Ethology 89, 73-83 (1991)
© 1991 Paul Parey Scientific Publishers, Berlin and Hamburg
ISSN 0179-1613

Department of Ecology and Evolutionary Biology,
The University of Connecticut, Storrs,
and Smithsonian Tropical Research Institute, Balboa

The Consequences for Communication of Call Overlap in the Tungara Frog, a Neotropical Anuran with a Frequency-modulated Call

JOSHUA J. SCHWARTZ & A. STANLEY RAND

SCHWARTZ, J. J. & RAND, A. S. 1991: The consequences for communication of call overlap in the tungara frog, a neotropical anuran with a frequency-modulated call. Ethology 89, 73—83.

Abstract

We presented male tungara frogs, *Physalaemus pustulosus,* with call-triggered computer-synthesized whines that either did or did not overlap the frogs' own frequency-modulated whines in time. When the stimulus was nonoverlapping, males added a high proportion of chuck notes to their calls. When the stimulus was overlapping, males responded with either no or only small increases in chucking. This suggests they have difficulty detecting whines while vocalizing. When female tungara frogs were given a choice between alternating whines and out-of-phase overlapping whines they did not discriminate. The result with males was similar to that previously obtained with species of frogs that have amplitude-modulated advemscment calls (SCHWARTZ 1987a), the result with females was different. We discuss our findings in relation to peripheral processing of spectral and temporal information in the anuran auditory system.

Corresponding author: Joshua J. SCHWARTZ, Department of Ecology and Evolutionary Biology, Box U-43, The University of Connecticut, Storrs, CT 06269, U.S.A.

Introduction

The acoustic environments in which animals communicate are often noisy. Sources of noise include wind, water (DUBOIS 1977), lightning (HOPKINS 1973) as well as biotic components of the environment. For example, interference problems can be created by the communication signals of conspecific and heterospecific individuals. Studies of neurobiology and behavior have illustrated ways animals from a variety of taxa enhance their ability to detect and transmit biologically relevant signals under such conditions (CODY & BROWN 1969; FICKEN et al. 1974; LITTLEJOHN 1977; LATIMER 1981; ZELICK 1986; NARINS & ZELICK 1988).

US Copyright Clearance Center Code Statement: 0179-1613/91/8901-0073$02.50/0

Male frogs often call in dense aggregations, and noise levels in these choruses are typically high. Because noise levels in choruses invariably fluctuate, one way individual male anurans can improve signal-to-noise ratios for call transmission is to adjust the timing of their vocalizations such that calls are broadcast when background noise levels drop (ZELICK & NARINS 1983). Call-timing shifts can occur on a coarse or a fine scale. For example, the timing of bouts of calling may shift relative to calling bouts of other species (LITTLEJOHN & MARTIN 1969; SCHWARTZ & WELLS 1983) or rapid timing adjustments may result in alternations of notes or calls with the vocalizations of other males (ZELICK & NARINS 1982, 1983; SCHWARTZ 1985).

SCHWARTZ (1987a) recently tested hypotheses on the function of call alternation in frogs using the species *Hyla microcephala*, *H. versicolor* and *Pseudacris crucifer*. In playback experiments, test males of all species responded with more aggressive calls to stimulus calls that were timed to alternate, as opposed to overlap, with their own calls. These data supported the hypothesis that neighboring males avoid overlapping calls because interference impairs their ability to assess the intensity of, and perhaps even detect, one another's calls.

Female-choice experiments supported the hypothesis that alternation also serves to preserve fine temporal information necessary for species discrimination by female *H. microcephala* and *H. versicolor*. Males of these two species have amplitude-modulated advertisement calls, and females are capable of fine levels of call discrimination based on amplitude modulation rate (GERHARDT 1978; SCHWARTZ 1987b). On the other hand, *Pseudacris crucifer* has a tone-like advertisement call that is slightly frequency modulated (20 % increase in frequency: 2800—3360 Hz) and lacks fine temporal structure. Unlike female *H. microcephala* and *H. versicolor*, females of this species did not discriminate against overlapping calls. DOHERTY & GERHARDT (1984) have shown that female *P. crucifer* also do not discriminate between constant-frequency and frequency-modulated synthetic calls, and males call antiphonally in response to constant-frequency synthetic calls (SCHWARTZ, pers. obs.). Frequency modulation is thus a stereotyped but "irrelevant" call property for *P. crucifer* (GERHARDT 1988).

Frequency-modulated signals are both common and taxonomically widespread among vertebrates (SIMMONS & STEIN 1980; BECKER 1982; RYAN 1985; TYACK 1986). Many species of anurans employ calls of this type (STRAUGHAN & HEYER 1976; CAPRANICA et al. 1984), and the range, direction, and rate of the frequency sweep, like amplitude modulation rate in other species, can be important in call recognition and species discrimination (RYAN 1983, 1985; ROSE et al. 1988).

The tungara frog, *Physalaemus pustulosus*, is a neotropical leptodactylid that produces a complex call consisting of a 'whine' and from 0 to 6 secondary 'chuck' notes (RAND & RYAN 1981). The whine is 300—400 ms in duration and its fundamental frequency sweeps from about 900 to 400 Hz (56 % drop in frequency). Upper harmonics of the whine are present in the call spectrum but are much reduced in amplitude relative to this dominant component (RYAN 1985). Chuck notes are 25-40 ms long and have a constant-frequency fundamental component that can be as low as 200 Hz in large males. Over 10 harmonics may be present in the chuck. Males add chuck notes to their calls in response to the calls of other males, and this enhances their attractiveness to females (RAND & RYAN 1981). When calls of other individuals are not audible, usually only whine notes are produced. Males that give complex calls are more susceptible to predation by frog-eating bats (RYAN et al. 1982).

Both male and female tungara frogs respond differently to whines with the natural downward sweep direction and those with sweep direction reversed. In an evoked-calling paradigm, males gave more whines and chucks in response to stimuli with frequency-modulated downsweeps than frequency-modulated upsweeps (RYAN 1983; ROSE et al. 1988). In two-choice experiments, females discriminated in favor of natural or synthetic whines with frequency-modulated downsweeps over upsweeps (RYAN 1983; RYAN & RAND in prep.). Therefore, unlike frequency modulation in *P. crucifer*, frequency modulation is not an irrelevant call property in *P. pustulosus*. This difference may occur because the dominant component of the frequency sweep of the tungara frog whine falls within the range of sensitivity of the amphibian papilla rather than just the basilar papilla. The tuning properties of neurons innervating the latter inner ear organ *suggest* that they may be less able to resolve frequency differences than those of the amphibian papilla (ZAKON & WILCZYNSKI 1988; RYAN 1988).

The purpose of this study was to supplement the previous study of SCHWARTZ (1987a) by investigating a species of frog with a *strongly* frequency-modulated advertisement call. Specifically, we wanted to determine the behavioral consequences of overlap of frequency-modulated calls for male-male and male-female communication. Therefore, the results of this study using *P. pustulosus* should cast light on the vulnerability of different information-coding schemes to acoustic interference and also contribute to a more thorough understanding of the evolution of patterns of call timing in chorusing frogs.

Materials and Methods

Tests with Males

Calling male *P. pustulosus* were collected after 19.00h in a flooded meadow in Gamboa, Panama during July and August 1989. They were placed individually in plastic bags containing a small amount of water, brought to a darkened room, transferred to plastic containers, and exposed to a stimulus of a recorded conspecific chorus. 8 experimental males, selected from those that began calling, were individually tested in an indoor, temperature controlled (27°C) room lined with mattress foam. After the male resumed calling the experiment began.

Experimental Stimuli

The acoustic stimulus was a synthetic whine designed to correspond closely to a natural whine (Fig. 1). It consisted of one spectral component exponentially sweeping from 900 to 450 Hz in 314 ms; the amplitude envelope was also exponentially shaped with a rise time of 35 ms and a fall time of 203 ms. The whine was digitally synthesized with a Commodore Amiga 2000 personal computer using software written by the first author. The program allows the user to specify stimulus duration, starting and ending frequency, pattern of frequency change (linear or exponential), and shape of the amplitude envelope. We used a sampling rate of 10 kHz (8 bits per sample), and low-passed filtered the computer's sound output at approx. 5 kHz using the Amiga's built in filter. The stimulus was stored in RAM during the experiment.

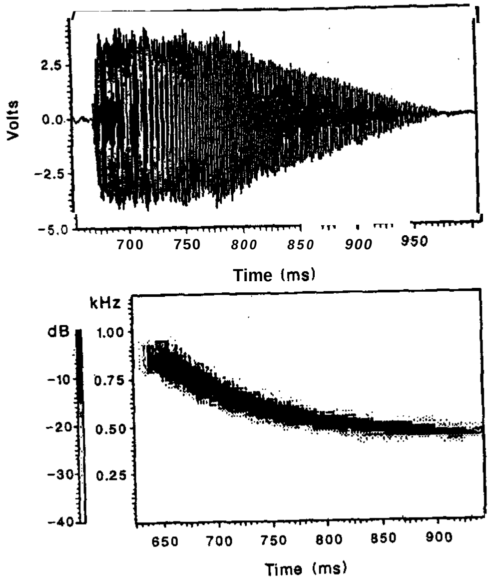

Fig. 1: Oscillogram (above) and sonagram (below) of the synthetic whine used in the experiments

During testing, the audio output of the Amiga was fed into one channel of a **Marantz PMD-430** stereo cassette tape recorder, amplified (Realistic SA10), and broadcast to subjects at 90 dB SPL (dB SPL re 20 μPa) from a speaker (ADS L200c) mounted in the wall of the arena. Stimulus amplitude (Peak SPL) was pre-adjusted with a calibrated Gen Rad 1982 precision sound-level meter set for flat weighting. Since measurements were made just in front of the frog's container, actual sound intensities experienced by subjects were somewhat lower than 90 dB SPL.

Recordings of the frog's calls were made using the second channel of the tape recorder and an Azden directional microphone (**ECZ-660**). The output of the microphone was split using a Y-cord and input to both the Marantz and an Applied Visions Future Sound (TM) audio digitizer for the Amiga. The whines of the subject were used to trigger stimulus output by the computer. We used six stimulus (post-trigger) delays: 50, 100, 200, 300, 500, and 1000 ms. To minimize within-treatment variation in stimulus timing, prior to tests, the gain on the digitizer was adjusted so that peak values of digitized calls input to the computer were approx. the same for all subjects. Trigger threshold for call output was then entered in the program; this was identical for all frogs. Threshold was usually crossed less than 15 ms after a male initiated a whine.

During tests, the computer monitored the timing of subject's calls. Because the inter-whine intervals of a calling male are much greater than the inter-note intervals within multi-note calls, it was easy to program the computer to respond only to whines. To prevent the stimulus output from itself being stored as a male's call (and perhaps triggering a response from the computer), the microphone was positioned as close as possible to the subject and facing 180° from the speaker. A software routine was used to check that the peak values of the digitized output of the speaker were indeed below the trigger threshold. If not, the microphone was repositioned. Prior to experimental broadcasts, frogs were recorded for an initial no-stimulus "solo" control period until they had given at least 30 calls. During broadcasts at each delay, we recorded at least 30 calls for most males (see Table 1 for exceptions).

For each male, we counted the number of chuck notes in recorded calls during the solo and stimulus periods. Data were statistically analysed using a Friedman two-way analysis of variance and Wilcoxon matched-pairs signed rank test on mean number of chucks per call.

Tests with Females

Gravid female *P. pustulosus* were captured in amplexus and tested in a square arena (2 x 2 m). in an apartment in Gamboa. The walls of the arena were formed by two mattresses and large cushions to minimize reflection of sound. Illumination was provided by a 25-W red bulb suspended from the ceiling. Individual females were placed under a small plastic funnel located equidistant (75 cm) from four Realistic Minimus 0.3 speakers (amplitude-frequency response: +/− 3 dB, 1.0—12.0 kHz). The speakers, placed at the perimeter of a circle, were separated by 90° and faced the center of the arena. After 30 s exposure to the test stimuli, the funnel was raised using a pulley, and the female was given 10 min to approach a speaker. The speakers continued broadcasting sound during this period. A positive response was scored if the animal made contact with or came within 10 cm of a sound source. Temperature during the experiments was approx. 26 "C.

Stimulus calls were identical to those presented to males and broadcast at a rate of 30 calls/min from each speaker. The quadraphonic arrangement of the speakers was necessary to mimic a situation in which two males alternate their whines and another two males overlap their whines. Stimulus calls were timed so that they either alternated or overlapped whines broadcast from the speaker on the opposite side of the arena. Overlapped calls, suffering three levels of acoustic interference, were used in separate tests: inter-call delays were 50, 100, and 200 ms. The inter-call delay of the alternating whines was 325 ms (Fig. 2). These stimuli were output in stereo using the Amiga computer and recorded using a Marantz PMD 360 stereo type recorder. The quadraphonic presentation of the

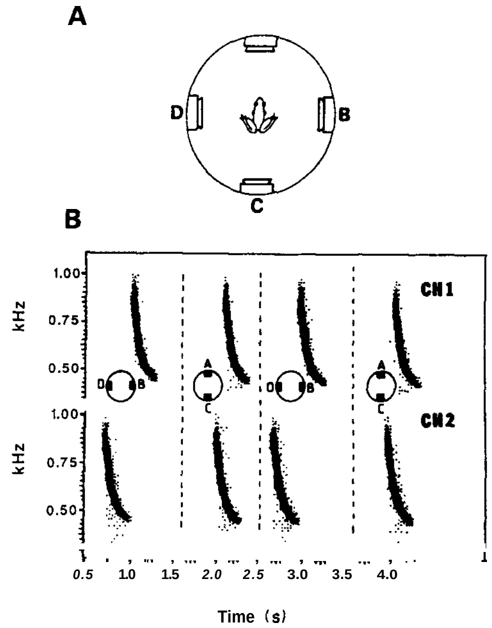

Fig. 2: A. Schematic diagram of the arena used in the four-speaker female-choice tests. B. Sonagrams showing the timing relationships of the alternating and overlapping whines used in one of the four-speaker female-choice tests (100 ms overlapping whine delay). Pairs of calls, each on a separate channel, were alternately output to speakers at opposite sides of the arena as indicated. In the figure, calls output to speakers A and C are overlapping while calls output to speakers B and D are alternating. *CH1*: Tape channel *1*, *CH2*: Tape channel 2

stimuli was obtained using call-triggered electronic relays to switch the stereo signal and ground lines from the tape recorder back and forth to the two pairs of speakers (see SCHWARTZ 1987a for additional details). Playback intensities for each speaker were regulated by separate Realistic L-pads and were equalized at the female release point at 90 dB +/− 1dB (peak SPL; dB re 20 μPa) with the Gen Rad 1982 sound-level meter. During successive days, the alternating and overlapping stimuli were broadcast from different pairs of speakers to neutralize any directional biases of the acoustic delivery system.

An additional experiment was conducted in the same room used for the tests with males (dimensions: 3 x 3 m). Individual females were released midway between two wall-mounted ADS L200c speakers and given a choice between calls that overlapped and those that alternated. The overlapped calls had an inter-call delay of 50 ms and were recorded on the same channel of a stereo tape; on the second channel, a single alternating call was recorded at each time midpoint between successive pairs of overlapped calls. Stimulus rate was 30/min from each speaker; stimulus intensity was equalized at 90 dB +/− 1dB (Peak SPL) at the female release point.

Results

Stimulus delay had a significant effect on the mean number of chucks per call (Table 1; Friedman test, $p < 0.01$), and only calls with delays of 100 ms or greater elicited a significant increase in the response measure relative to the no-stimulus, solo, levels (Wilcoxon matched-pairs signed rank test). However, the increases in chucking to the partially overlapped whines with delays of 100 and 200 ms were small.

In neither the 4-speaker nor the 2-speaker tests did females discriminate between the alternating and overlapping whines (Table 2). Moreover, order of the overlapping stimulus did not influence female choices: in no experiment was there a significant preference for the leading or following call.

Table 1: Responses of 8 male *Physalaemus pustulosus* to call-triggered computer-generated whines. Data are presented as mean number of chucks per call during stimulus and solo periods. Sample sizes for each treatment were 30 calls per male except for males 5 (50 ms, n = 24) and 6 (100 ms, n = 24); p-values are for a comparison of the stimulus and solo periods using a Wilcoxon matched-pairs signed rank test

		Delay (ms)					
Male	Solo	50	100	200	300	500	1000
1	0.77	0.47	0.87	1.30	1.00	1.63	1.79
2	0.97	0.87	1.00	1.00	0.97	1.57	1.17
3	0.00	0.07	0.20	0.13	0.57	0.80	0.53
4	0.27	0.03	0.67	0.30	0.67	1.30	0.63
5	0.00	0.04	0.20	0.13	0.97	0.77	0.90
6	0.60	0.67	0.54	0.90	1.00	1.70	1.83
7	0.00	0.00	0.03	0.00	0.13	0.46	0.46
8	0.00	0.70	0.30	0.03	0.90	1.03	1.43
Mean	0.33	0.36	0.48	0.47	0.77	1.16	1.09
Median	0.14	0.27	0.42	0.22	0.94	1.17	1.04
P		ns	0.02	< 0.01	< 0.01	< 0.01	< 0.01

***Table** 2:* Number of female *Physalaemus pustulosus* choosing alternating or overlapping whines in four-speaker and two-speaker choice tests and number of females that did not respond or just wandered around the arena. In parentheses: number of females choosing the leading whine of the overlapping stimuli. p-values are for a two-tailed binomial test

		Four-speaker tests		
Delay	Alternate	Overlap	No. resp.	P
50 ms	12	8 (4)	4	ns
100 ms	7	13 (7)	5	ns
200 ms	9	11 (5)	4	ns
		Two-speaker test		
50 ms	13	7	4	ns

Discussion

Although frequency sweep in the whine of P. *pustulosus* is a call property important in eliciting both male chucking and female phonotaxis, the results of this study were qualitatively similar to those obtained by SCHWARTZ (1987a) with male and female P. *crucifer*. When a synthetic whine overlaps with the whine of a calling male tungara frog, our results suggest that the male may have difficulty detecting the note or its frequency modulation. This was reflected in either no or only small increase in chucking to stimulus whines with delays less than 300 ms long relative to chucking during no-stimulus periods. The significant result obtained for the 100- and 200-ms delay may indicate some detection of the partially overlapping stimulus whines, but the chucking increases were often so small as probably to be biologically meaningless. An alternative to the detection hypothesis is that after a male initiates a whine, there is a brief behavioral refractory period caused by some neural constraint on calling (NARINS 1982).

Adjacent male tungara frogs tend to alternate calls (RAND & RAND unpubl. ms). Our data suggest they may avoid overlapping whine notes for two reasons. First, it may facilitate call detection and intensity assessment (SCHWARTZ 1987a). This, in turn, may help individuals maintain relatively fixed intermale distances in the chorus. In fact, if another male is detected calling very near, aggressive "mew" calls may be given (RYAN 1985). However, because previous unpublished work by one of us (RAND) indicated that males are usually reluctant to move in response to loud playbacks of conspecific calls, we favor a second possibility. Males should be better able to attract females if they add chucks to their calls when other males *are* whining; if they don't detect these whines because they are calling at precisely the same time, they could be at a disadvantage competing for mates with other males in the chorus.

Whine overlap, however, evidently does not *directly* impair a male's ability to attract a female. The four-speaker female-choice experiments showed that female behavior was essentially independent of both the inter-call delay in overlapped calls and stimulus order. It is unlikely that the presence of directional cues in the 4-speaker experiments can explain this absence of discrimination. In the 2-speaker experiment, where directional cues were not available to help separate the two overlapped whines, females also failed to discriminate. Moreover, an experiment with another small neotropical frog, *Hyla microcephala,* has shown that directional cues may not be great enough to enable the auditory system to isolate individual signals of the same intensity from one another during call overlap (SCHWARTZ, in prep.). In that experiment, when destructively overlapped amplitude-modulated calls were presented from two pairs of speakers separated by 5 and 120 degrees, females failed to discriminate in favor of the latter pair of sound sources — where directional cues were good.

The female-choice experiments showed that the critical information on frequency sweep direction was not obscured during call overlap. This suggests that the two whines, or portions of them, may be separately encoded in the auditory system of the female tungara frog, and the integrity of these signals maintained as information is transmitted from the auditory periphery to higher processing centers in the central nervous system. It is presumably in these centers where the detection mechanism for the direction of frequency modulation is located. In analogous experiments with *H. microcephala* and *H. versicolor,* the integrity of overlapped out-of-phase calls was evidently not preserved by the auditory system (SCHWARTZ 1987a). In these species, the critical information for species recognition is the rate of amplitude modulation rather than the direction of a frequency sweep. The encoding of species-specific spectral information may therefore be more immune to the effects of certain kinds of acoustic interference (call overlap) than the encoding of species-specific fine temporal information.

The behavioral data of both the SCHWARTZ (1987a) and the present study may be a manifestation of processes operating at the level of the auditory periphery. The eighth nerve probably encodes the amplitude modulation rate of an advertisement call as arrays of phase-locked neural firing that are transmitted to the CNS for decoding (ROSE & CAPRANICA 1985; SCHWARTZ & SIMMONS 1990). Peripheral auditory units spanning the entire range of frequency sensitivity can participate in this process. Therefore, when two amplitude-modulated calls overlap such that pulses are out of phase, either a degraded pulse rate or a pulse rate higher than that in a single call is transmitted in the temporal pattern of fiber firing.

Peripheral auditory fibers fire at rates proportional to sound energy within their tuning curves or frequency pass-band (within a limited dynamic range) (SACHS & YOUNG 1979; NARINS & WAGNER 1989). Therefore, frequency in a frequency-modulated or harmonically complex signal could be resolved by analyzing neural activity in the 8th nerve with respect to place (i.e. fiber best frequency). If two frequency-modulated signals overlap in time, the ability to resolve them should be a function of the time delay between them, the signal intensities, the shapes of auditory tuning curves, and the temporal integration characteristics of the auditory system. Theoretically, then, it should be possible to encode independently the frequency structure of two partially overlapping whines in the auditory system of a tungara frog (for a discussion of this problem in an FM bat see SIMMONS et al. 1989). Neurophysiological data on peripheral frequency coding in *P. pustulosus* have not been published and these data, coupled with modeling of the animal's auditory system would be needed to test the validity of this idea. For those anuran species that have been studied, tuning curves of auditory fibers innervating the amphibian papilla have Q_{10dB} values (unit best frequency divided by bandwidth at 10 dB above threshold) that range from about 0.5 to 4 (NARINS & ZELICK 1988; WILCZYNSKI & CAPRANICA 1984). Physiological data could also determine whether tungara frogs have typical Q_{10dB} values or unusually sharp tuning curves that might enhance their ability to detect frequency sweeps.

If the auditory system of *P. pustulosus* can extract sufficient information on frequency sweep in overlapped whines to elicit phonotaxis responses by females, why did calling males fail to respond, or at best respond only weakly, to overlapped broadcast whines? One possibility is that the production of loud sound during calling is sufficient acoustically to jam the whines of other frogs at or below the intensity of stimuli broadcast during our experiment. Another possibility is that sound transmission to the inner ear is somehow impeded during calling. Recent research indicates that the opercularis system of the anuran middle ear does not operate to impede stapedial movement during vocalization (JASLOW et al. 1988). However, the increase in buccal pressure concomittant with calling should stiffen the tympanic membranes of males and so act to dampen the transmission of sound (JASLOW et al. 1988). Data supporting this idea were recently obtained by NARINS (1990) who used laser doppler vibrometry to measure tympanic vibration during call broadcasts to calling male *Eleutherodactylus coqui.* If tympanic stiffening during calling produces a similar effect in *P. pustulosus,* then critical portions of the whine may have gone undetected during our overlapping broadcasts to males.

Acknowledgements

We thank Andrea SIMMONS, Prestor SALIENT, Mike RYAN, Gary ROSE, and Peter NARINS for helpful comments on the manuscript. We thank Charles HENRY for producing the oscillogram and sonograms of Figures 1 and 2 (Cambridge Electronics Design CED-1401 and accompanying software). Financial support was provided by a Smithsonian Institution Short Term Visitor Award and NIH grant NS08285 to JJS.

Literature Cited

BECKER, P. H. 1982: The coding of species-specific characteristics in bird sounds. In: Acoustic Communication in Birds. Vol. 1: Production, Perception, and Design Features of Sounds. (KROODSMA, D. E. & MILLER, E. H., eds.) Acad. Press, New York, pp. 214—252.

CAPRANICA, R. R., HARNED, G. D. & PASSMORE, N. I. 1984: Neuroethology of sound communication in the African running frog *Kassina senegalensis.* Neurosci. Abstr. 10, 399.

CODY, M. L. & BROWN, J. H. 1969: Song asynchrony in neighbouring bird species. Nature 222, 778—780.

DOHERTY, J. A. & GERHARDT, H. C. 1984: Evolutionary and neurobiological implications of selective phonotaxis in the spring peeper (*Hyla crucifer*). Anim. Behav. 32, 875—881.

DUBOIS, A. 1977: Observations sur le chant et les relations interindividuelles chez quelques grenouilles du sous-genre *Paa* du Nepal (Amphibiens, Anoures, Genre *Rana*). Bull. Soc. Zool. Fr. 102, Suppl. 2, 163—181.

FICKEN, R. W., FICKEN, M. S. & HAILMAN, J. P. **1974:** Temporal pattern shifts to avoid acoustic interference in singing buds. Science **183, 762—763.**

GERHARDT, H. C. **1978:** Temperature coupling in the vocal communication system of the gray treefrog ***Hyla* *versicolor.*** Science **199, 992—994.**

— — **1988:** Acoustic properties used in call recognition by frogs and toads. In: The Evolution of the Amphibian Auditory System. (FRITZSCH, B., WILCZYNSKI, W., RYAN, M. J., HETHERINGTON, T. & WALKOWIAK, W., eds.) John Wiley & Sons, New York, pp. **455—483.**

HOPKINS, C. **D. 1973:** Lightening as background noise for communication among electric fish. Nature **242, 268—270.**

JASLOW, A. **P.,** HETHERINGTON, T. E. & LOMBARD, R. E. **1988:** Structure and function of the amphibian middle ear. In: The Evolution of the Amphibian Auditory System. (FRITZSCH, B., WILCZYNSKI, W., RYAN, M. J., HETHERINGTON, T. & WALKOWIAK, W., eds.) John Wiley & Sons, New York, pp. **69—91.**

LATIMER, W. **1981:** Acoustic competition in bush crickets. Ecol. Entomol. **6, 35—45.**

LITTLEJOHN, M. J. **1977:** Long-range acoustic communication in anurans: an integrated and evolutionary approach. In: The Reproductive Biology of Amphibians. (TAYLOR, D. H. & GUTTMAN, S. I., eds.) Plenum **Press,** New York, pp. **263—294.**

— — & MARTIN, A. A. **1969:** Acoustic interactions between two species of leptodactylid frogs. **Anim.** Behav. **17, 785—791.**

NARINS, **P. M. 1982:** Behavioral refractory period in neotropical treefrogs. J. Comp. Physiol. A, **148, 337—344.**

— — **1990:** Does a treefrog protect himself from his **own** call? Abstract, Anim. Behav. Soc. **26th Ann.** Meeting, p. **125.**

— — & HILLERY, C. M. **1983:** Frequency coding in the inner ear of anuran amphibians. **In:** Hearing-Physiological Bases and Psychophysics. (Urn=, R. & HARTMANN, R., eds.) Springer-Verlag, Berlin, pp. **70—76.**

— — & WAGNER, I. **1989:** Noise susceptibility and immunity of phase locking in amphibian auditory-nerve fibers. J. Acoust. Soc. Am. **85, 1255—1265.**

— — & ZELICK, R. **1988:** The effects of noise on auditory processing and behavior in amphibians. In: The Evolution of the Amphibian Auditory System. (FRITZSCH, B., WILCZYNSKI, W., RYAN, M. J., HETHERINGTON, T. & WALKOWIAK, W., eds.) **John** Wiley & Sons, New York, pp. **511—536.**

RAND, A. S. & RYAN, M. J. **1981:** The adaptive significance of a complex vocal repertoire in a neotropical frog. **Z.** Tierpsychol. **57, 209—214.**

ROSE, G. J. & CAPRANICA, R. R. **1985:** Sensitivity to amplitude modulated sounds in the anuran auditory nervous system. J. Neurophysiol. **53, 446—465.**

— —, ZELICK, R. & RAND, A. **S. 1988:** Auditory processing **of** temporal information in a neotropical frog is independent of signal intensity. Ethology **77, 330—336.**

RYAN, M. J., **1983:** Frequency modulated calls and species recognition in **a** neotropical frog, *Physalaemus pustulosus.* J. Comp. Physiol. A, **150, 217—221.**

— — **1985:** The Tungara Frog. The Univ. of Chicago Press, Chicago.

— — **1988:** Constraints and patterns in the evolution of anuran acoustic communication. In: The Evolution of the Amphibian Auditory System. (FRITZSCH, B., WILCZYNSKI, W., RYAN, M. J., HETHERINGTON, T. & WALKOWIAK, W., eds.) John Wiley & **Sons,** New York, pp. **637-677.**

— —, TUTTLE, M. D. & RAMI, A. **S. 1982:** Bat predation and sexual advertisement in a neotropical frog. Am. Nat. **119, 136—139.**

SACHS, **M.** B. & YOUNG, E. D. **1979:** Encoding of steady-state vowels in the auditory nerve: Representation in terms of discharge rate. J. Acoust. Soc. Am. **66, 470—479.**

SCHWARTZ, J. J. 1987a: The function of call alternation in anuran amphibians: a test of three hypotheses. Evolution **41, 461—471.**

— — 1987b: The importance of spectral and temporal properties in species and call recognition in a neotropical treefrog with a complex vocal repertoire. Anim. Behav. **35, 340—347.**

— — & **SIMMONS,** A. M. **1990:** Encoding of a spectrally-complex communication sound in the bullfrog's auditory nerve. J. Comp. Physiol. A., in press.

— — & WELLS, K. D. **1983: An** experimental study of acoustic interference between two species of neotropical treefrogs. Anim. Behav. **31, 181—190.**

— — & — — **1985:** Intra- and interspecific vocal behavior of the neotropical treefrog *Hyla* ***microcephala.*** Copeia **1985, 27—38.**

SIMMONS, J. A. & STEIN, R. A. **1980:** Acoustic imaging **in** bat sonar: echolocation signals and the **evolution** of echolocation. J. Comp. Physiol. **135, 61—84.**

— —, FREEMAN, E. G., STEVENSON, S. B., CHEN, L. & WOHLGENANT, T. J. **1989:** Clutter interference and the integration time of echoes in the echolocating bat, *Eptesicus fuscus.* J. Acoust. Soc. **86, 1318—1332.**

STRAUGHN, I. R. & HEYER, W. R. **1976:** A functional analysis of the mating calls of the neotropical frog genera of the *Leptodactylus* complex (Amphibia, Leptodactylidae). Pap. Avulsos **Zool.** (Sao Paulo) **29, 221—245.**

TYACK, P. **1986:** Population biology, social behavior, and communication in whales and dolphins. **TREE 1, 144—150.**

WILCZYNSKI, W. & CAPRANICA, R. R. **1984:** The auditory system of anuran amphibians. **Progress** Neurobiol. **22, 1—38.**

ZAKON, H. H. & **WILCZYNSKI,** W. **1988:** The physiology of the anuran eighth nerve. In: The Evolution of the Amphibian Auditory System. (FRITZSCH, B., WILCZYNSKI, W., RYAN, M. J., HETHERINGTON, T. & WALKOWIAK, W., eds.) John Wiley & Sons, New York, pp. **125—155.**

ZELICK, R. **1986:** Jamming avoidance in electric fish and frogs: strategies of signal oscillator **timing.** Brain Behav. Evol. **28, 60—69.**

— — & NARINS, **P. M. 1982:** Analysis **of** acoustically evoked call suppression behaviour in a neotropical treefrog. **Anim.** Behav. 30, **728—733.**

— — & — — **1983:** Intensity discrimination and the precision of call timing in two species of neotropical treefrogs. J. Comp. Physiol. **153, 403—412.**

Received: February 8, 1991

Accepted: June 3, 1991 (G. Barlow)