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ACOUSTICAL PROPERTIES OF THE DISTRESS CALLS OF *ARTIBEUS JAMAICENSIS* AND *PHYLLOSTOMUS HASTATUS* (CHIROPTERA: PHYLLOSTOMIDAE)

PETER V. AUGUST

ABSTRACT.—Sound spectrographs of the distress vocalizations of *Artibeus jamaicensis* and *Phyllostomus hastatus* are presented and described. Distress calls consisted of long series of short duration pulses and each pulse covered a wide band of frequencies. Sound energy did not extend beyond 15 kHz. The acoustic structure of *Artibeus* and *Phyllostomus* distress calls is consistent with predictions derived from theory of ecological and behavioral acoustics.

Many species of bats produce loud, audible vocalizations when handled and nearby bats often respond to these calls by flying toward the source of the sound (Fenton et al., 1976; August, 1979; Ryan et al., 1985). In playback experiments using tape-recordings of *Artibeus jamaicensis* and *Phyllostomus hastatus* distress calls, August (1979) demonstrated: 1) large numbers of bats were attracted to the source of distress calls, 2) responding bats passed within 1-2 m of the tape recorder speaker but never landed on or near it, 3) both species responded to each other's call, and 4) the attraction of bats to a distress call is similar to mobbing behavior in birds and other mammals. Ryan et al. (1985) obtained identical results in similar experiments with *Artibeus lituratus*. In this paper, I describe the acoustical properties of *Artibeus* and *Phyllostomus* distress calls and discuss the structure of these vocalizations in light of predictions derived from theory on ecological and behavioral acoustics.

MATERIALS AND METHODS.—The bat distress calls reported herein were recorded in the field from specimens captured at Fundo Pecuario Masaguaral, 45 km S Calabozo, Estado Guarico, Venezuela (8° 33′ N, 67° 36′ W) and Aguas Buenas Cave, 3.2 km S Aguas Buenas, Puerto Rico (18° 14′ N, 66° 6′ W). Recordings of hand-held bats were made with a Uher Report IC 4000 tape recorder and a Uher M514 microphone at a tape speed of 19 cm/sec. Manufacturer specifications indicated that this recording system had an upper frequency limit of 20 kHz. Sound spectrographs were produced on a Kay Sonograph on wide band setting and a Saicor Real-Time Frequency Analyzer coupled to a Honeywell Fiber-optic Visicorder. Frequency and pulse parameters were measured on the real-time spectrograph record.

RESULTS.—A representative spectrogram of an *Artibeus jamaicensis* distress call is given in Figure 1A. *Artibeus* distress calls consisted of a long series of short, discrete pulses (Table 1). Each pulse had a basal frequency of around 1 kHz, a first harmonic at 2 kHz, and a wide band of sound energy between 6-14 kHz. Three kinds of pulses were found. Short pulses (<110 msec) had subtle frequency modulation (leftmost and two rightmost pulses in Fig. 1A). Two longer duration pulse types (>110 msec) were found; one showed little frequency modulation (middle pulse, Fig. 1A),

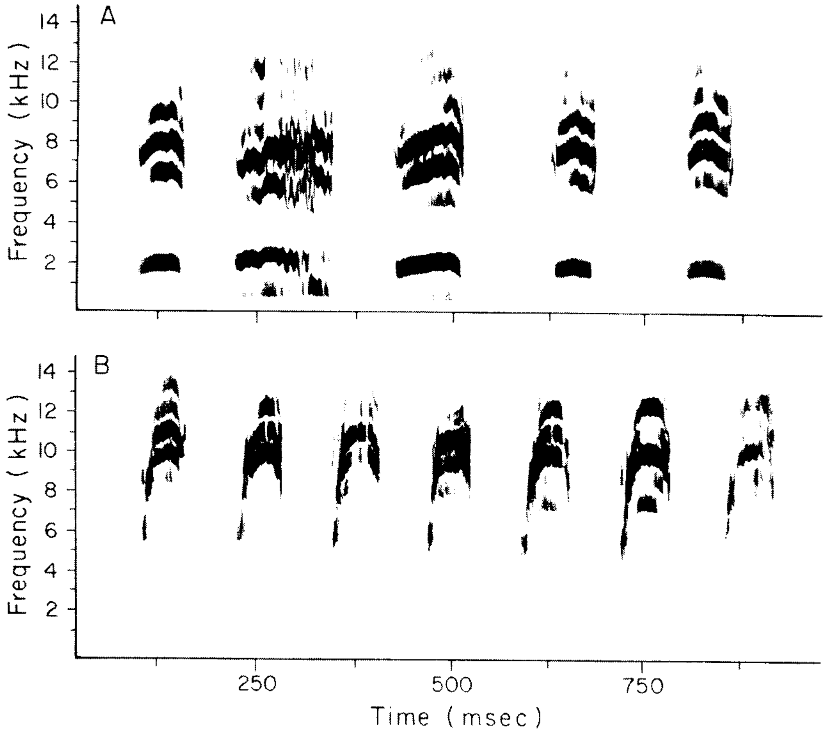

FIG. 1.—A) Sound spectrograph of the distress call of an adult male *Artibeus jamaicensis* recorded on Hato Masaguaral, Venezuela. B) Sound spectrograph of the distress call on an adult female *Phyllostomus hastatus*.

whereas the second had considerable frequency modulation (second pulse from left, Fig. 1A).

The distress calls of *Phyllostomus hastatus* (Fig. 1B) were generally similar to those of *A. jamaicensis* and consisted of repeated, short broadband pulses (Table 1). Most *P. hastatus* distress vocalizations had a weak band of sound energy at approximately 1 kH_z (not seen in Fig. 1B). Most of the energy was contained within a modulated band of sound between 6-15 kH_z.

Ultrasonic components (>20 kH_z) might have been present in *A. jamaicensis* and *P. hastatus* distress vocalizations, but would not have been captured by the recording system used here. Because bats would respond to playbacks of the sounds described in Fig. 1 and Table 1, I concluded that ultrasounds, if present in bat distress calls, were not needed to attract responders.

DISCUSSION.—Vocalizations that initiate mobbing behavior in birds and mammals are quite similar. Typically, they consist of repeated short pulses, each pulse covering a wide band of frequencies. The distress vocalizations of *A. jamaicensis* and *P. hastatus* were similar to the mobbing calls of birds

TABLE 1.—*Acoustical parameters of* A. jamaicensis *and* P. hastatus *distress calls. Pulse duration is the mean (±SD) of 10 pulses. Abbreviations are VZ = collected from Venezuela site, PR = collected from Puerto Rico site.*

Species Individual	Seconds of recording	Bandwidth of max. energy (kHz)	Basal frequency (kHz)	Max. frequency (kHz)	$\bar{X}$ Pulse duration (msec)	Pulse repetition rate (pulses/sec)
Artibeus jamaicensis						
Adult♂, VZ	60	1-14	1	14	89±39	5.7
Adult♂, VZ	39	1-11	1	11	84±8	6.6
Adult♂, VZ	11	1-10	1	10	139±39	4.2
Adult♀, PR	50	1-9	1	10	109±17	6.0
Phyllostomus hastatus						
Adult♂, VZ	15	8.5-15	1	15	83±26	6.5
Adult♂, VZ	67	6-14	1	14	95±35	10.1
Adult♀, VZ	24	6-15	1	15	93±10	5.8

(Marler, 1957), primates (Vencl, 1977), and rodents (Emmons, 1978). This convergence in call design is especially interesting given that the echolocation calls of *A. jamaicensis* and *P. hastatus* are considerably higher in frequency (>50 kHz; Gould, 1977). A number of factors might contribute to the apparent convergence among bat and non-bat distress vocalizations.

Morton (1977) presented a set of motivation-structural (MS) rules to explain the general convergence in the structure of sounds produced by birds and mammals in similar behavioral contexts. Calls given in appeasement-fearful contexts tended to be tonal and high-frequency. Calls given in hostile-aggressive contexts covered a wide band of frequencies (usually noisy) and were low-frequency. The distress calls of *A. jamaicensis* and *P. hastatus* were given in hostile-aggressive situations and corroborate Morton's MS rule hypothesis, they were noisy and low-frequency.

The efficiency with which sounds transmit through the environment vary with frequency, bandwidth, and duration (Morton, 1975; Marten and Marler, 1977; Marten et al., 1977; Wiley and Richards, 1978; Richards and Wiley, 1980). High-frequency sounds are severely distorted by reverberation and attenuate rapidly due to molecular absorption by air and scattering by objects in the path of the sound (leaves, branches, etc.). Low-frequency sounds, however, attenuate less and transmit farther in cluttered environments. If initiating and recruiting participants in a mobbing response is an important function of *A. jamaicensis* and *P. hastatus* distress calls (August, 1979), then selection should favor calls that propagate well over long distances. The low-frequency, broad band composition seen in *A. jamaicensis* and *P. hastatus* distress calls is consistent with this hypothesis.

Radiation patterns of sounds leaving an emitter might also explain why *A. jamaicensis* and *P. hastatus* concentrate sound energy in the lower frequencies when distress calling. High-frequency sounds radiate from a source as a narrow beam of acoustic energy (Kinsler and Frey, 1962; Richards and Wiley, 1980). Low-frequency sounds radiate widely from an emitter. Again, if *A. jamaicensis* and *P. hastatus* distress calls function to recruit conspecific and heterospecific mobbers, selection would favor sounds that radiate laterally and behind the caller (i.e., low-frequency sounds), thus saturating a large volume of space with the acoustic signal.

A striking feature of *A. jamaicensis* and *P. hastatus* distress vocalizations was the high repetition of individual pulses. Pulse repetition rates varied between 4-10 H_z. Calling bouts can last many minutes; in fact, biologists sometimes use distress calling bats to attract other bats to mist nets (Tuttle, 1976). The long, repetitive nature of distress calls might convey significant information to recipients. Gould (1971, 1983) emphasized the importance of repetition as a means of conveying arousal state. The high state of arousal in distress calling bats might be encoded in pulse repetition rate rather than frequency level, pulse duration, or modulation of frequency or amplitude. Zippelius (1974) contended pulse repetition rate by distress-calling neonate rodents is the "decisive" call component in initiating maternal retrieval behavior; call frequency is not important. Support for this hypothesis might be found in August's (1979) demonstration that a human imitation of a bat distress call can initiate mobbing. The imitation call differed from the bat calls by having a broader frequency range and not having complex frequency modulation within pulses. The pulse repetition rate (4.5 pulses/sec) was, however, similar.

The acoustic design of the distress calls of *A. jamaicensis* and *P. hastatus* was consistent with predictions derived from MS rules and eco/behavioral acoustics. The distress calls of these two species were similar to the distress calls of *Myotis lucifugus* and *Eptesicus fuscus* (Fenton et al., 1976) with respect to pulse bandwidth. However, *Myotis* and *Eptesicus* calls differed in that they contain a significant amount of sound energy in ultrasonic ($>$20 kH_z) frequencies. *Artibeus jamaicensis* and *P. hastatus* distress calls might also include ultrasonic components, but if present, they were not necessary to elicit a mobbing response. The selective benefits to the calling bat or responders are unknown. In fact, much remains to be done on elucidating the evolution and maintenance of mobbing behavior in birds and mammals in general (Curio, 1978). Bats should prove to be an excellent model to test many of the hypotheses of why distress calls are given and why mobbers mob.

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Address of author: *Conservation and Research Center, Nat. Zool. Park, Front Royal, VA 22630.*