Behavioral Responses of the Frog-Eating Bat, *Trachops cirrhosus*, to Sonic Frequencies

Michael J. Ryan[1]*, Merlin D. Tuttle[2], and Robert M.R. Barclay[3]**

[1] Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 14850, USA,
and Smithsonian Tropical Research Institute, Balboa, Panama
[2] Vertebrate Division, Milwaukee Public Museum, Milwaukee, Wisconsin 53233, USA
[3] Department of Biology, Carelton University, Ottawa, Canada K1S 5B6

Summary. The frog-eating bat, *Trachops cirrhosus* (Phyllostomatidae), locates frogs by using the frogs' vocalizations and shows a behavioral response to constant frequencies in the sonic range. The minimum intensity needed to elicit a behavioral response to a constant frequency (i.e. threshold intensity) increased as the frequency decreased from 15 kHz to 5 kHz. This is consistent with audiograms of other bats that have been tested in the sonic range. However, the threshold of *T. cirrhosus* decreases with frequencies below 5 kHz, which is unusual among bats so far tested in this frequency range. This decreased threshold coincides with the frequencies which characterize frog calls that the bats use to locate their prey.

Introduction

Microchiropteran bats are well known for their ability to emit ultrasonic calls, and to use the echoes of these calls to form an acoustical image of their environment (e.g. Griffin 1958; Simmons et al. 1979). As is the case with other small mammals (e.g. Sales 1975; Heffner and Heffner 1980), microchiropteran bats are usually most sensitive to ultrasonic frequencies (e.g. Henson 1970; Pollak et al. 1972; Long and Schnitzler 1975; Brown et al. 1978; Suga and O'Neill 1981). We have shown that the bat *Trachops cirrhosus* (Phyllostomatidae) eats frogs and uses the frogs' vocalizations to locate the frog (e.g. Tuttle and Ryan 1981; Ryan and Tuttle, in press). In general, the energy in frog calls is concentrated in frequencies

below 5 kHz (Loftus-Hills and Johnstone 1970). *T. cirrhosus* produces, and presumably hears, an echolocation call which contains energy from 50–100 kHz (Barclay et al. 1981). This raises an immediate question. How sensitive is *T. cirrhosus* to the relatively low frequencies which characterize frog calls?

The question of microchiropteran sensitivity to low frequency sounds is of general interest because it seems that *T. cirrhosus* might not be the only species to use sonic acoustic cues to locate prey (e.g. *Macroderma lyra*, Fiedler 1979; *Eptesicus fuscus*, Buchler and Childs 1981; *Antrozous pallidus*, Bell 1982; *Tonatia sylvicala*, Tuttle et al. submitted), and many studies of bat audition have not investigated sensitivity to sonic frequencies (i.e. < 20 kHz). In this study we determine a behavioral audiogram for *T. cirrhosus* using constant frequencies of 0.2–15 kHz. We then compare this audiogram to the average power spectrum of the calls of the most common species of local frogs.

Materials and Methods

The experiments were conducted in a large, outdoor, flight cage at the Smithsonian Tropical Research Institute's field station on Barro Colorado Island (BCI), Panama, in March and April, 1981. Bats were mist netted along streams and were returned to their original site of capture after the experiments.

The minimum intensity needed to elicit a behavioral response (i.e. the threshold intensity) from *T. cirrhosus* to a variety of sonic frequencies was determined. Four bats were tested and each bat was tested in two trials. High levels of background noise from chorusing frogs and insects prohibited testing during the night. Therefore, all experiments were conducted from 800–1600 h and only during times when there was a relatively low level of background noise.

Bats hung from the screened ceiling during the experiments, and a speaker was mounted on a tripod at the same height as the bat's head. The speaker was 1–3 m from the bat and 90° from the front of the bat. The order of stimulus presentation was random, and each pure tone stimulus was presented at

* Present address: Museum of Vertebrate Zoology, University of California, Berkeley, California 94720, USA
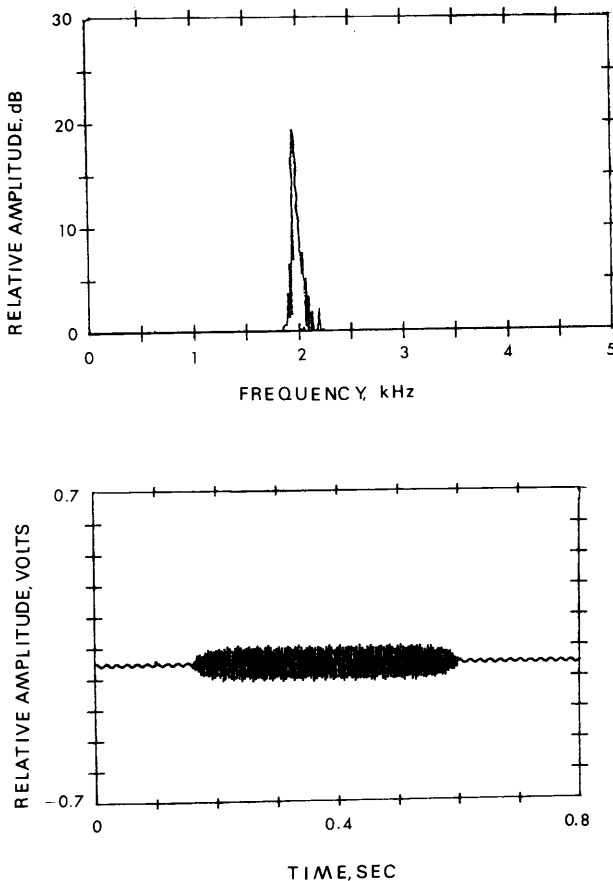** Present address: University of Manitoba Field Station, Portage la Prairie, Manitoba, Canada R1N 3A1

Fig. 1. Power spectrum (frequency vs relative amplitude, top) and an oscillogram (time vs relative amplitude, bottom) of the 200 Hz stimulus used to determine the behavioral frequency audiogram of *Trachops cirrhosus* in 1982. Stimulus was analyzed with a Nicolet model 444A spectrum analyzer

a rate of 1 stimulus/2.3 s with a Nagra IV-D tape recorder and a small extension speaker. A response was noted when the bat cocked its ears and turned toward the speaker. When a response was noted, we recorded the playback level of the tape recorder, waited approximately 30 s, and then repeated the stimulus presentation beginning at an intensity slightly lower than the intensity to which the bat had just responded. We continued this procedure until the bat responded at the same minimum intensity in two successive stimulus presentations of a given frequency. This was considered the threshold intensity for the frequency tested. The intensity of the stimulus was then measured at the bat's head with a Brüel and Kjaer sound pressure level meter.

In each trial the threshold intensities for eliciting behavioral responses to frequencies of 0.2 kHz, 0.5 kHz, 1 kHz, 3 kHz, 5 kHz, 7 kHz, 9 kHz, 11 kHz, 13 kHz and 15 kHz were determined. Each bat was tested in two trials. Stimuli were produced with an Eico model 377 sine wave generator, and were of constant frequency. We attempted to produce all stimuli with durations of 500 ms and rise and decay times of 50 ms. Prior to the playback experiments, the stimuli were monitored with a Sennheiser MKH 104 microphone and a Tektronix model 212 oscilliscope, as they were played through the speaker over the

range of intensities used during the experiments. Visual inspection of the waveform did not reveal distortion of the stimuli.

Although we attempted to produce stimuli with the same durations, and rise and decay times, lack of facilities prohibited us from having these properties precisely standardized. This was of some concern, since in another study we have shown that *T. cirrhosus* can discriminate among species of frogs using primarily the temporal features of the frogs' calls (Ryan and Tuttle, in press). Therefore, in 1982 stimuli of the same constant frequencies used in 1981 were generated with a Hewlett Packard model 200 CDR wide range oscillator and pulses were formed with a Grason-Stadler model 1200 series modular programming system. All of these stimuli had identical durations of 500 ms, and rise and decay times of 50 ms (Fig. 1). During a brief visit to Panama in March, 1982, the behavioral frequency audiogram of a *T. cirrhosus* was determined using these stimuli and the methods just described.

For two bats we determined the threshold intensity for the simple advertisement call of the frog *Physalaemus pustulosus*. This call is a frequency modulated 'whine' which has a dominant frequency that sweeps from approximately 1 kHz to 0.4 kHz in 400 ms (Rand and Ryan 1981). This is one of the most common frogs on BCI, and suffers heavy predation from *T. cirrhosus* (Ryan et al. 1981).

The logarithmic measure of dB SPL was converted to the linear measure of absolute pressure (0 dB SPL$=2\times10^{-5}$ Nm^{-2}) for the determination of means and standard deviations, and absolute pressures were then converted back to dB SPL for graphical presentation. Therefore, in Fig. 3 the standard deviations are asymmetric around the means.

We also determined the average power spectrum (frequency versus relative amplitude) of the advertisement calls for the 16 most common frogs in the area. The calls were recorded at various times by MJR or Dr. A. Stanley Rand of the Smithsonian Tropical Research Institute, using a Nagra III or IV-D tape recorder and a Sennheiser MKH 104 microphone. The calls were analyzed with a Princeton Applied Research model Fast Fourier Transform real time spectrum analyzer.

Results

The minimum intensities needed to elicit a behavioral response from *T. cirrhosus* at each frequency for all trials are shown in Fig. 2 A–D. Not all bats responded to all frequencies. In the six trials in which bats responded to the higher sonic frequencies (9 kHz, 11 kHz, 13 kHz, 15 kHz), the thresholds increased as the frequencies tested decreased from 15–5 kHz. In 7 of 8 trials the highest threshold was at 5kHz. In all trials the thresholds were lower at the lower frequencies tested (0.2 kHz, 0.5 kHz, 1 kHz) than at the middle frequencies (3 kHz, 5 kHz, 7 kHz).

The mean (±1 S.D.) audiogram shows considerable consistency both among and within individuals. There were lower thresholds at the upper and lower range of the frequencies tested, and thresholds were higher at middle frequencies. The highest threshold was at 5 kHz (Fig. 3). Figure 3 also shows thresholds for the bat tested in 1982, in which all stimuli had identical durations, and rise and decay times. These thresholds usually fall with-
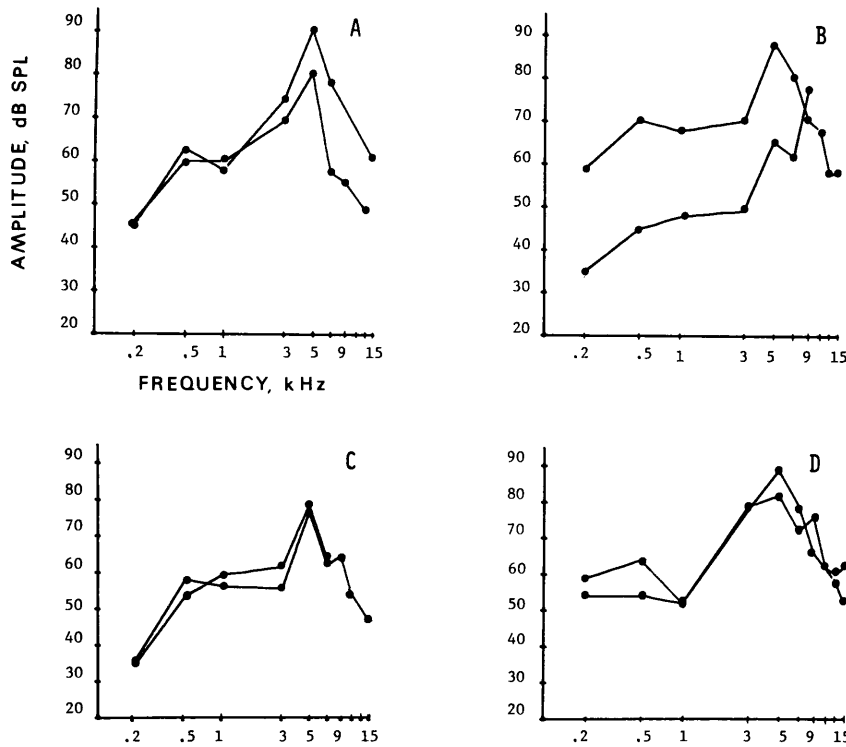
Fig. 2. Threshold intensities needed to elicit a behavioral response to various constant frequencies from 4 *Trachops cirrhosus*, two trials per bat, in 1981
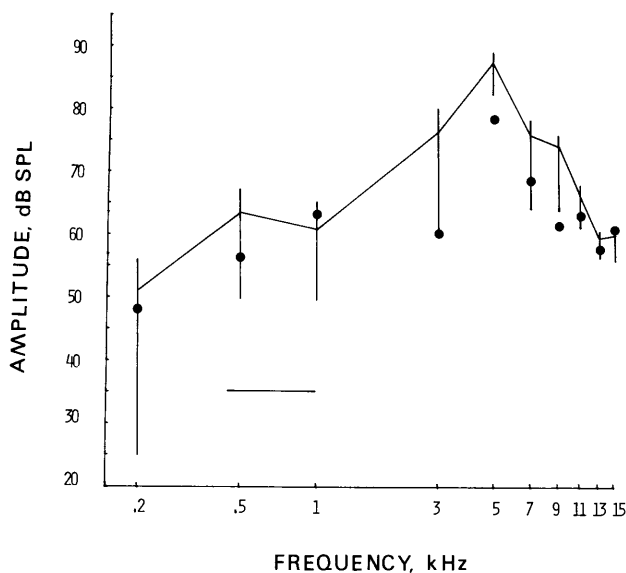

Fig. 3. Mean (± 1 S.D.) threshold intensities needed to elicit behavioral responses to various constant frequencies from *Trachops cirrhosus* (Fig. 1). Large dark circles represent the responses from the bat tested in 1982. Solid line is the mean threshold response of two bats to the simple *Physalaemus pustulosus* advertisement call
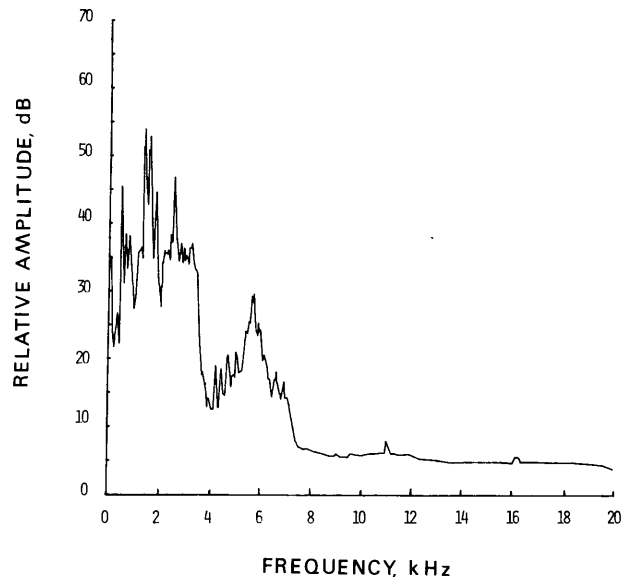
Fig. 4. Average power spectrum (frequency vs relative amplitude) of advertisement calls of the 16 most common local frog species

in the standard deviations of the mean responses, and the audiogram from 1982 has the same general form as the mean 1981 audiogram. This suggests that audiograms of the bats tested in 1981 result from spectral differences among the stimuli, and

are not an artifact of minor inconsistencies in the temporal properties of the stimuli.

The mean threshold intensity needed to elicit a response to the *P. pustulosus* call was 35 dB SPL (Fig. 3). This intensity is lower than the threshold

Table 1. Spectral characteristics of advertisement calls of the 16 most common local anurans in the Barro Colorado Island area, Panama

Species	Frequency (kHz)			
	Dominant frequency			2° Frequency or harmonic
	Peak	Min.	Max.	(Min./Max./Peak)
Bufo typhonius	1.85	0.89	2.43	
Bufo marinus	0.67	0.50	0.91	
Leptodactylus pentadactylus	0.48	0.39	0.73	
Smilisca sila	0.45	0.62	1.15	1.15, 1.63, 2.23
Hyla foliomorta	0.81			2.64, 4.79, 5.68
Hyla phlebodes	3.68	2.25	4.10	5.58, 6.66
Hyla microcephala	6.06	5.23	6.88	2.15, 2.97, 4.00
Hyla rufitela	0.94	0.75	1.09	1.53, 1.80, 2.63
Hyla boulengeri	2.82	1.96	4.05	
Colostethus nubicola[a]	7.08	5.96	7.67	1.13, 1.63
Agalychnis callidryas	1.57	1.19	2.42	
Centrolenella fleischmanni	5.26	4.55	5.49	
Eleutherodactylus diastema	3.64	3.06	4.04	5.88, 6.22, 6.42
Eleutherodactylus fitzingeri	2.07	1.36	3.93	
Physalaemus pustulosus[b]	2.20	0.94	4.07	0.48, 0.65, 0.94

[a] *Colostethus nubicola* is diurnal, thus probably has little overlap in activity pattern with *T. cirrhosus*

[b] *Physalaemus pustulosus* advertisement call is a whine plus one chuck (see Rand and Ryan 1981)

for any of the constant frequencies that are within the range of the dominant frequency of the frog call.

Spectral properties of the advertisement calls of the 16 most common local species of frogs are presented in Table 1. The average power spectrum of these calls (Fig. 4) is an estimate of the distribution of frequencies available for localization to *T. cirrhosus* when hunting for frogs. Peak energy concentration of these calls was 1.8 kHz, with secondary peaks of energy at 0.6 kHz and 2.8 kHz. There also was a minor concentration of energy at 5.9 kHz. A comparison of the mean frequency audiogram (Fig. 3) with the power spectrum (Fig. 4) demonstrates that these bats are especially sensitive to those frequencies that characterize frog calls.

Discussion

It is assumed that *T. cirrhosus* can hear frequencies in its echolocation calls, 50–100 kHz (Barclay et al. 1981). If *T. cirrhosus* is similar to some other bats investigated, its hearing should be maximally sensitive in this frequency range (Neuweiler 1968; Pollak et al. 1972; Long and Schnitzler 1975; Brown et al. 1978; Schuller 1980; Suga and O'Neill 1981). Our previous studies have shown that these bats are able to locate frog calls, and can even use the calls to discriminate among species and call types within species (e.g. Tuttle and Ryan 1981; Ryan et al. 1982). This study shows that *T. cirrhosus* responds to the relatively low frequencies which characterize frog calls. In fact, the thresholds of the bat increase from 15 kHz to 5 kHz, but thresholds then decrease at frequencies below 5 kHz, the frequency range which contains most of the energy in frog calls. These results as well as those of another study (Ryan and Tuttle, in press) demonstrate that *T. cirrhosus* is quite able to distinguish frog species by using spectral and temporal features of the sonic frequencies in the frogs' calls.

For several reasons, we expect that our experiments provide only minimal estimates of the sensitivity of *T. cirrhosus* to low frequency sounds. First, bats were tested in a flight cage in a forest, thus there were always a variety of background noises, although the intensity of the background noises during daylight hours was usually very low. Second, bats were tested during a time of day when they might not have been maximally motivated to respond to sound stimuli. And finally, the bats had lower threshold intensities in response to the frog call tested than to the pure tones within the range of the dominant frequency of the frog call, suggesting that the pure tone stimuli were not optimal for eliciting a response from the bats. Based on our experience with this species, we think that the absolute threshold is considerably lower than our experiments show, but this will be demonstrated only in a more controlled experimental situation.

A common feature of bat audition is that microchiropterans appear to be maximally sensitive to those frequencies in the echolocation call, and sensitivity decreases with lower frequencies (e.g. Henson 1970; Long and Schnitzler 1975; Brown et al. 1978; Suga and O'Neill 1981), although few studies have investigated sensitivity to frequencies outside the range of the echolocation call, and especially to sonic frequencies. Among the few bats tested with frequencies less than 15 kHz, the sensitivity almost always decreases with lower frequen-

Table 2. Rate of threshold increase over low frequency ranges (<15 kHz) in various microchiropteran bats. All studies cited also tested responses to ultrasonics. If 15 kHz was not tested the threshold was estimated from that of the nearest higher and lower frequency tested. Methods: *1* cochlear microphonic potentials; *2* evoked potentials from the inferior colliculus; *3* behavioral response

Species	Methods	Rate of increase (dB/kHz)	Frequency	
			Range	Reference
Tadarida brasiliensis	1	3.9	15–1 kHz	Henson 1964
Tadarida molossa	1	3.5	15–2 kHz	Henson 1964
Desmodus rotundus	1	1.1	15–1 kHz	Vernon and Peterson 1966
Rhinolophus ferrumequinum	2	5.9	15–1 kHz	Neuweiler et al. 1971
Hipposideros speoris	2	5.0	15–10 kHz	Schuller 1980
Hipposideros bicolor	2	9.0	15–10 kHz	Schuller 1980
Rhinolophus rouxi	2	6.0	15–10 kHz	Schuller 1980
Rhinolophus rouxi	2	−1.5	15–5 kHz	Schuller 1980
Rhinolophus ferrumequinum	3	7.3	15–2 kHz	Long and Schnitzler 1975
Eptesicus fuscus	3	6.2	15–3 kHz	Dalland 1965
Antrozous pallidus	3	1.0	15–5 kHz	Brown et al. 1978

cies (Table 2). The sensitivity of *T. cirrhosus* also decreases with frequencies from 15–5 kHz. However, *T. cirrhosus* is unusual among most bats tested in that sensitivity then increases at frequencies below 5 kHz.

Although most of the other bats exhibit decreasing sensitivities with decreasing frequencies, the rate of sensitivity decrease is not the same for all bats. Particularly interesting is the relatively slower decay of sensitivity in *Antrozous pallidus* and *Desmodus rotundus*. Recently, it has been suggested that *A. pallidus* uses sounds that result from wing fluttering to locate moths. The frequencies in those sounds range 1.4–14.2 kHz, and the peak energy concentration is 4.7–8.6 kHz, depending on the size of the moth (Bell 1982). The vampire bat, *D. rotundus*, preys upon large mammals and it is not inconceivable that acoustic cues produced by the prey, either from vocalizations or movements, might be used in prey localization.

The hearing sensitivity of some bats was not tested below 10 kHz. Schuller (1980) tested one *Rhinolophus rouxi* down to 10 kHz and another individual to 5 kHz. In the former test, the results are similar to those of other bats tested; hearing sensitivity decreases with decreasing frequencies (Table 2). However, the bat tested to 5 kHz shows an increased sensitivity to frequencies below 10 kHz (Table 2). These results suggest that it is not prudent to make generalizations about the sensitivity of microchiropteran bats to sonic frequencies until more species are tested over a greater range of frequencies. Clearly, knowledge of the extent to which other microchiropterans rely on sonic acoustic cues to locate prey, and their sensitivites to these frequencies is essential to an understand-

ing of the sensory basis of prey localization by bats.

References

Barclay RMR, Fenton MB, Tuttle MD, Ryan MJ (1981) Echolocation calls produced by *Trachops cirrhosus* (Chiroptera: Phyllostomatidae) while hunting for frogs. Can J Zool 59:750–753

Bell GP (1982) Behavioral and ecological aspects of gleaning by a desert insectivorous bat *Antrozous pallidus* (Chiroptera: Vespertilionidae). Behav Ecol Sociobiol 10:217–223

Brown PE, Grinnell AD, Harrison JB (1978) Development of hearing in the pallid bat *Antrozous pallidus*. J Comp Physiol 126:169–182

Buchler ER, Childs SB (1981) Orientation to distant sounds by foraging big brown bats (*Eptesicus fuscus*). Anim Behav 29:428–432

Dalland JI (1965) Hearing sensitivity in bats. Science 150:1185–1186

Fiedler J (1979) Prey capture with and without echolocation in the Indian false vampire bat, *Megaderma lyra*. Behav Ecol Sociobiol 6:155–160

Griffin D (1958) Listening in the dark. Yale University Press, New Haven

Heffner R, Heffner H (1980) Hearing in the elephant (*Elephas maximus*). Science 208:518–520

Henson OW (1964) Echolocation and hearing in bats with special reference to the function of the middle ear muscles. Ph D thesis, Yale University, New Haven (Connecticut), USA

Henson OW (1970) The ear and audition. In: Wimsatt WA (ed) The biology of bats, vol 2. Academic Press, New York

Loftus-Hills JJ, Johnstone BM (1970) Auditory function, communication, and the brain-evoked response in anuran amphibians. J Acoust Soc Am 47:1131–1138

Long GR, Schnitzler HU (1975) Behavioral audiograms from the bat, *Rhinolophus ferrumequinum*. J Comp Physiol 100:211–219

Neuweiler G (1968) Neurophysiologische Untersuchungen zum Echoortungssystem der Grossen Hufeisennase *Rhinolophus ferrumequinum*. Z Vergl Physiol 67:273–306

Neuweiler G, Schuller G, Schnitzler HU (1971) On- and off-responses in the inferior colliculus of the greater horseshoe bat to pure tones. Z Vergl Physiol 74:57–63

Pollak G, Henson OW, Novick A (1972) Cochlear microphonic audiograms in the pure tone bat *Chilonycteris parnellii*. Science 176:66–68

Rand AS, Ryan MJ (1981) The adaptive significance of a complex vocal repertoire in a neotropical frog. Z Tierpsychol 57:209–214

Ryan MJ, Tuttle MD (in press) The ability of the frog-eating bat to discriminate among novel and potentially poisonous species of frogs using acoustic cues. Anim Behav

Ryan MJ, Tuttle MD, Taft LK (1981) The costs and benefits of frog chorusing behavior. Behav Ecol Sociobiol 8:273–278

Ryan MJ, Tuttle MD, Rand AS (1982) Bat predation and sexual advertisement in a neotropical frog. Am Nat 119:136–139

Sales GD (1975) Auditory evoked responses in small mammals. In: Bench RJ, Pye A, Pye JD (eds) Sound reception in mammals. Academic Press, London

Schuller G (1980) Hearing characteristics and Doppler shift compensation in south Indian CF-FM bats. J Comp Physiol 139:349–356

Simmons JA, Fenton MB, O'Farrell MJ (1979) Echolocation and the pursuit of prey by bats. Science 203:16–21

Suga N, O'Neill WE (1981) Auditory processing of echoes: representation of acoustic information from the environment in the bat cerebral cortex. In: Busnel RG, Fish JF (eds) Animal sonar systems. Plenum Press, New York

Tuttle MD, Ryan MJ (1981) Bat predation and the evolution of frog vocalizations in the neotropics. Science 214:677–678

Tuttle MD, Ryan MJ, Belwood J (submitted) Acoustical partitioning of resources by two phyllostomatid bats

Vernon JA, Peterson E (1966) Hearing in the vampire bat, *Desmodus rotundus*, as shown by cochlear potentials. J Aud Res 6:153–163