2pAB9. Behavioral responses of anuran amphibians to biotic, synthetic and anthropogenic noise

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Many species of animals, including man, face the formidable task of communicating in noisy environments. In this paper, I shall discuss the effects of biotic, synthetic and anthropogenic noise on the calling behavior of anuran amphibians. Moreover, the role of spectral, temporal and spatial separation in minimizing masking by background noise will be examined. For example, presenting high-level, periodic (or aperiodic) tones at the male's Co-note frequency to males of the Puerto Rican treefrog, Eleutherodactylus coqui results in a clear shift in their calling pattern in an attempt to minimize acoustic overlap with the interfering playback stimulus. Amphibians also have a remarkable ability to shift their call timing in response to small intensity shifts in the background noise. Males of E. coqui are capable of reliably detecting a change in interfering tone intensity as small as 2-4 dB. Finally, I shall present behavioral evidence that biotic/anthropogenic noise may act as a strong selective force in sculpting the acoustic communication systems of several species of Old World frogs. Supported by grants from the NIDCD (no. DC-00222), UCLA Academic Senate (3501) and the P. F. Veneklasen Research Foundation.

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To avoid acoustic interference, acoustically communicating animals have evolved multiple behavioral adaptations to facilitate information transmission and thus information transfer. In this paper, I shall discuss three of these behavioral adaptations - the roles played by spectral, temporal and spatial separation in minimizing masking by background noise. To obtain data on these adaptations, one paradigm is to perform acoustic playback experiments. In the first part of this paper, I will try to answer the question: "What can we learn about frog vocalization behavior from acoustic playback experiments?" Finally, the effects of anthropogenic (man-made) noise on the calling behavior of anuran amphibians will be mentioned.

Amphibian field acoustic playback experiments involve setting up a loudspeaker in the animal’s environment, broadcasting an auditory stimulus to the calling frog, and recording the animal’s behavioral responses. The kinds of responses by males to playback stimuli that have been recorded include: 1. Call alternation with the stimulus (Awbrey, 1978; Narins and Capranica, 1978); 2. Antiphonal calling, in which there is a short-latency response by the frog to the stimulus (Narins and Capranica, 1978; Narins, 1982; Feng et al., 2006); 3. Synchronous calling, in which the frog under test calls in synchrony with the stimulus to attempt to “jam” the stimulus (Ryan, 1986); 4. Shifting of dominant frequency (Lopez et al., 1988); 5. Increasing call rate or complexity (Schwartz and Wells, 1984, 1985; Penna et al., 2005; Love and Bee, 2010); 6. Ceasing to call completely (Whitney and Krebs, 1975); 7. Orienting toward the loudspeaker (Narins et al., 2003); 8. Approaching the loudspeaker (Narins et al., 2005); 9. Aggressive behavior (Narins et al., 2005); 10. Increasing call intensity (Lopez et al., 1988).

Amphibian assemblages of New World arboreal frogs in the genus *Eleutherodactylus*, which exhibit remarkable phenotypic plasticity in the face of interfering sounds, have been extensively studied. For example, males of the Puerto Rican Coqui, *E. coqui*, produce a two-note advertisement call (“Co-Qui”) in which the “Co” note serves during male-male territorial encounters while the “Qui” note is most attractive to conspecific females. The first behavioral adaptation I shall discuss is known as spectral separation or frequency sharing. In a given assemblage of vocalizing animals (e.g., eleutherodactylid frogs in the Luquillo National Forest in Puerto Rico), there may be 6-8 species calling sympatrichly and syntopically. These species exhibit a range of body sizes from the largest (*E. coqui*, mean SVL: 35 mm) to the smallest (*E. gryllus*, mean SVL: 20 mm). Since the call frequencies in anuran amphibians are correlated with body size (Ryan, 1988; Meenderink et al., 2010), the frog calls in these assemblages range in frequencies from nearly 8 kHz to 2 kHz (Narins, 1995). Each species occupies a well-defined frequency range particular to that species, not unlike the allocation by the FCC of carrier frequencies in the FM radio band. By the assigning a unique carrier frequency to each broadcast station within that station’s range, the FCC ensures that nearby FM broadcasters will not cause undue mutual interference. This process assumes that the intended receivers (FM radios or conspecific frogs, in this example) possess sufficient frequency selectivity or resolution to filter out the adjacent stations. While this is virtually always true for the FM radio receivers, the frequency resolution of the behaving frog’s auditory system has not been measured over a frequency range sufficiently wide to determine if neighboring heterospecific frog vocalizations would be attenuated below their behavioral response thresholds.

In one set of acoustic playback experiments designed to determine the frequency specificity of the auditory system of the behaving Coqui in its natural habitat, 50 presentations of a synthetic, low-intensity (< 40 dB SPL at the frog) “Co” note, with a repetition period of 4 s, and a frequency adjusted by ear to be that of the calling male under test (typically 1.1 kHz), were broadcast to males of *E. coqui* calling in the Puerto Rican rain forest (Narins and Capranica, 1978). The number of one-note responses in response to 50 stimulus presentations was counted and threshold was arbitrarily designated as 10/50 one-note responses. The stimulus intensity was increased in 2 or 4 dB steps until the threshold criterion was reached and then the process repeated, changing only the frequency of the Co-note stimulus in steps of 100 Hz above and below the calling male’s Co frequency. In this way, a frequency audiogram could be obtained for a male calling in his natural habitat. Results showed that the lowest threshold was observed for a stimulus frequency of 1100 Hz (the frequency of the male’s Co note), and higher thresholds were observed for all frequencies tested, both above and below 1100 Hz (Narins and Capranica, 1978). However, the lowest call note frequency of the next smallest frog in this assemblage, *E. portoricicensis*, is 1.6 kHz (Narins, 1983), a frequency not tested in the *E. coqui* experiments (the highest frequency tested was 1.3 kHz, which required a stimulus intensity of 83 dB SPL to obtain the threshold response criterion). Thus, it is likely that the auditory system of *E. coqui* can discriminate between conspecific calls and calls of the congeneric sibling species *E. portoricicensis*, but the definitive tests are lacking.

Another set of acoustic playback experiments was designed to test the second acoustic avoidance adaptation behavior observed in frogs and other vertebrates - that of temporal separation or time sharing (Zelick and Narins, 1982, 1983; Gerhardt and Schwartz, 1995). Synthetic, high-level, 900-ms. pure tones with a repetition period of 2.4 s were broadcast for three minutes to males of *E. coqui* calling in the Puerto Rican rain forest. The intensity of the stimulus tones was adjusted to be 92 dB SPL at the position of the frog under test. The six males that were tested in this way each altered his calling pattern such that calls were initiated in the 1.5 s gap between the high-level
tones, and thus avoid overlap with the interfering stimulus (Zelick and Narins, 1982). This remarkable result demonstrates the ability of male frogs to both (a) detect an interfering sound within its hearing range, and (b) alter its calling behavior to minimize acoustic overlap (interference) with this interfering sound.

Moreover, even when the gap between stimulus tones was systematically reduced from a 50% duty-cycle stimulus (tone on 50% of the stimulus period, which was adjusted to be that of the frog under test) to a 90% duty cycle stimulus (tone on 90% of the stimulus period), males of the Coqui frog were still able to initiate calling in the “silent” gap between stimuli significantly more often than would be expected by chance (Zelick & Narins, 1983).

In fact, these frogs were able to initiate calling in the 750-ms gaps separating randomly occurring short and long interfering tones, suggesting that the cue for call initiation is the offset of the interfering tone, or in other words, a rapid reduction in the local noise level surrounding the frog (Zelick and Narins, 1985). To directly test this idea, frogs in their natural habitat were exposed to a high-level periodic tone for 1.5 s followed by a reduction in the tone level by 17, 14, 11, 8, 4 and 2 dB for 1.0 s, and the resulting call patterns examined. With a relatively large intensity difference between “tone burst” and window (> 10 dB) all the animals tested initiated calls preferentially in the window. Fifty-nine percent of the frogs still initiated significantly more calls during the window than would be expected by chance when the window was only 4 dB less intense than the tone. Only 16 percent of the frogs were able to initiate calls in the window for the smallest intensity difference (1-3 dB) tested (Zelick and Narins, 1983).

Another behavioral adaptation for extracting signals from noise is known as spatial separation. This behavior often involves frogs in multispecies assemblages. Say species A and species B produce calls that have similar (but not identical) spectral and temporal parameters. Then species A might aggregate in different regions of a site and/or may choose separate microhabitats from species B within the site. These behaviors are thought to reduce the possibility for (a) cross-species interactions, for example, when the calling of one species inhibits the calling of another (P´aez et al., 1993; Wong et al., 2009), (b) acoustic interference (Arak, 1984; Drewry and Rand, 1983; Hodl, 1977; Littlejohn, 1977; Garcia-Rutledge and Narins, 2001) and (c) cross-species matings (Hödl, 1977; Oldham and Gerhardt, 1975; Patecek, 1992).

A related behavior that may serve to reduce interference of signals by background noise is known as spatial release from masking; this has been elegantly demonstrated in Cope’s gray treefrog (Hyla chrysoscelis) by Bee (2007). In this experiment, females’ phonotaxis responses to a target stimulus were assessed when the target stimulus was separated by 7.5 degrees or 90 degrees from the masking noise. Phonotaxis responses were significantly faster and more accurate when the target and masker were separated by 90 degrees compared to a separation of 7.5 degrees. Thus, spatial release from masking appears to be a potential mechanism used by these frogs to extract signals from high-level background noise. It remains to be demonstrated in the field that females of this or any species actually orient themselves in a direction to spatially separate the male’s call from the interfering noise. It is also possible that the importance of spatial separation may be that a female frog somehow "knows" the most likely habitat harboring a conspecific male, and is thus more likely to avoid heterospecific matings (Arak, 1984). Future studies of spatial distributions of frog species within a multispecies assemblage are needed to shed light on the presumptive role of spatial release from masking.

In a series of more recent experiments, another variation of spectral separation to avoid signal masking has been discovered in three species of Old World frogs. The first of the species studied was the concave-eared torrent frog (Odorrana tormota) from Anhui Province, China. Males of this species are nocturnal, are found calling from the vegetation along rapidly-flowing streams, and possess transparent eardrums that are recessed in an ear canal, similar to the mammalian ear canals. It was the unusual ear morphology that caught the attention of Professor Kraig Adler at Cornell University who relayed this information to the author. This prompted the first expedition to the Tau Hua Creek in Huangshan Hot Springs, China, to make the first recordings of the calls of these remarkable animals. Their vocalizations are surprisingly rich in nonlinearities such as period doubling, sudden appearance and disappearance of multiple harmonics and subharmonics, frequency-modulated warbles, chaotic regimes, etc., generally absent in most other frog species’ calls (Feng et al., 2002; Narins et al., 2004; Feng et al., 2009). Moreover, males produce advertisement calls with fundamental frequencies at ca. 5 kHz that contain significant ultrasonic (US) harmonics (Narins et al., 2004), and playback of just the ultrasonic harmonics results in clear changes of the calling patterns of males (Feng et al., 2006; Narins et al., 2007). In addition, evoked potential recordings from the inferior colliculus indicate that they are capable of detecting these components up to 34 kHz (Feng et al., 2006).

Another sympatric species, Odorrana graminea (formerly O. livida) was also shown to detect frequencies in the ultrasonic range, up to 22 kHz (Feng et al., 2006). Males of this species produce calls with prominent ultrasonic harmonics up to 48 kHz and beyond (Shen et al., 2011a). It is interesting that females of this species cannot detect ultrasonic frequencies, but do respond to playbacks of pure tones as high as 16 kHz (Shen et al., 2011b). It is of note that this high frequency detection limit is ca. an octave higher than that of the non-ultrasonic frog with the second highest known detectable frequency (8.2 kHz- Loftus-Hills and Johnstone, 1970).
The other frog species that has been shown to communicate with ultrasound is *Huia cavitypanum*, the “hole-in-the-head frog” of Sabah, Malaysian Borneo (Arch et al., 2008). The interest in this frog stemmed from the fact that males of this species also possess transparent ear canals, terminated with flexible membranes (eardrums). Males may be found calling at night from the vegetation along the edge of the Nyipa River, a fast-flowing stream within the Gunung Mulu National Park in Sabah. Field recordings showed that males produce a variety of audible calls containing ultrasonic components, and moreover, they have the remarkable ability to shift the fundamental frequency of their calls above 20 kHz during a single calling bout (Arch et al., 2009). In addition, evoked potential recordings from the midbrain of males of this species revealed that they can detect frequencies, up to 39 kHz (Arch et al., 2009).

It is now believed that the sunken, transparent eardrums in both *O. tormota* and *H. cavitypanum* are adaptations for high-frequency detection in these frogs. The recessed membranes are correlated with shorter, and therefore less massive middle ear ossicles, and the transparent membranes are thinner (3-4 um) and therefore less massive than a typical frog eardrum, allowing them to vibrate at high frequencies (Feng et al., 2006; Narins et al., 2007).

Why do these remarkable frogs use the ultrasonic range for communication? One hypothesis is that the upward shift in both the call frequencies and the upper limit of hearing are the result of strong selective pressure from the environmental noise produced mainly by the rivers in both frogs’ habitats (Narins et al., 2004; Arch et al., 2008, 2009). Sound recordings of both the Tau Hua Creek in China and the Nyipa River in Malaysia reveal broadband spectra with energy principally at low frequencies, but falling off slowly up to 20 kHz and beyond (Narins et al., 2004; Arch et al., 2008). Human conversation is extremely difficult near these rivers; it is thought that these frogs have evolved a high-frequency communication system to avoid masking by the broadband noise produced by the torrential streams in their habitat, i.e., spectral separation of their calls from the masker (Narins et al., 2004; Arch and Narins, 2008).

Anthropogenic noise can also affect frog chorusing behavior. For example, Sun and Narins (2005) showed that in the face of airplane flybys or playback of motorcycle engine noise, call rates of some frog species in a multispecies calling assemblage in Thailand increased whereas others decreased. During exposure to playback of intermittent engine sounds, males of the hyilid *Dendropsophus triangulum* near Iquitos, Peru, concentrated more of their calling in the 15-s noise bursts than in the 30-s quiet intervals between bursts (Kaiser and Hammers, 2009). Males of *Litoria ewingi* in southern Australia appear to raise the dominant frequency of their calls an average of 123 Hz/dB of traffic noise (Parris et al., 2009). Whereas males of *Dendropsophus microcephalus* exposed to anthropogenic noise in Belize decreased both the number of days present at the chorus and the nightly chorus duration relative to controls (Kaiser et al., 2011), anuran communities near traffic noise in Puerto Rico were unaffected by traffic noise (Herrera Montes and Aide, 2011). Clearly, responses to playbacks of anthropogenic noise to individual frogs or choruses of frogs can vary widely between species and habitats. For comprehensive reviews of this burgeoning field, see Schwartz and Bee (2013), and Simmons and Narins (2013).

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REFERENCES


