

## Echolocation by Free-tailed Bats (*Tadarida*)

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**Summary.** The echolocation of bats in the genus *Tadarida* is highly adaptive to different acoustic conditions. These bats use different types of sonar signals with a diversity usually observed in comparisons across families of bats. *Tadarida brasiliensis* and *T. macrotis* search for airborne prey in open, uncluttered spaces using narrow-band, short CF signals with no FM components. They add broadband FM components while dropping the CF components when approaching or capturing prey. Only one harmonic is present in these insect-pursuit signals. When flying in cluttered situations or echolocating in a laboratory room, *T. brasiliensis* uses multiple-harmonic FM signals. Stationary bats tend to use linear frequency sweeps and moving bats tend to use curvilinear frequency sweeps or linear period sweeps. When emerging from a roost they initially use a short-CF/FM signal, changing to an FM signal as they fly away. The acuity of perception of target range in *T. brasiliensis* is about 1.0 to 1.5 cm and is determined by the bandwidth of the target-ranging sonar signals as represented by their autocorrelation functions. Many less adaptable species of bats use signals corresponding to part of the sonar repertoire of *Tadarida*. The functions of short CF or narrowband signals for detection and FM or broadband signals for resolution and acoustic imaging identified from comparisons among such species are confirmed by observations of echolocation by *Tadarida*. The differences observed in echolocation among many species and families of bats appear to be evolutionary adaptations to some of the same features of the acoustic environment to which *Tadarida* responds behaviorally.

**Abbreviations:** CF, frequency modulated; FM, constant frequency; LPM, linear period modulation; LFM, linear-frequency modulation

### Introduction

Free-tailed bats, of the family Molossidae (from the Greek word for "mastiff," which these bats resemble), are very successful and widely distributed throughout the warmer regions of the world (Koopman, 1970). The genus, *Tadarida*, is known from fossils in Europe dating back over 20 million years (Romer, 1966). One common species, the Mexican free-tailed bat, *Tadarida brasiliensis*, is migratory throughout much of its range in North America, traveling from the central and southwestern United States into Mexico to escape winter (Villa and Cockrum, 1962; Cockrum, 1969). Colonies of *T. brasiliensis* can contain over 10 million bats, and in some localities they forage for insects as great clouds of bats that sometimes reach altitudes of 3000 m (Williams et al., 1973). The wings and shoulder articulations are thought to be highly advanced in molossids (Vaughan, 1970a, b; Findley et al., 1972), and they probably feed on strong-flying insects pursued in the open air. Their capabilities for sustained flight, their spectacular success as life-forms, and their many interesting habits suggest that orientation to the environment by molossids will be of particular interest to study.

Echolocation, the biological sonar of bats, provides a valuable scientific example for understanding the mechanisms of the nervous system for processing signals (Griffin, 1973; Sales and Pye, 1974). Basic concepts involved in research on echolocation come from zoology, neurobiology, psychology, and communications theory (Simmons, 1977). Knowledge of the nature of echolocation sounds as signals and their capacity for carrying information about targets to bats is important for appreciating the evolution of bats, a major group of mammals, and the perceptual

world of each of the 800 living bat species (Simmons et al., 1975). Considerable progress has occurred in research on the role of the auditory system as the bat's sonar receiver (Grinnell, 1973; Henson, 1970; Schnitzler, 1973; Suga, 1973). Comparative analysis of the sonar of differing species of bats can enrich all of these scientific undertakings, and, accordingly, we report here the results of several studies on echolocation in free-tailed bats.

## Methods

Echolocating bats of the species *Tadarida brasiliensis* from the Animas Valley of New Mexico were used as subjects for laboratory experiments on target ranging. Field observations were made on *T. brasiliensis* emerging from and entering day roosts in Austin, Texas, and *T. brasiliensis* and *T. macrotis* foraging for insects in the vicinity of Logandale, Nevada. Bats were kept in the laboratory in a warm, moist room and fed on a diet of mealworms (*Tenebrio* larvae).

The orientation sounds used by these bats were recorded in the laboratory with a Brüel and Kjaer Model 4135 condenser microphone (wind-screen removed) and in the field with a plastic-diaphragm condenser microphone similar to equipment previously designed for picking up bat sounds (McCue and Bertolini, 1964). The signals were stored on a Pemtek Model 110A portable instrumentation tape recorder. In the field the sounds were analyzed with a portable frequency display device which shows the sweep structure of frequency-modulated signals on an oscilloscope (Simmons, Fenton, Ferguson, Jutting, and Palin, in preparation; Partridge, 1967). The tape-recorded sounds were digitized into 10-bit numbers and stored in a Digital Equipment Corp. PDP-11/40 computer. Signals were sampled at a rate of 300 kHz. The data arrays were processed with the Fast Fourier transform to display the characteristics of the signals in the frequency domain (spectra) and the time domain (autocorrelation functions). These arrays were broken into 10 to 50 overlapping segments for analysis of time-frequency patterns (sound spectrograms). Amplitude and bandwidth measurements were based on 50 signals of each type. Target-range discrimination experiments were carried out using previously-described procedures (Simmons and Vernon, 1971). The bat was presented with two identical targets located at different distances, or ranges, and trained to respond to the closer target by moving towards it. Correct responses were rewarded with food, a piece of a mealworm. The absolute range of the targets was 30 cm, and the acuity with which the bat could detect differences in range around 30 cm was measured. The data are in the form of percent correct responses at each difference in distance that was tested (30 cm versus the following distances in order: 27, 28, 28.5, 29, 29.5, and finally 30 cm). Each bat was pretrained on larger range differences, and 25 trials were run for each bat at each range difference after the bat's performance had stabilized (reached asymptote). The bats were blinded to prevent the use of visual cues in the discrimination task.

Random noise was presented to the bats during some discrimination trials to determine the bat's adaptive response to this type of acoustic interference. Noise signals were produced with an Elgenco noise source and an LTV Model EST-2 electrostatic loudspeaker located 60 cm away from the bat. The noise field could be made as loud as  $1.0 \text{ N/m}^2$  ( $\pm 6 \text{ dB}$ ) from 20 to 100 kHz, which is sufficiently uniform for the observations made here. Levels of interfering sound are expressed here in dB re  $1.0 \text{ N/m}^2$  RMS overall sound pressure across the 20 to 100 kHz frequency band.

## Results

### Range Discrimination

Figure 1 shows the performance of two individual bats of the species *T. brasiliensis*, on target range discrimination. From the data presented in the graph, it is evident that *T. brasiliensis* can detect differences of 1.0 to 1.5 cm in the distances to targets, using 75% correct responses as a "threshold" criterion. These bats' performance is comparable to other species, including the insectivorous bats, *Eptesicus fuscus* and *Pteronotus suapurensis* (Simmons, 1973).

Figure 2 shows the time-frequency structure or sound spectrogram of the type of sonar sound used by *T. brasiliensis* for target range discrimination (28 vs. 30 cm). The signal consists of a short, downward frequency modulated (FM) sweep (nearly linear with frequency) with strong first and second harmonics and a reduced but appreciable third harmonic. Note in Figure 2 that the harmonics do not overlap in frequency; they are separated by silent bands. The autocorrelation function of the sound (Fig. 3) presents descriptive information about the bandwidth of the sonar signal in the time domain. (The autocorrelation function represents the bat's signal transformed or compressed into an impulse with the same time-resolving characteristics as the original sound.) The signals used by *T. brasiliensis* for target ranging varied in bandwidth by less than 5%, and this autocorrelation function may be considered typical of the target-ranging sounds.

### Emergence from Roost

Members of a colony of *T. brasiliensis* were observed as they flew out of their roost to begin hunting for insects. The bats exited from the roost through a small hole in the brick wall of a building, located about 4 m above a sidewalk, and flew out over the sidewalk and street, avoiding signs and telephone poles as they climbed in altitude. The recordings described here were made of bats at altitudes of 4 to 10 m and at distances of 1 to 12 m from the roost opening.

The sonar sounds used by *T. brasiliensis* when emerging from the roost are illustrated by the signal in Figure 4. This signal, recorded from a bat in flight about one meter from the exit, is very broadband, with considerable overlap of harmonics compared to the signal shown in Figure 2. Furthermore, the signal emitted by the bat as it launched into flight begins with a short constant-frequency (CF) component with a duration of 1.5 ms at 55 kHz. Figure 5 shows the

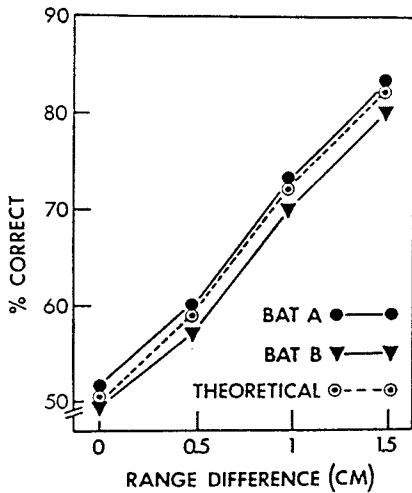


Fig. 1. Performance of two individual *Tadarida brasiliensis* on discrimination of target range differences at an absolute range of 30 cm under conditions of quiet or ambient noise. Graph compares behavioral data (bats A and B) with a theoretical performance curve derived from the envelope of the autocorrelation function of bat's sonar sound as recorded during the discrimination

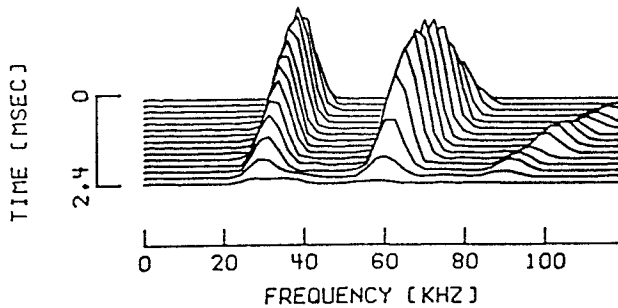


Fig. 2. Time-frequency structure, or sound spectrogram, of target-ranging sonar signal used by *Tadarida brasiliensis*. Signal is graphed with time progressing from top to bottom

initial part of the waveform for better definition of the CF component. Exact measurement of the CF frequency is difficult due to Doppler shifts produced by the bat's motion. This short CF component is present whenever bats emerge from the roost; it is similar in appearance to the short CF components in the sonar sounds of bats in the families Mormopidae and Hipposideridae (Simmons et al., 1975). As the bat flew further away from the roost opening, at distances of 6 to 12 m and altitudes of 5 to 10 m, the short CF component dropped out. The sonar sounds used by *T. brasiliensis* flying away from the roost area consisted of multiple, overlapping harmonics in the descending FM pattern shown in Figure 4, without the CF component. At this point the bats were flying rapidly in relatively straight paths, faster than the controlled maneuvering observed in *T. brasiliensis* as it pursues prey.

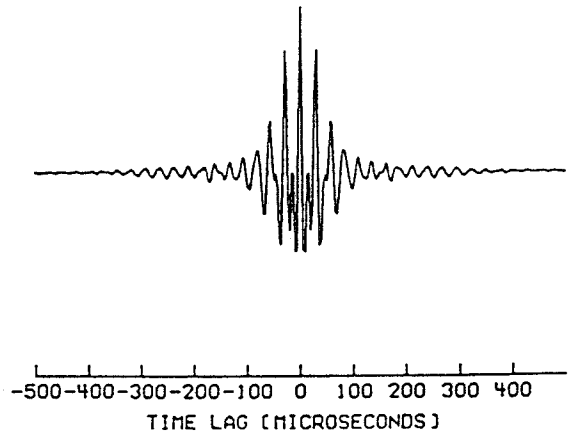


Fig. 3. Autocorrelation function for target-ranging sonar signal used by *Tadarida brasiliensis*. This graph represents the bandwidth of the signal in time domain for comparison with target-ranging performance

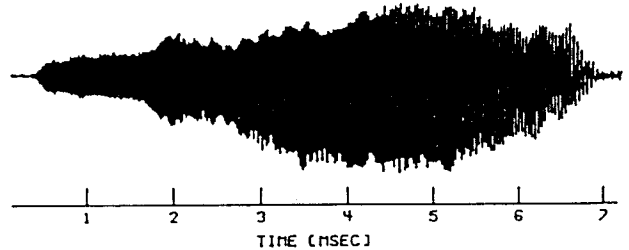


Fig. 4. Waveform and time-frequency structure of a short-CF/FM orientation sound used by *Tadarida brasiliensis* taking flight when emerging from its roost

### Feeding Behavior

*Tadarida brasiliensis* and *T. macrotis* were observed hunting for and capturing insects at altitudes of several meters to over 25 m above the ground. Recordings were made of the orientation sounds used by these bats as they searched for, pursued, and captured prey. At times a bat would complete a capture within

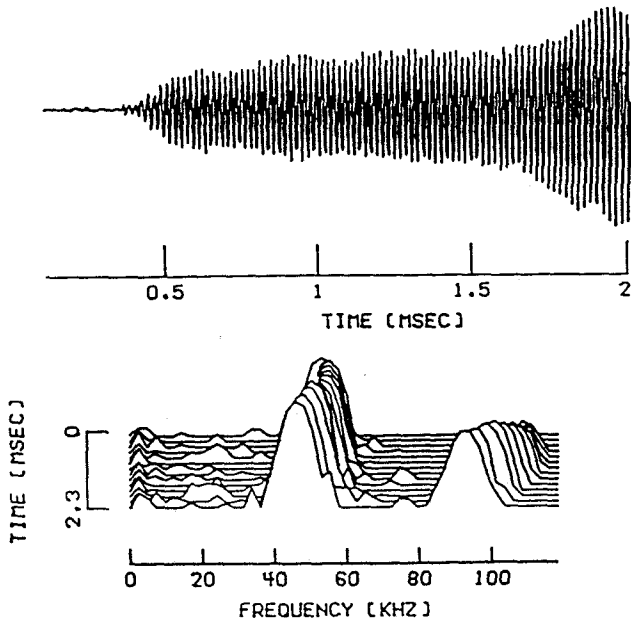


Fig. 5. Expanded view of initial portion of signal shown in Figure 4 to show details of CF component

a few meters of the microphone, so high-quality recordings of the signals were available. The signals described here were made by bats pursuing prey and flying about 5 m above the ground. These bats behaved much like vespertilionid bats (*Eptesicus fuscus*, for example) when feeding: flying on irregular paths, fluttering or partially hovering quite abruptly, capturing insects in their flight membranes, and immediately flying on in search of more prey (Griffin, 1958; Griffin et al., 1960; Webster and Griffin, 1962).

Although *Tadarida* have reputations as very fast fliers (Hayward and Davis, 1964; Vaughan, 1970b; Findley et al., 1972), these two species flew slowly and with great control of motion when pursuing prey. The wings were broadly spread and the tail membrane appeared extended, giving a flight silhouette with greater membrane surface than for *T. brasiliensis* emerging from roosts and flying away at high speed. The extended tail membrane altered these bats' free-tailed appearance in flight, a fact observed previously with high-speed photographic techniques (Edgerton et al., 1966). The insects upon which the bats were feeding were small and could not be seen or identified. Individual bats would pursue small pebbles tossed into the air, giving echolocation "buzzes" that were faintly audible to us as they followed the pebble in its fall back to the ground. The bats began feeding an hour before sunset and continued until after dark. Insect-capture maneuvers by *Tadarida* were accompanied by echolocation sounds in patterns typical of bats using sonar to track prey (Griffin, 1958; Grif-

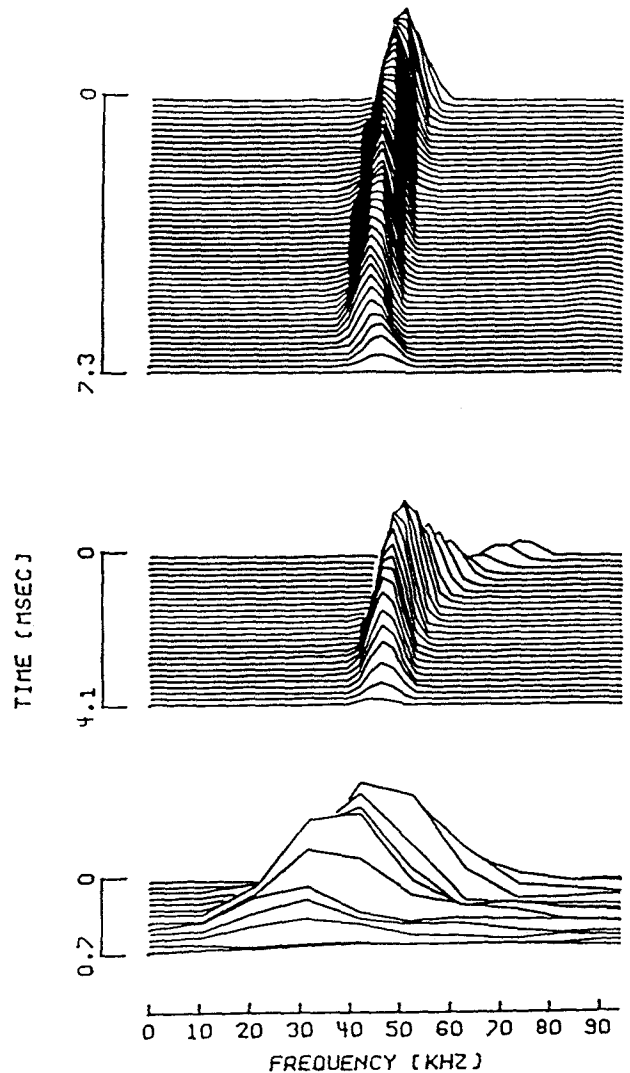


Fig. 6. Time-frequency structure of sonar sounds used by *Tadarida brasiliensis* during search (top), approach (middle), and terminal (bottom) stages of insect pursuit. Note nearly constant frequency during search, addition of an FM sweep during approach, and disappearance of the CF component and a general lowering of frequencies in the terminal stage

fin et al., 1960; Webster and Griffin, 1962; Webster and Brazier, 1965).

Figure 6 gives examples of orientation sounds used by *T. brasiliensis* during search, approach, and terminal or capture phases of the observed prey-capture behavior. This species apparently searches for insects with essentially a constant-frequency (CF) signal at about 50 kHz, and it changes to a progressively broader-bandwidth frequency-modulated (FM) signal as it closes in on the insect. All of these field recordings of *T. brasiliensis* indicate only one harmonic in the sounds, which is different from sounds used by this species in other situations. The exact frequency of the CF component is difficult to determine due to Doppler shifts.

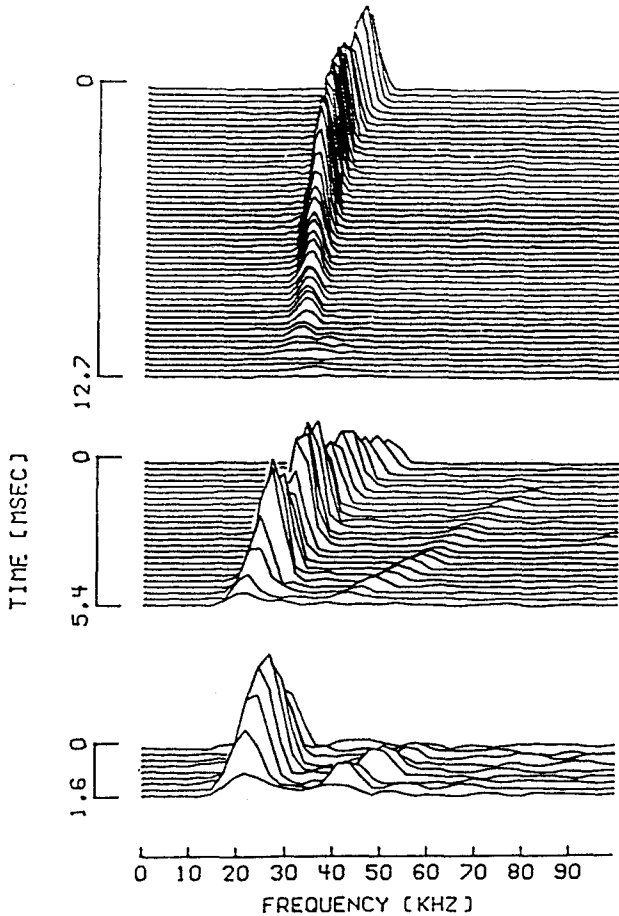


Fig. 7. Time-frequency structure of sonar signals used by *Tadarida macrotis* during search (top), approach (middle), and terminal (bottom) stages of insect pursuit. Search signal is narrowband, either CF or a shallow FM sweep, approach signal is FM, and terminal signal is FM

A similar pattern of foraging and acoustic behavior was observed in *T. macrotis* flying and feeding in company with *T. brasiliensis* at our study site. For *T. macrotis* the search signals are CF or shallow-sweeping FM sounds around 40 kHz, and broader FM sweeps appear as the bat approaches the prey (Fig. 7). Weak second harmonics appear in many approach and terminal "buzz" signals. The two species were readily distinguished by size (*T. macrotis* is 50% larger than *T. brasiliensis*) and by the illustrated differences in the frequencies of their orientation sounds as these were observed with portable frequency display equipment (Simmons, Fenton, Ferguson, Jutting, and Palin, in preparation).

Many signals were recorded with the bat and the microphone aligned towards each other and separated by a distance of less than 4 or 5 m, so no significant atmospheric absorption or acoustical artifact distorts

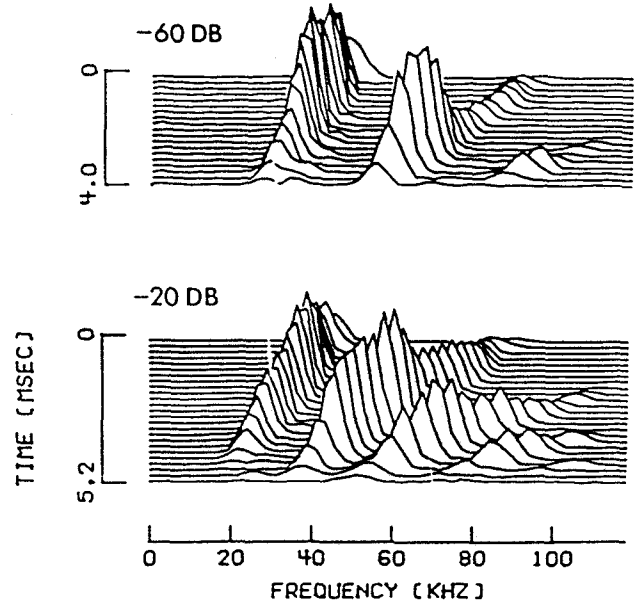


Fig. 8. Time-frequency structure of target-ranging sonar signals used by *Tadarida brasiliensis* in the presence of two levels of interfering noise ( $-60$  and  $-20$  dB re  $1.0 \text{ N/m}^2$  RMS sound pressure). Compare these signals with the target-ranging signal used in ambient noise (Fig. 2). Ambient noise was less than  $-70$  dB

these recorded sounds. The absence of a broad FM sweep in the search-phase signals used by the bats thus appears to be a valid observation, as is the predominance of a single harmonic component. It is difficult to classify the search signals as CF or shallow FM due to Doppler shifts. In both species the repetition rate of the sonar sounds ranged during searching from less than 5 sounds/s to over 100 sounds/s in the terminal phase. The details of temporal patterning of these sounds are considered in a separate paper (Simmons, Fenton, and O'Farrell, in preparation).

#### Adaptation to Noise Jamming

The ability of molossid bats to adapt to interfering noise was observed in the laboratory by presenting intense, broadband random noise to bats emitting sounds while held in the hand or while performing in target range discrimination trials. Figure 8 shows the signals used in the compensating behavior of *T. brasiliensis* as it attempts to avoid jamming. In the presence of noise the bat uses more intense and longer duration sounds than in quiet conditions (Fig. 2). An increase in signal power is general across the entire signal bandwidth when the noise is greater than  $-60$  dB re  $1.0 \text{ N/m}^2$  RMS sound pressure, and the duration of the signal in any narrow frequency region within the signal's bandwidth is increased relatively

uniformly since the frequency sweep is approximately linear (Figs. 2 and 8). *T. brasiliensis* thus responds to broadband random noise during range discrimination by increasing signal amplitude and duration to boost transmitted energy across the entire frequency band of the signals. The bandwidth is also increased somewhat and overlap of harmonics becomes pronounced. The progression of this adaptive response is shown by comparison of Figure 2 (target ranging in ambient noise) and Figure 8 (target ranging in noise at  $-60$  dB and  $-20$  dB re  $1.0$  N/m<sup>2</sup> RMS sound pressure at the bat's location during range discrimination). Under ambient conditions the interference was less than  $-70$  dB. The bats stopped target ranging performance if the interference became stronger than  $-10$  dB. The signals illustrated in these two figures were recorded while the bat successfully performed discrimination of targets at ranges of 28 and 30 cm.

Under ambient conditions the orientation sounds used by *T. brasiliensis* for target ranging were  $+5$  to  $+15$  dB re  $1.0$  N/m<sup>2</sup> peak sound pressure, and the echoes from the targets were  $-5$  to  $+5$  dB re  $1.0$  N/m<sup>2</sup> peak sound pressure at the bat's location. The bat increased sound pressure during discriminations in noise, bringing peak echo strength up to 0 to  $+10$  dB. Thus the bat's acoustic response to noise occurred when the RMS sound pressure of the noise was substantially lower than the peak sound pressure of the echoes used for the discrimination. The bats stopped performing when the interfering noise RMS sound pressure approached within an order of magnitude of the peak echo sound pressure. Quantitative analyses of signal-to-noise ratios in this experiment are not feasible, since the echo and noise strengths are not known with sufficient accuracy, since the bats used a variable number of sounds (1 to 30 signals per trial) for the discriminations, and since the directional separations of targets and loudspeaker ( $20^\circ$ ) provide opportunities for unspecified binaural interactions to occur.

## Discussion

When echolocating, the bat tries to communicate to itself information about its surroundings by interrogating the environment with sounds. The perceptual process of echolocation consists of building a description of the physical features of objects in terms of a description of the acoustic features of echoes. Central to an understanding of echolocation is the process of signal description, which must be undertaken no less by the scientist studying bat sonar than by the bat in interpreting echoes (Altes, 1976; Simmons, 1977).

A description of sounds based on Fourier analysis of waveforms (Schwartz, 1970) provides a convenient beginning for discussion of echolocation because experimental evidence indicates that there is at least a superficial quantitative relationship between such descriptions of echolocation signals and the acuity of target perception by echolocation (Simmons, 1973; Simmons et al., 1975), because optimal-probabilistic processor models of some auditory pitch phenomena suggest that such descriptions may be similar to those actually employed by the auditory system (Goldstein, 1973; Goldstein et al. in press), and because a web of circumstantial evidence links target perception by echolocating bats with temporal mechanisms for pitch perception in other animals (Suga, 1970; Pollak et al., 1977; Johnson and Titlebaum, 1976; Simmons and Lavender, 1976; Simmons, 1977; Popper and Fay, 1973).

In the conditions observed *Tadarida* uses echolocation in the simplest acoustic setting of any bat that we have watched, and the signals which these bats use in different situations clearly illustrate some basic principles of communications theory in animal orientation. The relationships discussed below between the bat's echolocation sounds as vehicles for information and the situations in which they are used reveal that the evolution and perhaps also the experience of free-tailed bats takes into account sophisticated aspects of sonar signal design.

## Types of Sonar Sounds

*T. brasiliensis* uses two families of sonar signals in different situations. Figure 6 illustrates the single-harmonic family, ranging from a CF or slightly FM signal at about 50 kHz to a descending, curvilinear FM sweep as the bat proceeds from search through approach and terminal phases of the insect-pursuit process. This sequence is a continuous progression, with signals of intermediate characteristics between the first and the second and the second and third signals shown in Figure 6. The signals in this prey pursuit family correspond roughly to the second-harmonic component in the multiple-harmonic signals used by the bat in cluttered situations (Figs. 2, 4, 5, and 8). The feeding behavior of *T. brasiliensis* is interesting in that the bats pursue their prey rather far above the ground and in the absence of significant obstacles to flight. The bats invariably abandon using the single-harmonic signals when echolocating in cluttered situations, such as rooms or roosts, where there are significant obstacles within a few meters distance.

The second family of signals consists of multiple-

harmonic FM sweeps used when obstacles or background objects are present. These signals have been observed previously and are the kind usually attributed to *Tadarida* (Griffin, 1958; Vernon and Peterson, 1965). When the bat is stationary, the sweeps in these signals descend linearly with frequency (Figs. 2 and 8). When the bat is flying, these sweeps descend in a curvilinear manner, approximating linear period modulation (LPM) signals (Fig. 4). The bat sometimes attaches a short CF component of about 55 kHz to the beginning of the first harmonic of multiple-harmonic sounds (Fig. 5).

The nearly constant-frequency or narrowband signal used to search for prey contains its energy from 45 to 55 kHz (Fig. 6), and the multiple-harmonic FM signals used for target ranging or more generally in clutter show a notch or null in the same 45 to 55 kHz region (Fig. 2). When the multiple-harmonic signals are increased in duration and expanded in sweep range when the bat is in noise or is in flight, this spectral notch is filled in (Figs. 4 and 8). Furthermore, the bat can add the initial short CF component to multiple-harmonic signals at this same frequency region (Fig. 5). Vocalization mechanisms in these bats would be interesting to study, and the existence of perceptual criteria for choosing signals may provide an example of animal "expectations" in a well-defined situation.

It has long been known that many species of bats which spend much of their time flying in dense foliage or other extremely cluttered situations use sonar signals with three or more harmonics (Neuweiler, 1977; Sales and Pye, 1974; Simmons et al., 1975). It is gratifying to observe as an adaptive behavior within one flexible species the same phenomenon that appears across different species, each one perhaps relatively more "locked in" to its acoustic environment. Observation of the use of multiple-harmonic signals by *T. brasiliensis* in cluttered situations and single-harmonic signals in open spaces constitutes a successful test of the hypothesis that multiple-harmonic signals are of particular value when operating in clutter. The addition of harmonics to a signal is a ready means of broadening signal bandwidth, thus gaining improved resolution of a variety of features of complex, distributed targets (clutter) by improving the quality of the acoustically-obtained image of these targets. The quality of the image improves with broader signal bandwidth because (a.) there are more frequencies available to determine frequency-dependent echo characteristics of targets or (b.) the autocorrelation function of the signal is compressed into a narrower time window, providing increased resolution of multi-planar structure of complex targets.

In the absence of clutter, as when pursuing prey,

*Tadarida* apparently uses CF signals or narrowband FM signals when searching for a target and progressively broader-bandwidth FM signals when closing in on an already-detected target to gather more detailed information about its nature. Previous laboratory and field studies have established the role of short CF or narrowband signal components in detection tasks by *Eptesicus* (Simmons et al., 1978). The use of purely CF signals by *T. brasiliensis* confirms these observations and suggests that many species of bats which use short-CF/FM or FM/short-CF signals (Simmons et al., 1975) do not drop the FM component due to a greater concern for cluttering objects than occurs with *Tadarida* when pursuing prey. These other species are always "keeping an ear out" for obstacles, even while pursuing prey.

The short CF component, used by *T. brasiliensis* just as it emerges from the roost but not after it has flown a few meters on its way (Fig. 5), may serve to detect targets that may be present in the area of emergence and past which the bat must launch itself. Once in flight the bat climbs in altitude, and this CF component disappears from the sounds. The appearance of this short-CF/FM signal in the repertoire of orientation sounds of *T. brasiliensis* further illustrates the great adaptability of the behavior of this species when compared to our present understanding of the behavior of other species of echolocating bats.

*Tadarida* apparently uses short CF sounds, short-CF/FM sounds, FM sounds with one or several harmonics, and FM sounds tailing off in relatively constant frequencies. With the exception of very long CF signals, *Tadarida* exhibits the whole range of echolocation signals found, species-by-species, among all other Microchiropteran bats. The recent discovery of the use of long-CF/FM sonar sounds by *Plecotus phyllotis* (Simmons and O'Farrell, 1977), a bat that would ordinarily have been thought to use only FM sounds, suggests that the use of long CF components cannot be ruled out for *Tadarida* without many more negative observations.

#### Range Discrimination

For range discrimination in the laboratory *T. brasiliensis* uses downward-sweeping FM signals that exhibit nearly linear frequency modulation (LFM), with two or three harmonics present (Fig. 2). The sounds are similar to target-ranging signals used by *Eptesicus fuscus* and by *Phyllostomus hastatus* in bandwidth and presence of harmonics, except that these other bats use curvilinear FM sweeps that approximate upward linear period modulation (LPM). The harmonics used by *E. fuscus* and *P. hastatus* also occur in overlapping

frequency bands (Simmons, 1973), whereas the harmonics in the target-ranging signal of *T. brasiliensis* do not overlap but are separated by silent bands several kHz wide (Fig. 2). In many respects these *T. brasiliensis* signals resemble the terminal FM sweeps used by *Pteronotus suapurensis* for target ranging in that the harmonics used by this bat do not overlap and LFM sweeps are sometimes used. *Pteronotus suapurensis*, however, uses a short-CF signal preceding and attached to the FM signal, even for target ranging. The autocorrelation function for the target ranging signal of *T. brasiliensis* has an envelope peak about 80  $\mu$ s wide (Fig. 3), which is similar in width to the autocorrelation envelope peaks (or ambiguity functions for stationary targets) for the FM signals of a wide variety of bat species (Simmons, 1973).

The envelope of the autocorrelation function of the signal can be viewed as describing the shape of the signal's occurrence as an image in time if the information contained across the signal's bandwidth contributes to determining the time of occurrence of each echo. Previous experiments have indicated that the performance of the bat (% correct responses) for a given range difference can be predicted accurately from the magnitude of the envelope of the autocorrelation function for the appropriate time delay. The autocorrelation envelope from Figure 3 was used to derive a theoretical target-ranging performance curve, assuming that this correlation function is equivalent to the crosscorrelation of transmission and echo for a stationary target, and that a correlation magnitude of 1.0 is equivalent to complete ambiguity and discrimination performance at chance levels (50% correct responses).

Figure 1 shows the predicted or theoretical performance of a bat using the signal in Figure 2 for target range discrimination and also the actual performance of two individual *T. brasiliensis*. Variations in autocorrelation width among target-ranging signals were less than 5%. These two curves match closely, suggesting (as for other species of bats) that the envelope of the autocorrelation function of the target-ranging signal used by *T. brasiliensis* somehow defines the shape of the bat's perceptual image or representation of the target along the range dimension.

### Adaptability of Echolocation

The observations reported here suggest that *Tadarida* are more flexible in their use of echolocation tailored to the perceptual requirements of different situations than are other species. It is evident that *Tadarida* cannot simply be classified as "FM bats." Although the categories of different kinds of orientation sounds

(FM, CF, FM/short-CF, short-CF/FM, long-CF/FM) describe the signals used by bats, they appear not to describe in simple categories the bats, themselves. At present many species of bats are known to use only one type of sonar sound, and it is likely that some of these species are in fact not very adaptable and truly use only one type of orientation sound in all situations. Others are probably more adaptable, however, and it remains for us to demonstrate their flexibility by observing them in new situations. Whether *Tadarida* are actually more adaptable than other bats is not at present known. *Eptesicus fuscus*, for example, uses multiple-harmonic FM or FM/short-CF sonar signals in all the situations so far observed, whereas *Tadarida brasiliensis* uses a broader range of signals in these same situations. Do *Eptesicus* forage for food in situations as free of obstacles as *Tadarida*? If so, perhaps they then use signals similar to *Tadarida*.

These comparative observations of echolocation by free-tailed bats clearly reveal a new pattern of orientation sounds used during insect pursuit: short CF or narrowband signals gradually broadening in bandwidth to become FM signals. The strategy for pursuit of prey implied by these signals is very basic. The bat begins by searching for targets and makes a transition from the use of narrowband detection signals to the use of broadband target-descriptive signals after detection occurs and the bat approaches closer to the prey. The gradual transition suggests that the echolocation requirements for target detection (narrow signal bandwidth) and for target description (broad signal bandwidth) are opposed to one another, and that the bat continuously adjusts the signals to maintain an optimal balance of the two perceptual intentions. That we can directly observe the bat's perceptual interests in the signals illustrates the scientific value of echolocation in bats as an animal model of acoustic communication and spatial orientation.

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