Old World frog and bird vocalizations contain prominent ultrasonic harmonics

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Several groups of mammals such as bats, dolphins and whales are known to produce ultrasonic signals which are used for navigation and hunting by means of echolocation, as well as for communication. In contrast, frogs and birds produce sounds during night- and day-time hours that are audible to humans; their sounds are so pervasive that together with those of insects, they are considered the primary sounds of nature. Here we show that an Old World frog (*Amolops tormotus*) and an oscine songbird (*Abroscopus albogularis*) living near noisy streams reliably produce acoustic signals that contain prominent ultrasonic harmonics. Our findings provide the first evidence that anurans and passerines are capable of generating tonal ultrasonic call components and should stimulate the quest for additional ultrasonic species. © *2004 Acoustical Society of America.*

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I. INTRODUCTION

Animal vocal signals are extraordinarily diverse. Their sound intensities range widely, and their dominant frequencies may extend from below the human hearing range (infrasounds) to a few Hertz through the audible range (20 Hz to 20 kHz) and into the ultrasonic range (to >200 kHz). It is thought that coevolution of the vocal and auditory systems results in the generation of sound communication signals that are correlated with the ability of an individual (or a conspecific individual) to detect and perceive that signal. Nevertheless, the hearing range of an animal need not coincide precisely with the frequency range of its vocalizations (Konishi, 1971). The logical outcome is a wide diversity of auditory processing abilities among animals (Stebbins, 1983). Common exceptions to this correlation are impulsive, click-like signals that are broadband, often containing frequencies exceeding the auditory system's upper range of detectable signals.

Most anuran amphibians (frogs and toads) produce advertisement calls containing frequency components in the range from ~ 100 Hz to 5–6 kHz (Capranica, 1965; Glaw and Vences, 1994). In contrast, birdsong may contain frequencies as low as 80–90 Hz and harmonic components as high as 10.7 kHz, a range of about seven octaves (Greenwalt, 1968). *Amolops tormotus* is an arboreal frog in the family Ranidae restricted in its distribution to two provinces in central China (Zhou and Adler, 1993). Males of this species call nightly from the low vegetation along the banks of rivers and streams. Their vocal repertoire is extraordinarily rich; individual calls exhibit multiple upward and downward frequency sweeps, rapid frequency "steps" and sudden onset and offset of selective harmonic components within a call note (Feng *et al.*, 2002). *Abroscopus albogularis* (family Sylviidae), a leaf warbler distributed from Nepal to S. China and N. Indochina, inhabits evergreen forests and bamboo thickets in the same regions at altitudes up to 2440 m (Meyer de Schauensee, 1984). Its call has been described as "a shrill twitter" (MacKinnon and Phillipps, 2000). Both the frog, *A. tormotus*, and the songbird, *A. albogularis*, call from the vegetation along creeks and streams in Anhui Province, China. During the rainy season the water level rises precipitously, resulting in increased background noise levels in the vicinity of the streams (Feng *et al.*, 2002). In the present study, the advertisement call of the frog *A. tormotus* and the song of the songbird *A. albogularis* in their natural habitat were recorded using an ultrasonic microphone and a digital recording system to examine the vocal features of their vocalizations and their relationship to the stream noise.

II. METHODS

All recordings were made between 1900 and 2400 h along the Tau Hua Creek (30° 06′N, 118° 10′E) in Huang-

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shan, China on 10–17 May 2002. Animal vocalizations were recorded using a custom-built, PC-based recording device (PCTape), and a custom-made ultrasonic microphone (Department of Animal Physiology, University of Tubingen) with a flat (±3 dB) frequency response from 15 to 120 kHz with a roll-off of 10 and 6 dB/oct at <15 kHz and >120 kHz, respectively. Signals were digitized using a 16-bit A/D converter (Analog Devices AD7723) at a sampling rate of 192 or 256 kHz, with 8× oversampling. Data were saved as wave files and analyzed (FFT, 1024), and displayed using SELENA, a custom-designed program (S. Andrzheevski, St. Petersburg). Field comments were recorded with a separate microphone, which was fitted with a switch to allow remote control of PCTape.

III. RESULTS

We recorded and analyzed spontaneous vocalizations (not evoked by acoustic playbacks) from 40 frogs (*A. tormotus*) and two songbirds (*A. albogularis*) along the stream of the Tau Hua Creek. Measurement of the ambient noise generated by the running water with a precision sound level meter (GenRad 1982) with various filter settings showed that the noise was broadband with a peak near 100 Hz decaying by 19 dB at 2 kHz and by 63 dB at 28 kHz.

The frog, *Amolops*, typically produces two-note calls composed of short tone pips [Fig. 1(a)], or one-note calls having short [Figs. 2(b)and (c)] or long duration [Figs. 1(b), 1(c), and 2(a)]. These calls show varying degrees of frequency modulation (FM); sudden onset and offset of harmonic and subharmonic components are often observed. Notably, these calls display a distinct first formant in the ‘‘audible range’’ and a prominent second formant at ~60 kHz; in some calls there is a spectral trough around 32–45 kHz [Figs. 1(c), 2(a), and (c)]. Sometimes, a third formant can be observed at 105 kHz [Fig. 1(c)]. It is clear these calls have significant energy in the ultrasonic range. A fortuitous simultaneous recording of a passing bat and a two-note call of the frog, *A. tormotus*, reveals that many frequency components of the frog’s call are shared with and even exceed those in the bat’s frequency-modulated echolocation pulses [Fig. 3(a)]. Similar to *A. tormotus*, the pulsed song of the songbird, *A. albogularis* [Fig. 3(b)], is characterized by distinct formants in the audible and ultrasonic ranges, with harmonics up to 54 kHz [Fig. 3(b)].

IV. DISCUSSION

The vocal repertoire of males of the arboreal frog, *Amolops tormotus*, is extraordinarily rich and individual calls share many features of birdsong and primate vocalizations, such as multiple upward and downward FM sweeps, rapid frequency transitions, and multiple harmonics (Feng *et al.*, 2002). The previous and the present studies further show that their calls often exhibit nonlinear features, e.g., sudden onset and offset of harmonic and subharmonic components within a call note—these are unique among known amphibian vocalizations. In mammals and birds, nonlinear acoustic properties are generated by the larynx (Herzel *et al.*, 1995; Fitch *et al.*, 2002) and the syrinx (Fee *et al.*, 1998), respectively. The origin of nonlinearities in frogs has yet to be determined.

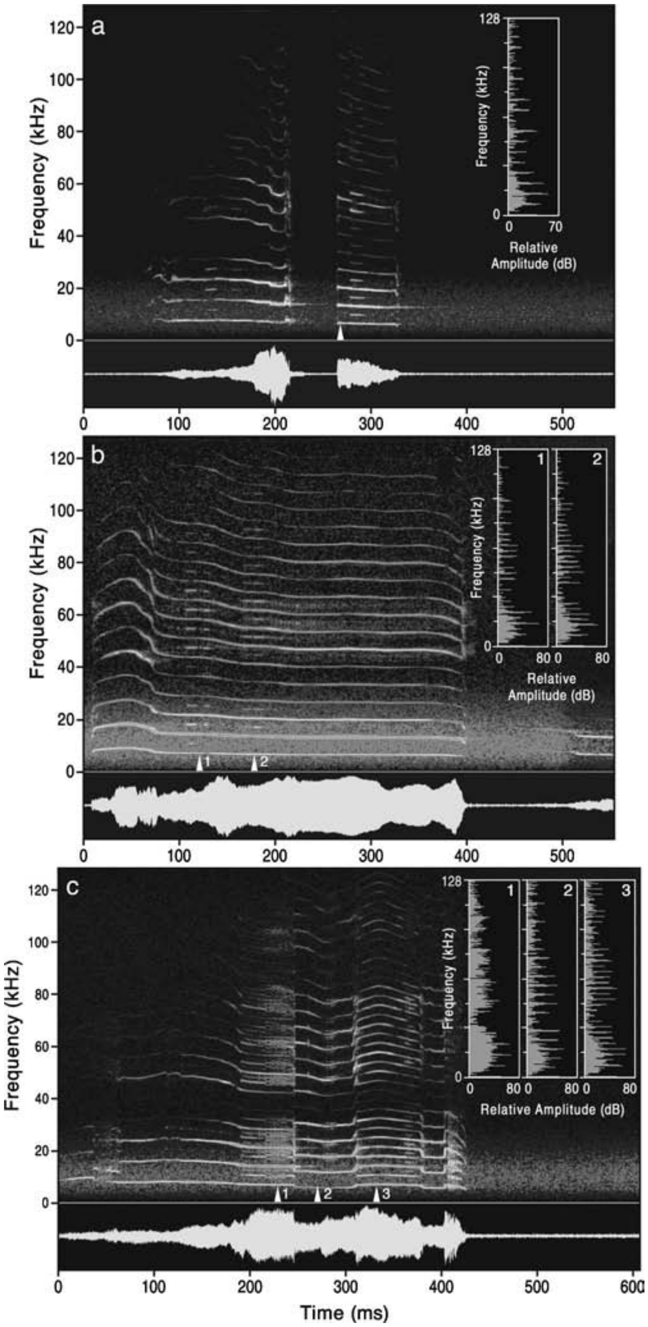

FIG. 1. Sound spectrograms (top panel), waveforms (bottom panel), and instantaneous amplitude spectra [insets, taken at indicated points (arrowheads)] of vocal signals of the frog, *Amolops tormotus* in Anhui Province, China. (a) A two-note call. The background noise (up to 20 kHz) is due to the rushing water in the Tau Hua Creek. Note that the roll-off of background noise energy below 15 kHz in the amplitude spectra is attributed to the limited-low frequency response of the ultrasonic microphone. (b)(c) One-note long calls of the frog, *A. tormotus*. The initial warble FM in (b) is followed by a constant-frequency tone with multiple harmonics; sudden onset of subharmonics can be seen in two instants (point 1, 2). For the one-note long call in (c), there is a sudden onset of subharmonics 200 ms into the call followed by a chaotic noisy segment (point 1) that itself ceases suddenly at 240 ms (point 2). For all plots, dynamic range: 90 dB; temperature range during recordings: 17–18 °C.

Published sound spectrograms of the calls of *A. tormotus* (Feng *et al.*, 2002) give a hint of the presence of ultrasonic

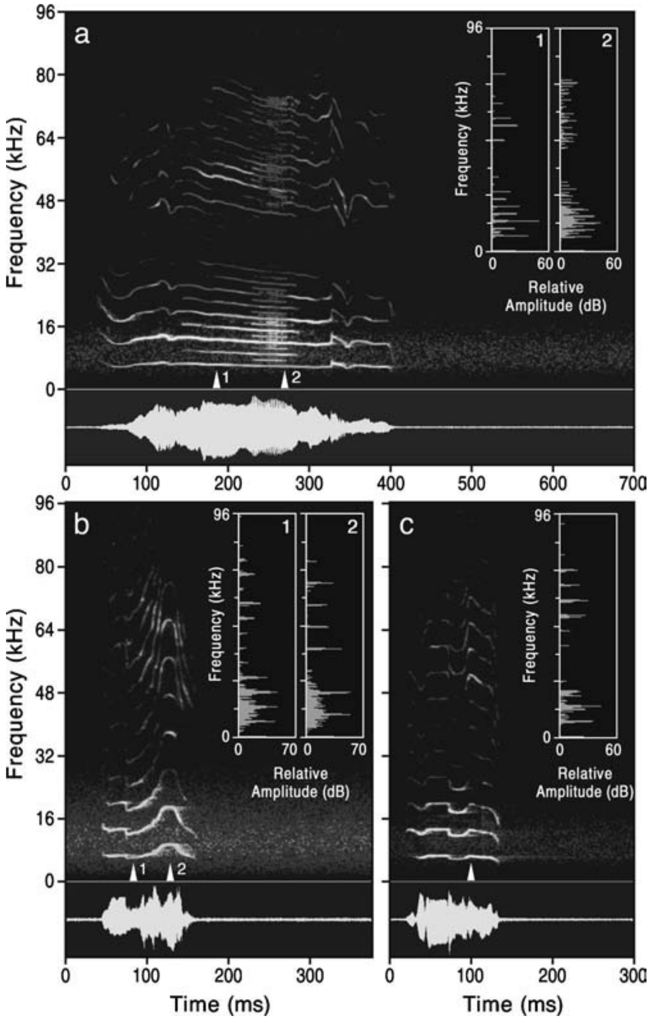

FIG. 2. Long call of the frog, *Amolops tormotus* (a), and two short calls [(b) and (c)] showing significant energy in the ultrasonic range and a spectral notch in the range of 32–45 kHz. Other data same as Fig. 1.

components, but the recordings were low-pass filtered at 22 kHz by the frequency responses of the microphone (Sennheiser ME-66) and tape recorder (Sony TC-D5M) and by the limited frequency range of the sound analysis software (Canary version 1.2.4). In the present study, use of a wideband microphone and a high-speed digital recording system with an extended range up to 128 kHz allowed unambiguous documentation of the ultrasonic harmonic components in the vocalizations of both the frog, *A. tormotus,* and the songbird, *A. albogularis*.

Among the vertebrates, ultrasonic harmonics of acoustic signals are known to be produced only by mammals, including whales (Sales and Pye, 1974), dolphins (Au, 1993), bats (Griffin, 1958), and rodents (Ehret, 1992). Our findings provide the first evidence that anurans and passerines are capable of generating tonal ultrasonic call components and should stimulate the quest for additional ultrasonic species.

These results raise several questions: Why do these animals produce signals containing ultrasonic components? That is, what function do they perform? Well-trained opera singers are able to produce a distinct high-frequency formant near 3 kHz (known as the singer's formant) that allows their voices to stand out from the loud orchestra in the background

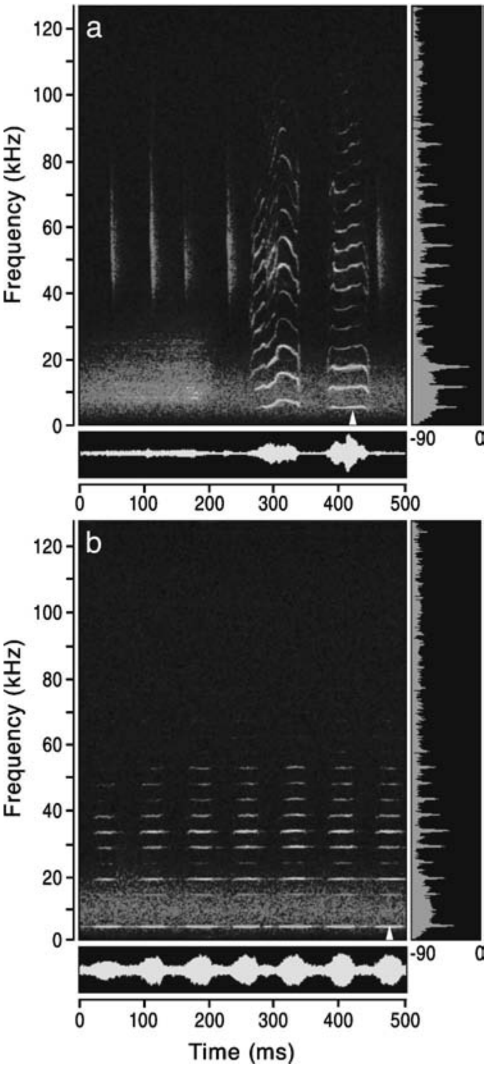

FIG. 3. Sound spectrograms (top left panel), waveforms (bottom panel), and average amplitude spectra [top right panel, 36-ms window centered at indicated points (arrowheads)] of animal vocalizations recorded at the study site. (a) Simultaneous recording of a short, two-note call of the frog, *A. tormotus*, and the FM echolocation pulses of a passing bat. (b) Pulsed song of the Rufous-faced warbler (*Abroscopus albogularis*); harmonics up to 54 kHz are evident. Other data same as Fig. 1.

(Sundberg, 1987). Thus, in this case, spectral salience may be viewed as an adaptation to overcome masking produced by the orchestra. In a recent study, Slabbekoorn and Peet (2003) showed that urban great tits (*Parus major*) in noisy locations sing with a higher minimum frequency than those in quieter locations, presumably avoiding masking of their songs by the predominantly low-frequency background noise. In the present study, we show that an Old World frog (*Amolops tormotus*) and an oscine songbird (*Abroscopus albogularis*) living near noisy streams produce acoustic signals that contain significant ultrasonic harmonics, which may also be the result of selective pressure to avoid masking by the wideband river noise that extends over the entire range of human hearing (Figs. 1 and 3). Alternatively, ultrasonic harmonics in the calls may be targeted at prey species or may be simply be an epiphenomenon—a by-product of the sound production mechanism. At present, our data do not allow us to distinguish between these alternatives.

Can *Amolops* or *Abroscopus* perceive these ultrasonic signal components? Current psychoacoustical data support an upper limit to frog and avian hearing of 5 kHz (Fay, 1988), and 12 kHz (Konishi, 1973), respectively. It must be noted, however, that systematic study of the response of the anuran or avian auditory system to ultrasound is lacking. In light of the results of the present study, it is important that the limits of hearing for these two groups of vertebrates be reevaluated.

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