



# Acoustic interference limits call detection in a Neotropical frog *Hyla ebraccata*

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(Received 25 March 1998; initial acceptance 29 May 1998;  
final acceptance 8 August 1998; MS. number: A8159)

Problems associated with communication in noisy environments include detection, discrimination, and localization of appropriate signals. I investigated the effects of broadband background noise on call detection by female *Hyla ebraccata*, a Neotropical treefrog. In playback experiments, I offered females a choice between two stimuli: chorus noise alone or chorus noise plus a computer-synthesized call. By systematically increasing the level of chorus noise, I determined that females could no longer reliably choose between the two speakers when the signal-to-noise ratio was +1.5 dB or lower. By taking the distribution of calling males into account, I estimated that females detect only the nearest male. If a female were to sample more than a very few males, she would need to move around the chorus. By doing so, she probably increases the costs of mate choice. Thus, the noise of a chorus impairs the ability of females to detect conspecific calls and thereby limits their ability to choose between mates. These limitations could have serious implications for the evolution of signallers' and receivers' behaviour.

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Animals often communicate in suboptimal conditions. Sometimes the intended receivers are engaged in other activities at a distance from the signaller. Often other animals produce irrelevant signals overlapping those of the signaller. Animals that breed in dense aggregations, such as orthopterans and anurans, often encounter these problems in acoustic communication. In addition to the problem of overlap of signals of nearby males, any one signal often attenuates to match levels of background sounds within a few metres of the source. Despite this, many experimental studies of acoustic communication have intentionally minimized background sound. While these studies document the capabilities for communication in ideal conditions, they leave open the question of performance in natural conditions.

Many studies of anurans have shown that overlapping calls are less attractive to females than nonoverlapping calls (Schwartz & Wells 1983a, 1984; Wells & Schwartz 1984), especially if overlap obscures fine temporal properties of the call (Schwartz 1987). Thus, it is not surprising that males generally avoid overlap with neighbouring males (Schwartz & Wells 1983a, b, 1984; Narins & Zelik 1988; Narins 1992a, b; Schwartz 1993, 1994; Greenfield 1994; Grafe 1996). This avoidance of overlap reduces interference between signals of nearby males. Even when

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overlap is avoided, however, the problem of the nearly continual background sound produced by the chorus remains (Wiley 1994).

Gerhardt & Klump (1988) studied the effects of background sound in green treefrogs, *Hyla cinerea*. They showed that a female could detect a single male's calls mixed with the sounds of a chorus when the intensity of the calls was equal to that of the chorus noise. Sound spreads spherically from a calling male (Gerhardt 1975), therefore sound from a signalling frog attenuates 6 dB with each doubling of distance. By combining information about call detection in noise with information about the sound pressure levels (SPLs) of a calling frog at 1 m and typical chorus noise, Gerhardt & Klump (1988) estimated that a female could hear only the nearest three to five males in a chorus as distinct signals.

Females are able to use the spatial distribution of calls to improve detection. Female *H. cinerea* can detect the presence of a conspecific call in broadband background noise when the speaker broadcasting the call is spatially separated from the source of the background noise but not when the call is broadcast adjacent to the speakers broadcasting background noise (Schwartz & Gerhardt 1989). In many natural choruses, calls of individual males are not spatially separated from background sounds.

In Gerhardt & Klump's (1988) study, most of the background sound consisted of other *H. cinerea* and thus included frequencies more or less matching the call.

Other species can also mask calls, provided their frequencies fall within the masking bandwidths of the subject's auditory system. This situation would make the detection of single conspecific calls more difficult in large multispecies choruses than in largely monospecific ones.

Many tropical frogs call in complex choruses that include species with similar frequencies. The present study used Gerhardt & Klump's methods to investigate the ability of female *Hyla ebraccata*, a common Central American treefrog, to detect calls of a single male in background sound from a complex natural chorus. The results suggest that females of this species might hear fewer males as distinct signals than do female *H. cinerea*. Together with Gerhardt & Klump (1988), these results emphasize the importance of measuring the abilities of receivers to detect signals in natural situations.

## METHODS

### Study Site and Species

*Hyla ebraccata* is a common treefrog in Atlantic lowland tropical rainforests throughout much of Central America (Duellman 1970). I studied acoustic communication in *H. ebraccata* in 1993 and 1994 at La Selva Biological Station, Heredia Province, Costa Rica. The study site (experimental swamp I) was a seasonal marsh located at 250 m north on Camino Experimental Sur (CES) with an elevation of approximately 15 m. Vegetation in the marsh was mostly *Spathiphyllum friedrichsthali* (Araceae) and *Panicum grande* (Poaceae). *Pentaclethra macroloba* (Mimosaceae) and *Ficus* sp. (Moraceae) were the dominant trees at the edges (Donnelly & Guyer 1994).

*Hyla ebraccata* males are small (mean  $\pm$  SE snout-vent length [SVL]=25.0  $\pm$  0.8 mm, mass=0.9  $\pm$  0.1 g) and attract females (SVL=31.7  $\pm$  1.3 mm, mass=2.4  $\pm$  0.3 g with eggs) with pulsed advertisement calls. Males at La Selva give calls that are short (mean  $\pm$  SE duration=162  $\pm$  2 ms), with a mean dominant frequency of 3256.3  $\pm$  19.8 Hz and pulse repetition rate of 97.2  $\pm$  0.5 Hz (Wollerman 1998). Males initiate amplexus (Miyamoto & Cane 1980; Morris 1991) although females often sit undetected near calling males (Morris 1991; personal observation). Amplexant pairs deposit eggs on leaves overhanging water; tadpoles drop from the leaf into the water below after they have hatched.

### Experimental Procedures

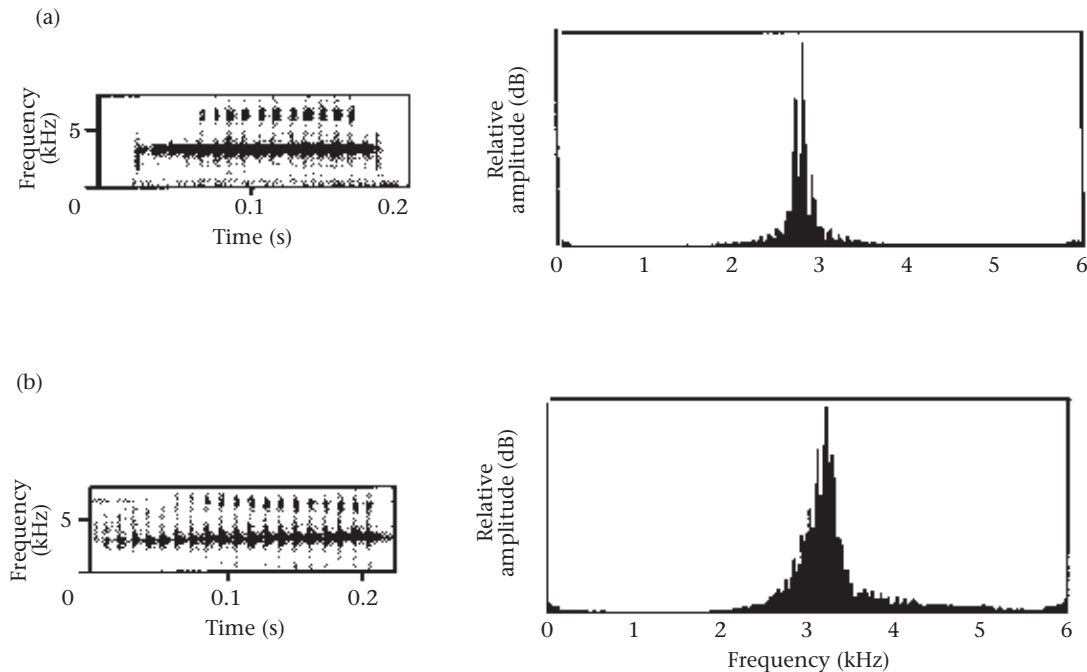
These experiments were designed to determine the minimal signal-to-noise ratio at which females detect a computer-synthesized call in the presence of chorus noise. Two speakers were used: one broadcast chorus noise plus a computer-synthesized call, the other chorus noise alone. Calls used in these experiments had the characteristics of the population mean. I assumed that if females could detect the computer-synthesized call in the chorus noise, they would approach that speaker.

For these experiments, I collected gravid females, identified by eggs visible through the body wall, from the study site between 2000 and 2400 hours. All females were tested in a laboratory at La Selva between 2230 and 0600 hours and released by dawn. Conditions in the semi-enclosed laboratory were similar to those in the ambient environment; the temperature was 25  $\pm$  1°C. During tests, SPL in the laboratory was between 50 and 55 dB (Extech Instruments digital sound level meter 407735, fast response, flat weighting). The experimental arena (1.8 m long by 1.0 m wide) had walls of foam padding (7.5 cm thick) and was lit by a 10-W red light bulb positioned to one side midway between the two speakers. Before using each female in these experiments, I required that she successfully orient to a single speaker broadcasting computer-synthesized calls by approaching it within 5 cm. In both preliminary and experimental trials, females generally performed actions indicative of sound localization in frogs, including head scanning and zigzag jumping (Gerhardt 1995).

In July and August 1993, I tested females with one signal-to-noise ratio (+6 dB). Chorus noise (played with a Marantz PMD 221 tape recorder) and computer-synthesized calls (played with a Sony TC-D5M tape recorder) were mixed with a Realistic 32-1200c stereo sound mixer connected to a Realistic 32-2031 amplified speaker at one end of the arena. The opposite speaker (same model) broadcast chorus noise played on a Sony Pro-Walkman tape recorder. Although I did not test the frequency response of these speakers, females did not have a preference when identical calls were broadcast from the two speakers ( $G_1=0.07$ ,  $N=15$ ,  $P<0.9$ ; Wollerman 1998). Receivers sometimes find signals easier to detect if they are correlated with background noise (if they occur at a predictable time in the background noise). In this series of tests, all stimuli were uncorrelated. In each trial, I began the three tape recorders at slightly different times. In addition, slight variation in tape speeds made it unlikely that the stimuli remained precisely synchronized throughout a trial.

In June and July 1994, I tested females with three signal-to-noise ratios (+3, +1.5, and 0 dB). In these experiments, chorus noise from a Marantz PMD 440 tape recorder was split using a Y-cord. One signal was then passed through an amplifier (Amplivox Model S702) to a Realistic Minimus-7 playback speaker. The other signal was mixed with computer-synthesized calls from a Sony TC-D5M stereo tape recorder. The combined output from the mixer passed through an amplifier (a second Amplivox Model S702) to a Realistic Minimus-7 speaker at the opposite end of the arena. Frequency responses for both speakers were flat ( $\pm 3$  dB) between 100 and 6000 Hz. Chorus noise broadcast at opposite ends of the arena in this experiment was correlated because it came from a single tape; however, chorus noise was uncorrelated with the call.

The signal-to-noise ratio was defined as the difference between the SPL of the signal and the SPL (not the spectrum level) of the chorus noise. Most studies of masking use spectrum level (dB/Hz) of the noise to define the signal-to-noise ratio. This definition is only useful for



**Figure 1.** (a) Spectrogram (left) and power spectrum (right) of the computer-synthesized call used in call detection threshold experiments. (b) Spectrogram (left) and power spectrum (right) of a natural *H. ebraccata* advertisement call.

situations in which the masker is white noise and has a flat amplitude spectrum. Natural chorus noise, such as that used here, has a variable amplitude spectrum and so the SPL of the noise is the more appropriate measure. I measured SPL at the centre of the arena with a digital sound level meter (flat weighting; calls were measured with the peak hold response, chorus noise with the fast response). Chorus SPL was calibrated for each speaker independently. The sound intensity ( $I$ ) of continuous sounds broadcast simultaneously from two speakers is twice that of one speaker with a resultant change in SPL of +3 dB ( $=10 \log 2I/I$ ). For example, if one speaker broadcast chorus noise at 77 dB, two speakers together produced noise with SPL 80 dB.

For the +6 dB signal-to-noise ratio, the SPL of the call was  $82 \pm 0.5$  dB and the chorus noise at each speaker was  $73 \pm 0.5$  dB. For all other signal-to-noise ratios, chorus SPL at each speaker was standardized at  $74 \pm 0.5$  dB. To achieve signal-to-noise ratios of +3, +1.5, and 0 dB, call SPL was  $80 \pm 0.5$  dB,  $78.5 \pm 0.5$  dB, or  $77 \pm 0.5$  dB, respectively. I checked the SPL for all stimuli (chorus noise and calls) every fifth test and adjusted levels if necessary. The SPL of the combined output of both speakers was confirmed periodically throughout each night.

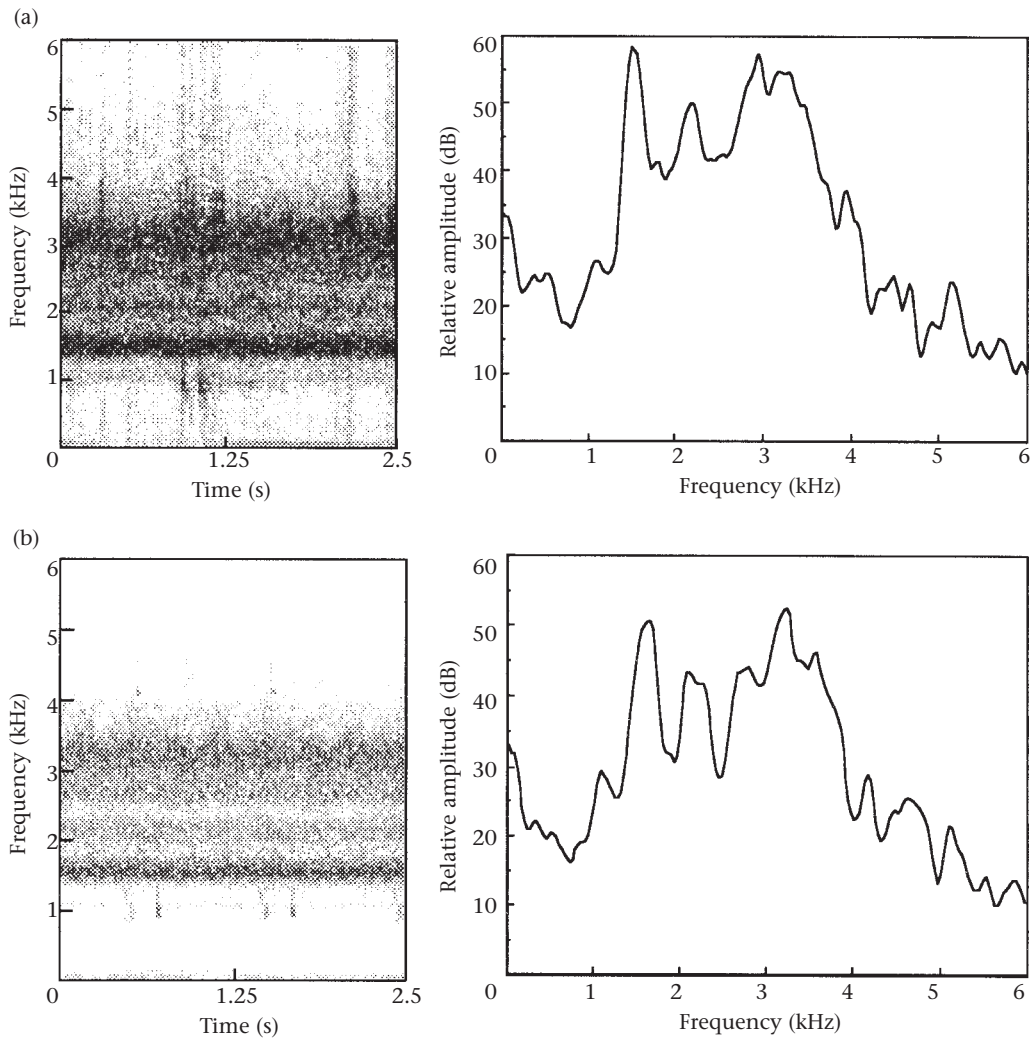
During each trial, I placed the female in a covered container (8 cm long, 6 cm wide, and 5 cm deep) midway between the two playback speakers and allowed her to listen to calls from the speakers for 1–2 min. I then released the female by pulling a string attached to the lid. Frogs that did not leave the container within 10 min were retested later in the evening, if time permitted. The female was allowed 10 min after leaving the container to approach within 5 cm of a speaker. If a female did not choose a speaker within this period, the chorus noise was

turned off and the female was given 5 min to orient to the speaker broadcasting calls alone. To eliminate biases to one side of the arena, I alternated each stimulus between the two sides in successive tests. Ninety females were tested in total: 16 with +6 dB signal-to-noise ratio, 26 with +3 dB signal-to-noise ratio, 24 with +1.5 dB signal-to-noise ratio, and 25 with 0 dB signal-to-noise ratio. Each female was tested only once. Preferences were tested for statistical significance with a log-likelihood ratio ( $G$  test).

Some females (approximately half in each signal-to-noise ratio) chose a speaker quickly. For these females, it is clear that the signal-to-noise ratios of interest are those at the centre of the arena, the point at which the female chose one side or the other. Not all females chose immediately, however. For each of these females, the signal-to-noise ratio changed as she moved around the arena. If a female moved closer to the speaker broadcasting signal plus noise, the signal-to-noise ratio increased. If she approached the speaker playing noise alone, the signal-to-noise ratio decreased. It is important to note that I monitored the signal-to-noise ratio at the centre only.

### Playback Tapes

I used SoundEdit software (22 kHz sampling rate) on a Macintosh 68030 computer to create a short (10-ms) computer-synthesized pulse. I then modified the amplitude envelope of the pulse to produce a logarithmic rise time of 1.3 ms and a linear fall time of 6.4 ms. Amplitude modulation was 100%. Pulses were joined together to create a call 0.16 s long with a rise time of 50 ms and a fall time of 10 ms (Fig. 1a), equal to the means for natural



**Figure 2.** Spectrograms and relative amplitude spectra of chorus used in call detection experiments. (a) Spectrogram (left) and relative amplitude spectrum (right) of chorus noise used in the +6 dB signal-to-noise ratio experiment (recorded 20 August 1992, temperature=24°C). (b) Spectrogram (left) and relative amplitude spectrum (right) of chorus noise (chorus 2) used in the other three signal-to-noise ratios (+3, +1.5 and 0 dB). Chorus 2 and chorus 4 were recorded 30 May 1993 (temperature=24°C for both recordings at 2230 and 2330 hours, respectively). The spectrogram and relative amplitude spectrum of chorus 4 were virtually identical. Analyses of all recordings were performed with Avisoft software (16 kHz sampling rate, spectral measurements are accurate to the nearest 125 Hz, temporal properties are accurate to the nearest 30 ms).

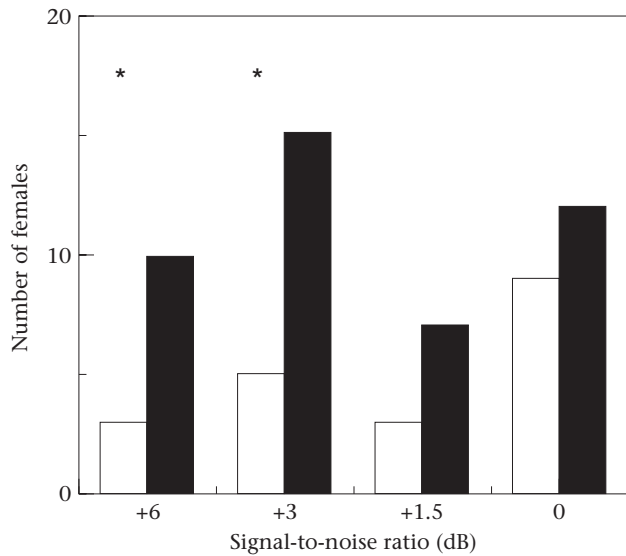
calls (Fig. 1b). Calls were recorded on a Marantz PMD 221 tape recorder from the Macintosh sound port (8-bit precision, 48 dB signal-to-noise ratio) after being band-passed (250–5000 Hz, 24 dB/octave) with a Krohn-Hite 3700 filter. Before using these taped calls in female choice experiments, I checked them for spectral and temporal accuracy by comparing them to natural calls with a Uniscan II real-time spectrum analyser and SuperScope (digital oscilloscope software on a Macintosh computer).

Samples of natural chorus noise were recorded from experimental swamp I. In 1993, I used one tape (Fig. 2a), prepared by repeating a 1-min section of digitized chorus noise recorded in 1992. In 1994, two tapes of chorus noise (Fig. 2b) were prepared by repeating short digitized segments (1–2 s) of chorus noise recorded in 1993 at different times on the same night (called chorus 2 and 4, respectively). Tapes were then recorded on a Marantz

PMD 221 recorder after band-pass filtering (150–6000 Hz, 24 dB/octave, Krohn-Hite 3700 filter). Half of the females were tested with chorus 2, the other half with chorus 4. Chorus noise on all tapes had very similar amplitude spectra (Fig. 2a, b). To determine whether chorus tape influenced responses in the four signal-to-noise ratios, I compared the responses of females to chorus 2 and chorus 4 with a two-tailed Fisher's exact test.

### Analysis of Spatial Patterns

In 1993, I determined the spatial distribution of *H. ebraccata* males in experimental swamp I. Censuses were conducted on 10 different nights. Every 5 m along a transect of 70 m, I measured the distance and the compass direction of each calling male located within 3 m of the transect. Data were converted to X–Y coordinates and



**Figure 3.** Results of detection threshold experiments. □: noise alone stimulus; ■: noise plus signal stimulus. \* $P < 0.05$ .

nearest-neighbour distances calculated for all frogs. The distribution of nearest-neighbour distances was compared to a random distribution with a goodness-of-fit test ('Campbell' software; Krebs 1989). This test is best for distributions in which both aggregation and regularity could occur (Campbell 1990). I also calculated the average nearest-neighbour distance for all frogs on each night.

## RESULTS

For the tests performed in 1994 (+3, +1.5 and 0 dB signal-to-noise ratios), I combined data from the experiments with different chorus tapes because female responses did not depend on the chorus noise with which they were tested (Fisher's exact tests: +3 dB,  $P = 0.6$ ; +1.5 dB,  $P = 1.0$ ; 0 dB,  $P = 1.0$ ). Females preferred the noise

plus signal stimulus to the noise stimulus in tests with +6 dB signal-to-noise ratio ( $G$  test:  $G_1 = 3.98$ ,  $N = 13$ ,  $P < 0.05$ ; Fig. 3) and +3 dB signal-to-noise ratio ( $G$  test:  $G_1 = 4.44$ ,  $N = 19$ ,  $P < 0.05$ ; Fig. 3). With the other two signal-to-noise ratios (1.5 and 0 dB), females chose randomly between the two speakers ( $G$  tests: 1.5 dB signal-to-noise ratio,  $G_1 = 1.65$ ,  $N = 10$ , NS; Fig. 3; 0 dB signal-to-noise ratio,  $G_1 = 0.43$ ,  $N = 21$ , NS; Fig. 3).

## Distributions of Calling Frogs

The overall density of frogs at the study site was 0.08 males/m<sup>2</sup>. On average, a calling male's nearest neighbour was 1.8 m ( $\pm 1.9$  m SD) distant. Nearest-neighbour distances between calling males were divided into three classes ( $\leq 1.0$ , 1.1–2.0,  $> 2.0$  m) for goodness-of-fit tests. Males of *H. ebraccata* were nonrandomly distributed in the study area on four of nine nights (Table 1). The number of neighbours in the nearest distance class ( $\leq 1.0$  m) was higher than expected, and the number of frogs in the other distance classes were lower than expected for most censuses. Thus, it appears that these frogs were aggregated on about half of the nights.

## DISCUSSION

### Masking Thresholds

My results show that continuous background noise can impair call detection in *Hyla ebraccata*. This is consistent with studies of call detection in the green treefrog (Gerhardt & Klump 1988; Schwartz & Gerhardt 1989) and in the bushcricket, *Conocephalus brevipennis* (Bailey & Morris 1986), which have shown that broadband background noise limits the ability of females to detect males. Females located calls in the presence of chorus noise with +3 dB but not +1.5 dB signal-to-noise ratio. The detection threshold for *H. ebraccata* in the conditions of this experiment is thus between +1.5 and +3 dB. Using similar

**Table 1.** Analyses of nearest-neighbour distances for males' locations on nine nights in 1993

Date	N	Upper limits of nearest-neighbour distance classes						$\chi^2$	P
		1.0 m		2.0 m		$> 2.0$ m			
		OF	EF	OF	EF	OF	EF		
6 June	39	10	9.9	21	17.0	8	12.1	2.4	NS
13 June	21	13	5.7	8	9.4	0	6.0	15.7	$< 0.001$
21 June	35	10	8.1	12	14.7	13	12.3	1.0	NS
25 June	32	19	6.8	5	12.9	8	12.3	28.1	$< 0.001$
29 June	33	13	7.2	11	13.5	9	12.3	6.0	0.05
11 July	17	2	2.0	8	4.8	7	10.2	2.5	NS
12 July	27	7	4.9	11	10.0	9	12.0	1.72	NS
16 July	18	7	2.3	6	5.2	5	10.5	6.9	$< 0.01$
19 July	27	8	4.9	12	10.0	7	12.0	4.4	NS

N: the number of calling *H. ebraccata* males observed on that night. OF: observed frequency; EF: expected frequency.

Goodness-of-fit tests (Krebs 1989; Campbell 1990),  $df = 2$ , except for 11 July and 16 July for which the first two classes were combined to obtain expected values  $\geq 5$ , so  $df = 1$ .

methods, Gerhardt & Klump (1988) found that female *Hyla cinerea* could not detect a call at a signal-to-noise ratio of  $-6$  dB, although they could at 0 dB. Evidently either *H. ebraccata* is more susceptible to masking by chorus noise than *H. cinerea*, or mixed-species chorus noise is a more potent masker than conspecific chorus noise alone.

One important difference between this study and that of Gerhardt & Klump (1988) was the use of correlated noise. The experiment with *H. cinerea* used uncorrelated chorus noise; that is, the chorus noise broadcast from one speaker was independent of that broadcast from the other speaker (Gerhardt & Klump 1988). In the experiment reported here, I used uncorrelated noise in one test ( $+6$  dB signal-to-noise ratio) and correlated noise in the other three tests. In all cases, the signals (computer-synthesized calls) were not correlated with the noise. No studies of the effect of correlated noise have been completed for any frog species and so the effect of correlated noise on the results of this experiment are unclear.

Frogs' ears are tuned to species-specific bands of frequencies (Zakon & Wilczynski 1988), so not all frequencies of noise affect masking equally. Consequently, the signal-to-noise ratios measured in these experiments underestimate those actually perceived by the subjects. The masking bandwidth, defined as the minimal bandwidth of white noise that masks a signal, can be estimated by converting the critical ratio, the difference between the SPL of the stimulus and the SPL of the masking noise (Scharf 1970), to a critical ratio band (CR band). White noise has a flat spectrum, and so one can easily measure the spectrum level (dB/Hz) of the noise to calculate the masking bandwidth of neurons in the auditory system. Most studies of masking thresholds in frogs have used white noise (Ehret & Capranica 1980; Ehret & Gerhardt 1980; Moss & Simmons 1986; Simmons 1988).

Based on their measurements of critical ratios for *H. cinerea*, Ehret & Gerhardt (1980) estimated that the CR bands of *H. cinerea* for two tones (900 and 3000 Hz) were 141 and 158 Hz, respectively. Assuming that *H. ebraccata* and *H. cinerea* have similar CR bands, I can estimate the energy of the chorus contained in a 150-Hz bandwidth centred on 3240 Hz, the dominant frequency of the computer-synthesized calls used in these experiments. This range of frequencies (3162–3316 Hz) contributed 20% of the overall chorus energy in chorus 2 and 13% in chorus 4. Thus, the SPL of this band of frequencies was 70 dB for chorus 2 and 68 dB for chorus 4, respectively. These results give a perceived signal-to-noise ratio of approximately  $+8$  dB for the '0 dB' experimental condition.

While no psychoacoustic experiments have been performed on *H. ebraccata*, other behavioural experiments suggest that the critical ratio band of auditory fibres in the ear of *H. ebraccata* might be wider than 150 Hz. Schwartz & Wells (1983a) found that male *H. ebraccata* were inhibited from calling when pulses of sounds at frequencies of 2, 3 and 4 kHz interrupted their calls. This indicates that males can hear calls much higher or lower than 3256 Hz (the median dominant frequency in this

population). Whether this result can be extended to females is unclear. There are differences between the sexes in the tuning and thresholds of the neurons in the inner ear in some anurans (Zakon & Wilczynski 1988; McClelland et al. 1997). To my knowledge, no information is available about differences between the sexes in masking bandwidths.

The background chorus noise presented in this experiment contained the calls of many co-occurring species, but nevertheless lacked many aspects of normal chorus noise. The spatial distribution of males in a natural chorus could provide a release from masking for females (Schwartz & Gerhardt 1989), although not for all species (Schwartz 1993). Natural chorus noise is organized into 'unison bout singing', periods of calling punctuated by quiet intervals (Schwartz 1991, 1994). Within the periods of calling, the chorus noise varies in overall amplitude. Male frogs are adept at inserting their calls into short gaps between the calls of neighbours (Loftus-Hills 1974; Narins 1982, 1992a, b; Zelick & Narins 1983, 1985; Narins & Zelick 1988; Schwartz 1993). In fact, *Eleutherodactylus coqui* can take advantage of decreases in the ambient chorus noise of as few as 4 dB (Zelick & Narins 1983). It seems likely that females are also able to take advantage of the natural temporal fluctuation in background chorus noise to detect calls. Future investigations of the spatial arrangement of males or the ability of females to take advantage of amplitude fluctuations in chorus noise would help in understanding the influence of background noise on mate choice in choruses.

### Detection of Males by Females

From information about the masking threshold for *H. ebraccata* and the density of calling males it is possible to calculate the number of males that a female can expect to hear from any one point in the chorus. If attenuation of calls occurs only by spherical spreading of the sound, as expected if male frogs are point sources of sound (Gerhardt 1975), intensity decreases 6 dB for each doubling of distance. The mean SPL of males' calls at 1 m is 85.1 dB. Thus, when a female is 2 m from a calling male, the SPL of the male's calls are approximately equal to that of the surrounding chorus noise (80.6 dB).

A female located randomly in a chorus has a listening area in which she can hear any calling male. The threshold of a female *H. ebraccata* for detecting calls in background noise is between  $+3$  and  $+1.5$  dB signal-to-noise ratio. Under field conditions similar to those in the experiments reported here, a female is probably unable to hear any male farther than 1.5 m away (a signal-to-noise ratio of approximately 3.5 dB). Thus, she has a listening area of 7.1 m<sup>2</sup> (a circle with a radius of 1.5 m). The average density of males at the study site is 0.08 individuals/m<sup>2</sup>. If males are distributed evenly, then a female is likely to hear only one male at any position within the chorus (0.08 males/m<sup>2</sup> multiplied by the listening area, 7.1 m<sup>2</sup>). The statistical analyses of nearest-neighbour distances of calling males indicate that, at least on some nights, males tend to be aggregated. Thus, if a

female is within a group of males, she can probably hear more than one male.

My calculations suggest that female *H. ebraccata* might hear fewer males at any one point in the chorus than do female *H. cinerea*, which can apparently hear the nearest three to five males (Gerhardt & Klump 1988). However, my higher detection threshold and lower estimate of the number of males that a female detects might reflect differences in experimental methods and not differences in auditory capabilities of *H. cinerea* and *H. ebraccata*. For example, I chose chorus noise that represents a realistic, but extreme, situation for female *H. ebraccata*. It is unclear if Gerhardt & Klump (1988) did likewise. In addition, issues of correlated noise and the lack of information about CR bands for *H. ebraccata* make comparisons between the two studies difficult.

The tuning of the auditory system of frogs suggests that conspecific noise should be the most important source of background interference during communication (Zakon & Wilczynski 1988). None the less, some heterospecific sounds can be sources of interference in communication in frogs. In Panama, male *H. ebraccata* routinely breed at the same sites and times as *H. microcephala* (Schwartz & Wells 1983a, b, 1984). The advertisement calls of these two species are similar (Schwartz & Wells 1984); and the calls of *H. microcephala* are an important source of interference for female *H. ebraccata*. When Schwartz & Wells (1983a) broadcast computer-synthesized calls (at 85 dB SPL) either alone or overlapped by pulses of *H. microcephala* chorus (at 90 dB SPL), female *H. ebraccata* preferred the nonoverlapped calls. Other studies have found similar results. For example, male *E. coqui* will alter their calling in response to playback of calls of *E. portoricensis*, a congener that shares breeding sites with *E. coqui* (Narins 1982; Zelick & Narins 1983). Systematic investigation of the influence of different chorus characteristics can clarify the relative importance of heterospecific and conspecific sources of interference.

Regardless of the exact number of males that a female hears at any one point in the marsh, it is clear that she must move around the chorus if she is to sample more than a few males. Observations by Morris (1991) suggest that female *H. ebraccata* do sample a number of males before entering amplexus. She found that females moved within 2 m of as many as seven different calling males before mating. On the other hand, female *Hyperolius marmoratus* released in a chorus choose the nearest male nearly 50% of the time, most likely because predation by snakes is high (Grafe 1997). We need more studies of mate choice in natural conditions to understand the role that acoustic interference has in the evolution of search behaviour (Real 1990; Wiley 1994) and of the traits used in mate choice (Pomiankowski 1987).

### Acknowledgments

I thank Haven Wiley, Joe Poston and members of the Animal Behavior Group at The University of North Carolina at Chapel Hill for valuable discussions of my research. Haven Wiley was very generous with his equipment and with comments on the manuscript. Don

Forester, Walter Wilczynski and four anonymous referees also provided valuable comments on the manuscript. Laura and Devon Byrd and Bill Nelson were very helpful with logistical support during the writing of this paper. Funds for this research were provided by Pew Charitable Trust, Jesse Smith Noyes Foundation, the Department of Biology and the Graduate School at The University of North Carolina, Sigma Xi Grants-in-Aid of Research, Association for Women in Science and the Animal Behavior Society.

### References

- Bailey, W. J. & Morris, G. K. 1986. Confusion of phonotaxis by masking sounds in the bushcricket *Conocephalus brevipennis* (Tettigoniidae: Conocephalinae). *Ethology*, **73**, 19–28.
- Campbell, D. J. 1990. Resolution of spatial complexity in a field sample of singing crickets *Teleogryllus commodus* (Walker) (Gryllidae): a nearest-neighbour analysis. *Animal Behaviour*, **39**, 1051–1057.
- Donnelly, M. A. & Guyer, C. 1994. Patterns of reproduction and habitat use in an assemblage of neotropical hylid frogs. *Oecologia*, **98**, 291–302.
- Duellman, W. E. 1970. *The Hylid Frogs of Middle America*. Lawrence, Kansas: University of Kansas Press.
- Ehret, G. & Capranica, R. R. 1980. Masking patterns and filter characteristics of auditory nerve fibers in the green treefrog (*Hyla cinerea*). *Journal of Comparative Physiology A*, **141**, 1–12.
- Ehret, G. & Gerhardt, H. C. 1980. Auditory masking and effects of noise on responses of the green treefrog (*Hyla cinerea*) to synthetic mating calls. *Journal of Comparative Physiology A*, **141**, 13–18.
- Gerhardt, H. C. 1975. Sound pressure levels and radiation patterns of the vocalizations of some North American frogs and toads. *Journal of Comparative Physiology A*, **102**, 1–12.
- Gerhardt, H. C. 1995. Phonotaxis in female frogs and toads: execution and design of experiments. In: *Methods in Comparative Psychoacoustics* (Ed. by G. M. Klump, R. J. Dooling, R. R. Fay & W. C. Stebbins), pp. 209–220. Basel, Switzerland: Birkhäuser Verlag.
- Gerhardt, H. C. & Klump, G. M. 1988. Masking of acoustic signals by the chorus background noise in the green tree frog: a limitation on mate choice. *Animal Behaviour*, **36**, 1247–1249.
- Grafe, T. U. 1996. The function of call alternation in the African reed frog (*Hyperolius marmoratus*): precise call timing prevents auditory masking. *Behavioral Ecology and Sociobiology*, **38**, 149–158.
- Grafe, T. U. 1997. Costs and benefits of mate choice in the lek-breeding reed frog, *Hyperolius marmoratus*. *Animal Behaviour*, **53**, 1103–1117.
- Greenfield, M. D. 1994. Synchronous and alternating choruses in insects and anurans: common mechanisms and diverse functions. *American Zoologist*, **34**, 605–615.
- Krebs, C. J. 1989. *Ecological Methodology*. New York: Harper & Row.
- Loftus-Hills, J. J. 1974. Analysis of an acoustic pacemaker in Strecker's chorus frog, *Pseudacris streckeri* (Anura: Hylidae). *Journal of Comparative Physiology A*, **90**, 75–87.
- McClelland, B., Wilczynski, W. & Rand, A. S. 1997. Sexual dimorphism and species differences in the neurophysiology and morphology of the acoustic communication system of two neotropical hylids. *Journal of Comparative Physiology A*, **180**, 451–462.
- Miyamoto, M. M. & Cane, J. H. 1980. Notes on the reproductive behavior of a Costa Rican population of *Hyla ebraccata*. *Copeia*, **1980**, 928–930.
- Morris, M. R. 1991. Female choice of large males in the treefrog *Hyla ebraccata*. *Journal of Zoology, London*, **223**, 371–378.

- Moss, C. F. & Simmons, A. M. 1986. Frequency selectivity of hearing in the green treefrog, *Hyla cinerea*. *Journal of Comparative Physiology A*, **159**, 257–266.
- Narins, P. M. 1982. Effects of masking noise on evoked calling in the Puerto Rican coqui (Anura: Leptodactylidae). *Journal of Comparative Physiology A*, **147**, 439–446.
- Narins, P. M. 1992a. Biological constraints on anuran acoustic communication: auditory capabilities of naturally behaving animals. In: *The Evolutionary Biology of Hearing* (Ed. by D. B. Webster, R. R. Fay & A. N. Popper), pp. 439–454. Berlin: Springer-Verlag.
- Narins, P. M. 1992b. Evolution of anuran chorus behavior: neural and behavioral constraints. *American Naturalist*, **139**, S90–S104.
- Narins, P. M. & Zelick, R. 1988. The effects of noise on auditory processing and behavior in amphibians. In: *The Evolution of the Amphibian Auditory System* (Ed. by B. Fritzsche, W. Wilczynski, M. J. Ryan, T. Hetherington & W. Walkowiak), pp. 511–536. New York: J. Wiley.
- Pomiankowski, A. 1987. The costs of choice in sexual selection. *Journal of Theoretical Biology*, **128**, 195–218.
- Real, L. A. 1990. Search theory and mate choice. I. Models of single-sex discrimination. *American Naturalist*, **36**, 376–405.
- Scharf, B. 1970. Critical bands. In: *Foundations of Modern Auditory Theory* (Ed. by J. V. Tobias). New York: Academic Press.
- Schwartz, J. J. 1987. The function of call alternation in anuran amphibians: a test of three hypotheses. *Evolution*, **41**, 461–471.
- Schwartz, J. J. 1991. Why stop calling? A study of unison bout singing in a Neotropical treefrog. *Animal Behaviour*, **42**, 565–577.
- Schwartz, J. J. 1993. Male calling behavior, female discrimination and acoustic interference in the neotropical treefrog *Hyla microcephala* under realistic acoustic conditions. *Behavioral Ecology and Sociobiology*, **32**, 401–414.
- Schwartz, J. J. 1994. Male advertisement and female choice in frogs: recent findings and new approaches to the study of communication in a dynamic acoustic environment. *American Zoologist*, **34**, 616–624.
- Schwartz, J. J. & Gerhardt, H. C. 1989. Spatially mediated release from auditory masking in an anuran amphibian. *Journal of Comparative Physiology A*, **166**, 37–41.
- Schwartz, J. J. & Wells, K. D. 1983a. The influence of background noise on the behavior of a neotropical treefrog, *Hyla ebraccata*. *Herpetologica*, **39**, 121–129.
- Schwartz, J. J. & Wells, K. D. 1983b. An experimental study of acoustic interactions between two species of neotropical treefrogs. *Animal Behaviour*, **31**, 181–190.
- Schwartz, J. J. & Wells, K. D. 1984. Interspecific acoustic interactions of the neotropical frog, *Hyla ebraccata*. *Behavioral Ecology and Sociobiology*, **14**, 211–224.
- Simmons, A. M. 1988. Masking patterns in the bullfrog: I. Behavioral effects. *Journal of the Acoustic Society of America*, **83**, 1087–1092.
- Wells, K. D. & Schwartz, J. J. 1984. Vocal communication in a neotropical treefrog, *Hyla ebraccata*: advertisement calls. *Animal Behaviour*, **32**, 405–420.
- Wiley, R. H. 1994. Errors, exaggeration and deception in animal communication. In: *Behavioral Mechanisms in Evolutionary Ecology* (Ed. by L. A. Real), pp. 157–189. Chicago: University of Chicago Press.
- Wollerman, L. 1998. Stabilizing and directional preferences of female *Hyla ebraccata* for calls differing in static properties. *Animal Behaviour*, **55**, 1619–1630.
- Zakon, H. H. & Wilczynski, W. 1988. The physiology of the anuran eighth nerve. In: *The Evolution of the Amphibian Auditory System* (Ed. by B. Fritzsche, W. Wilczynski, M. J. Ryan, T. Hetherington & W. Walkowiak), pp. 125–155. New York: J. Wiley.
- Zelick, R. & Narins, P. M. 1983. Intensity discrimination and precision of call timing in two species of neotropical treefrogs. *Journal of Comparative Physiology A*, **153**, 403–412.
- Zelick, R. & Narins, P. M. 1985. Characterization of the advertisement call oscillator in the frog *Eleutherodactylus coqui*. *Journal of Comparative Physiology A*, **156**, 223–229.