

# Echoes of bat-pollinated bell-shaped flowers: conspicuous for nectar-feeding bats?

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## Summary

Nectar-feeding glossophagine bats searching for flowers are guided by their echolocation system as well as olfactory cues in detecting and recognizing nectar sources. Therefore, chiropterophilous plants, which depend on these bats as pollinators, may be expected to have evolved acoustically conspicuous flowers that facilitate detection. As it is poorly understood how bats manage to find and recognize flowers acoustically, we investigated the echoes of some of the flowers pollinated by bats.

Echoes of bell-shaped bat-pollinated flowers have characteristic features with respect to the echoes they reflect to a calling bat and differ from the echoes of leaves or other objects in their surroundings: the echoes are comparatively long and of complex spectral composition.

Owing to the specific shape of the flowers, characteristic ‘spectral directional patterns’ result when the spectra of the echoes are plotted against the angle of sound incidence.

We suggest that bats are able to recognize such flowers – and probably other objects as well – not only by a characteristic spectral composition of the echo but also by comparing sequential echoes, at the same time taking into account their exact calling position relative to the object.

Key words: bat-pollination, echolocation, plant echo, acoustic object recognition, glossophagine bat, chiropterophilous flower.

## Introduction

The flowers of many tropical plant species are visited and pollinated by small nectar-feeding bats (Vogel, 1958, 1968, 1969a,b; Dobat, 1985); it is estimated that approximately 1000 plant species are pollinated by bats in the neotropics alone (Winter and v. Helversen, 2001). Neotropical flower-visiting bats belong to the family of leaf-nosed bats (Phyllostomidae). In particular, the subfamily Glossophaginae contains species that are highly specialized for nectar exploitation. Like hummingbirds, glossophagine bats are able to hover in front of a flower while licking nectar with tongues almost as long as their bodies, and this allows the exploitation of even small amounts of nectar (v. Helversen and v. Helversen, 1975a,b). These adaptations – hovering flight and extremely long tongues – allowed a large number of species of many different plant families to use these bats as pollinators.

To revisit known nectar sources, the bats use, above all, their excellent spatial memory. This corresponds to the long flowering period of most bat-pollinated plants, to the advantage of both: the bats can rely on the nectar source, and the plants can rely on being found and pollinated. To find new flowers, glossophagine bats use their well-developed senses of olfaction (e.g. Vogel, 1968, 1969a,b; Knudsen and Tollsten, 1995; v. Helversen et al., 2000) and vision (e.g. Suthers et al., 1969; J.

Lopez, Y. Winter and O. v. Helversen, manuscript in preparation) but, as in all microchiropteran bats, their orientation is mainly guided by their highly developed echolocation system (Griffin and Novick, 1955; Howell, 1974). This enables them to manoeuvre even in dense and clutter-rich vegetation. Typically, the echolocation calls of glossophagine bats are very short (0.5–3 ms) and mostly faint, which is why they have been described as ‘whispering bats’ (Griffin and Novick, 1955). The calls are multiharmonic, broadband, downward-modulated frequency sweeps. In many of the smaller species like *Glossophaga*, the frequency modulation starts at very high frequencies of about 140 kHz and ends at about 60 kHz (D.v.H., M.W.H. and O.v.H., unpublished observations).

Since the pioneering work of Donald Griffin, a large number of studies have investigated how insectivorous, aerial-hawking bats can detect and locate flying prey (for reviews, see Griffin, 1958; Neuweiler, 1989, 1990; Schnitzler and Kalko, 1998). Bats can also discriminate among different prey objects presented in uncluttered situations (Simmons et al., 1974; Simmons and Chen, 1989; v. d. Emde and Schnitzler, 1990) using temporal as well as spectral cues of the echoes (Simmons et al., 1990; Mogdans and Schnitzler, 1990; Schmidt, 1992).

However, it is not yet understood how bats recognize motionless objects in clutter-rich surroundings and to what extent they are able to find such objects. Many observations in the field suggest that frugivorous and nectarivorous bats cope excellently with this problem, and a small number of experimental studies have demonstrated it (Bradbury, 1970; Kalko and Condon, 1998; v. Helversen and v. Helversen, 1999; Schmidt et al., 2000). However, recognition of motionless prey is severely impeded by clutter-rich surroundings; trawling *Myotis* bats could detect prey only on smooth surfaces that reflect away most of the sound energy (Siemers et al., 2001), and it has even been claimed that other *Myotis* species are 'acoustically blind' to motionless prey in echo-cluttering habitats (Arlettaz et al., 2001).

Most bat-pollinated flowers can be assigned to one of two morphologically different types: 'pincushion-type' flowers, with long and numerous stamens, and 'bell-shaped' flowers. Bell-shaped flowers may differ widely in size, ranging from very large, cup-like flowers to small flowers no bigger than a 'head mask' for the bat (Vogel, 1968, 1969a,b; Dobat, 1985). Large, cup-like flowers, such as the flowers of the Balsa tree (*Ochroma lagopus*), allow the bats to land and, typically, are visited by large unspecialized bat species, while small, bell-shaped flowers can be exploited only by specialized bats. Although the small glossophagine bats could easily land on the flowers (and do so occasionally), they typically lick nectar while hovering in front of them (v. Helversen and v. Helversen, 1975b). Exploitation during hovering implies that the rapidly approaching bat has to meet the entrance of a flower with its snout or tongue or both, with the precision of a few millimetres, to gain access to the nectar. This seems to be no easy task: indeed, in some of their approaches the bats miss the target, as revealed by infrared video recordings in the field (D.v.H. and O.v.H., unpublished observations).

While insects, as prey of insectivorous bats, should have evolved to produce inconspicuous echoes that are difficult to localize or that even mislead their predators, bat-pollinated plants, in competition for these effective pollinators, should have evolved acoustically conspicuous flowers that facilitate detection, thereby reducing the bat's foraging costs in terms of time, risk and energy. Therefore, to be easily detected, bat-pollinated flowers may be expected to have evolved shapes, textures and structures generating echoes that are distinctly different from the general echoes of the surrounding vegetation.

In this study, we investigated the echoes of some bell-shaped flowers of bat-pollinated plant species. We consider two questions: (1) do bell-shaped forms give rise to unique echoes, which allow them to be discriminated from those of other objects, and (2) are the echoes of bell-shaped flowers particularly suited to lead the bat to the nectar chamber?

## Materials and methods

### Flowers

We measured the echoes of bell-shaped flowers in four bat-pollinated plant species: *Amphitecna latifolia* Mill. A. H.

Gentry (Bignoniaceae), *Crescentia cujete* L. (Bignoniaceae); *Vriesea gladioliflora* Wendland (Bromeliaceae) and *Markea neurantha* Hemsl. (Solanaceae). The flowers of *A. latifolia* and *C. cujete* are cauliflorous and have a frontal diameter of approximately 25 mm and 45 mm, respectively. *V. gladioliflora* has a long, rod-like inflorescence housing approximately 30 buds, which open one by one on successive nights. The diameter of the corolla opening is approximately 20 mm in this species. While the flowers of these plants are oriented more or less horizontally, the inflorescences of *M. neurantha* are flagelliflorous, causing the openings of the flowers to be directed downwards. The frontal diameter of the corolla is approximately 30 mm.

Flowers of *M. neurantha*, *V. gladioliflora* and *C. cujete* were collected at the OTS (Organization for Tropical Studies) field station, La Selva, Costa Rica; the flowers of *A. latifolia* were kindly provided by Dr Günter Gerlach, Botanical Garden, Munich.

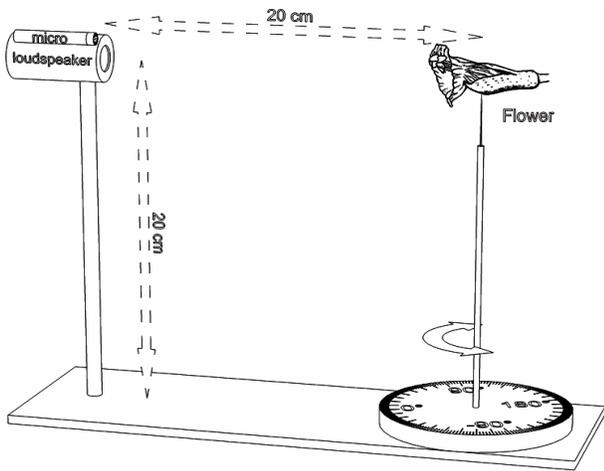
### Artificial hollow forms

For comparison, we also investigated the echoes of three artificial concave objects, all with the same circular opening diameter: a hollow hemisphere ( $r=18$  mm), a paraboloid ( $y=0.111x^2$ , cut at a height of  $y=36$  mm) and an ellipsoid ( $a=44$  mm,  $b=20$  mm), cut perpendicularly to the long axis so that a circular opening with  $r=18$  mm and a depth of 25 mm resulted. The three forms were made of plastic (thickness, 0.5 mm) with an acoustic impedance  $10^4$  times as great as that of air – thus absorption can be neglected (Fletcher, 1992).

### Echo measurements

The objects to be irradiated were impaled by a long, very thin insect pin or a similarly thin palm prickle at the top of a thin holder mounted in the centre of a small turntable. Revolving the turntable allowed irradiation of the objects from all directions in one plane. The front view of the object was adjusted to  $0^\circ$ . The loudspeaker and microphone were fixed at a distance of 20 cm from the target at the same height as the target object (Fig. 1).

As temporal structure and spectral composition of an echo depend not only on the angle of sound incidence but also on the position of the microphone relative to the sound source, we tried to mimic the dimensions of a bat's mouth and ears, i.e. they had to be as small and close to each other as possible. We used a custom-built condenser speaker with a membrane of 15 mm diameter and 1/4" microphones without protecting grid (either Brüel & Kjaer 4135 with sound level meter 2209 or GRAS 40BF with preamplifier 26AB and power module 12AA). The distance between the centres of the microphone and the loudspeaker was 18 mm. The microphone was placed coaxial to the loudspeaker, approximately  $45^\circ$  laterally above the horizontal with respect to the midpoint of the loudspeaker membrane. The frequency responses of the loudspeaker and microphone allowed measurements between 20 kHz and 140 kHz, which, on the whole, covered the frequency range of the echolocation calls used by most flower-visiting bats.



Impulse response

Echoes were measured as impulse response functions of the scattering object, i.e. as the echo that the object would produce when irradiated with a single click of very short duration (a Dirac impulse). The disadvantage of such short impulses is that they contain relatively little energy. Because the size of the loudspeaker had to be small in order to mimic the proportions of a bat's head, we did not compensate this lack of energy by employing a larger speaker but used the so-called 'maximum length sequences' (MLS) method to measure the impulse response function. The basis of the MLS method is the playing

Fig. 1. Experimental setup for measuring the echoes of flowers (and other objects). Microphone (Brüel & Kjaer or GRAS 1/4" condenser microphone) and loudspeaker (15 mm diameter) were as close to each other as possible, with their centers at a distance of 18 mm apart. The flower was fixed on top of a thin holder, which projected from a slender rod, at a distance of 20 cm from the loudspeaker–microphone array, and could be rotated by hand on a turntable.

of a predetermined sequence of impulses of variable length and intervals instead of repeating only one single impulse. This results in a much better signal-to-noise ratio. MLSs are designed to have no internal periodicity and therefore show a perfectly narrow autocorrelation function. The impulse response is not directly accessible from the recordings but can be obtained from the recorded signal by combining it with the original MLS in a 'fast Hadamard transformation' (FHT). The impulse response of the object is then selected in the time domain, and its frequency response (spectrum) calculated from the impulse function using fast Fourier transformation (FFT; window size 256 or 1024 samples for artificial forms and natural flowers, respectively; rectangular window).

We used an MLS of 16383 samples length with a duration of 32766 ms. Replay and recording were sample-synchronous at a sampling rate of 500 kHz. The MLS signal was continuously replayed *via* the loudspeaker by a custom-built sound generator (USSY, Technische Hochschule Darmstadt). The microphone signal was digitized with 12-bit resolution and recorded by a custom-made hard disc recorder (Institut für Technische Elektronik, Universität Erlangen).

As the frequency response of the loudspeaker was not sufficiently flat, we first had to determine the impulse response of the loudspeaker alone. This is usually done with the microphone facing the loudspeaker. As we wished to keep the position of the loudspeaker and microphone constant throughout all measurements, we replaced the object with an even plate of metal directed perpendicularly to the angle of sound incidence. The plate was large enough to reflect the sound wave back to the microphone (plate diameter approximately 40 cm). Thus, we obtained the same impulse response as we would have if we had placed the microphone on the acoustic axis facing the loudspeaker at twice the distance from the flower (i.e. 40 cm). The frequency response (spectrum) of the loudspeaker was then calculated from its impulse response as above. The actual spectra of the flower echoes, without influence of the loudspeaker frequency characteristic, were

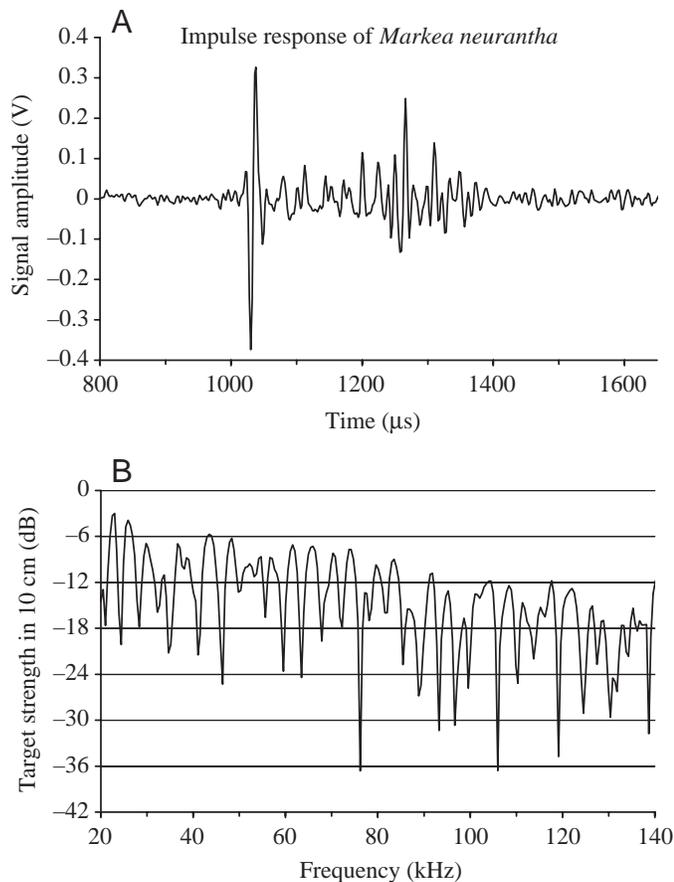


Fig. 2. Impulse response (A) and spectrum of the impulse function (B) of an echo of the flower of *Markea neurantha*, irradiated from 4° lateral to the longitudinal axis of the bell. The grey tone gradation corresponds to the attenuation steps of the echoes in Figs 3E, 4E, 5E and 6E.

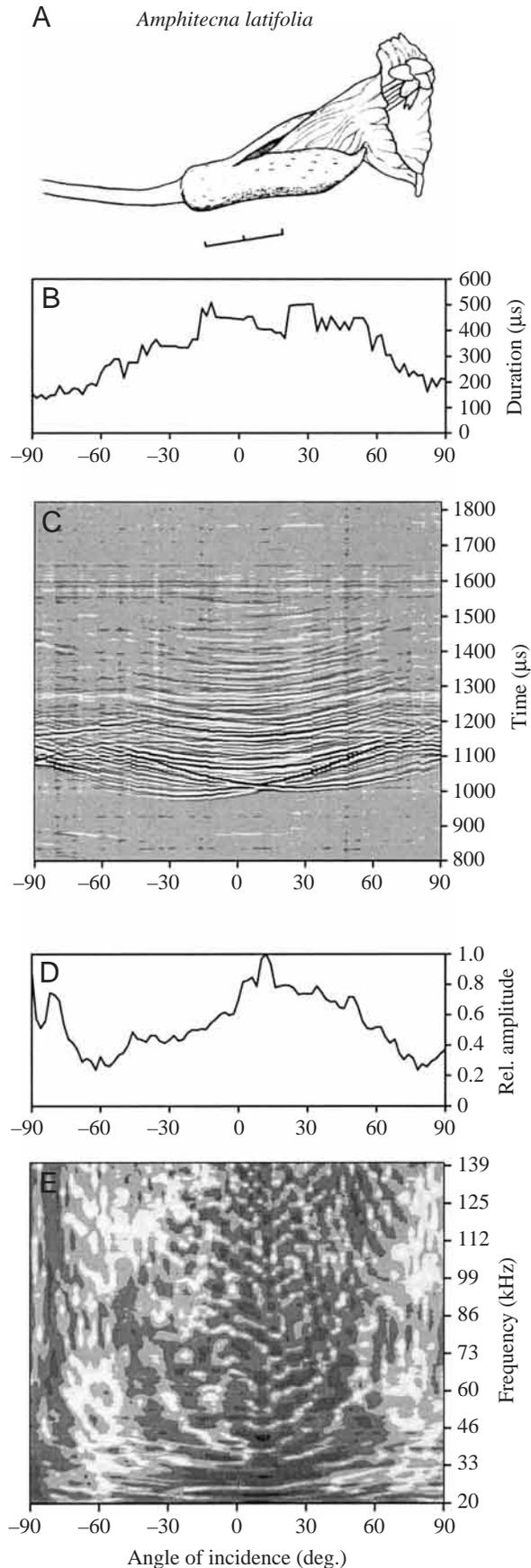


Fig. 3. Echo fingerprints of flowers in *Amphitecna latifolia*. (A) Sketch of the flower (scale bar, 20 mm). (B) Duration of the impulse response for 90 directions in the horizontal plane ( $-90^{\circ}$  to  $+90^{\circ}$  in  $2^{\circ}$  increments). (C) The directional pattern of the impulse response (black, positive amplitudes; white, negative amplitudes; see Fig. 2). (D) Overall amplitude of the echo. (E) Spectral directional pattern from 20 kHz to 140 kHz (black, 0 dB to  $-6$  dB; grey tone gradation in steps of 6 dB corresponding to the scale given in Fig. 2).

calculated as the (complex) difference spectrum between the spectra of the loudspeaker and the echo. These spectra represent the 'spectral target strength' for reasons given below. Finally, the actual impulse response of the object could be derived from this calibrated spectrum by employing inverse fast Fourier transformation (IFFT). All calculations were performed using the program Monkey Forest (Audio & Acoustics Consulting, Aachen, Germany).

#### Target strength

By definition, the target strength of an object is the reflected echo amplitude measured at a reference distance relative to the incident amplitude at the place of the object (e.g. Møhl, 1988). When the echo-generating object is regarded as a source of new spherically spreading sound waves, a reference distance has to be defined. The reference distance chosen was 10 cm. To ease the calculation of the target strength, the distance between the object and the loudspeaker/microphone was set at double the reference distance (20 cm): owing to spherical spreading loss, the echo amplitudes recorded at 20 cm are attenuated by 6 dB compared with the reference distance of 10 cm. As we measured the incident sound amplitude at an effective distance of 40 cm, which was twice the distance between the loudspeaker and the object, the recorded incident amplitude was also 6 dB lower than at the position of the object. Because the target strength is defined as the relationship between both, the two attenuations of 6 dB cancelled each other, and the relationship of the measured values directly indicated the target strength. This is also true for the calibrated spectrum mentioned above, which can therefore be regarded as 'spectral target strength'.

#### Relative amplitude and duration of the impulse response

Signal amplitudes were calculated as the sum of the magnitudes of the calibrated power spectrum between 20 kHz and 140 kHz. Defining a threshold just above the noise level, we estimated the duration of the impulse response for every direction of incidence.

## Results

### Impulse response and spectrum

As a first example, we show the impulse response that we observed when we irradiated the flower of *Markea neurantha* at the  $4^{\circ}$  position (Fig. 2A). Two prominent amplitude peaks were visible, one from the outward tilted distal edge of the

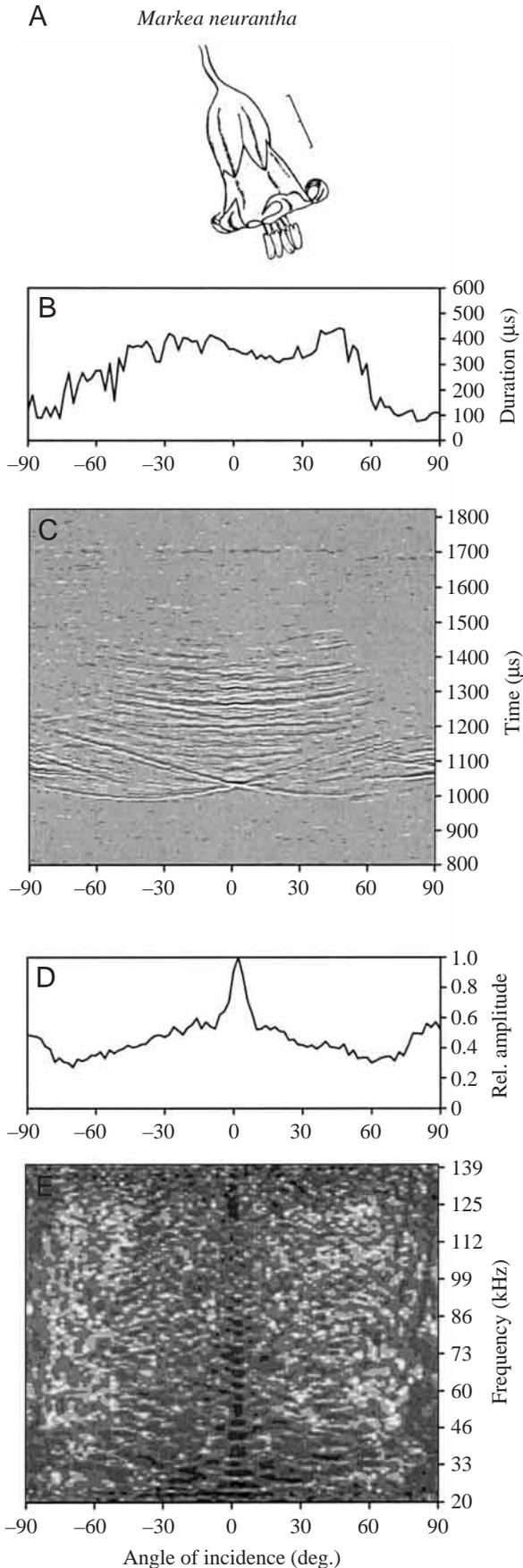


Fig. 4. Echo fingerprints of flowers in *Markea neurantha*. (A) Sketch of the flower (scale bar, 20 mm). (B) Duration of the impulse response for 90 directions in the horizontal plane ( $-90^{\circ}$  to  $+90^{\circ}$  in  $2^{\circ}$  increments). (C) The directional pattern of the impulse response (black, positive amplitudes; white, negative amplitudes; see Fig. 2). (D) Overall amplitude of the echo. (E) Spectral directional pattern from 20 kHz to 140 kHz (black, 0 dB to  $-6$  dB; grey tone gradation in steps of 6 dB corresponding to the scale given in Fig. 2).

corolla and another delayed by approximately  $200\ \mu\text{s}$  from the ground of the bell and from reverberations within the bell. The overall duration of the impulse function was approximately  $400\ \mu\text{s}$ , corresponding to a sound path length of 13 cm, which is a little more than double the flower depth.

From the impulse response we calculated the spectrum, which is shown in Fig. 2B. The amplitude is given in decibels and may be regarded as the spectral target strength, as discussed in the Materials and methods. Values between  $-5$  dB and  $-10$  dB at some frequencies are flanked by frequencies with very low echo amplitudes (0 dB would correspond to the amplitude reflected by the metal plate, as described in the Materials and methods).

#### Spectral directional pattern

Slightly revolving the turntable often resulted in a totally different impulse response. A resolution of  $2^{\circ}$  turned out to be sufficient to detect the minima and maxima. In principle, it would be necessary to measure the echoes from all directions in three dimensions but for the sake of clarity and to get a general idea we confined the measurements to the horizontal plane coplanar to the long axis of the flower tube.

Measurements between  $-90^{\circ}$  and  $+90^{\circ}$  allowed us to depict an 'acoustic fingerprint' of the flower. From the impulse response we derived the 'directional pattern of duration', and from the amplitude spectra the 'spectral directional pattern', by scaling the amplitudes as grey tone gradation over incidence angles ( $x$ -axis) and frequency ( $y$ -axis; Figs 3E, 4E, 5E, 6E).

Three of the flowers analysed in this way (*Amphitecna*, *Markea* and *Crescentia*) are similar in that they are exposed rather freely when blooming, which is brought about either by flagelliflory (*Markea*) or cauliflory (*Amphitecna*, *Crescentia*). The results presented in Figs 3–6 are measurements of the isolated flower without stem or peduncle, although in the two cauliflorous flowers (with a distance of 10–12 cm between the front of the flower and the stem) a partial overlap between the echoes of the flower and the stem might be expected in a natural situation.

In *Vriesea gladioliflora*, unlike other *Vriesea* species, which expose their flowers at the two opposite sides of a flat sword-like inflorescence, the flowers are not exposed freely but are embedded within the stalk, covered by their bracts. Even when the flowers are fully open, only the distal part of the flower's corolla is visible. As the bats will always experience the flower embedded in the stalk, we measured the echo of the flower together with a part of the stalk (approximately 15 cm long; Fig. 6A).

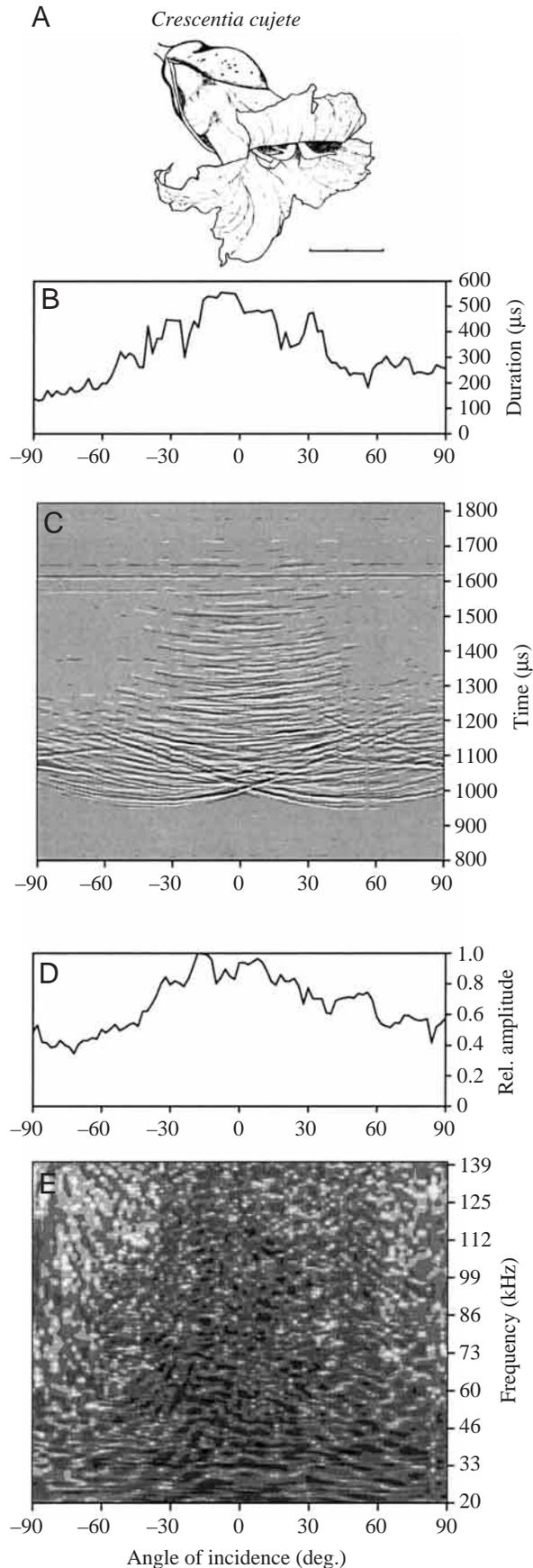


Fig. 5. Echo fingerprints of flowers in *Crescentia cujete*. (A) Sketch of the flower (scale bar, 20 mm). (B) Duration of the impulse response for 90 directions in the horizontal plane ( $-90^{\circ}$  to  $+90^{\circ}$  in  $2^{\circ}$  increments). (C) The directional pattern of the impulse response (black, positive amplitudes; white, negative amplitudes; see Fig. 2). (D) Overall amplitude of the echo. (E) Spectral directional pattern from 20 kHz to 140 kHz (black, 0 dB to  $-6$  dB; grey tone gradation in steps of 6 dB corresponding to the scale given in Fig. 2).

As may be expected, the overall echo amplitude in all four bell-shaped flowers showed a relative maximum at the position around  $0^{\circ}$ , when the opening of the bell was facing the speaker and microphone (Figs 3D, 4D, 5D, 6D). While *Markea* showed a prominent and rather narrow maximum, the range of angles with enhanced echo amplitudes was larger in *Amphitecna* and *Crescentia*.

Accordingly, the duration of the impulse response was also maximal at that frontal range (Figs 3B, 4B, 5B, 6B). In Figs 3C, 4C, 5C and 6C, the maxima (black) and minima (white) of the impulse function and their pattern can be seen as they change with the angle of the sound incidence. In all four examples, the first peaks deriving from the distal left and right edges of the flower can be traced with changing angle of incidence. Both the duration and the overall intensity of the echoes, of course, depend strongly on the shape of the bell.

The spectral directional pattern, the presentation of the spectral composition of the echoes as a function of sound incidence angle, is given in Figs 3E, 4E, 5E and 6E. In all four examples, in a range of approximately  $-60^{\circ}$  to  $+60^{\circ}$  relative to the opening of the bell, the echoes showed rapidly changing spectral compositions. In a single spectrum, sudden falls in intensity of more than 12 dB compared with the values for neighbouring frequencies were observed frequently at different frequencies and different angles of sound incidence. Thus, as a function of angle of sound incidence, the echoes differed in a characteristic manner with respect to their spectral composition, producing an acoustic fingerprint for every flower species.

In *Vriesea*, the echo was strongest when the stalk was ensonified from approximately  $-80^{\circ}$  laterally on the side of the stalk from which the flower originated. The echo of this part was nearly constant over the whole frequency range because of a rather flat, leaf-like part of the bract that reflected the sound back to the microphone. The echoes recorded in a frontal area from approximately  $-60^{\circ}$  to  $+60^{\circ}$  were less intense, and their spectral composition varied for different angles of incidence. At  $0^{\circ}$ , there was also a strong echo but with a complicated spectral pattern resulting from interferences enhancing some frequencies and cancelling others.

#### *Impulse response and echoes*

Bats do not have the impulse function at their disposal in that they use echolocation calls with a distinct duration and a distinct time course of the frequency spectrum. The frequency range of glossophagine bat calls is mostly within 140 kHz to 60 kHz. The echo of a call can be calculated by finite-impulse-

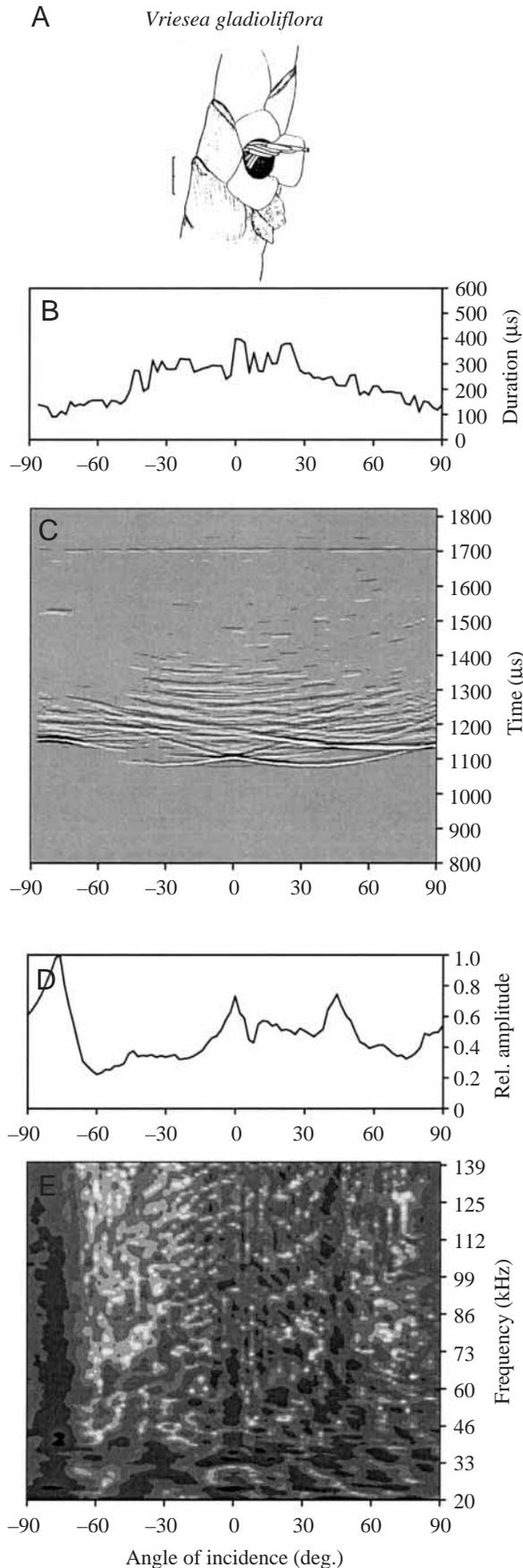


Fig. 6. Echo fingerprints of flowers in *Vriesea gladioliflora*. (A) Sketch of the flower (scale bar, 20mm). (B) Duration of the impulse response for 90 directions in the horizontal plane ( $-90^\circ$  to  $+90^\circ$  in  $2^\circ$  increments). (C) The directional pattern of the impulse response (black, positive amplitudes; white, negative amplitudes; see Fig. 2). (D) Overall amplitude of the echo. (E) Spectral directional pattern from 20 kHz to 140 kHz (black, 0 dB to  $-6$  dB; grey tone gradation in steps of 6 dB corresponding to the scale given in Fig. 2).

response-filtering (FIR) of the impulse function with the amplitude function of the call. In Fig. 7, the sonograms of two such impulse functions (at  $0^\circ$  and  $-30^\circ$ ) treated with the amplitude function of a typical call of *Glossophaga* give an impression of the echo as the bat would perceive it.

#### Echoes of artificial hollow forms

The echoes of natural flowers, as shown above, are determined not only by their shape but also by elastic properties, surface texture and other features of the corolla, and it seems difficult to separate the different components (see Hickling, 1967; Bozma and Kuc, 1991 for technical objects). Therefore, for a better understanding of the principal pattern of the echoes of bell-shaped flowers, and to test our method, we compared the directional patterns shown above with those of some simple concave forms, measured in the same way as the flowers. We chose hollow forms of a hemisphere, a paraboloid and an ellipsoid (see Materials and methods), all with the same opening diameter of 36 mm. Results are shown in Fig. 8.

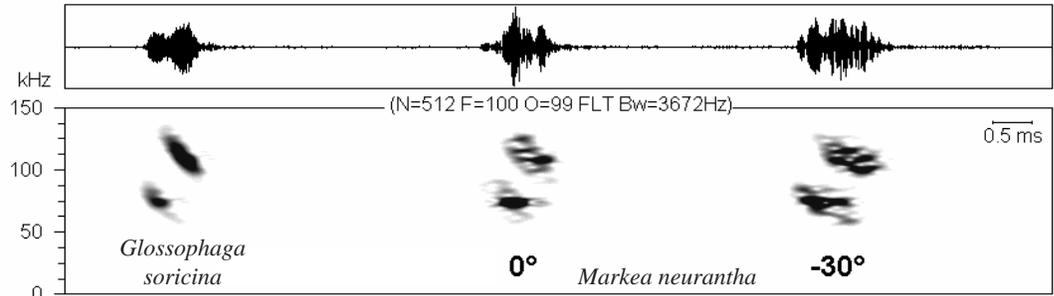
As expected, in all three forms, the loudest echoes were received when the concave side of the form was irradiated from (or from near) its main axis, but this was much more marked in the paraboloid and the ellipsoid than in the hemisphere. Furthermore, with each shape, typical bands of interference occurred, resulting from multiple reverberations at the inner side of the form. In the hollow hemisphere, due to the constant radius of curvature, the bands of interference remained constant for all angles of incidence (Fig. 8A), as expected from theoretical analysis (e.g. Freedman, 1962). In the other two forms, which had continuously changing radii of curvature, the bands of interference decreased in frequency with increasing deviations from the  $0^\circ$  axis. To test whether properties other than shape constituted the pattern of the echo fingerprint, we measured the spectral directional patterns of the same parabolic form twice, once as a shell of 0.5 mm thickness and then pressed in a solid cylinder of the same diameter. As the two measurements turned out to be very similar, we are confident that the directional spectral pattern of all three forms is due to their shape.

#### Discussion

##### A comparison with artificial hollow forms

The echoes of the three artificial objects showed characteristic patterns that were fairly symmetric with respect to the median plane. Single spectra from different bodies could

Fig. 7. Oscillogram (top) and sonagram (bottom) of a typical echolocation call of *Glossophaga soricina* and two echoes of the flower *Markea neurantha* (achieved by FIR-filtering the call with the impulse response at 0° and -30°). Sonagram parameters: window size (N); frame size (F); window overlap (O); window: flattop (FLT); resulting bandwidth (BW); software: SASLAB Pro 4.2; Avisoft.



be more or less identical, but the ‘spectral directional pattern’ as a whole was characteristic of each object. In some respects, the spectral directional patterns of the natural flowers were comparable and similar to those of the artificial objects but they appeared much patchier and less regular for the following reasons. Firstly, the shape of the natural flowers cannot be described by simple mathematical rules; therefore, such clear lines of interference are not likely to occur. Secondly, protruding stamina and the pistil, as well as the texture of the flower, will influence the echo. In *Crescentia*, and to some extent also in *Markea*, the surface of the corolla appears grooved and wrinkled, which possibly gives rise to the patchy spectral distribution. Moreover, the acoustic properties of the tissue of the corolla may also play a role; bat-pollinated flowers are known to be especially stiff and sturdy. (In *Vriesea*, we found the waxy petals to be 1.2–2 mm thick and also tightly enclosed by the very stiff sepals.)

#### *Can flowers be recognized by their echoes?*

The recognition of a small motionless object by an echolocating bat should be easier the more the echo differs from the echoes of the surrounding vegetation and other surrounding structures. Echoes of a single flat leaf consist primarily of simple reflections of the calls without sudden drops in intensity at certain frequencies and are not much longer than the echolocation call. Echoes of trees and bushes have been shown to be highly unpredictable, as the echoes of many different leaves superpose, but a statistical analysis was able to unearth features that characterize, for example, different tree species (Müller and Kuc, 2000). This is due to the different size, shape and configuration of leaves and to the specific architecture of the plants.

In contrast to the simple echoes of flat leaves, the flowers described here generate complex but predictable echoes owing to their specific and constant shapes and textures. In particular, echoes of bell-shaped flowers are characterised by their duration, spectral composition and directional pattern (see below).

#### *Duration*

Depending on the length of the bell, the duration of the echo may be increased relative to the echoes of leaves and other plane objects. Sound invading a tube will undergo numerous

reflections, and these higher order reverberations will possibly further increase the duration of the echo in addition to the time the sound has to travel into and out of the bell. Indeed, our measurements corroborate this idea.

#### *Spectral composition*

Several experimental studies have demonstrated that the spectral composition of an echo is important for detection and discrimination (Bradbury, 1970; Simmons et al., 1974, 1990; Mogdans and Schnitzler, 1990; Schmidt, 1992). In bell-shaped flowers, multiple reflections of an echo interfere with each other, enhancing some frequencies and erasing others. This gives rise to a ‘coloured’ spectral composition of the echo, which may be conspicuous in comparison with echoes of leaves. Our measurements show that the echoes of a bell-shaped flower have this ‘coloured’ appearance and, basically, resemble those of simple hollow forms, as demonstrated by the directional patterns (Fig. 8).

#### *Directional pattern*

We have shown that the spectral composition of the echoes depends strongly on the angle of incidence. Single echoes of different objects can be nearly identical and would not contain enough information for discrimination. Therefore, for recognition of specific forms, bats will have to evaluate the echoes of sequential calls, while taking into account their own position relative to the object. Besides learning the characteristic features of single echoes, bats may also be able to detect and learn the rules of echo changes determined by the shape of the flower. The actinomorphic symmetry of most bell-shaped flowers probably reduces the multiplicity of echoes. That bats are indeed able to compare successive echoes was shown in training experiments by Moss and Surlykke (2001).

#### *Can flower echoes help the bat to adjust its approach flight to the entrance of the nectar chamber?*

A flower must not only be detected and recognized as a nectar source: in the next step, the bat has to find the nectar, and the approach flight must be exactly directed towards the opening of the nectar chamber. As shown in the Results, the target strength and the duration of the echo increase drastically when the opening of a bell-shaped corolla faces the loudspeaker. A bat flying around a bell-shaped flower could

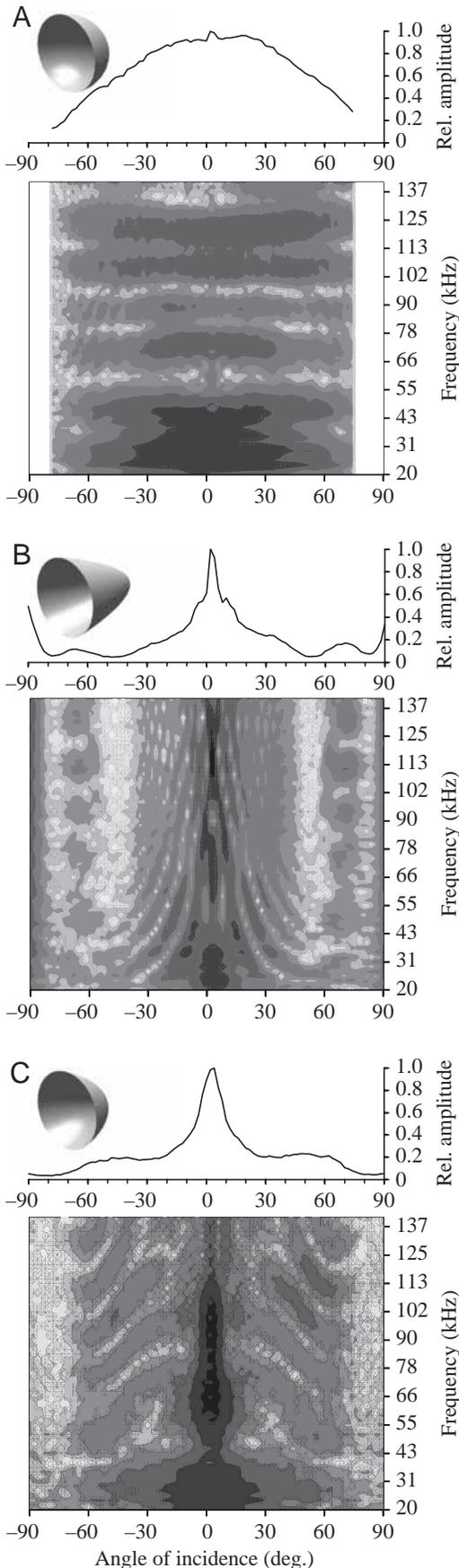


Fig. 8. Spectral directional pattern of a hollow hemisphere (A), a paraboloid (B) and an ellipsoid (C). All three hollow forms had the same circular opening with a diameter of 36 mm but different depths (for exact parameters, see text). Above each spectral pattern the relative intensity of the echo, averaged over the frequency range from 20 kHz to 140 kHz, is plotted as a function of the angle of sound incidence.

therefore detect the opening of the flower by evaluating the target strength alone (as shown in Figs 3–6), especially for the flowers of *Markea* and *Vriesea*. The echoes generated inside the tube could well function as a ‘guiding beam’, leading the bat exactly to the flower opening. Thus, bell-shaped flowers, in particular those with a long narrow tube, may ‘acoustically mark’ the entrance where the bat will find the nectar.

#### Adaptations for acoustic detection and recognition

The detectability of flowers by their echoes is probably reduced when other echo-generating structures are in close vicinity and clutter echoes are superimposed on the echoes of the flower. Most chiropterophilous flowers are exposed freely and therefore not only allow hovering in front of a flower (Vogel, 1968, 1969a,b; Dobat, 1985) but also facilitate their detection and recognition by avoiding overlap with clutter echoes. In many bat-pollinated plants, the typical exposition and the structure of the whole inflorescence may also give rise to specific echoes that can be detected from greater distances and thus guide the bat to the smaller structures of the flowers, which can only be identified from a shorter distance. For instance, the sword-like inflorescence of *V. gladioliflora* is inclined by approximately 40° with respect to the vertical and thus may be conspicuous even from a distance. The flowers open on the lower side and can be found by the narrow echo beam they reflect when the bat hovers along the inclined side of the stalk.

Cauliflorous flowers normally protrude at least several centimetres from the stem and probably allow a temporal separation of the echoes of the flower and those of the background. Where this is not so, as with some columnar cacti, special adaptations can be found; these cacti often present their flowers in the midst of a ‘cephalium’, a region densely covered with hairs. Besides the possible function of these cephalia to protect against heat and desiccation, the dense hairs may also serve to attenuate the echoes generated by the stem, thereby enhancing the contrast between flower and background echoes. Possibly, this is their main function, as in many species of columnar cacti the cephalium is restricted to the region where flowers are presented (v. Helversen and Winter, 2003).

At present, we do not understand how bats, guided by their echolocation system, manage to manoeuvre through a dense jungle of leaves, to recognize objects like flowers and fruits and to adjust their fast approach flight exactly to within a few millimetres of the opening of a flower. Our measurements suggest that bats probably extract more information from the echo sequences than has been hitherto supposed and that they do this by comparing the echoes of successive calls during flight.

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