

ADVANTAGES AND DISADVANTAGES OF TECHNIQUES FOR TRANSFORMING AND ANALYZING CHIROPTERAN ECHOLOCATION CALLS

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Bat researchers currently use a variety of techniques that transform echolocation calls into audible frequencies and allow the spectral content of a signal to be viewed and analyzed. All techniques have limitations and an understanding of how each works and the effect on the signal being analyzed are vital for correct interpretation. The 3 most commonly used techniques for transforming frequencies of a call are heterodyne, frequency division, and time expansion. Three techniques for viewing spectral content of a signal are zero-crossing, Fourier analysis, and instantaneous frequency analysis. It is important for bat researchers to be familiar with the advantages and disadvantages of each technique.

Key words: Chiroptera, echolocation, Fourier, frequency division, heterodyne, instantaneous frequency, techniques, time expansion, zero-crossing

Because of their nocturnal activity and small size, bats have been considered difficult to study. Microchiropterans use echolocation calls to orientate themselves and to locate and close in on prey (Griffin et al. 1960). Equipment capable of transforming ultrasound to frequencies audible by humans has been available for over 60 years (Noyes and Pierce 1938) and was used first to study echolocation calls of bats by Pierce and Griffin (1938). The most common techniques currently available to hear emissions of bats include heterodyne, frequency division, and time expansion. The majority of these transformations are performed on analog (or digital in the case of time expansion) signals by bat detectors. However, these techniques also can be applied digitally after the signal has been acquired, using either a more sophisticated bat detector or a computer.

Although these techniques allow humans to hear calls of bats, researchers also are interested in viewing the spectral content or frequency structure of a call. To do this, calls must be transformed from the amplitude–time domain into either the frequency–time domain (a spectrogram) or the frequency–amplitude domain (a power spectrum).

All of these techniques are in daily use in bat research, but many researchers do not fully understand the methods. Techniques and equipment available for study of ultrasound have been reviewed in recent years (Bradbury and Vehrencamp 1998; Fenton 1988; Hopp et al. 1998; Pye 1992), as have problems associated with such studies (Bazly 1976; Lawrence and Simmons 1982; Pye 1993). However, most reviewers have not dealt with these techniques in a bat-specific context, have not discussed practical limitations that are of interest to most bat re-

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searchers, have not discussed all the most common techniques in use, or have not been up to date enough to be of practical use.

MATERIALS AND METHODS

Heterodyne, frequency division, time expansion, zero-crossing, Fourier analysis, and instantaneous frequency analysis can be used within a framework that is applicable to those studying echolocation calls of bats. There are advantages and disadvantages of these techniques that are relevant to bat researchers. Specific brands of detectors and models change frequently, whereas techniques incorporated develop more slowly. A detailed listing of modern detectors and analysis systems has been published (Parsons and Obrist, in press).

(Super)Heterodyne

Technique.—Heterodyning was first used to transform echolocation calls of bats by Pierce and Griffin (1938), with an apparatus originally designed to study ultrasonic emissions of insects. The equipment, designed by Noyes and Pierce (1938), used only a single internal oscillator to lower the frequency of the input signal. However, most modern equipment uses a technique known as superheterodyning in which the input signal is mixed with signals from 2 oscillators (Fig. 1). When a call (F_{call} ; Table 1) is detected, it is mixed with a signal from an input oscillator (variable-frequency oscillator; F_{vfo}). The frequency of this oscillator is variable and usually is set by the user. The mixing of F_{call} and F_{vfo} ($F_{\text{call}} \times F_{\text{vfo}}$) results in production of a signal with 2 peak frequencies, 1 at $F_{\text{vfo}} + F_{\text{call}}$ and another at $F_{\text{vfo}} - F_{\text{call}}$. The resultant signal is passed through a narrow-band filter so that only part of the low-frequency peak ($F_{\text{vfo}} - F_{\text{call}}$) remains in the signal ($F_{\text{call}2}$). The filtered signal then is combined with a signal produced by a constant-frequency oscillator ($F_{\text{cfo}} \times F_{\text{call}2}$), producing a 2nd signal containing 2 frequency peaks ($F_{\text{cfo}} + F_{\text{call}2}$, $F_{\text{cfo}} - F_{\text{call}2}$). The low-frequency peak (F_{out}) is in the human hearing range but the other is not. Hence, the human ear (or audio speaker producing the sound) acts as a 2nd low-pass filter (Fig. 1).

Advantages.—Superheterodyne systems generally are cheap to produce and rugged, and the narrow range of frequencies transformed by superheterodyning leads to good signal-to-noise

ratios despite potentially high noise levels in the input signal. Stronger amplification of the signal also can be achieved because the internal oscillators use very different frequencies. The relatively high sensitivity of superheterodyning bat detectors has been demonstrated in the laboratory (Downes 1982; Waters and Walsh 1994) and the field (Parsons 1996; Waters and Walsh 1994). However, results can be influenced strongly by the frequency response of the microphone (Waters and Walsh 1994). Sensitivity of superheterodyning means that it can be useful for survey work where species identification is not necessary (e.g., O'Donnell and Sedgely 1994), particularly where use of less sensitive techniques may lead to undersampling. Given prolonged activity or presence of a bat, the narrow bandwidth transformed using this technique also can allow several call parameters to be approximated, including the highest and lowest frequencies, frequency of highest intensity, and position and number of harmonics. This approximation may allow researchers some degree of species identification if the species present do not produce echolocation calls that overlap significantly in frequency.

Disadvantages.—The narrow bandwidth transformed by superheterodyning also is the technique's most limiting factor. Superheterodyning does not preserve duration, absolute frequencies, or the frequency–time course of the original signal (Fig. 1). The narrow listening window also may lead to undersampling in survey work because bats calling at frequencies outside the window will be missed. J. D. Pye and J. A. T. Halls attempted to overcome this problem by developing a heterodyne system that listened through a number of frequency windows simultaneously (Pye 1992). The system was not successful because when a signal was detected no indication was given as to which window (or windows) it had passed through. Later detectors incorporated a scanning electronics circuit, allowing observers to quasi-simultaneously monitor a selectable frequency range (e.g., 20–80 kHz). This circuitry automatically pauses scanning at the tuning frequency where it detects a signal above the user-set threshold, giving the opportunity to observe the digital readout of the detected frequency.

Frequency Division

Technique.—Frequency division was first used to transform echolocation calls of bats when it

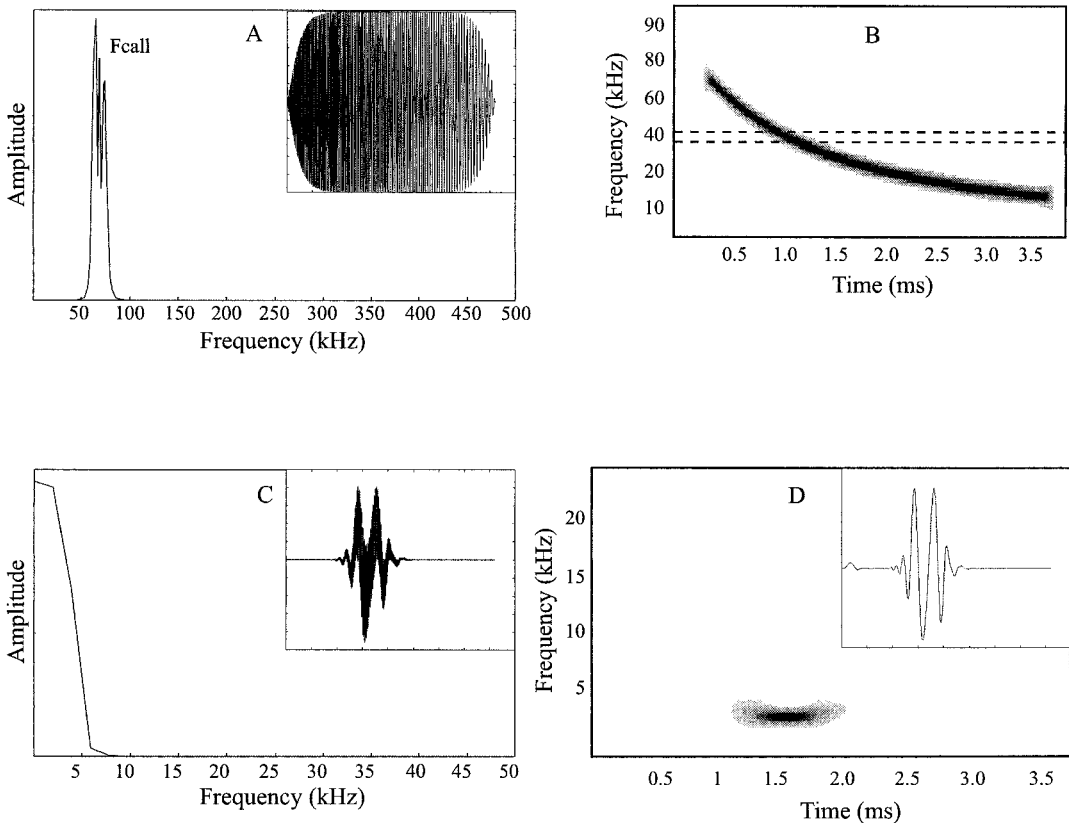


FIG. 1.—Results from an analysis of a simulated echolocation call using a digital superheterodyning system modeled in Matlab (version 5.3, MathWorks, Inc., Natick, Massachusetts). A) Power spectrum and waveform of the simulated echolocation call. B) Spectrogram of the simulated echolocation call. The dotted area shows the frequency range and bandwidth that will be transformed by the circuit. C) Power spectrum and waveform of the raw output signal from the superheterodyning circuit. The high-frequency component of the output signal is not visible in the power spectrum because it falls outside the displayed frequency range. D) Spectrogram and waveform of the output signal after the high-frequency component has been removed from the output signal using a low-pass digital filter. This panel shows the structure of the sound that can be perceived by humans. All power spectra and spectrograms were generated using 512-point fast Fourier transformation with Hamming windows.

was introduced into a bat detector by Andersen and Miller (1977). As with superheterodyning, frequency division is essentially an analog process. Frequency division simply divides the frequency of the incoming signal by a predetermined ratio, thus lowering its frequency. A zero-crossing system counts the number of times the incoming waveform crosses a zero voltage level and converts the signal into a sine or square wave. The amplitude of the sine or square wave is kept constant and so does not reflect the amplitude envelope of the original call. A circuit reduces the frequency of the incoming signal by

allowing only every n th cycle to pass through, i.e., the zero-crossing system inverts its output voltage when it has counted n zero-line crossings (Fig. 2). If the division ratio is set at 10, then only 1 in 10 cycles is allowed to pass. Many systems attempt to minimize the effect of noise by only dividing the incoming signal if its amplitude exceeds a threshold value. Finally, most systems multiply the output with the amplitude envelope of the original signal for optimum correspondence.

Advantages.—An obvious advantage of frequency division is that it does not “listen”

TABLE 1.—The effect of superheterodyning on an input signal centered at 4 different frequencies as performed by a bat detector. F_{call} = center frequency of input signal; F_{det} = tuned frequency of superheterodyning bat detector; F_{vfo} = center frequency of variable frequency oscillator; $F_{\text{call}2}$ = high frequency component of signal, produced by the combination of F_{call} and F_{vfo} , that is combined with F_{cfo} ; F_{cfo} = center frequency of constant frequency oscillator. F_{out} = center frequency of the signal presented to the user. Bandwidth of the output signal will depend on the characteristics of the individual detector or system.

F_{call} (kHz)	F_{det} (kHz)	F_{vfo} (kHz)	$F_{\text{vfo}} \times F_{\text{call}}$ (kHz)		F_{cfo} (kHz)	$F_{\text{cfo}} \times F_{\text{call}2}$ (kHz)	
			$F_{\text{call}2}$	Filtered		Filtered	F_{out}
27	30	479	506	452	455	907	3
76	80	527	603	451	455	906	4
121	120	574	694	454	455	909	1
198	200	655	853	453	455	908	2

through a narrow frequency window as do the superheterodyning systems. Therefore, frequency division is capable of transforming an entire signal, regardless of frequency (subject to performance of the associated microphone). This technique is particularly useful in survey work where a wide range of frequencies must be monitored simultaneously (e.g., Zingg 1990). Divided signals are suitable also for limited frequency analysis. Because frequency of the output signal can be significantly lower than that of the original, lower sampling rates are required for digitization with no loss in precision. The original duration of the call is more or less preserved in the output signal.

Disadvantages.—The frequency division technique has several drawbacks. Foremost is that the zero-crossing mechanism only tracks the harmonic with greatest amplitude, and thus no other harmonic information is contained in the output signal. In some bat species, frequency overlap between harmonics means that the harmonic with most energy may change over the course of the call. This can cause the zero-crossing system to jump between harmonics, leading to a misleading output signal, especially when analyzed spectrally (Fig. 3). A 2nd drawback is that in some frequency division systems, the amplitude envelope of the original signal may not be represented in the output. Hence, potentially important information such as the frequency with the most energy in a call is lost. Third, the degree of division will determine the frequency range that can be heard or recorded following transformation. If a division ratio is too low, calls of bats using high frequencies may be

missed. Fourth, use of an input amplitude threshold may decrease overall sensitivity of the detector (Parsons 1996) and may result in calls of lower amplitude (e.g., from “whispering” bats) being missed. Use of a threshold also may mean that parts of a call, particularly at the beginning and end, may be missed because they are not of sufficient amplitude to trigger the frequency division system. This, in turn, may lead to inaccurate measurement of the start and end frequencies of a call and its duration. The degree of error associated with these measurements will be determined by the threshold used. Fifth, by dividing the signal, information contained in those parts of the waveform that are not divided is lost and so is a large part of the frequency–time structure of the signal. Small changes in frequency structure of the original call may not be reflected in the divided signal. Sixth, use of frequency division relies on there being enough information in the original waveform to allow it to be accurately represented in the divided signal. This is most evident in very short calls or calls that exceed the threshold for only a short time. For example, a 40-kHz signal lasting 2 ms will contain only 8 cycles after being divided by 10. Andersen and Miller (1977) reported calls from pipistrelles (*Pipistrellus pipistrellus*) with durations of 0.3 ms emitted during a feeding “buzz” (Griffin et al. 1960). After frequency division, calls of such short duration were composed of only a single cycle and could not be meaningfully analyzed.

Time Expansion

Technique.—The frequency of a recorded signal can be lowered linearly by decreasing the

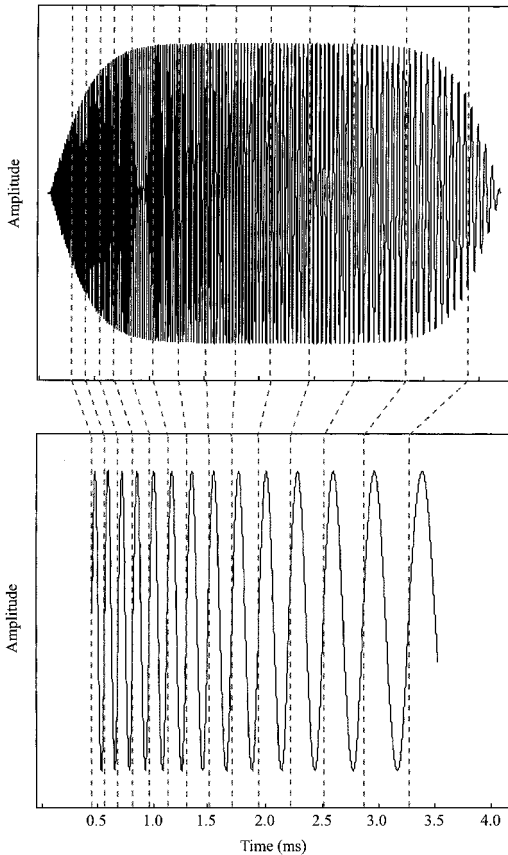


FIG. 2.—Waveform of a simulated frequency-modulated echolocation call before and after frequency division (10:1). A threshold of one-third the maximum amplitude of the waveform was used. For this reason, the frequency-divided signal has a shorter duration than the original signal. The original waveform has been split into sections comprising 10 cycles. Each of these sections corresponds to a single complete cycle in the waveform of the frequency-divided signal. The envelope of the original signal is not represented in the frequency-divided signal. The original waveform and the frequency division system both were modeled in Matlab. A sampling rate of 1 MHz was used to generate the original waveform.

replay speed of the recorder relative to the speed used during recording. Because of the inverse relationship that exists between time and frequency, duration of the signal will increase linearly as replay speed decreases. For example, a 40-kHz signal lasting 5 ms recorded using a tape

speed of 76.2 cm/s will become a 10-kHz signal lasting 20 ms if the tape is replayed at 19.05 cm/s. Unfortunately, size, weight, and cost of these tape recorders represent only a few of the drawbacks associated with their use, particularly in the field. However, in the mid-1980s, a method was developed to time-expand signals digitally. To be expanded in this way, the high-frequency signal must be digitized at a high sampling rate. The signal is then converted back into a waveform using a lower output rate. The degree of time expansion used depends on the difference between the 2 rates. The time-expanded signal can then be recorded using a more conventional tape recorder or redigitized at a lower sampling rate.

Advantages.—In recent times, digital time expansion has been incorporated directly into bat detectors, making the technique more widely available. The great advantage of this technique is that no information is lost from the incoming signal, making the output suitable for spectral analysis. When combined with a laptop computer and signal analysis software, output from a time-expansion system can provide field workers with high-quality information on bat ultrasound in near-real time. High sampling rates are not required because a time-expansion factor of 10 can bring signals of up to 220 kHz within the accurate digitization range of most modern computer sound cards, including those in newer laptops. Despite the higher cost, digital time-expansion equipment is an excellent value for money compared with the cost of traditional equipment such as air-dielectric microphones and instrumentation tape recorders. Some time-expansion detectors also are capable of outputting heterodyned, frequency-divided, and unmodified high-frequency signals, thus increasing their value.

Disadvantages.—Despite increasing availability and decreasing cost of digital technology, time-expansion units and detectors still are considerably more expensive than heterodyne or frequency division detectors. At present, it is not possible to sample continuously using time expansion. Most systems store 2–12 s of digitized sound before outputting the expanded signal. During the output phase, the system is not sampling from the environment. For example, a time-expansion detector will take 22 s to acquire and output 2 s of ultrasound (input = 2 s, output = 20 s), assuming a time-expansion factor of 10.

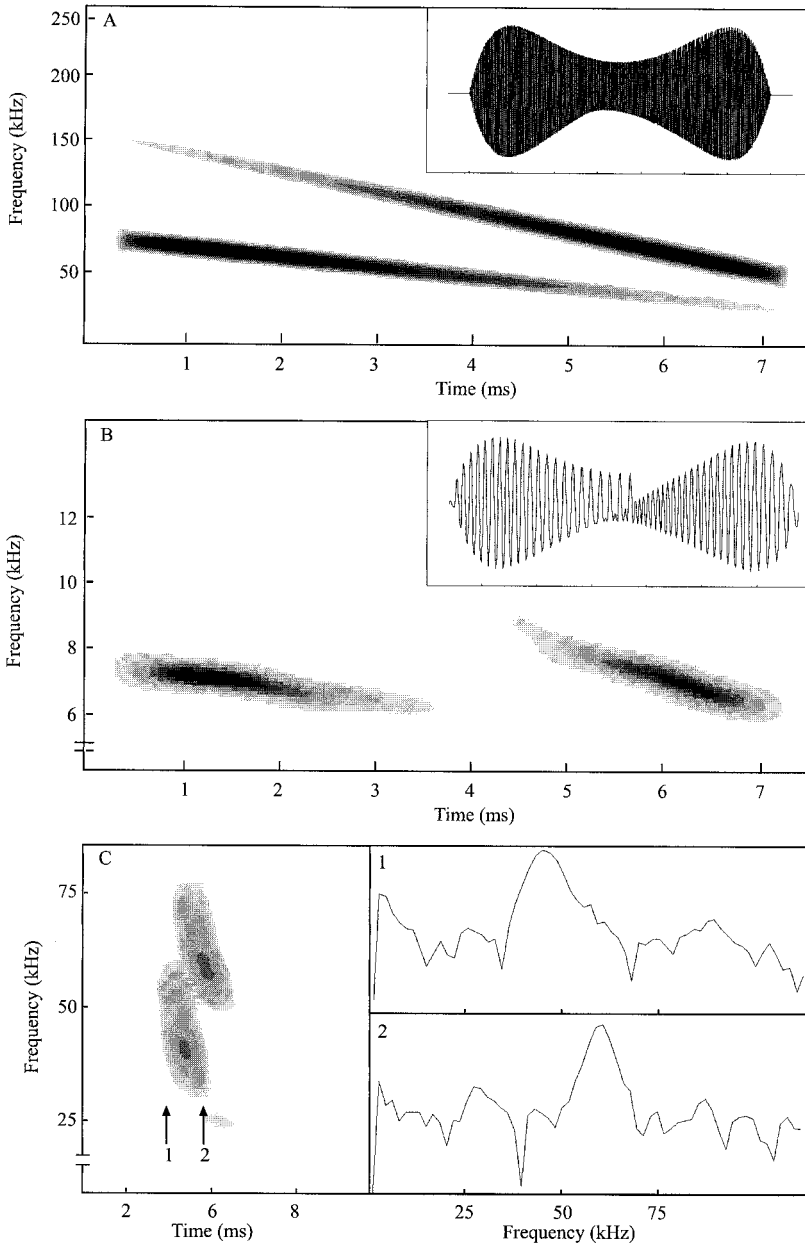


FIG. 3.—A and B) Spectrogram and waveform of a simulated frequency-modulated echolocation call with a single harmonic before and after frequency division (10:1). In this example, the frequency-divided signal jumps from the fundamental to the harmonic as it follows the part of the signal containing the most energy. The waveform and the frequency division system both were modeled in Matlab. A sampling rate of 1 MHz was used to generate the original waveform. C) Spectrogram and power spectra from an echolocation call produced by *Plecotus auritus*. In this call, energy swaps from the fundamental (C1; power spectrum 1) to the harmonic (C2; power spectrum 2) part way through the call. All spectrograms were generated using 512-point fast Fourier transformations; the power spectra were generated using a single 64-point fast Fourier transformation. In both cases, Hamming windows were used.

Thus, ideally the system is sampling only 9.1% of the available time. Use of higher expansion factors will further reduce sampling times. Frequency division and heterodyne systems are not limited in this way. Only with new approaches to real-time dumping of digital data at high speeds (parallel, IEEE 1394, or Firewire) to computer memory and hard disks will digital time expansion become a viable alternative to high-speed tape recording.

Zero-crossing Analysis

Technique.—Zero-crossing is used in frequency division to isolate individual cycles within a waveform. However, this technique also can be used to transform a signal from the amplitude–time domain into the frequency–time domain. Inverted output of a frequency-controlled voltage generator allows a real time display of instantaneous frequency of high-frequency signals on an oscilloscope (period meter—Simmons et al. 1979). In other cases, zero-crossings in the signal are determined digitally (i.e., after digitization) rather than on the analog waveform. However, the technique is essentially the same. After digitization, time is measured when the waveform crosses the average amplitude level of the signal (also known as the ambient sound pressure level) twice. As with zero-crossing in the analog domain, amplitude of the digital signal must be above a predetermined threshold level before it is analyzed. Because the time between successive zero-crossings is related inversely to twice the frequency of the signal at that point (every complete cycle will cross the zero-point twice), a frequency–time representation of the signal can be created (Fig. 4).

Advantages.—Zero-crossing is a simple technique that does not rely on the use of complex mathematical formulae to transform a digital signal into the frequency domain. Therefore, the technique is fast and, depending on the frequency of the incoming signal, usually can be carried out in real-time with appropriate analog circuitry, even without a computer. Unlike Fourier analysis, this technique does not suffer from the uncertainty principle so that resolution in the frequency domain is not compromised by a lack of resolution in the time domain.

Disadvantages.—Many of the problems associated with zero-crossing as an analysis method are the same as those associated with using it as part of a frequency division system. First, the

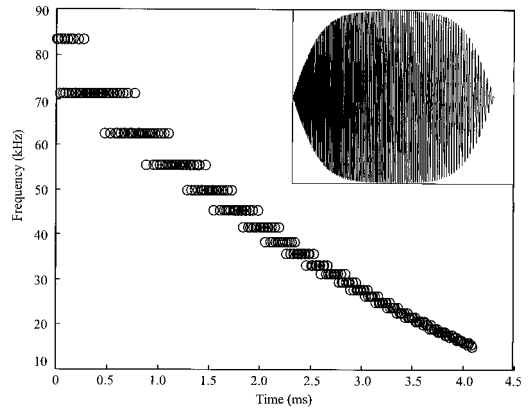


FIG. 4.—Frequency–time plot of a simulated frequency-modulated bat call after analysis by zero-crossing. The waveform of the original signal also is shown. A spectrogram of this signal can be seen in Fig. 1B. The frequency of the signal varies at the beginning of the signal. At high frequencies, small changes in the time between successive zero-crossings, which is influenced by the rate at which the signal was sampled, can cause large changes in frequency. However, as frequency of the call decreases, these small errors become less significant. The original waveform and the zero-crossing analysis both were modeled in Matlab. A sampling rate of 1 MHz was used to generate the waveform.

technique will analyze only that part of the signal that has the most energy associated with it. For this reason, all harmonic information contained in the original signal is lost, with only the loudest harmonic being analyzed. Use of a threshold also means that any part of the signal with amplitudes below this level will not be analyzed, possibly contributing to errors in estimating the start and end frequencies and the duration of calls. Many calls from species that use low-amplitude calls may not be accurately analyzed for the same reason. Zero-crossing also is extremely susceptible to the presence of noise in the signal, making the interpretation of frequency data difficult. As with all digital techniques, ability of digital zero-crossing to accurately represent the frequency–time course of the signal is dependent on the sampling rate used during digitization. If the sampling rate is low, each cycle in the waveform will be described by very few

data points and determination of the exact time of zero-crossings becomes difficult.

Fourier Analysis

Technique.—Fourier analysis probably is the most commonly used technique for calculating the spectral composition of a signal. Results of a Fourier transformation usually are represented in 1 of 2 forms, a power spectrum or a spectrogram. A power spectrum is used to present the frequency and amplitude content of part of a signal at a particular point in time (Fig. 3). This part can be the entire signal (i.e., echolocation call) or some fraction of it. A spectrogram differs from a power spectrum in that it also contains information on how frequency and amplitude of a signal change over time (Fig. 3). Essentially, a spectrogram is the result of a series of Fourier transformations applied sequentially to a signal.

A simple method for determining the frequency of an oscillating object is to look at it with a stroboscope. By slowly changing the flash rate, the object appears to be motionless at only 1 particular flash frequency, which coincides with the object's oscillatory frequency. A Fourier transformation attempts something similar. When applying a Fourier transformation to a waveform, the waveform is multiplied by an artificial waveform of a particular frequency, and the results are summed over a range of frequencies. If the input waveform consists only of 1 frequency, the sum of the multiplication will peak only at 1 particular frequency, just as in the example of the stroboscope. This peak will occur at the frequency that is equal to the frequency of the signal.

In reality, a Fourier analysis is somewhat more complicated because phase information must be included in the calculations. In terms of our stroboscope example, it is possible to "freeze" the oscillating object by choosing the appropriate flash rate, but the target could be frozen at any position ($0-2\pi$) of its cycle, depending on the phase difference between the stroboscope and the object. The Fourier transformation constructs the artificial waveform such that both frequency and phase match those of the real input waveform.

The size, or length, of a Fourier transformation is measured in points. The number of points used in a transformation represents the number values from the signal to be analyzed and the

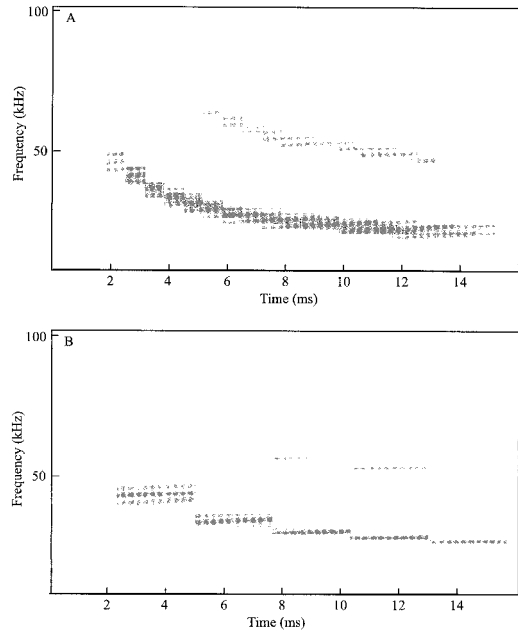


FIG. 5.—Spectrograms of the same echolocation call from *Eptesicus serotinus* using A) a 256-point Fourier transformation and B) a 1,024-point transformation. No window overlap was used in calculating the displays.

number of values returned by the transformation. For example, a 512-point Fourier transformation will analyze 512 sequential values from the waveform and return 512 frequency–amplitude values. Only 256 values of the sample will be usable; the remainder belongs to the imaginary part of the signal. The frequency resolving power of a transformation depends on the length of the signal being analyzed. The shorter the signal waveform to be matched with the artificial waveform, the worse the frequency resolution. The resolution of a transformation is constrained by the uncertainty principle (Beecher 1988), which states that frequency and time are inversely related. This principle can be represented by $\Delta t = n_f/s_f$ and $\Delta f = 1/\Delta t$, where n_f is the length of the Fourier transformation and s_f is the sampling rate used when the signal was digitized. Therefore, a trade-off exists between Δf (frequency resolution) and Δt (time resolution). As a general rule, the larger the number of points used in the transformation, the better the frequency resolution will be (Fig. 5). However, time resolution will be poor. If a small number of points are used, the inverse is true.

Fourier transformation on its own gives an adequate picture of the frequency content of a signal only if the input waveform is continuous. Sounds produced by bats, however, are often pulsed and therefore discontinuous. The start and end points of data to be transformed almost certainly will be nonzero values because sample points are unlikely to coincide with zero-crossings. Therefore, matching the signal with artificial waveforms used by the Fourier transform will be difficult and may lead to frequency side lobes appearing in the output. To avoid these spurious ripples, most signals are first weighted before being transformed. Most weighting functions (e.g., Hamming windows) are simple bell-shaped functions that taper off the far ends of the signal. In this way, truncated parts of the signal are de-emphasized and hence frequencies of the side lobes are reduced.

Advantages.—The main advantage of Fourier analysis is that very little information is lost from the signal during the transformation. The Fourier transform maintains information on amplitude, harmonics, and phase and uses all parts of the waveform to translate the signal into the frequency domain. Preservation of phase information by the Fourier transformation means that the signal can be transformed back into the time domain. Power spectra and spectrograms do not contain phase information. Fourier analysis does not rely on arbitrary thresholds; therefore, frequency and time resolution are calculated easily, making direct comparisons with other studies possible. This type of analysis also is relatively insensitive to noise, making it very useful for analyzing bat signals.

Disadvantages.—The major disadvantage of the Fourier transformation is the inherent compromise that exists between frequency and time resolution. The length of Fourier transformation used can be critical in ensuring that subtle changes in frequency over time, which are very important in bat echolocation calls, are seen. It may be that no single length of transform is ideal for a particular signal; several transformations, each of a different length, may be required before a signal can be described adequately. In a signal that is masked heavily with noise, the start and end points of a call may be more obvious in a spectrogram, because the high-amplitude noise is often of lower spectral density and lower frequency than the echolocation call of interest. However, because of the windowing cal-

ulation of the spectrogram, it is less advisable to measure duration of a signal from a spectrogram. Such measurements contain some degree of imprecision, which can be compensated for only after elaborate calibration of a specific spectrogram setting (window size, window shift) against the time–amplitude display.

Instantaneous Frequency

Technique.—Instantaneous frequency analysis is 1 of the lesser-known techniques for calculating spectral content of a signal. A waveform can be described in terms of sinusoids or cosinusoids. The period length of high-frequency signals is shorter than that of low-frequency signals. This means that pressure, or voltage, described by the sinusoid changes more rapidly between peaks and troughs at high frequencies than at low frequencies. Rate of pressure change depends on the frequency of the signal. The rate of change in sound pressure can be measured by calculating the time derivative of the sinusoid phase (Nyamsi et al. 1994):

$$f(x) = \frac{1}{2\pi} \frac{d\Phi}{dt} = \frac{1}{2\pi} \frac{x_r(t)\dot{x}_i(t) - x_i(t)\dot{x}_r(t)}{x_r^2(t) + x_i^2(t)},$$

where $f(t)$ is the instantaneous frequency of the signal, Φ is its phase, x_r is the real part of the signal, x_i is the imaginary part, and $\dot{\bullet}$ denotes the time derivative. Therefore, to calculate instantaneous frequency, real and imaginary parts of the signal and their time derivatives must be calculated. Time resolution of the instantaneous frequency method is better than that in any other method and is given by $\Delta t = 1/(s_f - 1)$, where s_f is the sampling frequency. Frequency resolution depends on frequency modulation of the signal itself and background noise level. If frequency modulation is high, the change in phase between 2 subsequent samples will be high. It is therefore impossible to define the frequency resolution of this method.

Advantages.—A clear advantage of using instantaneous frequency is that the uncertainty principle between frequency and time resolution is circumvented so that high resolution in frequency and time domains can be achieved simultaneously. The technique also uses all information contained in a signal and therefore is probably the best technique available for calculating frequency–time structure of echolocation calls. However, to function properly, spurious effects of noise must be suppressed, usually via

filtering. The Wiener filter is particularly suited to this task.

Disadvantages.—In theory, this method should be ideal for measuring the frequency–time course of chiropteran echolocation calls. In practice, however, it is very sensitive to noise and may cause difficulties in finding the exact start frequency of a pulse. The effect of noise can be reduced by smoothing the frequency–time data over a number of points, leading to a reduction in both time and frequency resolution. However, even if data are smoothed over 50 points, time resolution is better than that for Fourier analysis. If a curve is fitted to the smoothed points, the line can be extrapolated to the true start and end points of the call. Instantaneous frequency analysis also relies on the use of very specific filtering methods (Wiener). This method also is relatively intensive computationally, so it may not be suitable for real-time analysis of calls. Unfortunately, no information on amplitude or harmonic structure of the signal is retained after analysis.

DISCUSSION AND CONCLUSIONS

Before any signal is analyzed, researchers must realize that calls of different species of bat are not equally detectable. Some species produce extremely low-amplitude calls and some species of gleaners do not use echolocation at all to localize prey. Other species of bats produce very high-amplitude calls. Low-frequency calls may not be recorded, or recordings may not accurately represent the repertoire of a species. This potential source of error may be in addition to that potentially caused by the choice of transformation or analysis technique used.

The choice of technique to reduce the frequency of echolocation calls is not a simple one. The decision should be made based on the amount and quality of information that is required from the transformed signal. It is not necessary to collect minute detail on the structure of echolocation calls if simple measures of bat activity are all that are required. In such situations, use of heterodyne systems is most appropriate. However, in the situation where the signal must be analyzed in detail, the amount of detail required is not known, or the exact feature of

importance has yet to be determined, the method that alters the signal least must be used.

Transformation methods such as heterodyning and frequency division may appear to be suited for use by researchers and lay people wanting to analyze echolocation calls but who lack a detailed knowledge of the techniques involved. However, the opposite is true. Methods such as frequency division and heterodyning are capable of altering a signal so much that knowledge of the method is mandatory if results are to be interpreted accurately. In contrast, techniques such as time expansion, once viewed as the tool of the bioacoustician, are perhaps better suited to those with less technical knowledge. Time expansion may be termed a “what you see (or hear) is what you get” technique because the signal is unaltered by the expansion process.

All methods for accurately analyzing and displaying the spectral content of a signal are computationally intensive (if carried out on the original signal) and therefore difficult to perform in real time. A good understanding of how each technique works, particularly of their shortcomings, also is extremely important.

If an accurate representation of the spectral content of the original signal is required, it seems obvious that the technique of choice should remove the least amount of information from the signal. Although Fourier analysis is not ideal because of its coupling of time and frequency resolution, its resistance to interference from noise and its retention of amplitude, harmonic, and phase information make it well suited to the analysis of echolocation calls. However, if a less detailed description of the signal is required zero-crossing analysis may be more appropriate.

Use of transformed signals for identifying species of bat from their echolocation calls has received a great deal of recent attention; many researchers have used the Anabat detection and analysis system (Titley Electronics, Ballina, New South Wales,

Australia—O'Farrell and Gannon 1999; O'Farrell et al. 1999). The Anabat system displays the frequency–time course of frequency-divided echolocation calls using zero-crossing analysis. Much of the attention has revolved around use of subjective techniques to classify calls to species level (Barclay 1999; Robbins and Britzke 1999). However, studies have been published that incorporate use of quantitative classification methods with the Anabat system. Many species can be identified relatively easily from their calls when this system is used in conjunction with quantitative analysis methods such as discriminant functions analysis (Britzke et al. 1999; Krusic and Neefus 1996; Lance et al. 1996; Murray et al. 1999). However, other species produce echolocation calls that are so similar that they cannot be reliably distinguished from one another (e.g., *Myotis*—Krusic and Neefus 1996). By removing a large proportion of the information from the original signal, systems such as Anabat may be removing information required to separate these species. Researchers who use more detailed techniques but who fail to measure key variables also may fail to distinguish between calls of some species (Vaughan et al. 1997). In situations where key discriminating variables are not known, it is better to use transformation and analysis techniques, such as time expansion and Fourier analysis, that remove the least amount of information from the signal.

Use of these methods does not guarantee correct results, but their use will maximize the likelihood of correct identification. These methods have been shown to be effective for separating species that produce very similar calls, even separating individuals of the same species (Burnett and Masters 1999; Parsons and Jones 1999). Use of subjective measures to separate species must be avoided because these will vary significantly between researchers, thus making results difficult to repeat (Betts 1998; Weller et al. 1998).

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LITERATURE CITED

- ANDERSEN, B. B., AND L. A. MILLER. 1977. A portable ultrasonic detection system for recording bat cries in the field. *Journal of Mammalogy* 58:226–229.
- BARCLAY, R. M. R. 1999. Bats are not birds—cautionary note on using echolocation calls to identify bats: comment. *Journal of Mammalogy* 10:290–296.
- BAZLY, E. N. 1976. Sound absorption in air at frequencies up to 100 kHz. National Physics Laboratory, Teddington, United Kingdom, Acoustic Report Ac74:1–75.
- BEECHER, M. D. 1988. Spectrographic analysis of animal vocalizations: implications of the “uncertainty principle.” *Bioacoustics* 1:187–208.
- BETTS, B. J. 1998. Effects of interindividual variation in echolocation calls on identification of big brown and silver-haired bats. *The Journal of Wildlife Management* 62:1003–1010.
- BRADBURY, J. W., AND S. L. VEHRENCAMP. 1998. Principals of animal communication. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- BRITZKE, E. R., D. W. BOSSI, B. M. HADLEY, AND L. W. ROBBINS. 1999. The acoustic identification of bats in Missouri. *Bat Research News* 39:158.
- BURNETT, S. C., AND W. M. MASTERS. 1999. The use of neural networks to classify echolocation calls of bats. *Journal of the Acoustical Society of America* 106:2189.
- DOWNES, C. H. 1982. A comparison of sensitivities of three bat detectors. *Journal of Mammalogy* 63:343–345.
- FENTON, M. B. 1988. Detecting, recording, and analyzing vocalizations of bats. Pp. 91–104 in *Ecological and behavioral methods in the study of bats* (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.
- GRIFFIN, D. R., F. A. WEBSTER, AND C. R. MICHAEL. 1960. Echolocation of flying insects by bats. *Animal Behaviour* 8:141–154.
- HOPP, S. L., M. J. OWREN, AND C. S. EVANS (EDS.). 1998. *Animal acoustic communication. Sound analysis and research methods*. Springer-Verlag, Berlin, Germany.
- KRUSIC, R. A., AND C. D. NEEFUS. 1996. Habitat associations of bat species in the White Mountain National Forest. Pp. 185–198 in *Bats and forests symposium* (R. M. R. Barclay and R. M. Brigham, eds.). British Columbia Ministry of Forests, Victoria, British Columbia, Canada.
- LANCE, R. F., B. BOLLIH, C. L. CALLAHAN, AND P. L. LEBERG. 1996. Surveying forest-bat communities with Anabat detectors. Pp. 175–184 in *Bats and forests symposium* (R. M. R. Barclay and R. M. Brigham, eds.). British Columbia Ministry of Forests, Victoria, British Columbia, Canada.
- LAWRENCE, B. D., AND J. A. SIMMONS. 1982. Measure-

- ment of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *Journal of the Acoustical Society of America* 71:585–590.
- MURRAY, K. L., E. R. BRITZKE, B. M. HADLEY, AND L. W. ROBBINS. 1999. Surveying bat communities: a comparison between mist nets and the Anabat II bat detector system. *Acta Chiropterologica* 1:105–112.
- NOYES, A., AND G. W. PIERCE. 1938. Apparatus for acoustic research in the supersonic frequency range. *Journal of the Acoustical Society of America* 9:207–211.
- NYAMSI, R. G., T. AUBIN, AND J. C. BREMOND. 1994. On the extraction of some time dependent parameters of an acoustic signal by means of the analytical signal concept: its application to animal sound study. *Bioacoustics* 5:187–203.
- O'DONNELL, C. F. J., AND J. SEDGELEY. 1994. An automatic monitoring system for recording bat activity. Department of Conservation, Wellington, New Zealand, Technical Series 5:1–16.
- O'FARRELL, M. J., AND W. L. GANNON. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. *Journal of Mammalogy* 80:24–30.
- O'FARRELL, M. J., B. W. MILLER, AND W. L. GANNON. 1999. Qualitative identification of free-flying bats using the Anabat detector. *Journal of Mammalogy* 80:11–23.
- PARSONS, S. 1996. A comparison of the performance of a brand of broad-band and several brands of narrow-band bat detectors in two different habitat types. *Bioacoustics* 7:33–43.
- PARSONS, S., AND G. JONES. 1999. Can the use of signal curvature improve identification of bats in flight using echolocation calls alone? A test using discriminant analysis and artificial neural networks. *Journal of the Acoustical Society of America* 106:2189.
- PARSONS, S., AND M. K. OBRIST. In press. Recent methodological advances in the recording and analysis of chiropteran biosonar signals in the field. In *Echolocation of bats and dolphins* (J. Thomas, C. Moss, and M. Vater, eds.). The University of Chicago Press, Chicago, Illinois.
- PIERCE, G. W., AND D. R. GRIFFIN. 1938. Experimental determination of supersonic notes emitted by bats. *Journal of Mammalogy* 19:454–455.
- PYE, J. D. 1992. Equipment and techniques for the study of ultrasound in air. *Bioacoustics* 4:77–88.
- PYE, J. D. 1993. Is fidelity futile? The true signal is illusory, especially with ultrasound. *Bioacoustics* 4:271–286.
- ROBBINS, L. W., AND E. R. BRITZKE. 1999. Discriminating *Myotis sodalis* from *Myotis lucifugus* with Anabat—critique. *Bat Research News* 40:75–76.
- SIMMONS, J. A., M. B. FENTON, W. R. FERGUSON, M. JUTTING, AND J. PALIN. 1979. Apparatus for research on animal ultrasonic signals. *Life Science Miscellaneous Papers, Royal Ontario Museum, Toronto, Canada*, 1–31.
- VAUGHAN, N., G. JONES, AND S. HARRIS. 1997. Identification of British bat species by multivariate analysis of echolocation call parameters. *Bioacoustics* 7:189–207.
- WATERS, D. A., AND A. L. WALSH. 1994. The influence of bat detector brand on the quantitative estimation of bat activity. *Bioacoustics* 5:205–221.
- WELLER, T. J., V. M. SEIDMAN, AND C. J. ZABEL. 1998. Assessment of foraging activity using Anabat II: a cautionary note. *Bat Research News* 39:61–65.
- ZINGG, P. E. 1990. Akustische artidentifikation von fledermäusen (Mammalia: Chiroptera) in der Schweiz. *Revue Suisse de Zoologie* 97:263–294.

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