Flight height of trawling pond bats and Daubenton’s bats

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Abstract: This article presents an indirect way to estimate the flight height of trawling bats by measuring the small time intervals between pulses and echoes from the water surface. A particular study site, the historical Vauban ramparts around the town of Ieper, Belgium, allowed for time expansion recordings made from trawling pond bats (*Myotis dasycneme*) and Daubenton’s bats (*M. daubentonii*) when they were skimming the water surface close to the wall. The surface echoes were used to estimate the flight height. This method was confirmed by a detailed analysis of a feeding buzz performed by a pond bat close to the wall, where the bat finally broke the water surface, which was revealed by expanding waves in the water. The pulse-echo time interval gradually decreased from search to buzz phase, corresponding with a gradually decreasing flight height from circa 53 to circa 6 cm. Sound analysis of bat passes of Daubenton’s bats and pond bats in the search phase revealed the pond bat to have higher flight heights (median: 43 cm) than Daubenton’s bat (median: 24 cm).

Keywords: pond bat, Daubenton’s bat, *Myotis dasycneme, Myotis daubentonii*, flight height, trawling.

Introduction

The trawling technique, sometimes referred to as gaffing or water gleaning, is used by specialised chiropterans, which probably evolved from ancestral aerial hawking forms through morphological adaptations (Fenton & Bogdanowicz 2002). These bats catch insects from the water surface and/or fish and crustaceans just below the surface, by using their enlarged hind feet, which are equipped with long claws (Jones & Rayner 1988, Kalko & Schnitzler 1988, Jones & Rayner 1991, Britton et al. 1997). They also take flying insects in the air just above the water surface by using the tail membrane, a hunting strategy commonly referred to as aerial hawking (Jones & Rayner 1988, Todd & Waters 2007). Trawling bats emerged all over the world and appeared in different chiropteran families by convergent evolution (Fenton & Bogdanowicz 2002). Various opportunities may have triggered the emergence of trawling. Food resources close to, and on the water surface, are often abundant and largely unavailable to non-trawling species. Aldridge (1988) and Jones and Rayner (1991) suggest that flying close to the ground reduces the energy that bats expend (25 to 30% in Daubenton’s bat (*Myotis daubentonii*) and *Myotis adversus*). However these savings rapidly decrease with increasing height, as shown by Britton et al. (1997) who found lower savings (9%) in commuting pond bats (*Myotis dasycneme*) flying at an average height of 26 cm. Furthermore, prey is more conspicuous over smooth surfaces than textured ones, since a smooth surface will reflect much of the sound energy away from a bat, if the latter flies sufficiently low so that the emitted sound beam hits the surface at a narrow angle (Boonman et al. 1998, Rydell et al. 1999, Siemers et al. 2001). These low background echo levels make smooth surfaces favourable hunting grounds for echolocating bats. Siemers et al. (2005) found that prey protruding sufficiently above a smooth surface provide greater echo amplitudes compared to the same prey in mid-air because of a mirror effect, by which indirect echo reflections from the immediate surface add to the direct echo from the insect. Hence, trawling bats can detect similar sized prey at greater distances than hawking bats in mid-air. In spite of these advantages there is no evidence of obligate trawling forms having evolved. Even the most specialised ones, i.e. the piscivorous and insectivorous greater bulldog bat (*Noctilio leporinus*), have maintained the ability to hawk insects in mid-air and for at least part of the season extensively hunt airborne insects (Schnitzler et al. 1994). For some reason, non-trawling bats are unable or unwilling to continuously fly as low over a water surface as trawling bats and aerially hawking species that extensively hunt over water, e.g. gray bats (*Myotis grisescens*), fly and catch insects at higher heights (2-5 m) (Brack & Laval 2006).

The common search phase of trawling bats most often consists of a flight at 10 to 60 cm over the water surface with the body axis and feet positioned horizontally (Baagøe 1987). Only the most specialised species (*Noctilio leporinus*) are capable of making prolonged flights of at least 10 m, raking through the water surface (random rake technique, Schnitzler et al. 1994). They use their long calcars to turn their tail membrane forwards and keep it out of the water. During capture attempts trawling insectivorous bats perform pointed dips, during which the bat first descends to the surface, lowers its feet to a more vertical position until the claws rake the surface and turns the tail membrane backwards so that minimum interference with the water occurs. Finally the insect is scooped from the surface either with the feet or tail membrane. The bat brings head and foot together to transfer the prey item to the mouth and then regains height to continue its search flight at 10-60 cm (Jones & Rayner 1988,

Figure 1. View of the ramparts, stone walls and moats of Vauban's historical fortifications around the town of Ieper, Flanders, Belgium. The combination of tall vegetation, large open water surfaces, and sheltered microhabitats with a favourable climate, offers an insect-rich habitat and attracts many species of bats, including in spring when the bats awake from hibernating in several underground sites in and around this fortification.

Kalko & Schnitzler 1988, Jones & Rayner 1991, Britton et al. 1997).

There is still little available information about the flight heights of trawling bats. In Denmark, Baagøe (1987) established flight heights of 10 to 20 cm for trawling Daubenton's bats, and 10 to 60 cm for trawling pond bats. Based on photographs, hunting Daubenton's bats were found to fly at an average height of 15.8 ± 6.7 cm (min-max 8-28 cm) over tributaries of the river Rhine in Germany (Kalko & Schnitzler 1988). Pond bats commuting over a canal near a summer roost in Friesland (the Netherlands), flew at a height of 26 ± 2 cm, as recorded by stereo photogrammetry (Britton et al. 1997). Schnitzler et al. (1994) reported flight heights as low as 4 to 10 cm during low search phase flight of *Noctilio leporinus* in Neotropical Costa Rica.

This paper describes an indirect way of estimating flight height in trawling bats by means of time expansion recordings. Daubenton's bats and pond bats were hunting on the same spring nights over the same large water surface and used a similar flight style and at a similar distance to a rampart wall bordering the water surface. This was a good opportunity to test whether the two species used different flight heights in the same field conditions.

Methods

Study site

Observations of hunting Daubenton's bats and pond bats were made in Ieper (French/English name: Ypres), a town with 30,000 inhabitants in the western lowlands of Flanders (Belgium) at 25 m above sea level. The historical town centre is partly surrounded by rampart walls and large moats, remains of the fortifications built by the French architect Vauban in the 17th century (figure 1). The recordings and observations were made north of the Menin Gate Bridge. At this point the moat is about 200 m long and has an an average width of 50 m and a water depth of 1.5-2 m. The inner side of the moat is bordered by an 8 m high stone wall, the top of which is overgrown by tall trees, bushes and scrub. The outer side is bordered by a 2 m high grass covered talus, a small grass stretch with trees, a road, and houses.

Visual observations

A monocular image intensifier, the ITT Night Mariner 150 (ITT Industries, Roanoke, Virginia, USA), was used for visual observations. The monocular does not magnify and has a view angle of 40 degrees. A circuit of 49 GaAs infrared leds with a wavelength of 880 nm (Vision Nachtzicht Techniek, Born, the Netherlands) was mounted on the Night Mariner to improve the image contrast. When the lights were on, the scene viewed through the image intensifier was that of a dark green water surface with bright green bat silhouettes flying above it (figure 2). The observations were made from the top of the 8 m high stone wall, looking down on the trawling bats below. The image intensifier was used to estimate the distance between the bats and the wall (see below).

Sound recordings

A Pettersson D240 ultrasound detector with heterodyne and time expansion systems (Pettersson Elektronik AB, Uppsala, Sweden), with a memory storage time of 1.7 s, was used for acoustic observations, instant species identification in the field and sound recordings in the time expansion mode.

Recordings were made with the detector held on top of the wall taking care that it didn't protrude (so as to avoid reflections from the wall to the microphone). Sounds were recorded from bats in their search phase, flying in a straight line parallel to the wall and of bats performing feeding buzzes, circular manoeuvres with a diameter of about 1 m. The stages between the search phase and the final buzz were evaluated by analysing the pulse lengths and intervals, following Kalko and Schnitzler (1998). Combined heterodyne and time expansion recordings were stored on a stereo Minidisc Walkman MZ-R35 at a sampling rate of 44 kHz.

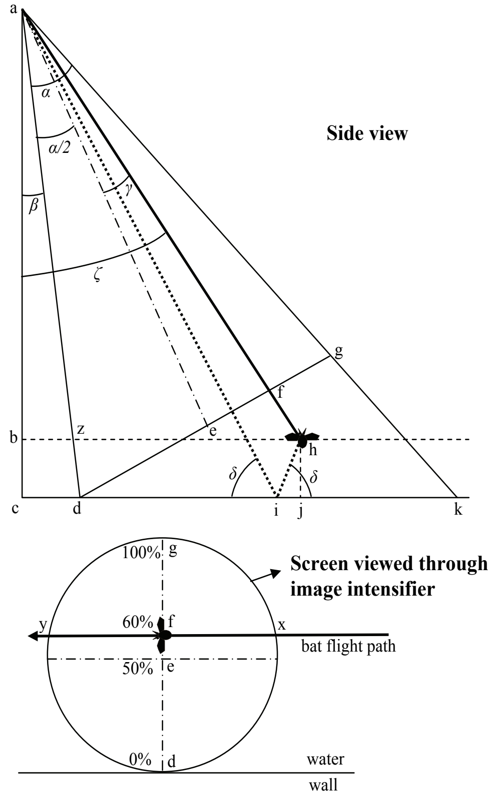

Figure 2. Schematic representation of visual observations made from the top of a rampart wall, of trawling bats hunting low over the water surface close to the wall. Side view of the scene (top) and field of view seen through an image intensifier (bottom) show the method of estimating bat flight height (*hj*) and the distance of the bat to the wall (*hz*). *a*: observation point (visual and acoustic), *h*: position of bat at moment when it crosses the perpendicular of the image intensifier screen, held in such a position that the bottom of the screen rakes the border line of the wall and –water. The full bold line in the side view represents the pathway of the pulse from the mouth of the bat to the microphone in *a*, the bold dotted lines show the pathways of the echo reflected by the water surface in *i*.

Sound analysis

The BatSound programme (Pettersson Elektronik AB) was used to analyse the time expansion recordings. Pulse-echo time interval (*dt*), pulse length and pulse interval were measured in spectrograms made from Fast Fourier Transforms, Hanning window, FFT size: 256 samples, FFT-overlap: -1. The pulse interval (PI) was defined as the time between the start of one pulse and the start of the next. Since pulses and surface echoes overlap in time, the oscillogram could not be used to measure *dt*.

Analysis of time expansion recordings of bats flying below the wall revealed that every pulse was followed by an almost exact copy with a delay of a maximum of 3.1 ms (figure 3). The second pulse is a strong reflection of a point (*i*) on the smooth water surface between the bat and the microphone where the angles of reflection (δ) are the same (figure 2). Siemers et al. (2001) described a similar ground echo in recordings made from an artificial bat positioned 12 cm above a smooth screen in laboratory conditions. The time delay they measured (0.73 ms) corresponded exactly to the height of 12 cm. The field recordings from this study only yielded these strong pulse-echo pairs from recordings made from above the bats; they were not so clearly observed in recordings made from ground level. In recordings made from ground level the reflection point on the surface may be too far away from the bat, so the energy of the sound beam when it hits the surface may be too weak to give a noticeable echo, due to atmospheric attenuation and spherical spreading. In recordings from (nearly) above the bat, the reflection point will be very close to the bat. While trawling bats in horizontal flight emit sound in a directional fashion (and not primarily directed downwards), the surface echoes are still strong enough to be picked up by a microphone at a distance of about 9 m.

Species identification

Trawling bats were identified in the field, by listening to the sounds in the heterodyne mode, with the detector being adjusted to 38 kHz. Dauben-

Variables and equations	**Definition**	**Example**
a	top of the wall where visual observations (image intensifier) and time expansion recordings (ultrasound detector) were done.	
d	bottom of the wall, this is the point where the water surface of the moat touches the wall.	
dk	water surface of the moat	
h	position of the bat at the moment when it crosses the perpendicular of the image intensifier screen at a certain percent of the screen diameter (image intensifier held so that the bottom of the screen raked the border line between wall and water surface).	
hj	bat flight height (cm)	55 cm
ad	length of the inclined side of the wall, measured using a chord (cm).	802 cm
α	field of view of the image intensifier (Deg)	40 Deg
β	angle of the wall inclination, measured using a water level and a protractor (Deg).	9.7 Deg
$ac = ad.\cos\beta$		791 cm
$ab = ac - hj$		736 cm
$bz = ab.\sin\beta$		124 cm
$cd = ad.\sin\beta$		135 cm
$ae = ad.\cos\left(\frac{\alpha}{2}\right)$		754 cm
$de = ad.\sin\left(\frac{\alpha}{2}\right)$		274 cm
$percentSD$	estimated intersection of the bat's flight path with the diameter of the screen of the image intensifier (perpendicular to the wall) expressed as percent of the full screen diameter (%).	60%
$df = 2.de.\frac{percentSD}{100}$		329 cm
$ef = df - de$		54.8 cm
$\gamma = \arctan\left(\frac{ef}{ae}\right)$		4.16 Deg
$\zeta = \beta + \frac{\alpha}{2} + \gamma$		33.8 Deg
$ah = \frac{ab}{\cos\zeta}$	pathway of direct pulse from mouth of bat to microphone (cm)	886 cm
$cj = bh = ab.\tan\zeta$		494 cm
$hz = cj - bz$	horizontal distance bat to wall edge (cm)	397 cm
$ai = \sqrt{ac^2 + \left(\frac{ac.cj}{ac + hj}\right)^2}$	pathway of echo from water surface to microphone (cm)	915 cm
$\delta = \arcsin\left(\frac{ac}{ai}\right)$	angle of sound reflection on the water surface (Deg)	59.7 Deg
$ci = ai.\cos\delta$		461 cm
$di = ci - cd$	distance reflection point water surface to wall edge (cm)	326 cm
$hi = \frac{hj}{\sin\delta}$	pathway of pulse from mouth of bat to reflection point on water surface (cm)	63.7 cm
$xy = 2.de.\cos\left[\arcsin\left(\frac{ef}{de}\right)\right]$	length of the bat's flight path between entry point (x) and exit point (y) of the image intensifier screen (cm)	538 cm
w	flight speed of the bat (supposed) (m/s)	4 m/s
t	time required by bat to cross the screen of the image intensifier (from x to y) at the supposed bat flight speed w (s)	1.3 s
v	speed of sound (cm/ms) at air temperature (°C)	33.1 cm/ms (at 5°C)
$dt = \frac{1}{v}(ai + hi - ah)$	pulse-echo time difference (ms)	2.8 ms

Table 1. Equations used to calculate the pulse-echo time interval *dt* from a known flight height *hj.* Right column: example of a calculation for a flight height of 55 cm and a bat-to-wall distance corresponding to an estimated 60% of the diameter of the screen (as observed through an image intensifier positioned so that the bottom of the screen was set to where the wall and water met (see figure 2).

ton's bats produce dry clicks at this frequency and pond bats relatively loud, wet, smacking sounds of a slightly higher pitch, since the detector was tuned a few kHz above the pond bat's QCF-frequency (33-35 kHz) (Limpens & Roschen 1995, Limpens 2001). Each identification was checked by analysing the corresponding time expansion recordings. The pulse series of pond bats included at least some characteristic FM-QCF-FM signals with the QCF part at 33-35 kHz. Daubenton's bats don't use QCF parts in their signals. Visual observations confirmed the acoustic identification. When passing close to the wall, the silhouettes of pond bats seen through the image intensifier were clearly larger than those of Daubenton's bats, and the difference in head-body size was particularly obvious. Pond bats also flew faster than Daubenton's bats, although no speed measurements were done.

In July 2000 samples of both species were caught in Japanese nets positioned under a low bridge over these moats and identification was confirmed by examination of the bat and measuring the forearm length (following Schober & Grimmberger 1998). In August 2000 a small pond bat maternity roost (20-30 individuals) was found about 5 km from the recording site, by radio tracking a juvenile pond bat that was caught in the Japanese net (Van De Sijpe 2001, Van De Sijpe 2003).

Flight height calculation method

The pulse-echo time interval *dt* can be calculated from a known flight height *hj* by applying the equations and relations shown in table 1 and figure 2. This calculation requires the following input data: the length of the inclined wall (*ad*) ,the view angle of the image intensifier (α), the angle of wall inclination (β), and the distance of the bat to the wall (*hz*). The length *ad* and the angle β were measured in the field, the angle α was taken from the image intensifier specifications and *hz* was derived by estimating the position of the bat in the screen of the image intensifier, expressed as percent of the full

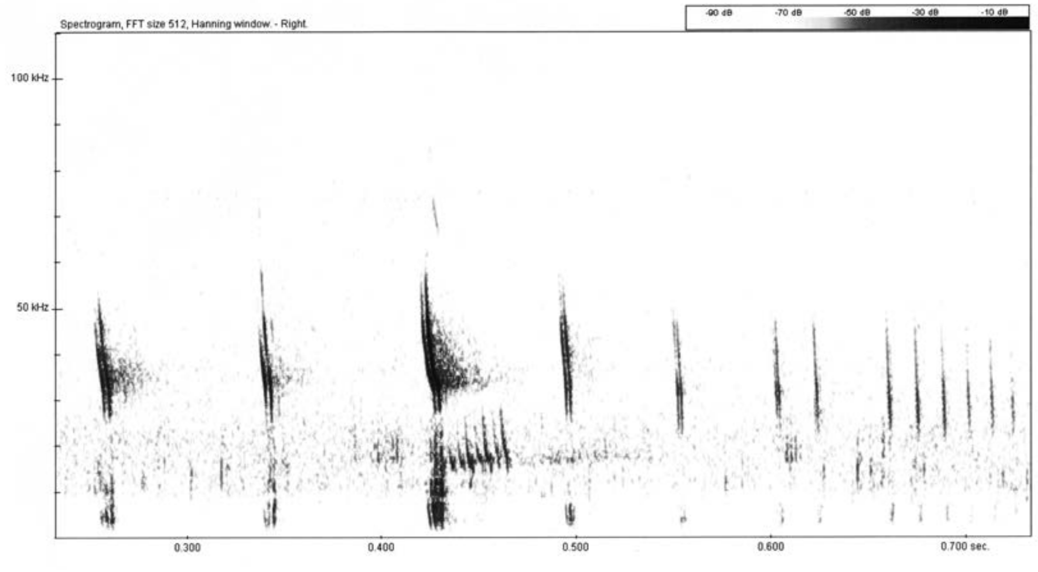

Figure 3. Spectrogram of a trawling pond bat in approach phase prior to a feeding buzz. The recording was made from the top of a high stone wall with the bat flying below over the water surface close to the wall. All the original pulses were followed by surface echoes, exact copies of the original pulse. As the bat approached the water surface to capture a prey item, the time interval of the pulse-echo pairs gradually shortens.

screen diameter (*percentSD*) at which the bat intersects the perpendicular (figure 2).

An iteration of the above calculation was done based on a measured pulse-echo time interval (*dt)* to find the unknown flight height *hj*. In the first step a flight height *hj* was assumed and *dt* was calculated and compared with the measured *dt*. The calculation was repeated until the calculated *dt* became equal to the measured *dt*.

Error estimates

Errors due to inaccurate estimation of the percent of the screen diameter
Assuming *dt* = 2.8 ms, and with the percent screen diameter estimated at 60%: the calculated flight height would be 55 cm. If the percent screen diameter was 70% the flight height would be 57.5 cm (4.5% error). At 80%, 90% and 100% screen diameter the error would increase to 10%, 16% and 24% respectively. For 50% screen diameter an error of 3.6% was found. Although the percent screen diameter is an estimate, the accuracy obtained in the field is estimated to be within ± 10%.

Errors due to incorrect timing of recording
Assuming *dt* = 2.8 ms, and with the percent screen diameter estimated at 60%: the calculated flight height would be 55 cm for a bat emitting a pulse precisely at the intersection with the perpendicular (*hz* = 369 cm). Incorrect timing of recording will cause a deviation from the perpendicular (figure 4). Assume that the recording is stopped when the bat emitted a pulse at *h*' (the exit point of the screen) instead of *h*. The distance *hh*' would be 269 cm, and the correct bat to wall distance would be 457 cm instead of 369 cm. This would give a flight height of 58 cm instead of 55 cm for the given dt of 2.8 ms, hence a 5.5% error. Bats flying at a speed of 4 m/s stay within the field of vision for a period of about 1.3 s, and will take circa 0.6 s to travel from *h* to *h*'. The time required by the bat to cross the entire screen is long enough for the observer to react in a more or less timely manner. In reality the error induced by incorrect timing of recording is estimated to be less than in the example above.

Errors due to discontinuous sound emission
Assume *dt* = 2.8 ms, and the percent screen diameter is estimated at 60%: the calculated flight height would be 55 cm for a bat emitting a pulse exactly at the intersection with the perpendicular. Bats flying at a speed of 4 m/s using a pulse repetition rate of 10 Hz (average pulse interval 100 ms) will travel a distance of 40 cm between two pulse emissions. Assume the recording was stopped exactly at the intersection with the perpendicular, but the bat emitted the last pulse 40 cm before the intersection, when at point u (figure 4). The flight height would be 55.1 cm (0.2% error).

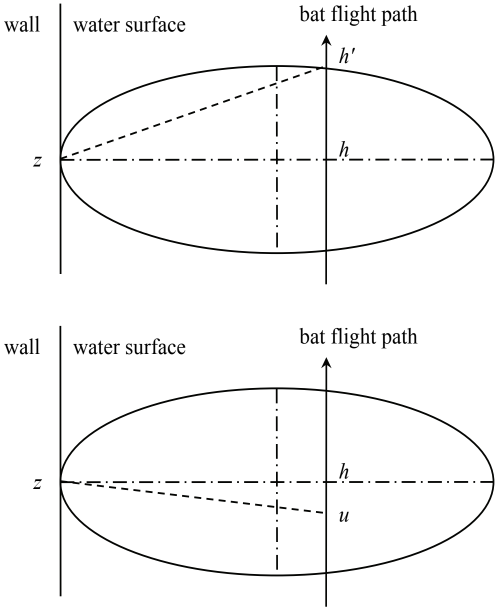

Figure 4. Examples used for error estimations due to incorrect timing of recording (above) and discontinuous nature of sonar emissions (below). The cross section of the horizontal plane through *z* and *h* (the flight height of the bat) with the conical space projected on the screen of the image intensifier is elliptical.

Data collection and statistical analysis

Sound recordings of pond bats and Daubenton's bats were made on the 29th of March 2004 and the 9th and 10th of April 2004. On these nights between 1-5 pond bats and 1-2 Daubenton's bats hunted over the water surface north of the Menin Gate Bridge. One time expansion sequence was analysed of a pond bat capture buzz close to the wall at circa 50% of the screen diameter and one bat pass of a pond bat in the search phase flying parallel to the wall was made at circa 60% of screen diameter. These sequences were used to estimate the change of flight height during the bat pass or manoeuvre. Additionally the flight height of bats in the search phase of hunting, when passing in front of the observer at circa 60% screen diameter was calculated for 30 bat passes of Daubenton's bats and 25 bat passes of pond bats. In parallel search phase flights pond bats did not fly closer to the wall than the estimated 60%, but during capture attempts they came closer (circa 50%). Daubenton's bats flew closer and both species flew also further away (>60%) but these recordings were not retained for analysis. To obtain an accurate value of flight height, it was necessary to find and record the pulse corresponding to the position of the bat as closely as possible to the intersection point with the perpendicular. The instant that the bat crossed the screen of the image intensifier in the centre, the time expansion button on the back of the detector was pushed and the contents of the detector's memory were transferred to the recorder. The pulse emitted by the bat when it passed the perpendicular of the screen then corresponded to the last pulse of the recorded time expansion sequence. Deviations that occurred have been discussed above.

Data sets of pulse-echo time interval, flight height, pulse length and pulse interval of pond bats and Daubenton's bats were statistically compared using Mann-Whitney non-parametrical tests with the Analyse-it programme running in Microsoft Excel (Analyse-it Software Ltd, Leeds, UK).

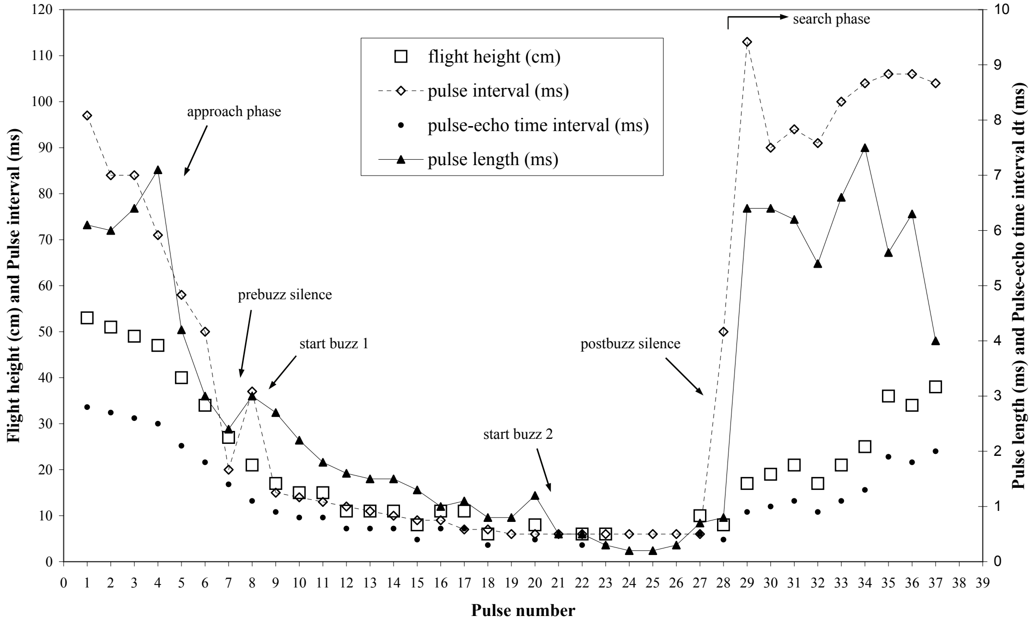

Figure 5. Change of pulse-echo time intervals, flight height, pulse length and pulse interval during a capture attempt by a trawling pond bat (39 consecutive pulses analysed). The various stages of the capture attempt were evaluated by pulse length and pulse interval changes, as per Kalko and Schnitzler (1998).

Results

Observations of hunting activity

Bat hunting activity over the Ieper town moats usually resumes every year by the middle or the end of March, following the winter months of inactivity. The often low temperatures in early spring, means that activity over the moats at this time is generally limited to four more or less cold-tolerant species: Daubenton's bat, pond bat, common pipistrelle (*Pipistrellus pipistrellus*) and Nathusius' pipistrelle (*Pipistrellus nathusii*). Both Pipistrelle species were active shortly after dusk but often disappeared after one to two hours, when the temperature dropped and the numbers of flying insects became too low. Both trawling bats continued their hunting activities for longer periods, even when the air temperature became as low as two to three degrees Celcius. Apparently there was still enough insect activity on the water surface or in the air just above it. Air temperature can be several degrees higher a few cm over water surfaces than a few metres higher (A.-J. Haarsma, personal communication).

During cold spring nights both Daubenton's bats and pond bats regularly flew close and parallel to the inner stone wall. The search flight was now and then interrupted by a manoeuvre (a tight circle when seen from above), which coincided with a feeding buzz (as heard through a bat detector) and visual observations revealed expanding circular waves in the water, indicating that the bat broke the surface. Later in the season, when temperatures increased the bats did not forage so close to the inner walls. The early spring bat activity was related to the mass emergence of non biting midges (Chironomidae) as revealed by visual observations with a torch. These midges and the emerging pupae also attracted many small surface dwelling fish, that were observed feeding on them. The moats are well protected against western winds by the high wall and tall trees on the rampart talus, and the shallow water is exposed to the morning and

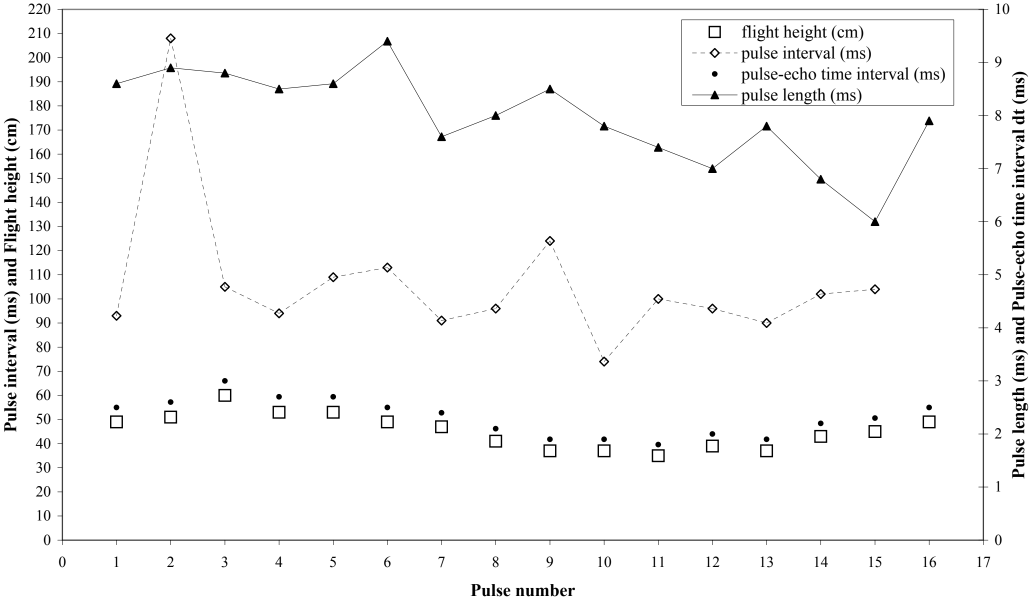

Figure 6. Change of pulse-echo time interval, flight height, pulse length and pulse interval during a bat pass of a trawling pond bat in the search phase of hunting.

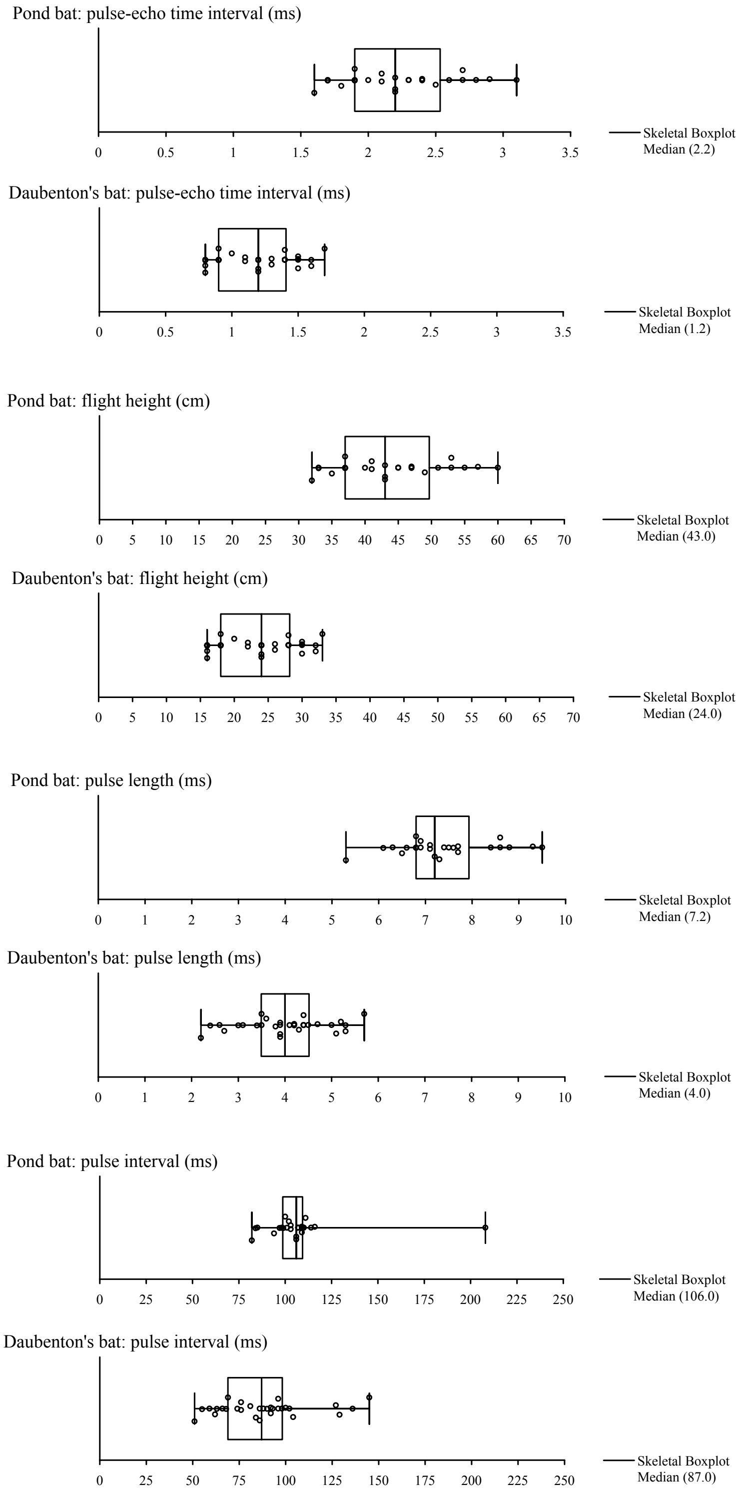

Figure 7. Dot and box plots of pulse-echo time interval, (ms) flight height (cm), pulse length (ms) and pulse interval (ms) including 25 recordings of pond bats and 30 recordings of Daubenton's bats in linear search flights parallel to a rampart wall at a distance of circa 4 m from the wall. Dots represent individual data, the box defines first quartile, median and third quartile, the traits define minimum and maximum values

midday sunshine. In early spring shallow water warms up quicker than deep water, and so insect activity starts earlier in shallow waters. The presence of several bat hibernacula in the immediate vicinity of the moats also influences the intense early season bat activity.

Changes of flight height during a pond bat capture buzz

Figure 5 shows the change of pulse-echo interval, flight height, pulse length and pulse interval of a series of consecutive pulses from a time expansion recording of a pond bat manoeuvring in a tight circle at a distance of circa 3 m from the wall (estimated 50% of screen diameter) whilst trying to catch an insect. The capture attempt was observed visually by using the image intensifier and expanding waves were observed in the water indicating that the bat briefly touched the water surface during the attempt. The time interval between pulse and surface echo gradually decreased from 2.8 ms in the initial search phase to values as low as 0.3 ms during buzz 1 and buzz 2 and increased again after the post-buzz silence towards 2 ms at the 9th search phase pulse following the post-buzz silence. This corresponds to a flight height change from 53 cm in the search phase to about 6 cm during the final stages of the capture buzz, and back to 38 cm at the ninth pulse following the post-buzz silence (figure 5). These results confirm that the method for estimating flight height appears to be quite accurate because trawling bats are known to gradually descend to the water surface (pointed dips) in order to pick up an insect sitting on the water surface. At the moment of capture the hind feet just rake the water surface, the mouth of the bat then is at a height above the water of slightly less than the head-body length (5.5–6.7 cm for the pond bat, according to Schober & Grimmberger 1998). Other recordings made of capture buzzes of both pond bats and Daubenton’s bats showed a similar pattern of gradually decreasing flight height from search to final buzz phase.

Changes of flight height during the linear search phase flight of a pond bat

Figure 6 shows the flight heights of a pond bat in a linear search phase flight, while passing parallel to the wall at an estimated distance of about 4 m (60 percent screen diameter). During 16 consecutive pulses the calculated flight height varied between 60 and 35 cm.

Flight heights of pond bats and Daubenton’s bats in the search phase

Figure 7 shows dot and box plots for pulse-echo time interval, flight height, pulse length and pulse interval for 25 recordings of pond bats and 30 recordings of Daubenton’s bats in the linear search phase. Pulse-echo time intervals were significantly greater in pond bats than in Daubenton’s bat (pond bat median 2.2 ms, Daubenton’s bat median 1.2 ms, $P<0.0001$) and so were the calculated flight heights (pond bat median 43 cm, Daubenton’s bat median 24 cm, $P<0.0001$). Pond bats used significantly longer pulses (pond bat median 7.2 ms; Daubenton’s bat median 4.0 ms; $P<0.0001$) and longer pulse intervals (pond bat median 106 ms; Daubenton’s bat median 87 ms; $P=0.0003$) than Daubenton’s bats.

Discussion

Comparison with literature data

The pond bat flight heights recorded in this study (6-60 cm) accord well with previous data (10-60 cm) published by Baagøe (1987). The median of 43 cm is also close to the height of circa 50 cm found by Siemers et al. (2005) who used videogrammetry in the artificial conditions of a flight room where pond bats searched for mealworms on a linoleum screen. However, the heights of hunting bats in the search phase (median 43 cm) were markedly higher than the ones of commuting bats obtained using photogrammetry by Britton et al. (1997) (26 ± 2 cm). This said, the data in this study are restricted to hunting activities and limited to a couple of nights in early season and at the same location. More data will be required to evaluate potential flight height differences due to behaviour (commuting vs. hunting), habitat type and/or season.

The flight height found for hunting Daubenton's bats (median 24 cm, min-max: 16-33 cm) is higher than the value reported by Kalko and Schnitzler (1988) by a photographic method (15.8 ± 6.7 cm, max 28 cm) and Baagøe (1987) (10-20 cm) but falls within the range of heights reported by Siemers et al. (2001) of Daubenton's bats flying over an artificial smooth surface (5-30 cm) in laboratory conditions.

Possible relations between height and flight behaviour in trawling bats

Bats fly by alternating upstrokes and downstrokes of their wing membrane. In order to avoid collisions with the water surface trawling bats have to fly as horizontally as possible especially when they fly very low over the surface and need to reduce the amplitude of their wing beats to avoid contact with the water. Piscivorous bats raking through the water with their claws for prolonged distances and flying as low as 4 cm above the surface (i.e. *Noctilio leporinus*) are the most extreme example. Insectivorous trawling bats catching prey from the surface by using pointed dips fall somewhere between the highly specialised piscivores and fully aerial hawking bats operating at heights of a few metres. Because of its lower flight height Daubenton's bat seems to be a more specialised trawling species than the pond bat.

The pond bat (17 g) has a higher wing loading (10.4 N/m²) compared to Daubenton's bats (7 g; 7.0 N/m²) and therefore is less manoeuvrable and tends to fly faster (Norberg & Rayner 1987, Schober & Grimmberger 1998). Britton et al. (1997) found flight speeds of 3.21 ± 1.92 m/s in hunting pond bats and 7.35 ± 1.26 m/s and 9.13 ± 0.41 m/s in commuting pond bats, depending on the location. Compared to Daubenton's bats the wing tips of pond bats are longer (wing tip length ratio pond bat: 1.43, Daubenton's bat: 1.22) and more pointed (wing tip index pond bat: 1.20; Daubenton's bat: 2.05) (Norberg & Rayner 1987). The wing tip values of pond bats are quite close to those of fast hawkers that operate at high altitude (*Nyctalus*, *Vespertilio*). High wing loading, long and pointed wingtips are adaptations to fast and agile flight at the expense of manoeuvrability. Pond bats prefer large open water bodies where speed and agility can be advantageous and manoeuvrability less important.

Daubenton's bat is a lightweight version of trawling bat with lower wing loading and shorter and more rounded wing tips, thus having a slower and more manoeuvrable flight (Norberg & Rayner 1987). Baagøe (1987), Kalko and Schnitzler (1988) and Jones and Rayner (1988) have reported flight speeds of 4.1 m/s, 3.4 ± 0.6 m/s and 3.87 ± 0.84 m/s respectively. Daubenton's bats are probably more efficient in trawling close to obstacles such as the edges of reedbeds and among the narrow spaces of riverine habitats thanks to their better manoeuvrability.

Daubenton's bat's lower flight height may provide it with greater energy savings thanks to the ground effect (Norberg & Rayner 1987, Britton et al. 1997) although the potential benefit of the ground effect on trawling bats should be studied more in detail.

Possible relations between height and echolocation behaviour in trawling bats

Pond bats and Daubenton's bats also differ in their echolocation behaviour (Ahlén 1990, Limpens & Roschen 1995). Pond bats use longer pulses with a smaller bandwidth, hence their distance of focus will be greater (Holderied et al. 2006, Boonman 2007, personal observations). They also use a lower peak frequency (pond bat: 33-38 kHz, Daubenton's bat: 38-45 kHz) and often a QCF part, both features that enlarge the detection distance (Schnitzler et al. 2003). In combination with the higher flight speed, these longer detection ranges may allow pond bats to scan larger areas of open water surface or larger volumes of air per unit of time than Daubenton's bats. As such pond bats may specialise on larger sized insects available in quite low densities. Higher flight heights may still provide small angles of incidence at the (larger) distance of focus, so pond bats may still also take advantage of the low background noise of smooth water surfaces, as stated by Siemers et al. (2001). In this study trawling pond bats performed several feeding buzzes in which the bat touched the water surface. The search phase heights found in this study (median 43 cm, min-max 32-60 cm) are apparently still low enough to detect small sized aquatic insects on the water surface. In summer pond bats sometimes use yet faster hunting flights while foraging low over open water for big insects (i.e. moths). In spite of the low flight heights in the search phase this strategy seems to be more a kind of fast aerial hawking than trawling, as the bats often catch the insects above their own search phase height (Van De Sijpe & Holsbeek 2007).

Daubenton's bats use a range of shorter pulse lengths of a higher peak frequency without QCF but with higher starting frequencies and larger bandwidths than pond bats (Boonman 2007). Although the shorter pulses probably limit the detection distance to a smaller volume of air in front of the bat, the shorter pulses and greater bandwidths yield more precise acoustic images at short range and a shorter distance of focus (Schnitzler et al. 2003, Holderied et al. 2006). This will be advantageous close to the bank side or near to floating aquatic vegetation where background echoes might interfere with prey echoes.

Potential niche differentiation between trawling bats

The two sympatric trawling insectivorous bats of the Northwestern Palaeartic, Daubenton's bat and the pond bat, differ in many aspects such as body size and weight, jaw and teeth row size, flight morphology, flight height, echolocation, roosting ecology and habitat preferences (Baagøe 1987, Norberg & Rayner 1987, Kapteyn 1995, Mostert 1997, Schober & Grimmberger 1998, Limpens et al. 1999, Krapp 2001, Dietz & von Helversen 2004). Although they are potential competitors since both hunt for prey exposed on the water surface and flying in the air just above it, niche differentiation seems to exist and might explain the large overlap of their distribution ranges and the fact that they sometimes hunt together in the same habitat.

Daubenton's bat is an efficient and successful trawling bat, given its large distribution area, high population density and the diversity of aquatic habitats it uses. Its range spans nearly the entire arboreal zone of the Palaearctic from the British Isles to the Far East, and also enters the Mediterranean zone in the south (Horáček et al. 2000) where Daubenton's bat competes with the Mediterranean trawling insectivorous and piscivorous long-fingered bat *Myotis capaccinii* (Aihartza et al. 2003, Levin et al. 2006, Biscardi et al. 2007). Based on DNA studies, Stadelmann et al. (2004) found that the lineage leading to the recent Daubenton's bat separated probably as late as the early Pliocene from a common ancestor shared with the forest-dwelling *Myotis bechsteinii*. The lineage leading to the recent pond bat apparently separated from an ancestral form in the earliest stages of the *Myotis* radiation, most likely some 10 million years ago in late Miocene (Stadelmann et al. 2004). Today the pond bat occupies a limited distribution area within the temperate humid and boreal zones of the western Palaeartic and is a rare species in large parts of its range (Horáček & Hanák 1989, Limpens et al. 1999, Horáček et al. 2000, Ciechanowski et al. 2007). This bat seems to only build large populations in areas with abundant large water surfaces and the core centres of its population are dispersed as islands in lowlands of northerly latitudes.

Further studies

Further work is recommended to study flight heights, speeds and flight mechanisms of trawling bats in more detail in order to better understand differences in behaviour and niche differentiation as well as to find answers to questions such as how trawling bats maintain the right height. The method described in this paper can be used in various locations where a microphone can be positioned above the bat. These would include high quay walls in villages, ramparts with wet moats bordered by walls, bridges over canals and rivers etc. If recordings can be made perpendicularly above the bats the equation for solving flight height will be much simpler than in this study, which involved oblique viewing. Other more accurate techniques such as flight path tracking by laser scans, stereo videogrammetry, or sound recording by multiple microphone arrays, as suggested by Jones and Holderied (2007) can also be recommended. The use of microphone arrays low over water may however be difficult since various reflections might result in ambiguous bat positions.

Conclusion

When foraging together over the Ieper town moats in March and April, both pond bats and Daubenton's bats used the trawling foraging tactic to feed extensively on emerging early season non-biting midges. By measuring the minute time intervals between pulses and echoes reflected by the water surface, the flight height of the bats at moments when the bats passed close to the stone wall could be estimated. This method confirmed literature data asserting that the medium-sized pond bat usually hunts higher over the water surface than the smaller Daubenton's bat. Whilst flying in a similar way in a same habitat and at a similar distance to the nearest clutter producing background (i.e. a stone wall), pond bats used longer pulses and longer pulse intervals than Daubenton's bats. Gradually decreasing time intervals during pond bat capture buzzes revealed that the bats descended to the water surface to catch insect prey and visual observations of circular waves in the water, seen from above, confirmed that the bat broke the water in the final stages of the capture buzz.

Acknowledgements: I would like to thank Alex Lefevre, coordinator of the Flemish bat group, for his advice on available literature about Daubenton's bats and pond bats, the two anonymous referees for their valuable comments and suggestions, which substantially improved this paper. Thanks also to Ben Verboom and Nick Parrott (Textual Healing) for improving the layout and English text.

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Samenvatting

Vlieghoogte bij harkende meervleermuizen en watervleermuizen

Dit artikel beschrijft een indirecte manier om de vlieghoogte van harkende vleermuizen te schatten aan de hand van zeer kleine tijdsintervallen tussen de pulsen en echo’s van het wateroppervlak. De bijzondere locatie van de Vauban-vestingen rond de stad Ieper, maakte het mogelijk om tijdexpansie opnamen te maken van harkende vleermuizen schuin boven de vleermuizen. De opnamen werden gemaakt op de top van een hoge muur die een brede vestinggracht begrenst aan de binnenzijde, terwijl watervleermuizen (*Myotis daubentonii*) en meervleermuizen (*Myotis dasycneme*) over het wateroppervlak jaagden en daarbij parallel en vrij dicht langs de muur vlogen. De sterke echo’s waren bruikbaar om de vlieghoogte vrij nauwkeurig te schatten, zo bleek uit een gedetailleerde analyse van een vangstmoment van een meervleermuis dicht langs de muur, waarbij in de finale fase de vleermuis de waterspiegel doorbrak en uitdijende golfjes in het water zichtbaar werden. De tijdsintervallen tussen puls en echo verminderden gradueel van zoekfase tot de finale buzz fase. Deze stemden overeen met een geleidelijke vermindering van de vlieghoogte van circa 53 cm in de zoekfase naar circa 6 cm in de buzz fase. Geluidsanalyses van jagende water- en meervleermuizen bracht aan het licht dat meervleermuizen hoger boven de waterspiegel vlogen (mediaan 43 cm) dan watervleermuizen (mediaan 24 cm) tijdens de zoekfase van de jachtvlucht.

Received: 26 March 2008
Accepted: 10 September 2008