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Hunting strategy and tympanate moth predation by the pond bat (*Myotis dasycneme*)

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Abstract: Visual observations of moth predation by pond bats *(Myotis dasycneme)* are described and related to typical secondary echolocation and flight behaviour patterns. When hunting over canals and rivers, the common search phase of pond bats combines low-level flight over the water surface with an quasi uninterrupted series of frequency modulated echolocation calls. During the season that moths become available the bats gradually switch to a faster and linear search flight, regularly interrupted by sudden rises and attacks upon moths. Observations of power dives of moths upon bat approaches reveal that these attacks are often aimed at tympanate moths. The bats counter the moths' escape reactions by additional aerial attacks or by an immediate switch from aerial hawking to trawling in response to the power-diving prey dropping to the water surface. During these search flights, bats switch between two distinct echolocation signals, the first predominantly frequency modulated, the second having a more pronounced QCF ending, with both differing from the basic trawling echolocation signal. In this fast aerial hawking search phase, pond bats typically switch between sequences of high intensity pulses and sequences of silences or possible stealth/whispering mode, creating a discontinuous call pattern. These sound sequences always include narrowband signals of a high intensity and long duration, increasing the detection distance to larger prey items. We assume that this discontinuous echolocation pattern facilitates the bats in successfully approaching tympanate moths by delaying or counteracting the moths ability to identify bats from a distance.

Keywords: pond bat, *Myotis dasycneme,* Chiroptera, tympanate moths, power dive, waterways, echolocation.

Introduction

The Palaearctic insectivorous pond bat *(Myotis dasycneme)* occurs mainly in lowland areas in cool and humid climates, often in open landscapes with abundant large, calm water surfaces (Kapteyn 1995, Mostert 1997, Horáček 1999, Limpens et al. 1999). This bat takes prey from the water surface with its large feet or tail membrane in pointed dips, a strategy also found in other trawling *Myotis* (Jones & Rayner 1988, 1991, Britton et al. 1997). Pond bats also feed by aerial hawking and use a variety of echolocation signals from brief broadband FM to long narrowband FM-QCF-FM (Ahlén 1990, Kapteyn 1993, Limpens & Roschen 1995, Britton et al. 1997, Ahlén & Baagøe 1999). Several authors have reported sudden rises and quick pursuits of insects by this species.

Although the pond bat is basically a trawling bat, some morphological aspects, such as its wing shape and tragus length, as well as aspects of its echolocation (the narrowband signal components) reveal striking similarities with open space aerial hawking bats (Norberg & Rayner 1987, Schober & Grimmberger 1998).

Food analyses in the Netherlands and Germany revealed small Diptera as the bulk of prey (76 and 70% of volume respectively). Lepidoptera (11 and 3% respectively), Trichoptera (1.5 and 27% respectively) and Coleoptera (11% in the Netherlands only) have been found in lower quantities (Britton et al. 1997, Sommer & Sommer 1997).

Many larger species of Lepidoptera: Noctuidae, Arctiidae, Notodontidae, Geometridae and

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Pyralidae possess tympanal organs which are sensitive to ultrasounds in the range of 20-60 kHz and enable them to detect the echolocation signals of most aerial hawking bats (Roeder 1966, Rydell & Young 2002).

Tympanate moths move away from the sound source when they detect echolocation calls of a low intensity at a low repetition rate (far-bat reactions) and react to calls of a high intensity and high repetition rate by unpredictable escape manoeuvres such as spirals, loops or power dives (near-bat reactions; Roeder 1967, Waters & Jones 1996). In spite of these defences, several gleaning and aerial hawking bat species feed heavily on eared moths. Aerial hawking species specialised in moth hunting emit echolocation calls with peak frequencies that are below or above the optimum hearing range of tympanate moths (allotonic frequency hypothesis; Fullard 1987). In general few moths are found in the diet of aerial hawking bats that use peak frequencies that are within the moths' optimum hearing range (Bogdanowicz et al. 1999).

This manuscript describes a special moth hunting technique ("fast aerial hawking low over water" - FH) used by the pond bat and compares this strategy to the typical midge ("trawling" T) hunting technique. This fast aerial hawking behaviour was found to be associated with feeding on tympanate moths 0.5-3 m over water. We discuss the hypothesis that the significant gaps in the echolocation pattern facilitate the bats' hunting of tympanate moths.

Materials and methods

Bat observations

Bat observations and recordings were carried out between 1998 and 2005 in Flanders (Belgium) at town moats, ponds, canals and lowland rivers. A monocular image intensifier ITT Night Mariner 150, supported by a powerful infrared light (Vision Nachtzicht Techniek), was used for combined visual-acoustic field observations. The infrared light contains 49 GaAs light emitting diodes with a wavelength of 880 nm, a radiation angle of 20 degrees and a range of 30-50 m. With these tools, water surfaces remain dark, but bats and large insects are seen as bright objects. Infrared illumination does not influence bat and moth activities (Arlettaz et al. 2001, Fullard & Napoleone 2001). Visual observations covered a total of 91 nights (field survey duration 0.5-1.5 h per night), about 450 observed bat passes and about 40 visual observations of sudden climb attacks.

Insect trapping

A mercury vapour light trap (Skinner trap, Alana Ecology Ltd.) with a HQL 125W (MBF-U) ultraviolet light was used for insect sampling along the banks. Insects were identified to family level, or species level where possible, using Chinery (1986). Insect trapping was done over 12 nights between March and October of 2005. The sessions lasted 1.5–2 h per night, starting one hour after sunset. The method is semi-quantitative and cannot replace a full range of insect trapping, which would have to include land-based as well as water-based trap methods. However, Brack & La Val (2006) showed that, based on a large scale faecal analysis and land-based light trapping comparison, diet and insect availability correspond largely in at least *Myotis grisescens*, a Nearctic bat feeding over water.

Ultrasound recordings

We identified pond bats directly in the field, based on heterodyne sounds. Identification was made only when at least some of the species' characteristic sounds were perceived (QCF at 32-35 kHz). Bats only using FM signals during the entire bat pass were not identified because of possible confusion with sympatric Daubenton's bat (*Myotis daubentonii*) (Ahlén 1990, Limpens & Roschen 1995).

A Pettersson D240 ultrasound detector was used for heterodyne and time expansion recordings in the field. All recordings were made at fixed observation points as close to the waterway as possible (<3 m). Recordings were stored on a Sony minidisc MZ-R35 stereo recorder at a sampling

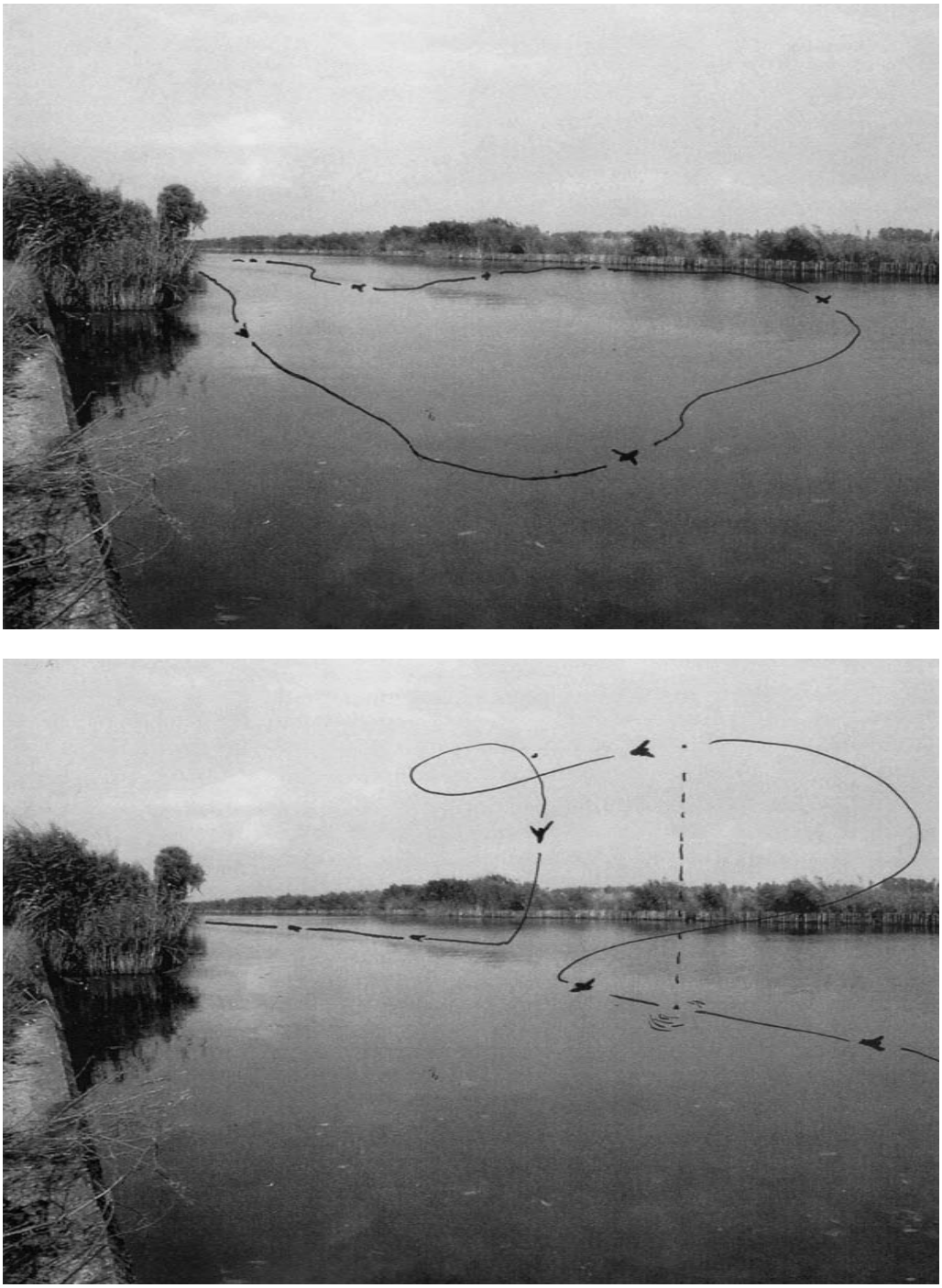

Figure 1. a (above): T-style: permanent low flight, ever changing directionality with distance, sometimes close to the banks. b (below): FH-style: rapid linear search flight over the midline of a canal, sudden climb, attack on a moth, moth escape (power dive) and final capture of a floating moth. *Photographs: Marc Van de Sijpe*.

rate of 44 kHz and transferred to the BatSound programme (Pettersson Elektronik AB).

In total, 60 call sequences were analysed in heterodyne, corresponding to 2656 pulses within a time frame of three years. Calls were recorded at four different geographically separate regions (minimum 50 km apart). Based on the numbers of commuting bats at least 1-30 individuals were present in each region. Calls were recorded at random within the regions. Ninety-four call sequences were analysed in time expansion, corresponding to 1084 pulses.

The time expansion mode was used to determine pulse length (PL), pulse interval (PI), QCF-frequency and peak frequency. The pulse interval PI is defined as the time between two consecutive pulses. We excluded intervals of <50 and >150 ms from our analysis. We assumed a PI of >150 ms to be indicative of an omission of one or more pulses, and a PI of <50 to correspond to an approach phase, possibly preceding a buzz and a catch.

Omitting pulses leads to considerable gaps between the series of pulses, which can be either silences or sequences of whispering calls which are not detected at distances of about 10 m. Both silence or stealth mode serve the same purpose of making the bat inconspicuous to tympanate prey. Gap length (GL) is defined as a period corresponding to more than five consecutively omitted/undetected pulses. The time interval of sound sequences between two consecutive gaps is called sequence length (SL). Silence/stealth mode gaps are not the result of temporally gliding sequences of the bats. Visual observations confirm that passing bats were beating their wings while being silent. The duration of approach phases and feeding buzzes was measured using heterodyne recordings because the time expansion recording capacity of the D240 detector was too short. The onset of the approach phase was defined as the signal with a PI at least 30% shorter than the typical search phase PI. The end of the buzz sequence was the first pulse following the post buzz silence (Kalko & Schnitzler 1998). Catch sequences are defined as the time interval between the start of the first approach phase and the final capture or abandonment of the insect. These sequences can include several buzzes and approach phases.

Results

Flight behaviour over large waterways

Acoustic and visual observations over large linear waterways (width 20-50 m) revealed two hunting strategies, referred to below as "Trawling" (T; figure 1a) and "Fast aerial Hawking at low heights over water" (FH; figure 1b). The two styles were separated by differences in echolocation: T = continuous pattern and absence of signals of long duration (>15 ms) and FH = discon-

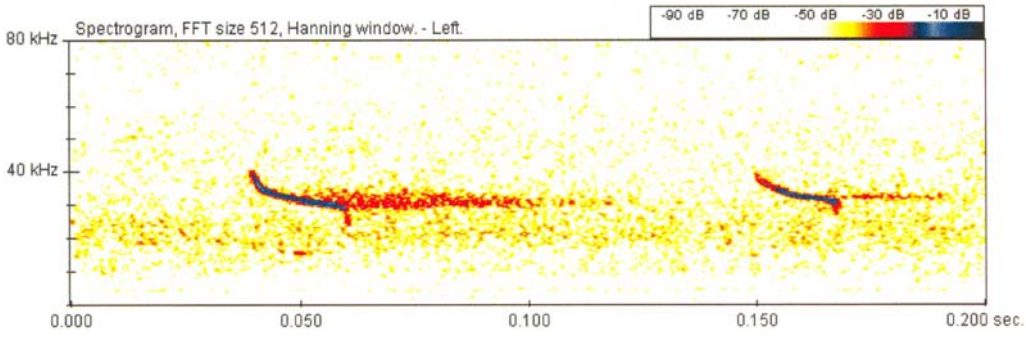

Figure 2. BatSound spectrogram of a time expansion recording: first two narrowband signals of a sound sequence (emitted after a silence/stealth mode gap) from a pond bat hunting in FH-style. Pulse lengths of 21 and 18 ms respectively.

tinuous pattern with calls of both short and long duration (figure 2).

In the T-style the bats fly in both straight and circular paths at a low height over water, sometimes even close to the banks (1-2 m). Visual observations revealed that the bats foraged on emerging midges.

The FH-flight was straight, often over the midline of the waterway, parallel to the banks and low over the water surface (height <0.5 m). In this way the bats patrol the waterways, covering stretches of 100-200 m, for periods up to one hour. During FH-search flights, the bats maintained a distance of at least 10 m from the nearest clutter producing bank. FH-style pond bat hunting was not observed over small canals (the minimum canal width for this activity was approximately 20 m). In FH-style, the bats regularly and suddenly change their flight track in order to climb and chase large insects (figure 2b). The flight speed during the search phase was variable (estimate: max 30 km/h), but considerably faster than in the Trawling T-style. This visually observed speed difference between T and FH was confirmed by the lower pulse repetition rate of the FH style, as aerodynamic models predict that flight speed is inversely proportional to wing beat frequency, hence also to pulse repetition rate (see below). In early spring the T-style was the only flight style observed, with the FH-style gradually replaced the T-style hunting as the season proceeded (figure 3).

Visual observations of bat – moth interactions

Visual observations revealed both successful and unsuccessful attacks on moths, together with moth power dives and other evasive reactions (erratic flight, escaping to the banks and gaining height). Moth hunting was only observed when the bats hunted in the FH-style. Insects were identified as moths (Lepidoptera), as opposed to lacewings (Neuroptera), caddis flies (Trichoptera) or beetles (Coleoptera) on the basis of their appearance, flight style and escape reactions,.

Light trap results

Several thousand Chironomids were caught, along with 153 larger insects. Insect sampling revealed that small Diptera (Nematocera, mainly Chironomidae) were, by two orders of magni-

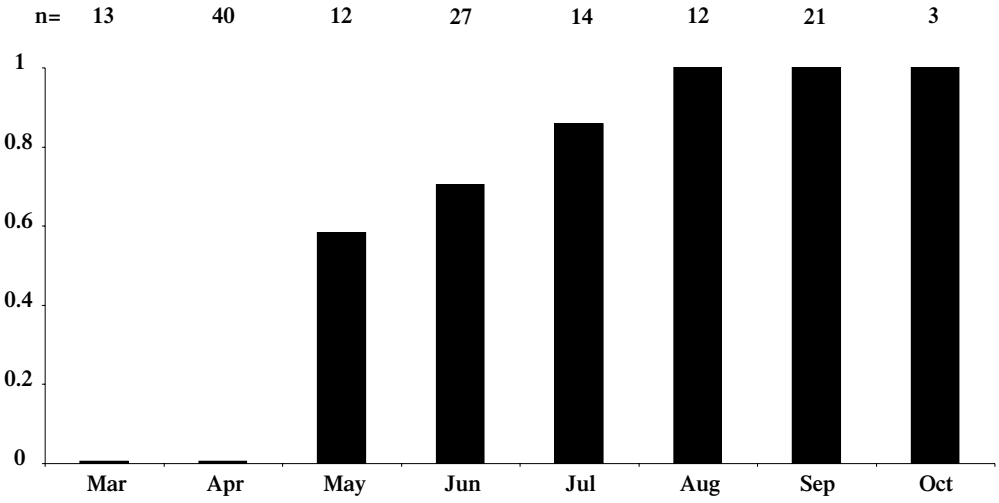

Figure 3. Proportion of hunting nights with positive visual and/or acoustical identification for FH type hunting (qualitative approach, pooled data 1998-2005). FH: Fast aerial hawking at low heights over water; *n*: number of hunting nights with positively identified hunting activity of pond bats; total surveys: 142 (0.5-1.5 h).

Table 1. Semi-quantitative results of light trapped insects, trapped on pond bat hunting sites during 2005, identified on family or order level; number of insects per 1.5–2h sessions. Total Lepidoptera: sum of the three major and other families identified. Chironomidae: >500, may include up to several thousand midges.

		31 Mar	3 Apr	5 Apr	7 Apr	12 Apr	2 Aug	4 Aug	6 Aug	7 Aug	25 Sep	26 Sep	3 Oct
Diptera	Chironomidae	23	23	20	4	>100	>500	>500	>500	>500	>100	>100	>100
Coleoptera			1				1	1		1	1		1
Trichoptera								2					
Lepidoptera	Noctuidae	4		1	1		12	5	18	11	4	4	6
	Arctiidae						1	2	2				
	Geometridae						2	1	1	2		4	
	Total Lepidoptera	4	0	1	1	0	15	10	23	17	4	8	6

tude, the most abundant insect group (table 1). There was a clear distinction between the densities of insects caught between mid April and early August (4 to 23 per catch versus >100 to >500). Larger insects such as Trichoptera, Coleoptera and Lepidoptera were found in lower numbers, with higher densities from the beginning of August (0 to 4 per catch versus 0 to 23). No samples were taken in the period May-July.

Heterodyne results

A heterodyne analysis was used to identify differences between T and FH flight patterns. For both T and FH flights, 30 bat passes of between 3.4 and 11.9 s were analysed. The pond bat's T-style hunting is characterized by an absence of larger gaps (>5 omitted pulses), with at most three consecutively omitted pulses (figure 4a). FH sonar is highly discontinuous with long silences between sound sequences (figure 4b). The majority of FH bat passes are characterized by short pulse sequences consisting of a small number of emitted pulses per sequence. Per bat pass there were 1-3 gaps and 1-3 pulse sequences. Gaps for FH-style hunting were long, up to 3570 ms, corresponding to 34 missing/undetected pulses. It is possible that the gaps in the echolocation pattern

Table 2. Heterodyne analysis of T- and FH-styles pond bat passes. PI average pulse interval (excluded intervals <50 and >150 ms), GL: gap length (FH-style only), SL: sound sequence length (FH style only), emitted N (SL): number of pulses in the sound sequences (FH-style only), % omitted: percentage of omitted/undetected pulses (total per bat pass).

	T Mean ± sd Median (Min-Max)	FH Mean ± sd Median (Min-Max)	Statistical testing T versus FH Mann-Whitney U
Total number of bat passes (n)	30	30	
Total number of pulses	2055	601	
Bat pass duration (s)	7.7 ± 1.6	6.2 ± 1.7	
PI (ms)	102 ± 4 103 (93-107)	117 ± 5 118 (104-124)	*** P< 0.001
GL (ms)	-	1963 ± 758 (n=43)	
SL (ms)	- -	1537 ± 861 (n=65) 1370 (470-5090)	
emitted N (SL)	-	8 ± 4 (n=65) 7 (3-27)	
% omitted	11 ± 9 (n=30) 8 (0-29)	61 ± 9 (n=30) 63 (38-74)	*** P< 0.001

are not real silences but a series of low-intensity/whispering calls that remained completely undetected at distances of 10 m due to atmospheric attenuation and spherical spreading. On a few occasions, single steep FM signals of very weak intensity were recorded in the FH gaps. T and FH call series tested as highly significant different (Mann-Whitney $P<0.01$) for pulse interval lengths and number and percentage of omitted/undetected pulses (table 2).

Time expansion results

Time expansion was used to describe the T and FH echolocation call parameters: 783 (T) and 301 (FH) echolocation calls were analysed (table 3). The analysis of FH bat passes always started with the first call emitted after a silence and in this type of analysis, only search phase calls were used with approach phase calls and catch buzz sequences being omitted.

FH calls were separated in two distinct groups based on pulse length, with FH1 calls having a pulse length of ≤12 ms and FH2 signals one of >12 ms (figure 5). FH1 calls were aimed at midges over water and FH2 calls at larger insects.

The most noticeable observation is that in general the T and FH1 call patterns, expressed as pulse length and slope of the call, are very similar (figure 6). Both are short calls with a steep slope, although the call duration and therefore the duration of the QCF-part in T-style calls may vary considerably (T median PL 8 ms).

FH2 style calls are significantly longer (median 18 ms) with a pronounced QCF-part. T and FH2 calls have similar ending frequencies (median 27.0 and 26.6 kHz) and these are significantly different from the median FH1 ending frequency (30.6 kHz, $P<0.001$). FH2 QCF-frequencies and peak frequencies are closer to T-style than to FH1 style calls (table 3). The difference in PI between T and FH-styles found in the heterodyne analyses is confirmed in time expansion (table 3). Assuming a 1/1 link between wing beat and pulse emission, the median T-style PI of 103 ms

Table 3. Time expansion analysis of search signals for bat passes in T- and FH-styles: T, FH1 and FH2. Parameters are all highly significantly different (Mann-Whitney $P\leq0.001$), except for pairs of data marked # which do not score significantly different even at a $P<0.05$ level.

	T	FH	
Total number of bat passes	55	39	
Total number of pulses	783	301	
		FH1	FH2
	Mean ± sd Median (Min-Max)	Mean ± sd Median (Min-Max)	Mean ± sd Median (Min-Max)
Total number of pulses		96	205
Starting frequency (kHz)	54.5 ± 7.1 55.4 (37.2-77.7)	48.8 ± 4.0 48.8 (39.6-63.4)	44.1 ± 3.1 43.6 (35.1-59.4
Ending frequency (kHz)	26.9 ± 2.3 27.0 (19.3-34.4) #	30.9 ± 2.5 30.6 (25.2-36.5)	26.7 ± 1.5 26.6 (21.6-32.5) #
Bandwidth (kHz)	27.6 ± 7.8 28.0 (9.8-59.0)	17.9 ± 5.1 17.9 (7.9-31.5) #	17.3 ± 3.3 17.2 (9.3-31.9) #
QCF-frequency (kHz)	33.4 ± 0.8 33.4 (31.2-35.9)	35.0 ± 1.1 35.1 (32.7-37.6)	32.8 ± 0.9 32.7 (29.9-35.5)
Peak frequency (kHz)	35.9 ± 1.9 35.4 (28.8-43.3)	37.9 ± 2.1 37.6 (33.8-43.3)	33.6 ± 1.6 33.3 (28.3-41.0)
PI (ms)	101 ± 16 103 (53-149)	121 ± 8 121 (105-140) #	117 ± 13 117 (74-144) #
PL (ms)	7.7 ± 2.4 8.0 (2.0-17.0) #	6.8 ± 2.7 7.0 (1.0-12.0) #	17.6 ± 2.3 18.0 (13.0-23.0)

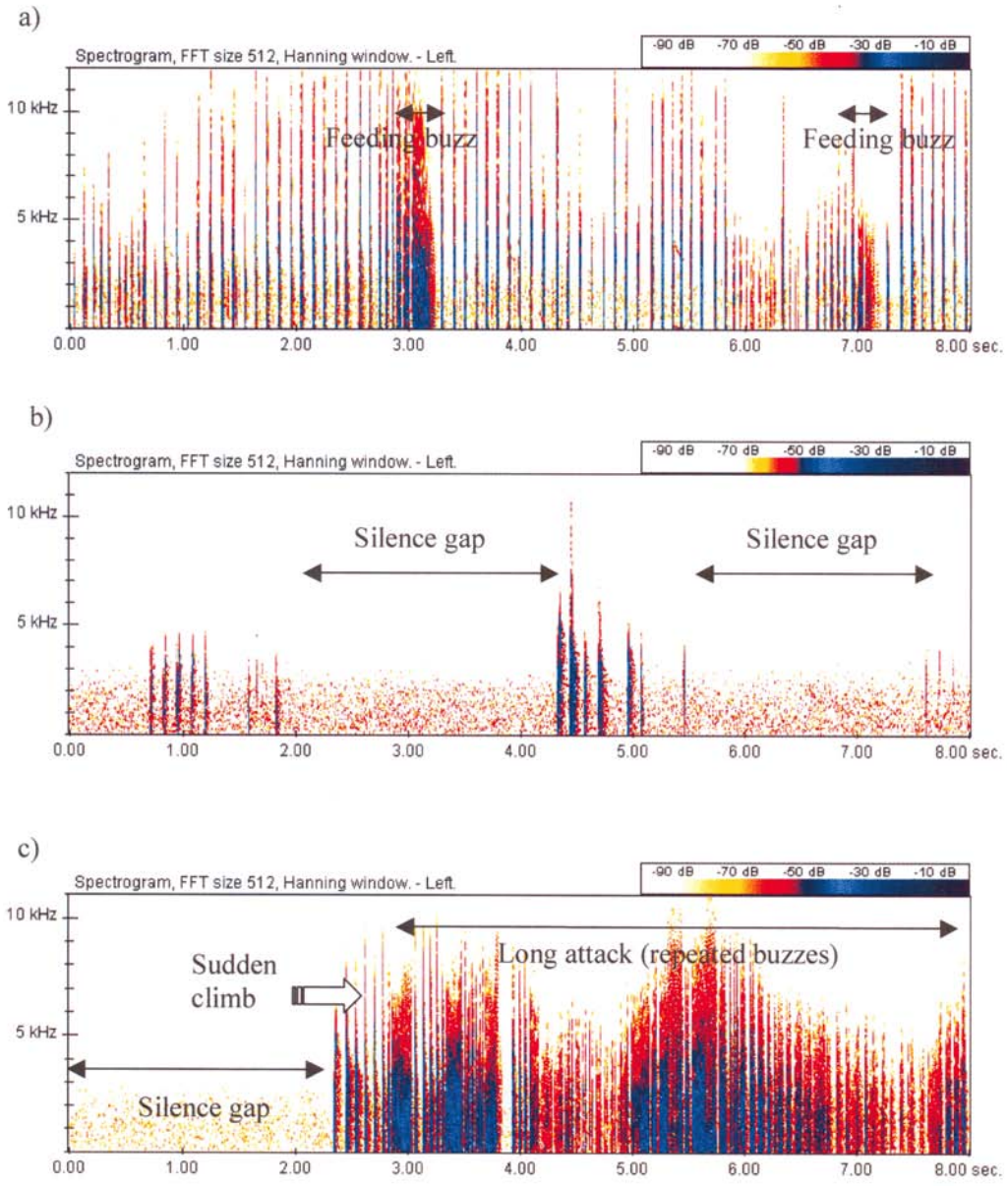

Figure 4. BatSound spectrograms of heterodyne recordings:
a) T-style search phase; echolocation is almost continuous (no gaps). Now and then short feeding buzzes occur (attacks on Chironomids on the water surface).
b) FH-style search phase; echolocation is highly discontinuous: 3 groups of pulses separated by long silence/ stealth mode gaps.
c) FH-style, from left to right: part of silence/stealth mode gap (0–2.3 s), start of sound emission at 2.3 s, start of approach phase at 2.7 s, coinciding with a sudden attack on a moth (2.7–8 s) involving several approach phases and feeding buzzes.

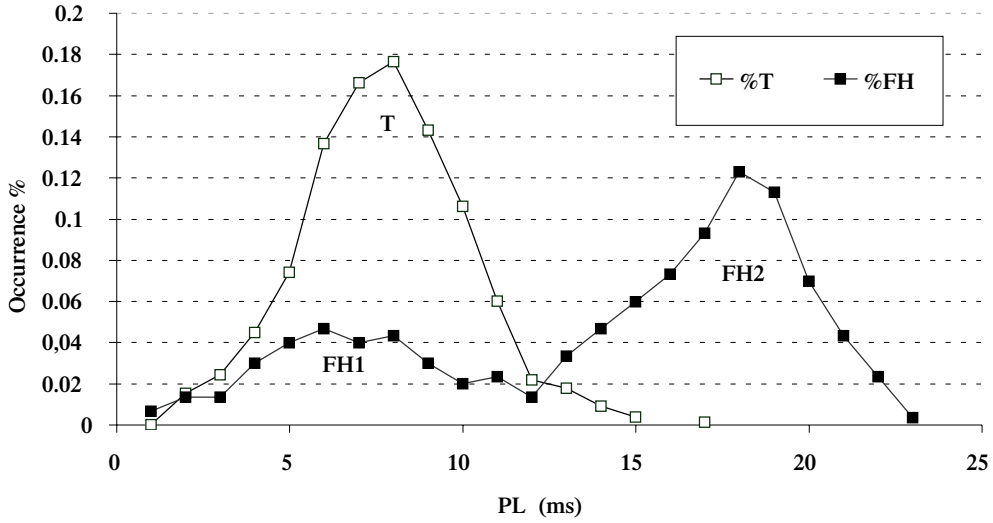

Figure 5. Distribution of pulse length (ms) of T-style (*n*=783) and FH-style (*n*=301) search phases of the pond bat for typical T, FH1 and FH2 calls.

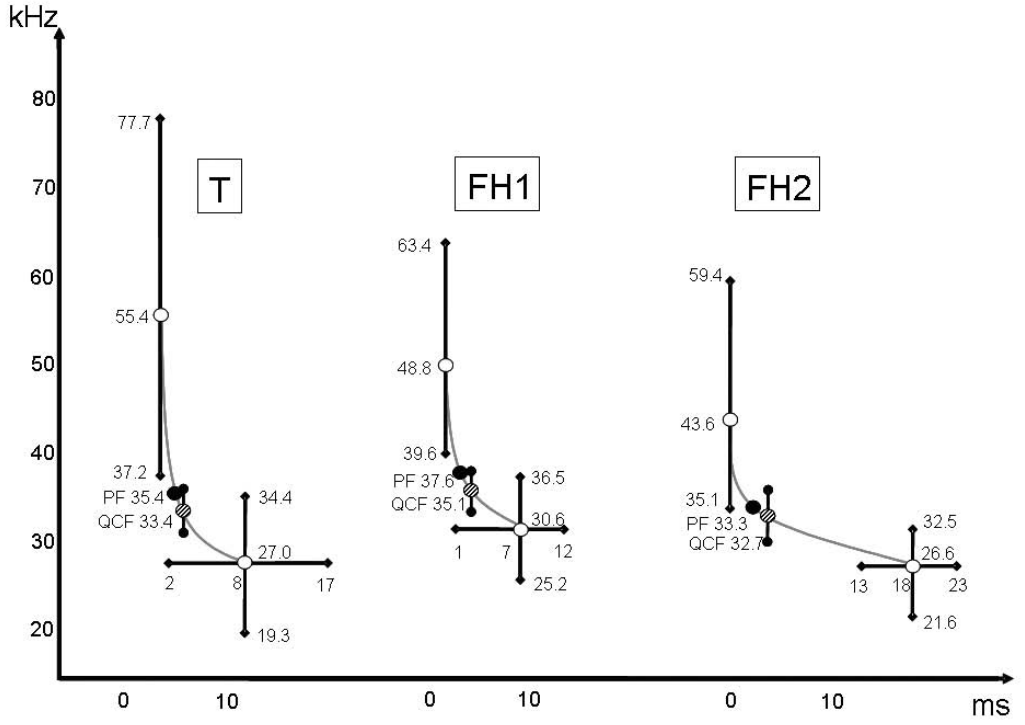

Figure 6. Signal structure indicating median, minimum and maximum values of start, end and peak frequency, QCF-frequency and pulse length (horizontal).

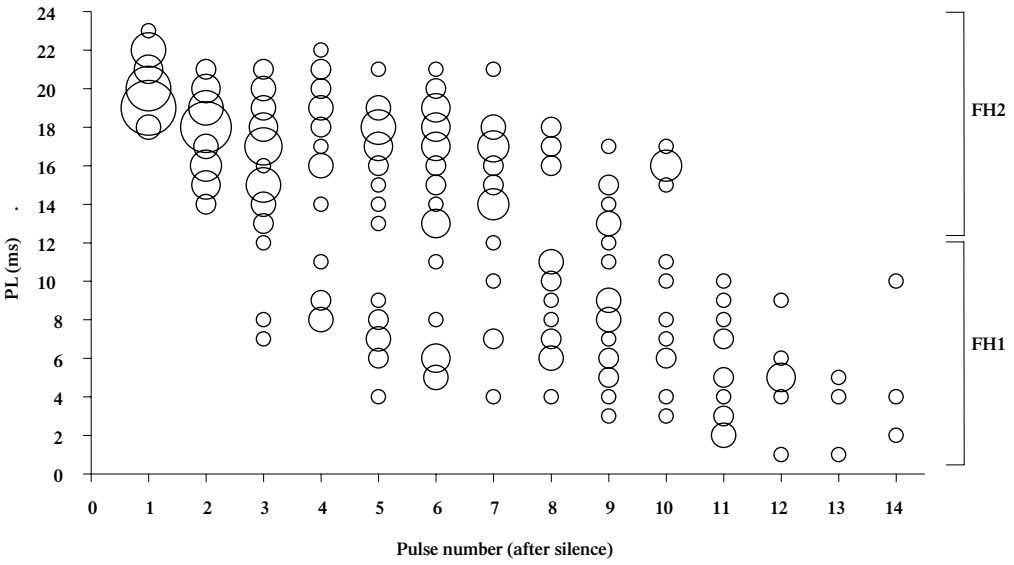

Figure 7. Change of pulse length (ms) versus pulse number in FH call series (pulse nr 1 corresponds to the first pulse emitted after a gap, pulse nr 2 with the second pulse, etc.).

corresponds with a flight speed of approx. 2.8 m/s, and the median FH1-style PI of 117 ms with a flight speed of 7.5 m/s for a pond bat of 17 g, according to the formula given by Bullen & McKenzie (2002).

FH-style hunting call pattern change

Figure 7 shows the pulse lengths for sequences of pulses in FH-style hunting, starting each time after a silence/stealth mode gap. The first two pulses of the sequences are always FH2 (>12 ms) and are gradually replaced by a mixture of FH1 (<12 ms) and FH2 type calls (9-68% FH1, 32-91% FH2). The mixing of FH1 and FH2 calls is random and this was obvious from the field recordings. Also it should be highlighted that, the FH2 calls are clearly stronger in amplitude than the following call FH1-style. Towards the end of the sequence (above a wing beat of 11), calls are exclusively FH1 style, which is considered to be a typical trawling call. After some time, this ends in a new, long gap.

Approach phase and feeding buzz durations

Table 4 compares the duration of the catch sequences for the pond bat's different hunting styles

Table 4. Approach phase + feeding buzz durations from heterodyne recordings of pond bats in T and FH styles and of Daubenton's bats (2000) and common serotines (1998) as a reference (own data), n: number of sequences analysed.

Species	Hunting style	Type of attack	n	Duration appr + buzz phase (ms)	
				Mean ± sd	Median (Min-Max)
M. daubentonii	T	trawling, slow flight	7	451 ± 67	440 (380-590)
M. dasycneme	T	trawling, slow flight	10	615 ± 162	605 (390-920)
M. dasycneme	FH1	sudden rise & pursuit in the air, fast flight	10	3402 ± 2335	3070 (1010-9410)
M. dasycneme	FH2	low catch over water / trawling, fast flight	5	538 ± 254	440 (340-1040)
E. serotinus	Aerial hawking	pursuit around street light	7	1646 ± 774	1250 (840-2980)

(T and FH), and compares this to similar sequences for Daubenton's bat and the common serotine (*Eptesicus serotinus*) (own data analysis).

In the FH-hunting strategy both long and short catch sequences occur. The long catch sequences (mean 3402 ± 2335 ms), are associated with FH2 search pulses and aerial hawking. Sudden climbs often include a lot of manoeuvring in order to catch a moth or another larger prey (figures 2b and 4c). Catch sequences as long as 25 s are reported in *Lasiurus borealis*, a Nearctic aerial hawking and moth hunter (Reddy & Fenton 2003). The pond bat's long catch sequences are comparable with those of the common serotine when chasing moths around street lights (average time 1646 ± 774 ms). Short buzzes associated with FH1 (538 ± 254 ms) and T-style (615 ± 162 ms) hunting are significantly shorter in duration and compare to the sequences of trawling Daubenton's bat (451 ± 67 ms). Even though the duration of an approach and catch of an FH1-style compares to the duration of a T-style trawling, it is associated with a faster search flight.

Discussion

Signal design

Short broadband FM signals (T and FH1) are typical for trawling behaviour (Jones & Rayner 1988, 1991, Britton et al. 1997). A short broadband FM signal, which quickly sweeps through many frequencies, improves spatial orientation (Schnitzler & Kalko 2001, Schnitzler et al. 2003) and assures an adequate separation of overlapping echoes (Boonman & Ostwald 2007) ensuring the detection of prey close to clutter producing objects. The short duration of calls limits the forward masking zone, allowing a search for small prey items.

Although the QCF part in the long T-style calls is uncommon in trawling bats (Siemers et al. 2001), these calls are also related to trawling behaviour involving the detection and capture of chironomid midges near to and on the water surface. In the FH-style hunting, the majority of search signals (FH2) have a much longer QCF part, resulting in pulse lengths up to 23 ms. QCF-calls are also documented in trawling *Rynchonycteris naso*, a Neotropical Emballonurid bat species (Jung et al. 2007), and in the Nearctic *Myotis volans,* known to forage over trees, cliffs and water (Fenton & Bell 1981). Both Neotropical trawling Noctilio species also emit mixed QCF-FM calls (Schnitzler et al. 1994, Kalko et al. 1998). These species are documented as hunting on larger prey.

QCF-components increase the detection distance because the bat's neuronal filter tuned to the QCF frequency is activated for a longer period, thereby enabling the detection of weak echoes (Schnitzler & Kalko 2001). In addition, long duration calls increase the detection distance by improving the chances of receiving acoustic glints of fluttering insects at moments when the insect's wings are perpendicular to the sound beam (Schnitzler & Kalko 1998). If acoustic glints play a role in target detection, it is likely to happen right at the beginning of the sound emissions after the silence/stealth mode gaps, at moments when the bats emit their longest pulses. Lepidoptera have typical wing beat frequencies of 5-85 Hz and small Diptera one of 100-1000 Hz (Knospe 1998). Average FH2 calls at the start of call series (PL 20 ms / PI 108 ms) yield a glint rate of one glint/pulse for an insect fluttering at 50 Hz.

FH2 calls: long range echolocation at low height

When flying close to clutter generating objects such as trees or the ground, bats need to shorten their calls to keep an overlap-free window open for prey detection (Jensen & Miller 1999). Aerial hawking bats use long QCF calls when hunting high over the ground in the open. When occasionally foraging at lower heights these bats shorten their calls and reduce or omit the QCF-part. Unlike structured land surfaces, smooth water surfaces do not generate clutter echoes for bats flying close to the surface. Ensonifying the surface from a sharp angle causes the sound beam to reflect away from the bat (Boonman et al. 1998, Rydell et al. 1999,

Siemers et al. 2001). In this particular situation the canal banks are the only sources of clutter echoes. If the bat maintains enough distance from the banks, it will experience an acoustically open environment in which the emission of narrowband signals of long duration becomes possible. Reflection from the water surface results in an interference pattern in the recordings, which can be seen as a sinusoidal amplitude modulation in each call. In the FH style, which seems to be a special case of open space aerial hawking, the pond bat combines the advantages of low flight height, increased flight speed and long range echolocation in order to optimise the detection, pursuit and capture of large, fast flying prey in the lower air. Interestingly, Kalko et al. (1998) observed moth hunting over water by the predominantly insectivorous *Noctilio albiventris*, including power dives of moths and counter attacks involving trawling manoeuvres by the bat.

Verboom et al. (1999) found that commuting pond bats emitted calls with a longer pulse length and pulse interval when flying over the midline of larger canals, suggesting that the canal banks play a role as acoustic landmarks when navigating through a landscape. FH2 type calls therefore may also play a role in spatial orientation, in detecting distant banks when flying over large open water surfaces. However these authors also describe long QCF in bats flying more than 100 m from the shore, suggesting these calls serve for more than spatial orientation. Britton et al. (1997) associated the emission of long QCF calls with hunting behaviour over a large lake. We assume therefore that our observations of FH behaviour are associated with hunting behaviour. Sudden rises are always associated with groups of FH2 calls. We never observed rises during the silence/stealth mode. Open space aerial hawkers, e.g. *Nyctalus* and *Vespertilio*, are also known to use long QCF calls while hunting on large prey at high altitude.

Maximum detection distances

Although detection distances are longer for prey low over water, than for the same prey in open air (Siemers et al. 2005), long duration FH2-type signals are probably not well suited for the detection of individual small prey items (e.g. midges) because, for an aerial hawking bat, the maximum detection distance (2 m at 35 kHz for Culicidae) is typically shorter than the actual forward masking zone (3 m for 18 ms signals) (Waters et al. 1995). Such small targets can better be detected with the shorter T- and FH1-style pulses because the forward masking zone is smaller (1.4 m for 8 ms signals). The longer FH2-signals are well suited for detecting larger prey items (e.g. moths) because of their greater target strengths and larger detection distances (maximum 12 m at 35 kHz for *Noctua pronuba*) (Waters et al. 1995, Britton et al. 1997). Because the first few signals after a silence are always the long FH2 type, the bat's interest at that particular moment is focussed solely on detection of large prey at a distance and/or landscape elements (navigation). If no large prey is revealed after the emission of the first long pulses, the bat continues its fast flight and typical FH sonar emissions. However, over time, more and more shorter pulses appear within the sequences, seeming to indicate a switch of the bat's interest towards potential smaller prey at a close range.

Discontinuous sound emission pattern

Tympanate moths are especially sensitive to ultrasounds in the range 30-40 kHz, with the detection threshold decreasing with increasing pulse length (Surlykke et al. 1999, Norman & Jones 2000). According to Surlykke et al. (1999), tympanate moths can detect approaching bats at up to a maximum of 30-90 m. Bat using frequencies around 35 kHz can detect large moths at up to a maximum of 12 m (Waters et al. 1995). Detection distances on both sides are highly dependent on amplitude, frequency and size. If the bats emit continuous pulse series, tympanate moths will detect them long before they can be detected themselves. Since moths have lower flight speeds than bats, they need larger detection distances to stay outside the sound beam of approaching bats. However, silence/stealth mode gaps in the FH-

style might delay far-bat escape reactions and increase the chances for an unnoticed approach. Silences of 2000 ms correspond with a travelled pathway of approx. 17 m at a bat's flight speed of 30 km/h. In this way the gaps in calls seem to be a strategy by the bats to counter the tympanate moth's ability to evade distant bats.

If economizing were an issue, we would expect the bat to more frequently omit single pulses as observed among species that hunt in the open, rather than omitting a large number of pulses consecutively.

The faint signals that sometimes occur in the silences leave the impression of a whispering sonar. Trawling bats scanning smooth water surfaces for aquatic insects have to use high intensity FM signals in order to detect small sized prey and even then they operate at low signal-to-noise ratios (Rydell et al. 1999). Because the scattered signals in the silences are so faint even at relatively short distances (10 m) it is unlikely that they are intended for prey detection. It is possible that these signals provide short-range spatial orientation to prevent collisions with (unpredictable) obstacles e.g. other bats or floating water birds. Daubenton's bats passing over water at similar distances emit a continuous pulse series of loud FM calls that are easily heard with a bat detector, in contrast to the few faint calls of the pond bat during an otherwise silent flight.

Pond bat diet

The few available food analyses indicate quite low percentages of Lepidoptera in the diet of the pond bat (Britton et al. 1997, Sommer & Sommer 1997). However, our visual observations showed that this bat does approach and catch tympanate moths over water. One needs to be extremely careful when analysing Lepidoptera in bat droppings, as the legs and wings may well be removed before ingestion, leaving only few possible traces of larger Lepidoptera in the droppings.

In early spring the absence or scarcity of large insects in general, and also over open water, apparently influences pond bats to use only the trawling technique (T-style). The yearly reappearance of FH behaviour in May and the growing frequency of this behaviour up to September/October seems to coincide with the emergence of most large nocturnal insects, including many Lepidoptera (Emmet 1992).

The majority of bat-moth interactions were observed over linear water elements, including canals and rivers, of 20-45 m width. The density of basically terrestrial insects may be higher over these linear elements than over large lakes due to a closer contact surface with the surrounding terrestrial habitat. Many Lepidoptera, especially Noctuidae, live on food plants which are common in canal and river banks, e.g. willow, common reed, reed mace, yellow iris, grasses, nettle and many other herbaceous plants (Emmet 1992). The light trap experiments confirm the presence of a wide variety of Lepidoptera.

Conclusion

The pond bat uses different hunting techniques when foraging low over water, the choice of these is highly dependent on the available food resources: a 'classical' trawling T-technique allows exploitation of motionless or slow flying aquatic insects near to and on the water surface. An alternative FH fast aerial hawking strategy through it's FH2 calls provides access to larger, faster prey items (including tympanate moths) flying in the lower air. This is a unique strategy because it combines a relatively fast flight at low height over large smooth water surfaces with long range echolocation calls. The prominent silence/stealth mode gaps in the echolocation pattern, the emission of long QCF calls immediately after each silence and the simultaneous visual observations of moth attacks and typical moth evasive reactions reveal that the pond bat is at least an occasional tympanate moth predator. As soon as these moths are available in sufficient numbers in their specific habitat (larger water surfaces) and when weather conditions are favourable, pond bats readily switch from slow T to fast FH hunting strategy.

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Samenvatting

Predatie op motten met tympanale organen door de meervleermuis (*Myotis dasycneme*) door middel van een speciale jachtstrategie

Dit artikel beschrijft zichtwaarnemingen van het jachtgedrag van de meervleermuis op motten met tympanale organen en legt een verband met

de echolocatie en het vlieggedrag. Wanneer de vleermuizen op motten jagen boven brede kanalen en rivieren vliegen ze snel en rechtlijnig heen en weer, laag boven het wateroppervlak, ver van obstakels die nevenecho's veroorzaken (oeverlijnen). Regelmatig wordt deze vlucht onderbroken waarbij de vleermuizen plots steil omhoog schieten en prooien achtervolgen hoger boven het water. Waarnemingen van motten die zich pijlsnel naar beneden laten vallen (de zogenaamde 'power dives') tonen aan dat minstens een deel van de aanvallen gericht is op motten met tympanale organen. De vleermuizen omzeilen de vluchtreacties van de motten door de grillig vliegende mot herhaaldelijk in de lucht aan te vallen of door onmiddellijk over te schakelen van aerial hawking naar trawling, zodra de mot na een duikvlucht op het wateroppervlak terecht komt. In de zoekfase wisselen de vleermuizen reeksen luide echolocatiepulsen af met stilteperioden of reeksen van zeer zwakke echolocatiepulsen, waardoor een discontinu patroon ontstaat. De reeksen echolocatiegeluiden die volgen op de stilteperioden bevatten steeds lange, smalbandige FM-QCF-FM signalen van hoge intensiteit, in het bijzonder aan het begin van elke pulsreeks. Dit signaaltype levert een grotere detectieafstand op in vergelijking met de typische korte FM-signalen van trawling vleermuizen, maar kunnen allicht enkel dienen voor waarneming van grote prooien. Wij beargumenteren dat de discontinue sonar het benaderen van motten met tympanale organen vergemakkelijkt door het vertragen of uitschakelen van de afweerreacties van de motten tegen verafgelegen ultrasone bronnen (de zogenaamde 'far-bat reacties'). De echolocatie van het jachtgedrag op motten, dat wij in dit artikel omschrijven als 'snel luchtscheppen laag boven open water' wordt vergeleken met het klassieke harken (trawling).

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