# Echolocation calls produced by *Trachops cirrhosus* (Chiroptera: Phyllostomatidae) while hunting for frogs

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The echolocation calls produced by *Trachops cirrhosus* in the field and in a flight cage were recorded as they hunted for frogs. The calls were of low intensity (<70 dB sound pressure level (SPL) at 10 cm), short (less than 1 ms), multiharmonic frequency modulated sweeps with energy from over 100 to around 50 kHz. During most successful attacks of frogs in the cage, these orientation sounds were produced by the bats which are also known to rely on frog calls to locate prey.

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Les cris d'écholocation de *Trachops cirrhosus* en nature et dans une volière ont été enregistrés durant une chasse aux grenouilles. Les cris sont de faible intensité (<70 dB SPL à 10 cm), de courte durée (moins de 1 ms), à modulation de fréquences multiharmoniques, à énergie de 100 à environ 50 kHz. La plupart des attaques réussies des chauves-souris dans la volière s'accompagnent de ces cris d'orientation; les chauves-souris s'aident aussi des cris des grenouilles pour localiser leurs proies.

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## Introduction

Although biologists have some appreciation of the variety of echolocation strategies used by bats (Simmons, Fenton, and O'Farrell 1979) and there has been an explosion of information in this field in the past 15 years (Grinnell 1980), relatively few species of bats have been studied in this regard and field studies are particularly uncommon. The low intensity of the echolocation calls of some bats, notably many phyllostomatids, or whispering bats (Griffin 1958), has kept studies of this group to a minimum (Gould 1977; Novick 1977).

*Trachops cirrhosus* is a medium-sized phyllostomatid (Phyllostomatinae) weighing about 30 g (forearm 58–62 mm) (Fig. 1) which occurs from southern Mexico to southern Brasil and Bolivia (Jones and Carter 1976) and is known to feed on small animals (Gardner 1977). These bats respond to frog calls (Tuttle and Ryan 1981), suggesting that they might rely on the sounds of prey rather than, or in addition to, echolocation much as *Megaderma lyra* (Megadermatidae) does (Fiedler 1979).

The purpose of this study was to record and analyze the echolocation calls of *T. cirrhosus* in the field and the laboratory when it was hunting and catching frogs.

## Methods and materials

Field and laboratory recordings of *T. cirrhosus* were made at the Smithsonian Tropical Research Station on Barro Colorado Island in Panama between 4 and 14 March 1980. Field recordings were attempted at a small pond where the bats came to hunt frogs, notably *Physalaemus pustulosus* (Leptodactylidae), and laboratory recordings were made in two large flight cages (4.3 m by 4.3 m by 2.1 m). Four *T. cirrhosus* were captured in the field in mist nets and maintained in captivity for 3–4 days each.

The bats were observed through a Javelin 221 night vision scope using light filtered through an infrared filter (Wratten No. 87). Recordings were made in the field as bats hunted frogs and in the flight cages when they were initially released and when they attacked hand-held frogs (Fig. 1) or those dropped to the floor of the cage. The bats were also recorded as they responded to the recorded calls of *P. pustulosus* played back at normal intensity (75 dB sound pressure level (SPL) at 1 m) from a Stellavox recorder with small extension speakers. In addition, the echolocation calls of six bats were monitored using a zero-crossing period meter (Simmons, Fenton, Ferguson et al. 1979) as they emerged from their day roost located in a hollow tree (Table 1).

The bats' vocalizations were recorded on a Lockheed store 4D tape recorder operated at 76 or 152 cm/s using a QMC PSM1 broad-band microphone sensitive to over 200 kHz

FIG. 1. Captive *Trachops cirrhosus* attacking moving fingers. Echolocation calls were recorded with the microphone shown held in the left hand. Photo by M. D. Tuttle.

(Simmons, Fenton, Ferguson et al. 1979). Recordings were analyzed by slowing the tape speed 16 or 32 times and playing them into a Princeton Applied Research fast Fourier transform Real Time spectrum analyzer model 4513 operated with a manual trigger to capture complete calls. A Kay 7029A sonagraph and Tektronix 5104 N dual beam storage oscilloscope were also used to analyze the vocalizations.

## Results

The echolocation calls of *T. cirrhosus* were of short duration ($\bar{X}$ = 0.58 ± 0.15 ms, $n$ = 20) and composed of two to four harmonically related frequency modulated (FM) pulses (Fig. 2; Table 2). From sonagrams (Fig. 2) it appears that the frequencies presented in the call represent harmonics of a suppressed fundamental whose frequency sweep would be approximately 25 to 13 kHz. Thus, both the fundamental and second harmonics are absent while the third is present and has a frequncy sweep averaging 79 to 53 kHz (Table 2). The two highest recorded harmonics were not produced in every call and were also absent from the beginning of some calls. The pulses were produced at intervals of 24.2 ± 4.9 ms ($n$ = 35) when the bats were cruising, but the interpulse intervals decreased to 12.5 ± 1.6 ms ($n$ = 16) in the

final stages of attacks on frogs. The pulses were of low intensity, detectable only when the bats flew within 1.2 m of the microphone, and although we did not attempt to obtain accurate readings of intensity, they were clearly below 70 dB (SPL at 10 cm). Bats monitored leaving their day roost produced echolocation calls that were twice as intense as those of hunting bats.

In most situations where we observed *T. cirrhosus* they produced calls which presumably served an echolocation function. Since our experiments did not involve sensory deprivation, we have no categorical proof of echolocation. However, on 32 of 35 trials we conducted (Table 1) the bats produced pulses like those described above and because of the intensity of the calls and variability in the position of the bat relative to the microphone, we cannot rule out production of calls on the other three trials. During the three trials when we detected no calls, the bats did not succeed in capturing the silent frogs. The strongest circumstantial evidence in favour of echolocation is the change in pulse repetition rates during attack, although this increase did not approach that characteristic of a "feeding buzz" of some vespertilionids, molossids, or other insectivorous bats (Simmons, Fenton, and O'Farrell 1979).

TABLE 1. Situations in which flying *Trachops cirrhosus* were monitored for production of echolocation pulses

| | No. of trials | |
|---|---|---|
| Conditions | Pulses produced | No pulses |
| **Darkness** | | |
| Departure from day roost | 6† | 0 |
| Frog thrown on to floor of flight cage* | 12 | 0 |
| Frog held in hand* | 8 | 1 |
| Taped frog calls* | 5 | 0 |
| Initial release into flight cage* | 2 | 0 |
| **Light** | | |
| Frog held in hand* | 3 | 2 |
| Taped frog calls* | 2 | 0 |

*Trials run in captivity using four wild-caught *T. cirrhosus*.
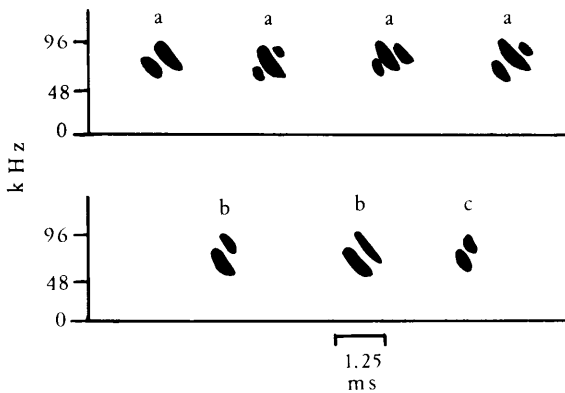†Represents number of bats.



FIG. 2. Tracings of sonagrams of calls made by *Trachops cirrhosus* (details of frequencies in Table 2). Calls marked *a* were produced by one individual, *b* by another, and *c* by a third.

TABLE 2. Frequency characteristics of the calls of *Trachops cirrhosus* as determined from fast Fourier transform (FFT) spectra and sonagrams. Of the 13 calls analyzed, 8 had two harmonics, 4 had three, and 1 had four

| Peak in power spectra* | $N_{calls}$ | Frequency (kHz) | |
|---|---|---|---|
| | | Maximum | Minimum |
| First | 13 | 79±6 | 53±11 |
| Second | 13 | 102±6 | 68±5 |
| Third† | 4 | 105 | 83 |
| Fourth† | 1 | 101 | 91 |

*The peaks appear to be harmonics of a suppressed fundamental (see text).

†The two highest harmonics were often not present during the complete call which results in their apparently nonharmonically related frequencies (see Fig. 2).

We were unable to record any signals from *T. cirrhosus* hunting over the pond even though some bats passed within 0.3 m of the microphone. Again, owing to the low intensity of the calls and the uncertainty of the position of the bat to the microphone we can not state categorically that the bats were not using echolocation.

*Trachops cirrhosus* is known to orient towards calling frogs or recordings of their calls (Tuttle and Ryan 1981). During our experiments on four occasions bats attacked the fingers of the hand holding a silent frog when the fingers were moved to produce noise (Fig. 1). During three of these attacks the bats produced detectable echolocation calls, but the responses to playbacks of recorded frog calls and the attacks on "noisy" fingers provide a strong indication that *T. cirrhosus* uses cues besides echolocation to locate prey.

## Discussion

The echolocation calls we recorded from *T. cirrhosus* are similar to those known from other phyllostomatids (Gould 1977; Novick 1977) and they are strikingly similar to the calls reported from the other gleaning species (e.g., *Megaderma lyra* (Schnitzler 1978); several species of *Nycteris* (Novick 1977)). *Trachops* calls differ from those of gleaning *Myotis auriculus* in intensity and the pattern of frequency change over time (Fenton and Bell 1979). However, all of the aforementioned bats produce short calls, a feature which may function to minimize pulse-echo overlap while hunting at short range (Novick 1977). The multiple harmonic structure of the calls of *Trachops, Megaderma,* and *Nycteris* should provide the bats with precise, unambiguous information about the position of targets (Simmons and Stein 1980).

*Trachops cirrhosus* uses both its own echolocation and acoustic information from prey (Tuttle and Ryan

1981), and their ability to respond to frog calls with maximal energy below 5 kHz (Ryan 1980) and to the echoes of their own echolocation calls (maximum energy near 75 kHz) suggests a remarkable range of hearing sensitivity.

Our field recordings are inconclusive regarding the use of echolocation by hunting *T. cirrhosus*. However, it is interesting to note that in captivity the bats appeared to use both echolocation and the sounds of prey to locate targets, whereas Fiedler (1979) found that *M. lyra* relied solely on the latter. The difference may reflect the hearing sensitivities of the respective prey; mice have good hearing sensitivity to ultrasonic sound (Sales and Pye 1974), while it is doubtful that the frogs hunted by *T. cirrhosus* can hear the bats (R. R. Capranica, personal communication).

A variety of factors other than the hearing sensitivity of prey make echolocation a mixed blessing (Fenton 1980) and may have selected for its limited use by *Trachops*. Sympatric with *T. cirrhosus* over much of its range is *Vampyrum spectrum*, another phyllostomatid that will include other bats in its diet (Gardner 1977) and that is sensitive to the frequencies of the *Trachops* calls (Bradbury 1970). On Barro Colorado Island *Philander opossum* (Didelphidae) hunts frogs at the same time and place as *T. cirrhosus* (Tuttle et al. 1981) and will also take bats when the opportunity arises (C. Handley, personal communication). Some didelphids are sensitive to ultrasonic sound (Ravizza et al. 1969).

The hearing sensitivity of predators and prey combined with the physical nature of the problem facing the bat may all influence the design of echolocation calls or the use of other acoustic cues by hunting bats. The strong similarity between the calls of *Trachops*, *Megaderma*, and *Nycteris* suggests convergence in design of calls that includes duration, intensity, and frequency–time patterning. Further investigation is required to clarify the factors exerting selective pressure on the design and use of echolocation calls.

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