated echolocation behavior, as well as morphological specializations such as enlarged feet for capturing prey from the water surface.

Key words Bats · Echolocation · Foraging · Evolution · Piscivory

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Introduction

The development of flight and echolocation give bats (Microchiroptera) access to a wide range of habitats and foods. Echolocation allows orientation at night and to a varying degree detection, classification, and localization of food. Signal structure varies widely across microchiropteran families and genera (e.g., Fenton 1995; Neuweiler 1990; Simmons and Stein 1980). To understand the adaptive value of variability in signal design, comparative field studies of bats living under similar ecological conditions are essential for linking use of signal types to ecological constraints imposed by foraging habitat, feeding mode, and type of food, also taking into consideration the phylogenetic relationships of species (e.g., Fenton 1990; Neuweiler 1989, 1990; Schnitzler and Kalko 1998; Simmons and Stein 1980). Bats foraging over water are excellent models for such studies. Members of several families capture prey from or near water surfaces. These include evening bats (Vespertilionidae: *Myotis*; subgenera *Leuconoe*, *Pizonyx*), sheath-tailed bats (Emballonuridae: *Rhynchonycteris naso*), New World leaf-nosed bats (Phyllostomidae: *Macrophyllum macrophyllum*), bulldog bats (Noctilionidae: *Noctilio albiventris* and *N. leporinus*), Old World false vampire bats (Megadermatidae:

Megaderma lyra), and slit-nosed bats (Nycteridae: *Nycteris grandis*) (e.g., Altenbach 1989; Audet et al. 1990; Britton et al. 1997; Gudger 1943; Harrison 1975; Hood and Jones 1984; Hood and Pitocchelli 1983; Jones and Rayner 1988, 1991; Kalko 1995a; Kalko and Schnitzler 1989a; Marimuthu et al. 1995; Maya 1968; Novick and Dale 1971; Patten and Findley 1970; Schnitzler et al. 1994; Suthers 1965, 1967). Although all of these bats forage in similar habitats, signal design is highly diverse ranging from short frequency-modulated (FM) signals to relatively long constant-frequency (CF) and mixed CF-FM signals.

Here we focus on the lesser bulldog bat, *Noctilio albiventris*, which feeds mainly on insects. Although this bat will eat small pieces of fish in captivity and parts of fish have been found occasionally in its feces (Howell and Burch 1974), fish do not play an important role in its diet (e.g., Hood and Pitocchelli 1983; Hooper and Brown 1968). We compare *N. albiventris* with its congener *N. leporinus* which is well-known for its fish-eating habits but occasionally also eats insects. An insectivorous ancestor resembling *N. albiventris* may have given rise to *N. leporinus* (Novick and Dale 1971).

Field studies of *N. leporinus* have revealed several hunting strategies: the bat takes prey from the water surface in a pointed dip, rakes with its claws through the water, and captures insects in the air (e.g., Hood and Jones 1984; Novick and Dale 1971; Schnitzler et al. 1994). In contrast, few published studies focus on foraging behavior of *N. albiventris* (e.g., Fenton et al. 1993). They indicate that it gaffs insects from the water surface (e.g., Brown et al. 1983; Hood and Pitocchelli 1983; Howell and Burch 1974; Suthers and Fattu 1973).

In both noctilionids, general structure and pattern of echolocation signals are similar (Roverud and Grinnell 1985a, b; Suthers 1965, 1967). They produce CF signals interspersed with mixed signals consisting of a CF component and steep FM components. This pattern is unique among bats known to take food from the water

surface. CF components facilitate the detection of moving prey amidst clutter-producing background (e.g., Neuweiler 1990; Roverud et al. 1991; Schnitzler and Kalko 1998), a challenge confronting both *Noctilio* when hunting over water or over land.

To link foraging with echolocation behavior and to elucidate behavioral and sensory adaptations which may have favored the evolution of the piscivory seen in *N. leporinus* we studied *N. albiventris* in the field at study sites in Costa Rica and Panamá.

Methods

Field sites and bats

From a boathouse (Fig. 1) and from a boat at mid-river we observed *N. albiventris* for 20 nights (20 October–10 November 1990) at the Tortuguero River, a tidal estuary about 60 m wide, at Tortuga Lodge, Costa Rica. We made additional observations of *N. albiventris* in Panamá on 35 nights (June 1991–September 1995) around Barro Colorado Island (BCI), a field station of the Smithsonian Tropical Research Institute in Lake Gatun (9 09′N, 79 51′W), Panama Canal, and at Gamboa on the Chagres River, about 10 km southeast of BCI. Recording and observation sessions started when the bats began to forage about half an hour after dusk, and usually ended around 12:30 a.m. We observed foraging bats with night vision goggles (type Wild) and/or headlights and followed them acoustically with a custom-made bat detector. *N. albiventris* and *N. leporinus* are widespread throughout tropical and subtropical South and Central America. *N. albiventris* is similar to *N. leporinus* but is readily identified in the field by its smaller size (30–35 g) and higher frequency echolocation calls.

Photography of hunting bats and sound recordings

We photographed bats under stroboscopic illumination with a custom-made multiflash array consisting of two 35-mm cameras (Nikon 301, 35-mm lens) and a custom-made flash unit (Heinze, Germany) with four flash tubes (guide number 50). We triggered the flash unit up to four times with flash intervals set to 50 or 100 ms, which gave 16 images of an individual bat on a single

Fig. 1 a Typical flight paths of hunting *Noctilio albiventris* including **b** pointed dip, **c** raking pass, **d** aerial capture and **e** a combination of aerial capture and pointed dip on the Tortuguero River near Tortuga Lodge (*A*), in front of the boat house (*B*) and the dock house (*C*), and near an anchored boat (*D*). The *boat* is somewhat enlarged and not drawn to scale
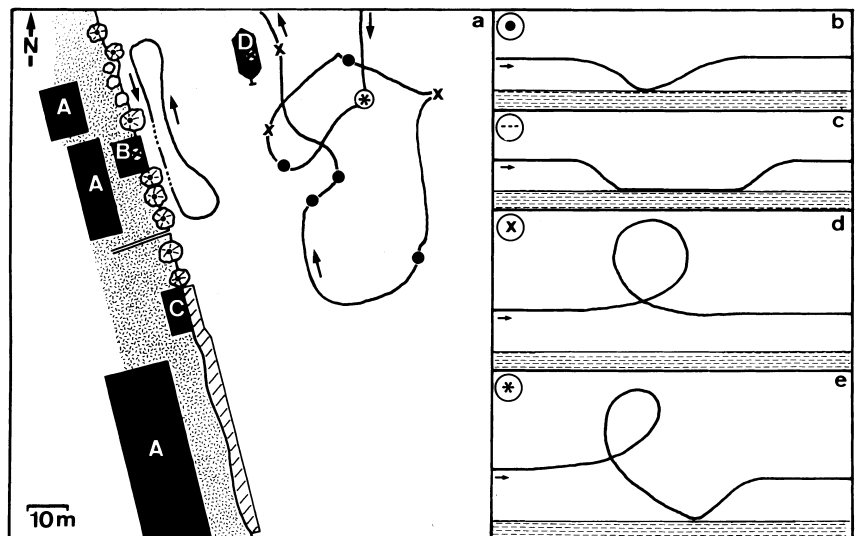
photograph. Simultaneously, the echolocation signals of the bats were picked up by ultrasound microphones of two bat detectors (model QMC 100), amplified and recorded on two amplitude-modulated channels of a high-speed tape recorder (Lennartz 6000/607, ¼-inch tape) at 76 cm/s. The frequency response of the system was flat within about 10–15 dB between 20–120 kHz. Synchronization pulses between flashes and sound recordings and spoken comments were recorded on the two frequency-modulated channels of the recorder. *N. albiventris* showed no obvious changes in echolocation or hunting behavior in response to the flashes.

For three-dimensional reconstruction we digitized the photographs (Bitpad One, Summagraphics, Fairfield, USA, maximum resolution 0.1 mm) and used custom-made computer programs for analyses. Sound recordings were analyzed at 1/16 speed with a digital frequency-analyzer MOSIP 3000 (Modular Signal Processor; Medav, Germany) using a fast Fourier transformation (FFT). A frequency range of 160 kHz was chosen for analysis with a Hanning Window 256. The sequences were displayed in consecutive 20-ms segments. Sound parameters were measured with a cursor on the screen. These settings resulted in a frequency resolution of 400 Hz, and time resolution of 40 ms (interpolated). The dynamic range was restricted to 60 dB to eliminate background noise. Measurement points were set 40 dB below maximum. Components >1 ms duration and sweep rates <0.4 kHz/ms were defined as constant frequency (CF). In case of mixed signals we define the onset of the FM component as the point where the frequency dropped 4 kHz below the highest frequency in the CF component. The FM portions often showed a characteristic pattern of nulls resulting from interference between the emitted signal and reflections from the water surface (Kalko and Schnitzler 1989a). Within sequences, the frequency of the signals deviated due to angle-dependent Doppler shifts. To minimize this error we used only pulses recorded when the bats flew almost straight toward the microphone. Quantitative data on echolocation behavior are given as mean values of sample size ±1 SD. A general *t*-test was used for comparisons.

The three-dimensional analysis of the photographs was merged with the sound recordings using custom-made software. We took 23 films (784 photographs; Kodak Tmax 400 black-and-white print film) and recorded 16 tapes at high speed (12 min real time each; Afga PE 49 professional) and three audiocassettes (90 min each) of echolocation sequences. For final analysis of echolocation we selected 121 sequences (40 in high search flight; 34 while raking; 24 in low search flight; 23 with pointed dips). Of our photographs 51% showed foraging or transecting *N. albiventris*, including 55 captures (10 aerial captures, 40 pointed dips, 5 captures from rakes). To illustrate correlation of foraging behavior with echolocation we selected 53 photographs (4 with high search flight; 2 with low search flight; 10 aerial captures and 28 pointed dips from high search flight; 5 rakes with captures; 4 rakes without captures) synchronized with good sound recordings. We also included all relevant information from the remaining photographs which were either not suited for 3D reconstruction or lacked good sound recordings. For more details on methods see Kalko (1995b), Kalko and Schnitzler (1993), and Schnitzler et al. (1994).

Results

Hunting strategies and echolocation behavior of *N. albiventris* foraging over water

At our study sites, *N. albiventris* arrived every evening about half an hour after dusk. They either foraged close to the shore, flying back and forth in a figure-eight pattern (40–50 m long) or hunted 20–30 m or more from the shore in large, meandering circles above the water (Fig. 1a). Foraging bats caught insects in the air (Fig. 1d), took prey from the water surface in pointed dips (Fig. 1b), used a combination of aerial captures and pointed dips (Fig. 1e), or raked with their claws through the water (Fig. 1c). Typically, foraging activity was high for the first 1–1.5 h, then tapered off to 2–3 bats/10 minutes. The level of activity changed from night to night. On the bright nights around the full moon, the activity dropped to a very low level, with no more than an occasional passing flight. We observed a similar decrease in activity in *N. leporinus* which foraged in the same areas (Schnitzler et al. 1994). However, we cannot rule out the possibility that the bats hunted elsewhere on those nights.

High search flight

In high search flight (>20 cm above water or ground) *N. albiventris* flapped its wings continuously, with about 4 full wingbeats/s at flight speeds of 7–7.5 m/s (Fig. 2a). It typically emitted groups of mostly two or three CF or CF-FM echolocation signals of medium duration (10 ms) near the top of each wing beat (Fig. 2a,b,f). In groups with two pulses, the first pulse was usually a CF signal followed by a mixed CF-FM signal (Fig. 2b,c). With more pulses in the groups, we found all possible arrangements of the two pulse types but usually the group ended with a CF-FM signal. Sometimes a bat also emitted long FM calls (Fig. 3a,b) with varying sweep rates, a call type most often observed when *N. albiventris* was foraging high (>2 m) over land.

Pulse duration of search signals varied. FM signals were longest (17–21 ms), followed by CF-FM and CF signals (10–11 ms) (Fig. 2c,g,i). In CF-FM signals, pulse duration of the CF component was about equal to the FM component (Fig. 2g,i). The interval between the last signal of a group and the first signal of the next group (intergroup interval) was 70–210 ms, approximately 2–4 times the interval (30–50 ms) between signals within a group (intragroup interval) (Fig. 2d,h). The duty cycle (amount of time filled with sound) in high search flight (Fig. 2j), varied from 5–7% between signal groups to more than 30% within signal groups (Fig. 2e).

CF signals typically began with a short (1–2 ms) upward modulation of 0.4–1 kHz, followed by a constant middle-portion where the frequency stayed within 0.4 kHz, and terminated in a short (2–3 ms) downward-modulated portion of 2–4 kHz bandwidth (Fig. 2 l). The frequency structure of the CF component of the CF-FM signals was similar to that of CF signals. CF-FM signals ended with a short (5 ms) downward FM sweep (Fig. 2m) and a bandwidth of 32 kHz (Fig. 2k). The energy of CF and CF-FM signals in high search flight was concentrated mainly in the first harmonic (Fig. 2l,m). Rarely, spectograms also revealed part of the second or third harmonic. The frequency of the recorded signals is higher than the emitted frequency due to Doppler shifts. We measured best frequencies of the CF component between 67 and 72 kHz.
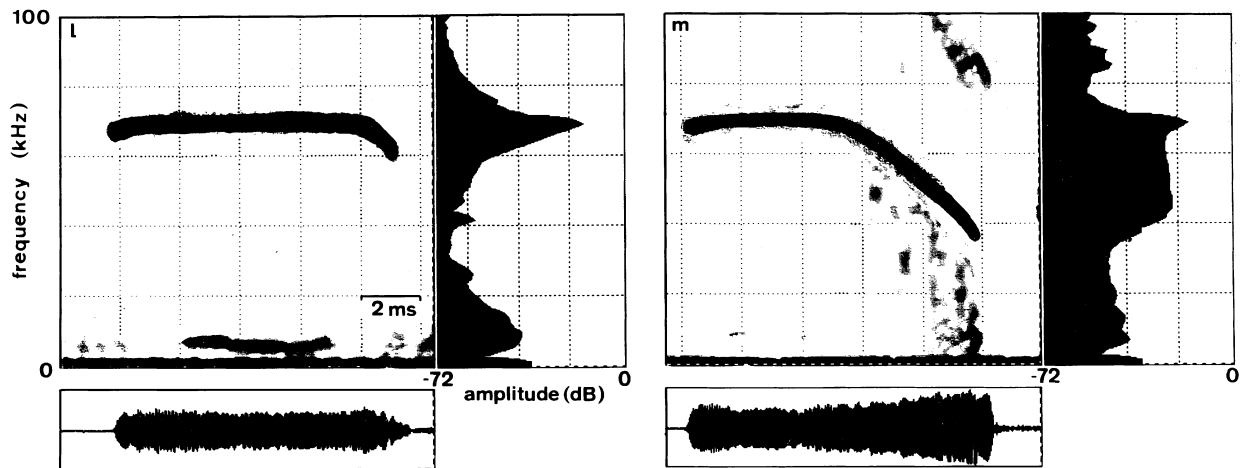
Fig. 2a–k (for legend see next page)

Aerial capture from high search flight

The predominant hunting strategy of *N. albiventris* in Costa Rica was capture of insects in mid-air during high search flight, mostly 2–5 m above the water. Prey ranged from small mosquito-sized insects which mostly could not be discerned on the photographs to medium-sized moths with head and body lengths of 1–3 cm (estimated from the photographs). *N. albiventris* captured prey with its uropatagium alone (tail scoop) or reached out with a wing to funnel the insect onto its interfemoral membrane (wing capture with tail scoop) (Fig. 4a). There is no evidence in our photographs with aerial captures where the prey was clearly visible ($n = 4$) that the bat seized insects directly with its mouth. Flight speed was reduced during captures to 1–2 m/s. Often the bat came almost to a standstill. The bat immediately retrieved the prey from its tail pouch (head down) and resumed search flight. It presumably stored the prey temporarily in its large cheek pouches (Murray and Strickler 1975). We often observed that moths reacted to approaching bats with evasive maneuvers that frequently led them onto the water surface. Repeatedly, the bats then turned around and scooped the still fluttering insects in a pointed dip from the water surface.

With the beginning of the approach flight, *N. albiventris* switched in echolocation behavior from search phase to the approach sequence, characterized by a continuous reduction in pulse duration and pulse interval (Figs. 4b–d, 5). Throughout the approach sequence the CF component of the signals was reduced and finally dropped. Prior to capture the bat produced a series of short FM signals (2 ms) at a high repetition rate (up to 160–180 Hz), the terminal phase (Fig. 4b). Except for the last signals of the terminal phase, the emitted signals did not overlap echoes returning from the prey (Fig. 5). Signal emission ceased when the bat was 15–20 cm from the prey. The duty cycle rose from 19–30% in high or low search flight to 40–45% in the terminal phase (Fig. 4e). Preparations for the capture coincided with the second half of the terminal phase in echolocation behavior. After a capture maneuver *N. albiventris* switched back to search phase after a pause of 90.2 ± 64.4 ms ($n = 10$, minimum 18.1 ms, maximum 180.3 ms) where no echolocation calls could be recorded. In two of the four photographs with aerial captures where the prey could be clearly seen the bat went through the whole capture maneuver but missed the insect (Fig. 4a).

Pointed dip from high search flight

N. albiventris took prey also directly from the water surface with its large feet in pointed dips that were directed to a spot where a fluttering insect drifted on the water surface (Fig. 6a). The bat slowed down from 7–7.5 m/s to 5–6 m/s ($n = 23$ sequences). The prey was immediately retrieved and processed as in an aerial captures. As in aerial captures the bat sometimes went through the whole capture maneuver but missed or lost the prey (Figs. 4a, 6a).

When the bat descended towards the target, it switched from search to approach phase (Fig. 6b, f). Echolocation behavior (Fig. 6b) changed much as it did in aerial captures. Shortly before dipping into the water the bat emitted a terminal phase (Fig. 6c–e, g). The pause after the terminal phase lasted 59.9 ± 49.8 ms ($n = 29$, minimum 11 ms, maximum 188 ms). We did not find a
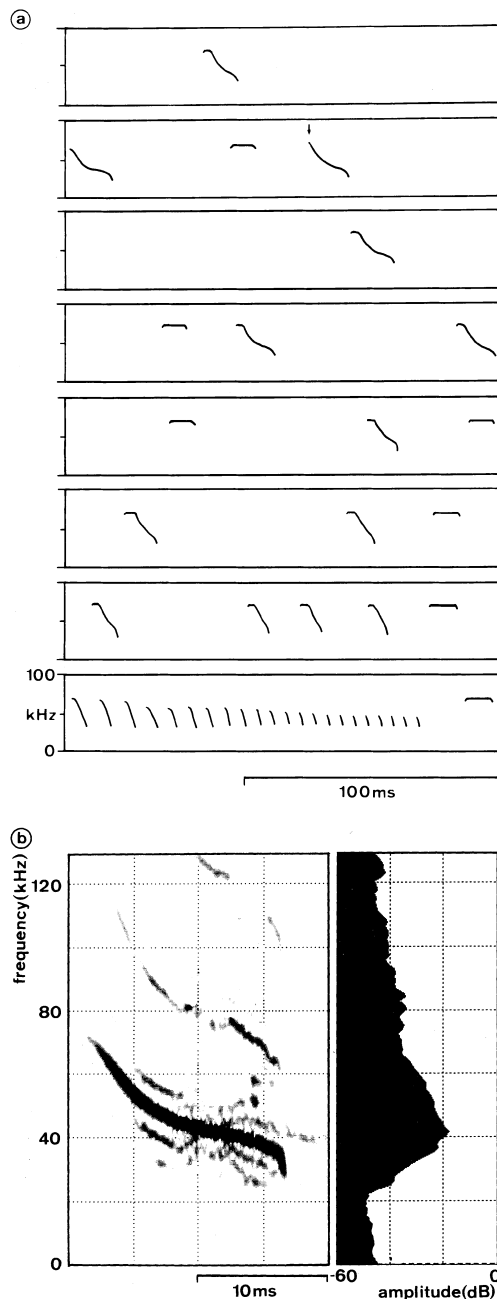
Fig. 3 a Echolocation sequence of *N. albiventris* flying in high search flight, including long FM signals and a terminal phase at the end; **b** sonagram and averaged spectrum of FM pulse marked with an *arrow* in **a**

clear correlation between capture success and duration of the pause. Of 13 photographs with pointed dips where the prey insect was visible to us, 11 captures were successful and prey was missed in 2 cases. Pauses after successful captures ranged from 22 to 188 ms; the pause after the unsuccesful captures were 32 and 46 ms, respectively. We measured time intervals of 300–600 ms between detection and actual capture ($n = 3$). This translates at estimated flight speeds of about 5 m/s into detection distances of 1.5–3 m. As in aerial captures, *N. albiventris* avoided, except for a few signals at the end

of the terminal phase, echo-overlap between emitted signal and returning echoes from prey.

Low search flight

Occasionally *N. albiventris* switched from high search flight to short segments of low search flight ($<20\%$ of photographs) when it flew within 20 cm of and parallel to the water surface (Fig. 7a). It continued to beat its wings (Fig. 7a) and employed a full wing beat amplitude during the upstroke. The amplitude of the downstroke was somewhat reduced compared with that of high search flight. Flight speed decreased from 6.5–7 m/s to 4–5 m/s at the end of the segment ($n = 24$ sequences). The bat stayed in low search flight for only 2–5 m before returning to high search flight.

Signal pattern differed strikingly from that of high search flight. Long series (50–200 ms) of short CF-FM pulses were interspersed with groups of longer signals, mostly one CF signal followed by 2–4 CF-FM signals (Fig. 7b,c). Overall, pulse duration in low search flight was much lower than in high search flight (6.5 vs. 10.9 ms) (Fig. 2f, 7f). Duration of pure CF signals and FM components, as well as bandwidth of the FM components resembled those of high search flight (Fig. 7g,i,k). Structure of short CF-FM signals within signal groups resembled approach phase signals. Pulse interval varied from 10 to 100 ms or more (Fig. 7d,h). Both intragroup and intergroup intervals were shorter in low search flight than they were in high search flight. Within groups of short CF-FM signals, intragroup intervals ranged mostly between 10 and 30 ms (Fig. 7h). Between groups of short CF-FM signals or longer CF and CF-FM signals, intergroup interval mostly lasted 40–70 ms (Fig. 7d,h). The duty cycle in low search flight (28%) (Fig. 7j) was much higher than it was in high search flight (Fig. 2j). It oscillated between 10 and 40%, or, rarely, more (Fig. 7e,j). Signal emission was correlated with wing beat. Groups of short CF-FM signals and groups of longer CF and CF-FM signals corresponded to one wing beat cycle.

Pointed dip from low search flight

This behavior appears to be very rare in *N. albiventris*. Behavioral patterns in two pointed dips from low search flight were similar to those in pointed dips from high search flight.

Directed random rake

On one occasion at our observation site in Costa Rica, thousands of small shrimp (estimated body length 0.5–1 cm from captured individuals) were frequently jumping out of the water. *N. albiventris* approached this site in low search flight and raked its claws through the
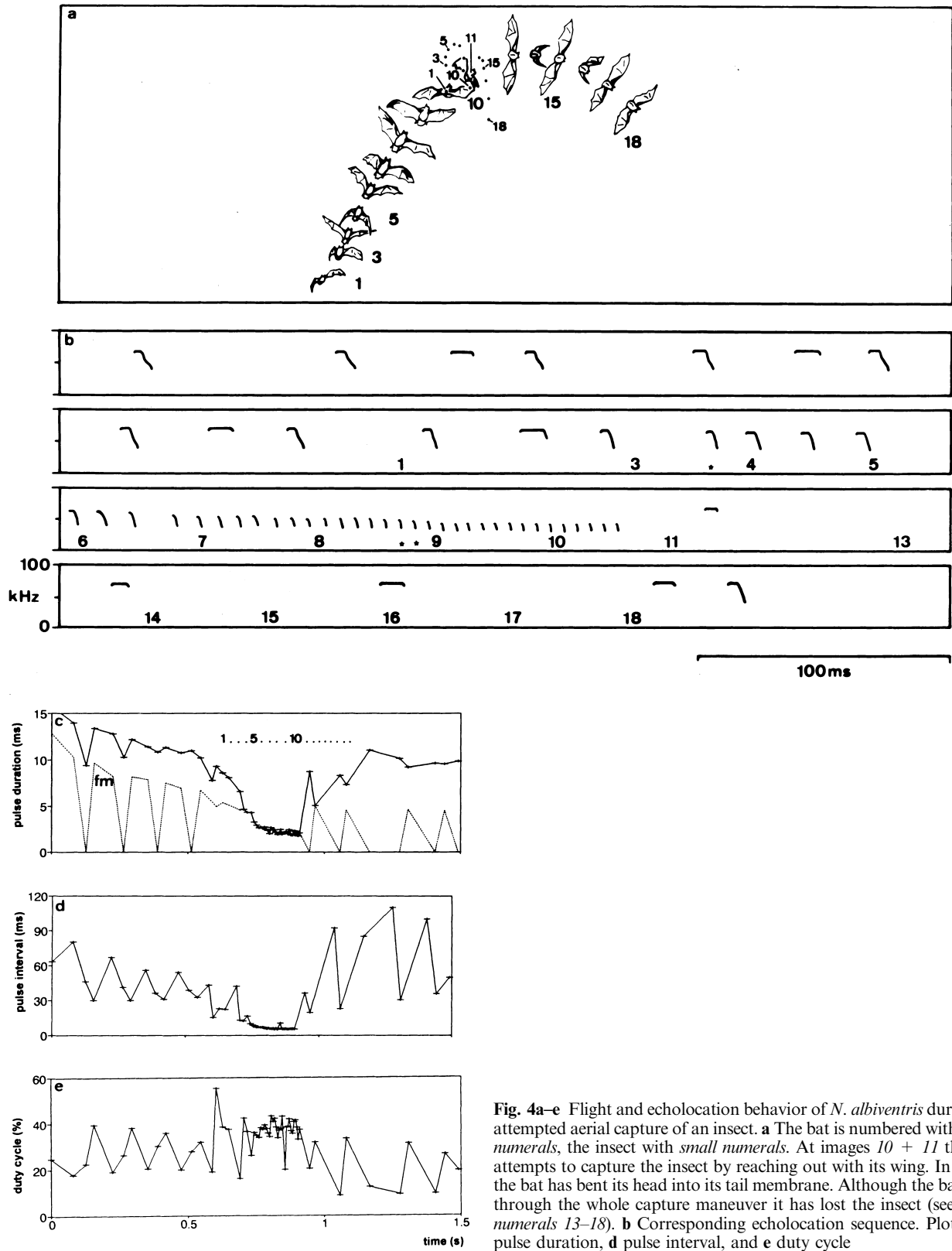
Fig. 4a–e Flight and echolocation behavior of *N. albiventris* during an attempted aerial capture of an insect. **a** The bat is numbered with *large numerals*, the insect with *small numerals*. At images *10 + 11* the bat attempts to capture the insect by reaching out with its wing. In 13–18 the bat has bent its head into its tail membrane. Although the bat goes through the whole capture maneuver it has lost the insect (see *small numerals 13–18*). **b** Corresponding echolocation sequence. Plots of **c** pulse duration, **d** pulse interval, and **e** duty cycle
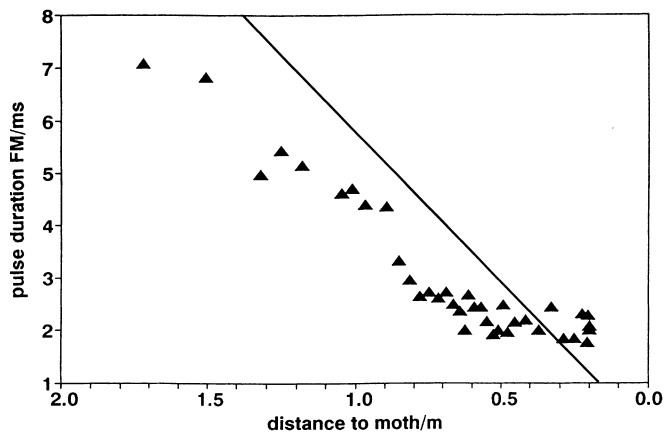
Fig. 5 Pulse duration of the FM component in relation to the bat's distance from the insect prey during search, approach, and terminal phases of an aerial capture by *N. albiventris*. The prey, a moth, was successfully caught in this sequence. The *solid line* marks the range of echo-overlap

water for distances up to 2–5 m (Fig. 8a). During the rakes the large interfemoral membrane was folded forward and upward by the strong calcars so the bat's legs were unobstructed. Wing beat amplitude, particularly the downstroke, was reduced. Wing beat rate increased from about 5 beats/s in high search flight to 6–8 beats/s. Flight speed dropped from 6–7 m/s to 4–5 m/s. Echolocation pattern and signal structure resembled those in high search flight (Fig. 8b–k).

Hunting strategy and echolocation behavior
of *N. albiventris* foraging over land

We observed *N. albiventris* foraging over land in Panamá. The bats hawked insects for 10–15 min every evening at heights of 15–20 cm above a clear-cut meadow adjacent to the Chagres River. On two nights they foraged at heights of 3–5 m around street lights in housing areas 300–500 m from the river. On one occasion we recorded foraging *N. albiventris* flying back and forth between buildings on BCI at flight heights of 3–5 m.

The pattern of the echolocation behavior was similar to that of aerial captures from high search flight over water except that the bats frequently emitted long (17–21 ms) FM signals (Fig. 3a). The long FM signals started with a short (3–4 ms), steep (7–10 kHz/ms) downward FM sweep that leveled out in a shallow-modulated (about 1 kHz/ms) component of 10–12 ms duration (Fig. 3b). The signal ended with another steep (10–12 kHz/ms), downward FM sweep of about 1 ms duration. In contrast to CF and CF-FM signals, spectrograms of long FM signals revealed also part of the second and third harmonic (Fig. 3b).

Discussion

Hunting strategies and capture techniques

We found high flexibility in hunting strategies in *N. albiventris*, ranging from aerial captures over water and land, pointed dips from high and low search flight to directed random rakes. Captures of prey by pointed dips have been reported previously (e.g., Hooper and Brown 1968; Novick and Dale 1971; Suthers and Fattu 1973), but aerial captures and the rare raking passes have not been described in published accounts. The observed flexibility in hunting strategies possibly allows *N. albiventris* to quickly adjust to prey availability and thus may enhance foraging efficiency.

N. albiventris is well adapted morphologically to grasp objects from the water surface in flight. With pointed dips it takes prey with its large feet and claws in a manner similar to other dipping bats, particularly *Myotis* of the subgenera *Leuconoe* and *Pizonyx* (Vespertilionidae), *Macrophyllum macrophyllum* (Phyllostomidae), and *N. leporinus* (e.g., Dalquest 1957; Findley 1972; Jones and Rayner 1988, 1991; Kalko and Schnitzler 1989b; Schnitzler et al. 1994; authors unpublished observations). In aerial captures over water or over land, *N. albiventris* like other aerial insectivores, uses its interfemoral membrane and/or a wing to snare its prey (e.g., Griffin et al. 1960; Kalko 1995b; Webster and Griffin 1962).

In contrast to *N. leporinus*, which we observed frequently raking for distances up to 10 m (Schnitzler et al. 1994), we documented raking passes only once in *N. albiventris*. Probably the limited use of raking by this bat is imposed by energetic and morphological constraints. Raking is energetically costly since the bat has to overcome the hydrodynamic drag created by dragging its immersed claws through water. Morphological adaptations for drag reduction including lateral compression of claws are not as well developed in *N. albiventris* as in *N. leporinus* (Fish et al. 1991). Furthermore, small body size limits its carrying capacity. Hence, the size of prey that it could catch would be much less than in *N. leporinus*, which frequently catches fish (e.g., Altenbach 1989; Brooke 1994; Schnitzler et al. 1994). Studies of *N. leporinus* have show that capture success is often very low in raking passes (Bloedel 1955; Schnitzler et al. 1994). Possibly, *N. albiventris* rakes only when it is assured of a high capture rate in exceptionally rich patches of small prey such as the mass of leaping crustaceans at our study site in Costa Rica.

▶

Fig. 6a–g Flight and echolocation behavior of *N. albiventris* during a pointed dip from high search flight. The bat goes through the capture maneuver but misses the prey. **a** Multiflash sequence and **b** corresponding echolocation sequence. Plots of **c** pulse duration, **d** pulse interval, and **e** duty cycle. Sonagram, averaged spectra, and oscillogram of **f** one signal of the approach and **g** two short FM signals of the terminal phase *marked* * in **b**
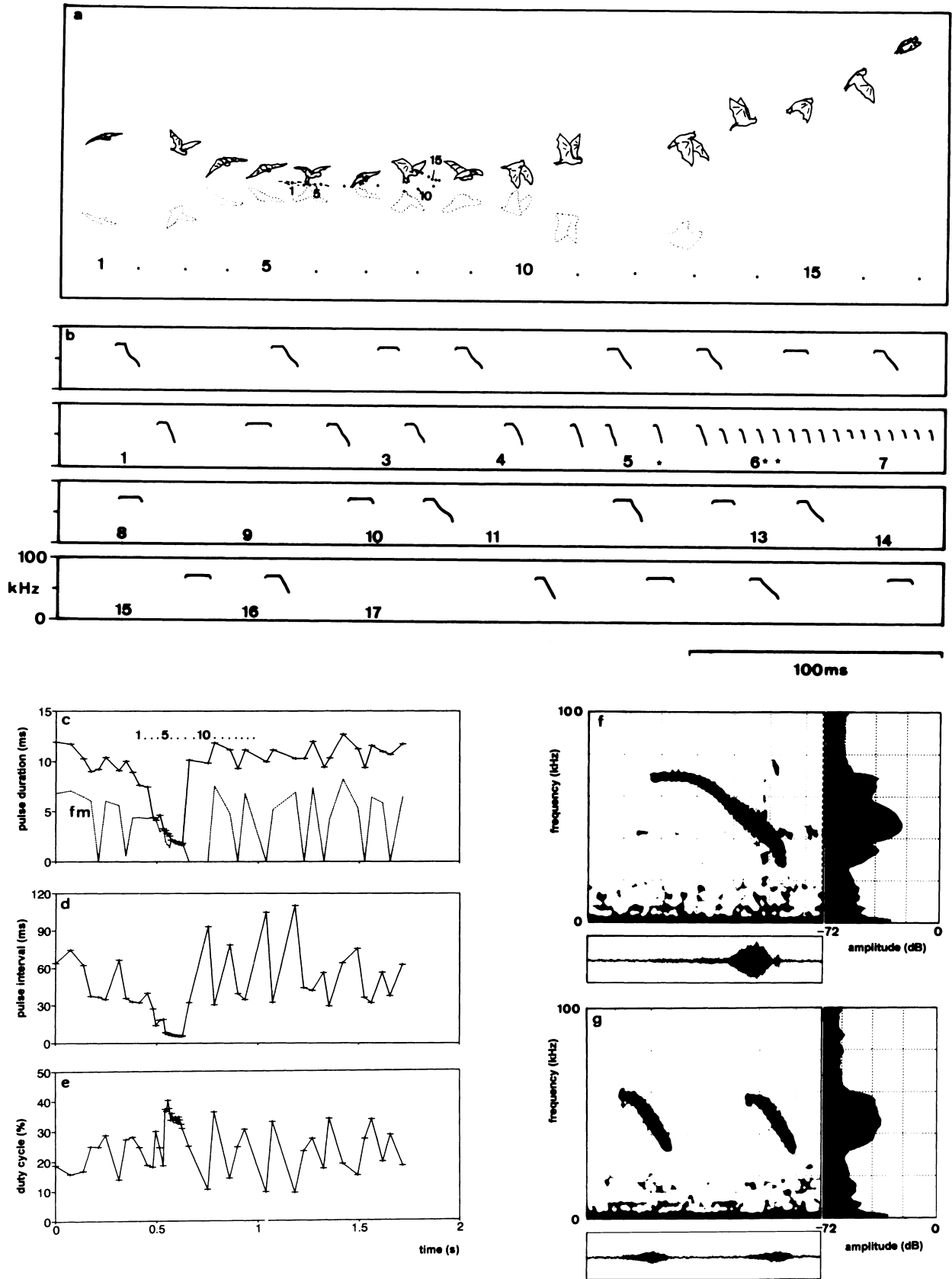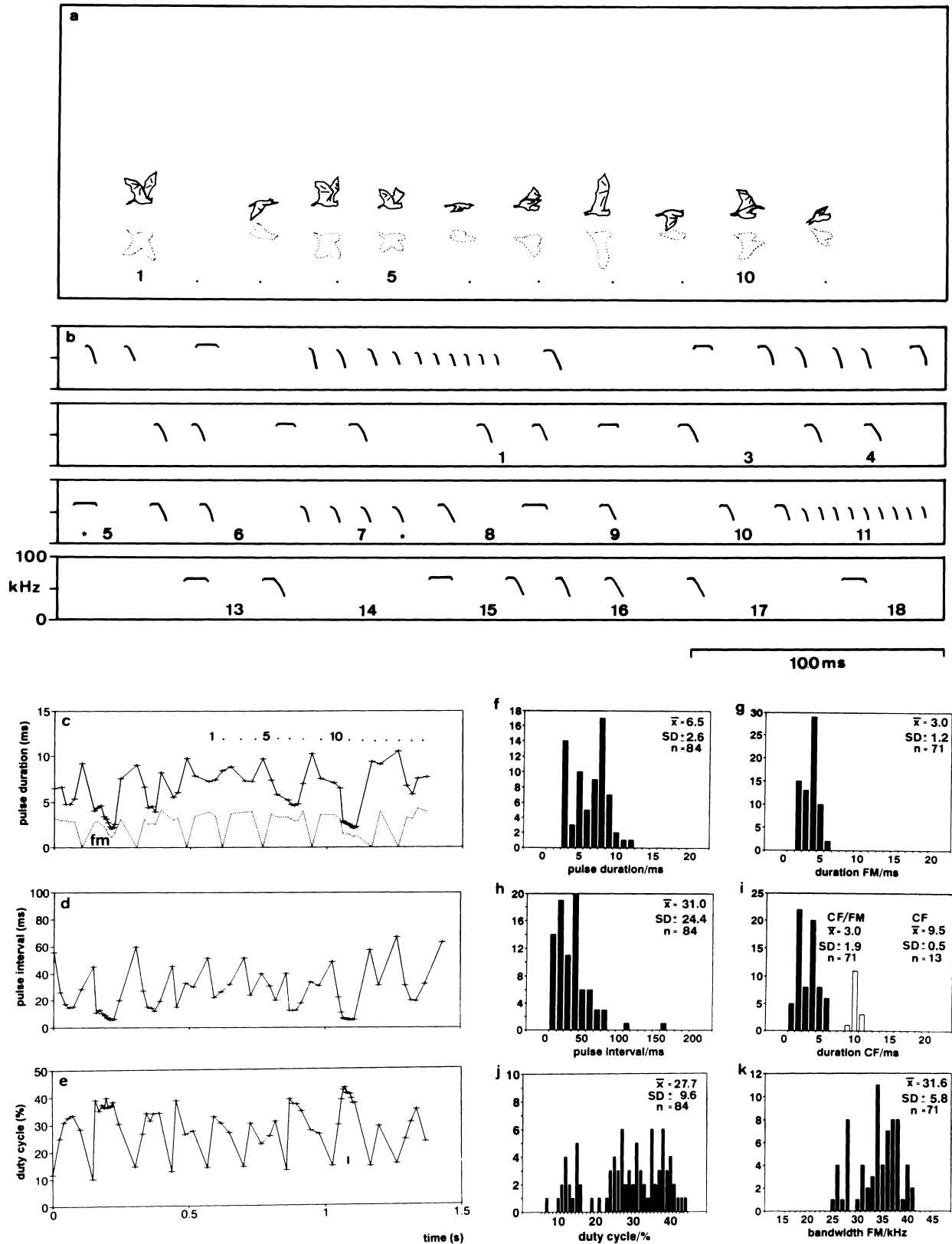
Fig. 6a–g

100 kHz

0

100 ms

c pulse duration (ms) — 1 . . . 5 . . . . 10 . . . . — fm

f pulse duration/ms — $\bar{x}=6.5$ SD$\pm$2.6 n=84

g duration FM/ms — $\bar{x}=3.0$ SD$\pm$1.2 n=71

d pulse interval (ms)

h pulse interval/ms — $\bar{x}=31.0$ SD$\pm$24.4 n=84

i duration CF/ms — CF/FM $\bar{x}=3.0$ SD$\pm$1.9 n=71 — CF $\bar{x}=9.5$ SD$\pm$0.5 n=13

e duty cycle (%) — time (s)

j duty cycle/% — $\bar{x}=27.7$ SD$\pm$9.6 n=84

k bandwidth FM/kHz — $\bar{x}=31.6$ SD$\pm$5.8 n=71

Fig. 7 Flight and echolocation behavior of *N. albiventris* during **a, b** low search flight with **c–e** plots of pulse duration, pulse interval, and duty cycle. **f–k** Histograms of all analyzed sequences from low search flight
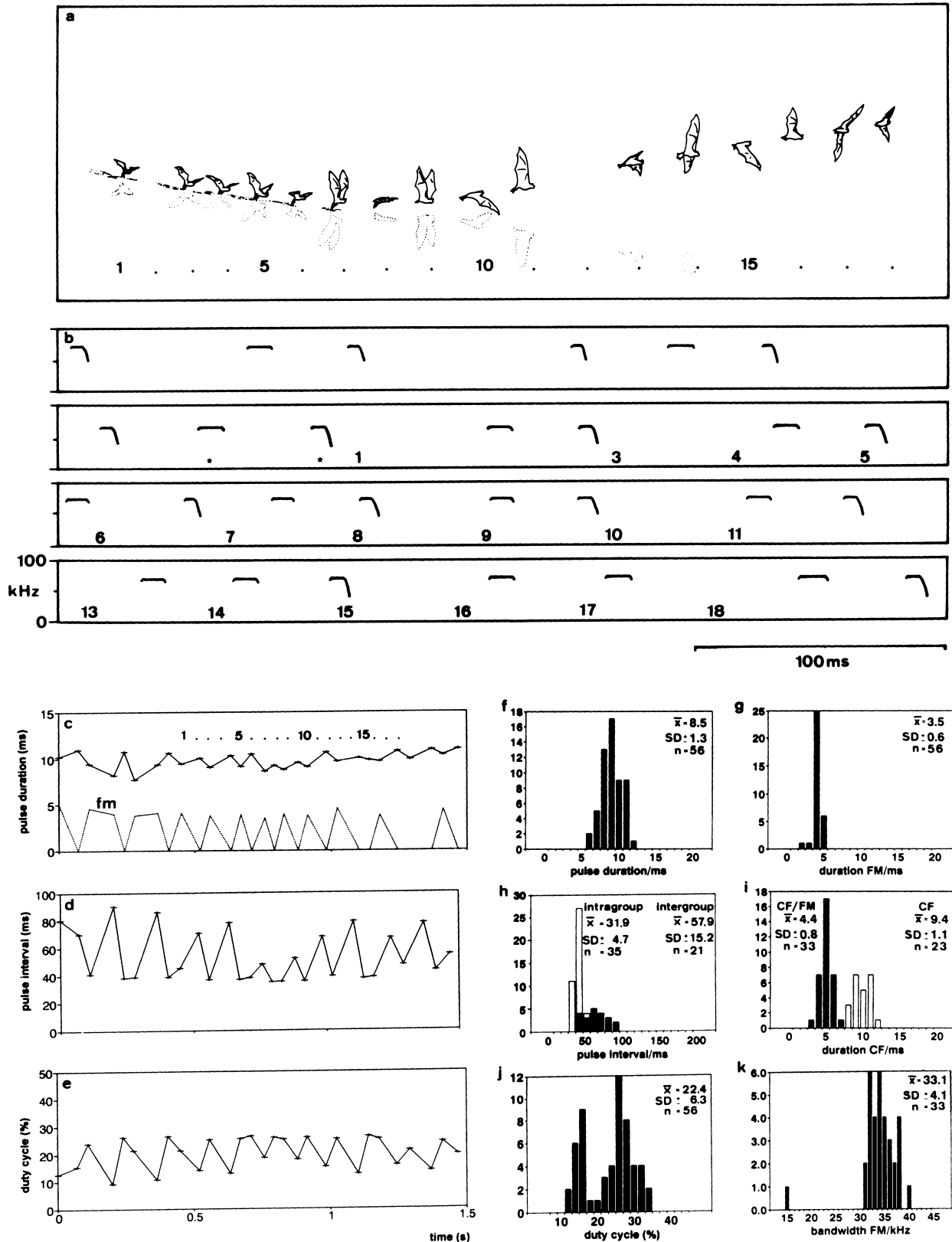
Fig. 8 Flight and echolocation behavior of *N. albiventris* during **a, b** a raking pass, with **c–e** plots of pulse duration, pulse interval, and duty cycle. **f–k** Histograms of all analyzed sequences of raking passes

Functional significance of call design
in foraging *N. albiventris*

Signal design is highly variable in *N. albiventris*, ranging from long CF, long and short CF-FM, and long FM signals in search phase, to short FM signals in approach and terminal phase. Variability in signal design is linked to the perceptual tasks that have to be performed by *N. albiventris* employing a variety of hunting strategies.

*Hunting for fluttering insects in the air
and from the water surface*

N. albiventris caught fluttering insects in the air or gleaned them from the water surface. While searching for prey, the bat emitted a mixure of CF and CF-FM search signals. Laboratory studies have shown that echoes of CF signals from flying prey such as fluttering insects are characterized by "acoustical glints", patterns of prey-specific amplitude and frequency modulations that encode wing beat rate, wing size, and other species-specific information (e.g., Schnitzler 1987; Kober and Schnitzler 1990; Schnitzler et al. 1983). Chances of perceiving such temporary glints depend on the duty cycle of the bat's echolocation sequence and the wing beat rate of the insects (Kober and Schnitzler 1990). With an average duty cycle of 19% in high search flight and 30% in low search flight, and estimated wing beat rates of 50–100 Hz in the prey, *N. albiventris* could perceive 9.5–30 glints (duty cycle × wing beat rate) per second. Since *N. albiventris* has a repetition rate of about 11 signals per second in high search flight and about 27 Hz in low search flight, it could perceive up to 1–3 glints in every signal.

We propose that *N. albiventris*, like other bats with CF signals (rhinolophids, hipposiderids, *Pternonotus parnellii* (Mormoopidae), and *N. leporinus*) use echolocation information for prey selection by evaluating the characteristic patterns of temporary acoustic glints in echoes from fluttering insects (e.g., vd Emde and Schnitzler 1986, 1990; Jones 1990; Kober and Schnitzler 1990; Schnitzler et al. 1994). In the case of *N. albiventris* hunting for fluttering insects drifting on the water surface, most unwanted targets (e.g., debris) float on the water surface and hence generate fairly stationary glints easily to be discriminated from the rhythmical pattern of temporary glints in echoes from fluttering insects (Kober and Schnitzler 1990; Schnitzler et al. 1994). From differences in their search patterns for food we infer that the two noctilionids evalute glint pattern with different search images. For instance, we never observed the insectivorous *N. albiventris* attacking jumping fish, which inevitably triggered foraging behavior in *N. leporinus* (Schnitzler et al. 1994), and when we used an underwater pump to produce a water jet that broke the water surface and mimicked a jumping fish, it elicited no response in *N. albiventris*, but *N. leporinus* attacked it. We conclude that this type of glint pattern is not part of the search image of *N. albiventris*.

A number of CF bats are known to compensate for the Doppler shift caused by their own flight movement relative to the surroundings. By lowering the emitted frequency, they keep the frequency of the CF component of the echo constant at the so-called reference frequency. Adaptations in the hearing system are characterized by a specialized cochlea (auditory fovea at the reference frequency) and an overrepresentation throughout the system of sharply tuned neurons in the frequency range of the prey echoes. These enable the bats to discriminate the characteristic echoes of fluttering insects from the overlapping, unmodulated emitted signal and from overlapping clutter (e.g., Neuweiler 1989; Schnitzler and Henson 1980). Laboratory studies have shown that *N. albiventris* also has the capacity for Doppler shift compensation (Roverud and Grinnell 1985c) although it is still unclear whether this compensation is as complete as in horseshoe bats (e.g., Schnitzler and Henson 1980) or incomplete as in *N. leporinus* (Wenstrup and Suthers 1984).

We propose that the CF components in the search signals of *N. albiventris* adapts it to forage for insects in "highly cluttered space" (Schnitzler and Kalko 1998) where prey echoes overlap clutter echoes from other objects. This is the case when *N. albiventris* takes prey in pointed dips or searches for prey flying lower than 2 m above the water or ground. At search signal durations of 6.5–10.9 ms, echoes from a target overlap with clutter echoes at distances of 1.1–1.9 m and less. Conversely, when the bat hunts for insects higher than the overlap-zone, echoes indicating potential prey in mid-air are followed by, but do not overlap, clutter echoes from the water surface. Thus, *N. albiventris* according to our definition is in "background cluttered space" (Schnitzler and Kalko 1998). In both cases, glint detection facilitates prey detection.

Behavioral and electrophysiological studies of *N. albiventris* suggest that CF signal components may also play a role in estimating distance. The onset of the CF component activates a gating mechanism which creates a time window during which distance information can be extracted by comparing the FM components of pulse-echo pairs of the CF-FM search signals (Roverud 1988; Roverud and Grinnell 1985a,b). However, both noctilionids drop the CF component of their signals during approach and terminal phase when distance information is also crucial. Thus, the mechanism for extracting distance information must differ in search and approach.

In contrast to other CF bats such as rhinolophids, hipposiderids, and *Pteronotus parnellii* which maintain a CF signal component throughout approach and terminal phase (e.g., Schnitzler et al. 1985), *N. albiventris* drops the CF component of its signals during approach phase and emits pure FM calls in the terminal phase. We conclude that in the final part of an approach the FM component alone delivers the necessary information for the pursuit of an insect prey after it has been detected and classified with flutter cues. Behavioral experiments suggest that for an echo of a FM signal in the terminal

phase 100 or more discrete filters are present for about 10 msec and that each filter analyzes information from a band of a few hundred Hertz (Roverud 1993).

Short FM signals or FM components are overlap-sensitive (Schnitzler and Kalko 1998). Consequently, bats with overlap-sensitive signals reduce signal duration and pulse interval during approach and terminal phase (Kalko and Schnitzler 1989b, 1993). Presumably, overlap would mask important information from the bat. At the end of the terminal phase, the duration of FM pulses in *N. albiventris* is longer (2 ms) than FM signals recorded in terminal phases of other bats (0.3–0.5 ms) when capturing insects from the water or in the air (e.g., Kalko and Schnitzler 1989b, 1993). Hence, in *N. albiventris* signals overlap the prey echo at distances of about 26 cm or less. However, like aerial insectivorous pipistrelle bats (Vespertilionidae) (Kalko 1995b), *N. albiventris* often stops signal emission 10–20 cm before the capture maneuver, thereby preventing potential overlap.

Gleaning prey from water surface with directed random rake

The pattern of echolocation signals produced during raking passes through patches with many jumping shrimps resembles that in high search flight, except approach and terminal phases are absent. This suggests that similar to raking *N. leporinus* (Schnitzler et al. 1994) raking *N. albiventris* do not localize single targets but search for prey in a random manner in a area where many temporary glints indicate prey. Possibly optical cues or the splashing sounds of potential prey also might assist *N. albiventris* in prey detection. Since we saw *N. albiventris* raking only once, we cannot say whether it would rake also in places where no target cues are present but where it had hunted successfully before, as we found it in the memory directed random rakes of *N. leporinus* (Schnitzler et al. 1994).

Comparison of foraging and echolocation behavior of *N. albiventris* and *N. leporinus*

Both noctilionids employed similar hunting strategies but differed in the frequency of the use of various types. Overall, aerial captures and pointed dips from high search flight were most used by *N. albiventris*, whereas pointed dips from high and low search flight and raking phases predominanted in *N. leporinus*.

Echolocation behavior was similar in the two species. There were few species-specific differences (e.g., Griffin and Novick 1955; Hartley et al. 1989; Schnitzler et al. 1994; Suthers 1965, 1967; Suthers and Fattu 1973). We found the CF part of search signals (66–72 kHz) in *N. albiventris* at least 10 kHz higher than in *N. leporinus* (53–56 kHz). We attribute the differences in call frequencies in the two species to differences in body mass, a relationship well documented for a variety of bats (e.g.,

Barclay and Brigham 1991). The smaller *N. albiventris* (30–35 g) produces higher frequency calls than the larger *N. leporinus* (65–75 g). Although duration of search signals was significantly shorter in *N. albiventris* than in *N. leporinus* ($t_{168} = 7.29$, $P < 0.001$), its FM component was significantly longer ($t_{95} = 4.54$, $P < 0.001$), 5.3 ms versus 3.9 ms. In *N. albiventris*, the FM component encompassed about half (50%) of a CF-FM signal but only 30% in *N. leporinus*. CF components were significantly shorter ($t_{95} = 12.05$, $P < 0.001$) in *N. albiventris* (4.4–5.5 ms) than in *N. leporinus* (5.4–8.9 ms). Furthermore, the bandwidth of the FM component was significantly higher ($t_{172} = 12.37$, $P < 0.001$) in *N. albiventris* (31–33 kHz) than in *N. leporinus* (24–26 kHz). In comparisons of the relative proportions of FM and CF components in long CF-FM signals, the FM part was more accentuated in *N. albiventris* and the CF part in *N. leporinus*.

Possibly a shorter CF component delivers adequate information to *N. albiventris* since it hunts mainly for fluttering insects, constantly producing acoustical glints in the rhythm of their wing beats. The preponderance of FM components may enhance localization accuracy, which is of particular importance to a bat capturing insects in three-dimensional space. Conversely, the longer CF components in *N. leporinus* enhance its chances of detecting the brief glint patterns produced by fish which jump out of the water for only 50–100 ms.

A possible scenario for the evolution of piscivory

The many similarities in hunting and echolocation behaviors of the two noctilionids provide clues to how hunting for fish may have evolved (Schnitzler et al. 1992). Like other CF bats noctilionids can detect fluttering insects by the glint pattern in the echoes. We suppose that the ancestor of *N. leporinus* was hunting for insects including moths much as *N. albiventris* does today (Novick and Dale 1971). Since many moths can hear, they often react to ultrasound with evasive movements and frequently drop. If a moth accidentally landed in the water, the ancestral bat may have wheeled and scooped up the still fluttering and thus glint-producing insect. Simultaneously, fish may attack, even jump for insects fluttering on the water surface. Since jumping fish that break the water surface also produce characteristic temporary glints, it seems probable that the insect-hunting ancestor of *N. leporinus* sometimes accidentally detected, localized, and caught a jumping fish instead of a fluttering moth. Since fish have higher nutritional value than moths, we assume that in areas where jumping fish were abundant a bat specialized to hunt fish could evolve. This scenario is supported by our observation that the behavioral separation of the two species is not complete. *N. leporinus* retains its ability to hunt for insects, and *N. albiventris* has evolved hunting modes such as low search flight and directed random rake to hunt for prey other than insects which produce

specific glint patterns. Morphological adaptations including the enlarged feet with laterally compressed claws further enhanced the ability of *Noctilio* to catch fish.

Signal design of phylogenetcially closely related species

Although there is some disagreement about the degree of relatedness of noctilionids on the superfamily level, there is broad consensus that the Noctilionidae and the Mormoopidae (leaf-chinned bats) form a monophyletic group (Hood and Smith 1982; Novacek 1991; Smith 1972, 1976; Simmons 1995) and that noctilionids could be particularly close to the genus *Pteronotus* (Mormoopidae) (Baker and Bickham 1980; Sites et al. 1981). Mormoopids, particularly *Pteronotus*, share many similarities in their echolocation behavior and ecology with noctilionids. All mormoopid bats feed on insects. The mustached bat, *Pteronotus parnellii* forages in highly cluttered space in the forest and produces rather long (20–30 ms) CF signals. The other *Pteronotus* hunt in background cluttered space such as forest edges and gaps and emit shorter signals (8–12 ms) composed of a short CF component followed by a downward FM component (Pye 1980; Schnitzler et al. 1991; authors, unpublished observations).

Due to similarities in signal structure we tentatively propose that noctilionids and mormoopids evolved from a common ancestor which used signals with CF components to improve detection of fluttering prey. Subsequent morphological modifications such as the enlarged feet in noctilionids allowed them to grasp objects from surfaces.

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