

VOCAL COMMUNICATION IN A NEOTROPICAL TREEFROG, *HYLA EBRACCATA*: ADVERTISEMENT CALLS

By KENTWOOD D. WELLS & JOSHUA J. SCHWARTZ

Biological Sciences Group, The University of Connecticut, Storrs, Connecticut 06268, U.S.A.

Abstract. We studied the vocal communication of *Hyla ebraccata* in central Panama. The advertisement call of this species consists of a pulsed buzz-like primary note which may be given alone or followed by 1–4 secondary click notes. Primary notes are highly stereotyped, showing little variation within or among individuals in dominant frequency, duration, pulse repetition rate or rise time. Males calling in isolation give mostly single-note calls. They respond to playbacks of conspecific calls by increasing calling rates and the proportion of multi-note calls, and by giving synchronized calls 140–200 ms after the stimulus begins. Responses to conspecific advertisement calls are usually given immediately after the primary note of the leading call, but the primary note of the response often overlaps with the click notes of the leading call. Experiments with synthetic signals showed that males synchronize to any type of sound of the appropriate frequency (3 kHz), regardless of the fine structure of the stimulus. Playbacks of synthetic calls of variable duration showed that males do not synchronize well to calls less than 150 ms long, but they do to longer calls (200–600 ms). The variance in response latency increased with increasing stimulus duration, but modal response times remained at around 140–200 ms. Similar results were obtained in experiments with synthetic calls having a variable number of click notes. Males showed no tendency to increase the number of click notes in their calls in response to increasing stimulus duration or increasing number of clicks in the stimulus. Females preferred three-note to one-note calls in two-choice playback experiments, whether these were presented in alternation, or with the one-note call leading and the three-note call following. Females showed no preference for leader or follower calls when both were one-note. When two-note calls were presented with the primary note of the follower overlapping the click note of the leader, females went to calls in which click notes were not obscured. Our results indicate that male *H. ebraccata* respond to other males in a chorus in ways which enhance their ability to attract mates.

Males of many species of frogs gather in dense choruses and call to attract females. Frogs in such choruses are faced with the problem of producing signals which can be perceived and recognized by conspecifics in a noisy environment. Usually males in choruses do not call independently, but respond to the calls of other individuals by altering their own vocalizations (Wells 1977a, b). Typical responses include shifting the timing of calls to avoid overlap with those of neighbouring males (Lemon 1971; Loftus-Hills 1971, 1974; Rosen & Lemon 1974; Awbrey 1978; Narins & Capranica 1978; Lemon & Struger 1980; Narins 1982), increasing the rate of calling (Lemon 1971; Ramer et al. 1983), adding notes to the call (Rand & Ryan 1981; Arak 1983a; Ramer et al. 1983) and increasing the production of aggressive calls (Rosen & Lemon 1974; Gambs & Littlejohn 1979; Brzoska 1982; Ramer et al. 1983).

These changes in calling behaviour are assumed to enhance a male's ability to maintain his territory or attract mates (Wells 1977a, b). However, there has been relatively little experi-

mental work designed to test this hypothesis. Most recent work on female choice in anurans has focused on features of calls which might provide females with information about male size or genetic quality (Ryan 1980, 1983; Gerhardt 1982), or on features which are important in species recognition (Gerhardt 1981a, b, 1982). Only a few workers have attempted to determine whether males in choruses respond to other males in ways which improve their ability to attract mates (Whitney & Krebs 1975; Passmore & Telford 1981; Rand & Ryan 1981).

For several years, we have been studying the vocal communication of a neotropical treefrog, *Hyla ebraccata*, in Panama. The vocal repertoire of this species consists of two basic types of calls, advertisement calls and aggressive calls. Sonagrams are given in Wells & Greer (1981) and Schwartz & Wells (in press). Advertisement calls consist of a buzz-like introductory note which may be followed by one or more secondary click notes (Fig. 1). Preliminary work showed that males give mostly single-note calls when calling alone. Males respond to the approach of non-

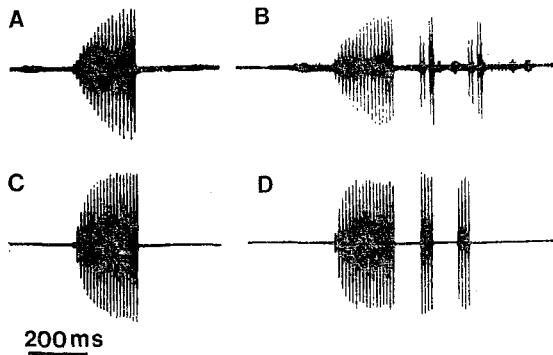


Fig. 1. Oscillograms of natural and synthetic *Hyla ebraccata* advertisement calls: (A) one-note natural call, similar to that used for stimulus A; (B) three-note natural call, similar to that used for stimulus B; (C) one-note synthetic call; (D) three-note synthetic call. Horizontal bar shows time scale.

calling individuals by giving a rapid series of single-note calls (Wells & Greer 1981). These may serve as 'courtship calls' (Wells 1977b) which make a male more conspicuous to a nearby female. Males respond to calls of other individuals by increasing the proportion of both multi-note and aggressive calls (Wells & Greer 1981). Aggressive calls are similar to advertisement calls, but have much higher pulse repetition rates and often are much longer (Wells & Greer 1981).

In this paper, we extend previous work with playbacks of natural calls to include a wider range of playback intensities and a detailed investigation of the timing of male responses to other males' calls. We also performed playback experiments with synthetic calls in which different temporal features of calls were systematically varied. This allowed us to determine which features of calls are important in evoking responses from males, as well as the ways in which male responses change as the stimulus changes.

Methods

Study Area

We conducted field work in June through August 1980, 1981 and 1982. The study site was a flooded field in Gamboa, Panama, near the Panama Canal. *H. ebraccata* males usually called from perches 1–2 m high near pools of water, although they sometimes called from the ground. Males generally were spaced at least 1–2 m apart. We did field work on male frogs between 1930 and 2330 hours. Temperatures ranged from 22.5

to 27.5°C (\bar{X} = 25.3, SD = 1.0, N = 134 nights) and rarely changed by more than 1°C during our work each evening. Relative humidity ranged from 86 to 100% (\bar{X} = 95.5, SD = 2.8).

Recording and Playback Techniques

We recorded calling males on a Uher 4200 Report Stereo IC tape recorder through a Sennheiser MKE 802 directional microphone placed approximately 1 m from the frog. Natural interactions were recorded at a tape speed of 9.5 cm/s, responses to playbacks at 4.7 cm/s. Playbacks were made through a University 4401 horn speaker mounted on a wooden baffle and placed 1 m from the frog. The amplitude–frequency response of the speaker was ± 3 dB from 1.1 to 14.5 kHz. The frog's responses were recorded on one channel of a stereo tape recorder through the Sennheiser microphone, while the stimulus was recorded on the second channel through a patch cord from the playback machine. Playback intensities were predetermined with a Gen Rad 1982 precision sound level meter set for flat weighting and calibrated with a Gen Rad 1562A sound level calibrator. We measured Peak SPL (expressed as dB SPL re 20 μ Pa) at 1 m with a random incidence microphone. SPL measurements of calling males in the field were made in the same way, but with the microphone at 50 cm. Our standard playback intensities were 85, 90, 95 and 100 dB SPL, corresponding to a separation of 2.8 to 0.5 m between calling males.

Stimulus Tapes

We made stimulus tapes of natural calls by re-recording a single call 20 times on a tape at a standard rate of 10 calls/min. This was close to the average calling rate of males in the field. Synthetic calls were produced on a custom-built sound synthesizer as described in Gerhardt (1974, 1978). Synthetic signals were band-pass filtered with a Krohn-Hite 3550 filter and recorded on a ReVox A77 or a Nagra S tape recorder. Bursts of filtered noise were synthesized with a Gen Rad P390B random noise generator, filtered with a Bruel & Kjaer 125 graphic spectrum analyser, and recorded on the ReVox tape recorder. All synthetic stimuli were recorded at a rate of 10 signals/min. The details of synthetic stimuli used in each experiment are described in later sections.

When pairs of calls were required for female choice experiments, they were recorded on two channels of the same tape. The timing relationship of the calls was fixed in one of two ways. In

some cases, calls were recorded from the synthesizer onto one channel of the tape at the desired repetition rate. With the ReVox recorder, it is possible to play calls from one channel and simultaneously record on the second channel. The recorded call was used to trigger the synthesizer after a fixed delay, and the new calls were recorded on the second channel of the tape. Alternatively, a pair of calls with the desired timing relationship was recorded on two channels of a tape. This was converted to a tape loop and re-recorded at the desired repetition rate.

Analysis of Recordings

Measurements of temporal relationships of stimulus and response to the nearest 0.5 s were obtained from strip charts produced on a Heath SR 206 two-channel recorder. More precise measurements (± 8 ms) of response latencies, as well as measurements of temporal features of calls, were obtained with a Tektronix 5111 storage oscilloscope. Frequency analysis of calls was performed on a Uniscan 4500 spectrum analyser (Unigon Industries). Responses to playbacks were analysed by computer with SAS statistical packages (SAS Institute, Cary, N.C., 1982) following standard non-parametric techniques (Siegel 1956). A significance level of 0.05 was used in all tests.

Female Choice Experiments

We conducted experiments in an arena inside a darkened apartment in Gamboa at about 26°C. The arena, 3 m long, 1.6 m wide and 1 m high, had uniformly coloured blankets on each side which shielded test animals from extraneous light, but did not restrict their movements. A 25-W bulb was suspended 1 m above the centre of the arena. Initially, two Heppner mid-range horn speakers (amplitude-frequency response: ± 4 dB from 1.1 to 14.5 kHz) mounted on wooden baffles were placed 2.8 m apart at opposite ends of the arena, and females were released midway between them. In one experiment, the females showed a bias toward the left speaker, so we moved the speakers to opposite corners of the right end of the arena, 1.3 m apart and angled toward a release point 2.1 m from the centre of each speaker. Cushions were placed behind the speakers to minimize sound reflections. Playback intensities were regulated by separate Realistic L-pads and equalized at the release point at 85 dB (± 1 dB) peak SPL. Sound intensities were spot-checked with the sound level meter at various points in the arena to ensure that radiation of sound was symmetrical from the two

speakers. When alternating stimuli were presented from the two speakers, the speaker which began a playback sequence was determined randomly. The stimulus being played from a particular speaker was switched between nights.

We captured females in amplexus between 2230 and 0100 hours and conducted tests the same night between 2230 and 0300 hours. Each female was placed at the release point in a plastic box. Testing usually began within 1 min. After playbacks were started, the lid was lifted off the box with a string from outside the arena. A positive response was scored if the female moved to within 10 cm of one speaker; most moved directly toward a speaker and made contact with it. If a female hopped onto the arena walls or showed extensive undirected wandering, her response was scored as an escape and she was tested again later in the evening. Females that failed to respond within 20 min were removed and re-tested later. Most females were used in two playback experiments involving different stimulus choices each night, but only one response per female was scored in each test. Each female was toe-clipped before being released to ensure that she was not used twice in the same experiment. Some were subsequently recaptured and used in new experiments. Responses were analysed with two-tailed binomial tests.

The Advertisement Call

The advertisement call consists of a pulsed introductory note which may be followed by one or more click notes (usually one or two, rarely more than four; Fig. 1). The calls are very stereotyped in dominant frequency, duration, pulse repetition rate and rise time, with very little variation either within or between individuals (Fig. 2). In general, coefficients of variation for each individual and for all calls pooled were less than 10%. In designing synthetic advertisement calls for playback experiments, we used values for temporal and spectral features near the average for calls recorded in the field, or at the modal value if the distribution was skewed. The intensity of calls given by males in the field also was very uniform. Seven males calling from unobstructed elevated sites had modal intensities of 99–102 dB SPL at 50 cm (median = 100, $N = 10$ –15 calls per male). Calling rates of males calling without stimulus playbacks ranged from 5 to 25 calls/min (median = 11). The high degree of variability in calling rate ($CV = 38\%$) resulted in part from different levels of interaction with other males in the chorus.

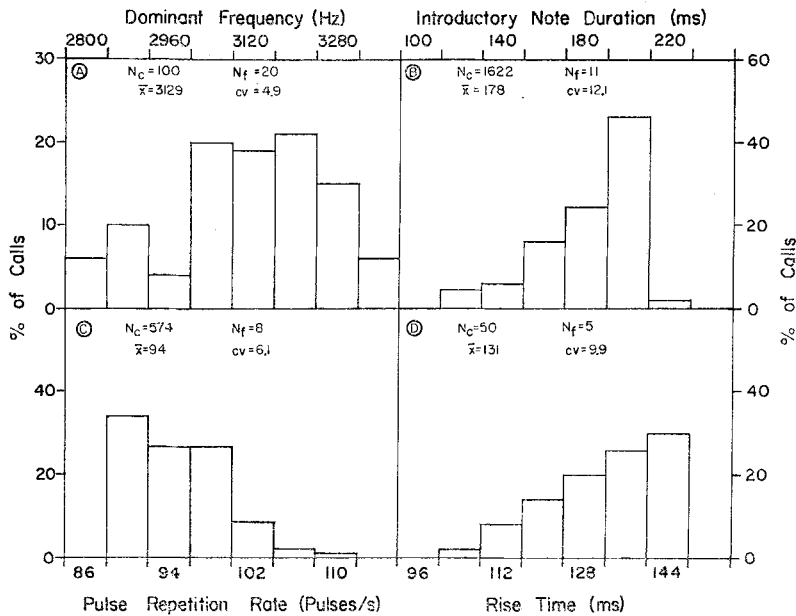


Fig. 2. Spectral and temporal features of *Hyla ebraccata* advertisement calls: (A) dominant frequency; (B) duration of the introductory note; (C) pulse repetition rate; (D) rise time. N_c = number of calls; N_f = number of frogs; CV = coefficient of variation.

Responses of Males to Natural Call Stimuli

Methods

Two natural call stimulus tapes were used. Stimulus A was a series of 20 single-note calls (Fig. 1A), stimulus B a series of 20 three-note calls (Fig. 1B). In each test, a relatively isolated male was recorded for 1 min without a stimulus and then presented with the first 2-min stimulus playback. The male was then recorded for another 1-min no-stimulus period and presented with a stimulus at a second volume. This alternation of 2-min stimulus and 1-min no-stimulus periods continued until the stimuli had been presented at all playback intensities. Because high-intensity playback sometimes caused males to move away, most stimuli were presented in order of increasing intensity (85, 90, 95, 100 dB). However, in some cases, the 100-dB playbacks were presented first. The change in playback order did not appear to alter male responses, but the sample size at high intensities was so small that we could not test this statistically. The frogs usually returned to pre-test calling patterns within a few seconds after the end of a stimulus tape. Most males were tested with both stimuli, but some were not tested at every volume. Stimulus B was not presented at 85 dB to any of the frogs.

In our analysis, all no-stimulus periods for each frog were pooled and used for comparison with responses to stimulus playbacks.

Quantitative Changes in Calling Behaviour

The frogs showed a significant increase in calling rates in response to both stimuli at 90 and 95 dB, but not at 85 dB (Table I). Although more individuals showed increased calling rates at higher playback intensities, a Friedman two-way ANOVA showed that calling rates did not differ significantly in response to stimulus A at 85, 90 or 95 dB ($\chi^2 = 3.45$, 2 *df*, $P > 0.10$). Responses to stimulus A did not differ significantly from those to stimulus B at 90 dB ($P = 0.542$) or 95 dB ($P = 0.802$; two-tailed Wilcoxon tests). Some males exhibited reduced calling rates in response to stimulus A at 100 dB, but the small sample size makes meaningful statistical comparisons impossible. There was no tendency for stimulus B to inhibit calling at 100 dB.

Males significantly increased the proportion of multi-note calls in response to both stimuli at all playback intensities, except where sample sizes were very small (Table I). This was true if both advertisement and aggressive calls were included in the analysis, or if only advertisement calls

Table I. Median Calling Rates (calls/min) and Median Proportion of Multi-note Calls (PMC) During No-stimulus Periods and During Playbacks of Stimulus A and B at Different Intensities

Stimulus	<i>N</i>	Intensity (dB SPL)	Calling rate	<i>P</i>	PMC (all calls)	<i>P</i>
None	12	—	9.5	—	0.43	—
A	11	85	11.5	0.166	0.71	0.023
A	12	90	14.2	0.001	0.69	0.027
A	12	95	13.3	0.001	0.71	0.005
A	4	100	7.7	0.034	0.65	0.072
None	10	—	11.5	—	0.44	—
B	10	90	14.3	0.001	0.67	0.004
B	10	95	15.2	0.029	0.78	0.003
B	5	100	10.0	0.251	0.95	0.022

P values are for one-tailed Wilcoxon matched-pairs signed-ranks tests comparing calling during playbacks with no-stimulus periods.

N = number of frogs tested at each playback intensity.

were used. The proportion of multi-note calls was not affected by playback intensity for stimulus A ($\chi^2 = 2.23$, 2 *df*, $P > 0.30$; Friedman two-way ANOVA), but it was for stimulus B (one-tailed Wilcoxon test, $P = 0.026$). The proportion of multi-note calls given in response to the multi-note stimulus (B) did not differ significantly from that in responses to stimulus A at 90 dB ($P = 0.312$), 95 dB ($P = 0.920$) or 100 dB ($P = 0.068$; two-tailed Wilcoxon tests).

Synchronized Call Responses

The timing of male responses to stimulus calls was not random. In most cases the first advertisement call was given within a few hundred milliseconds after the beginning of the stimulus call (Fig. 3). We refer to this rapid answering of a stimulus as a 'synchronized response,' which we operationally defined as any advertisement call given within 1.0 s of the beginning of the stimulus. Since stimulus calls were 6.0 s apart, the expected percentage of calls falling in each 1.0-s period would be 16.7% if the frogs called randomly with respect to the stimulus. However, 54% of all responses to stimulus A ($N = 1070$) and 82% of all responses to stimulus B ($N = 470$) fell in the first 1.0 s ($P < 0.001$ for both; *G*-test for goodness of fit; pooled data for all playback intensities). Most synchronized responses occurred 140–200 ms after the onset of the stimulus (see synthetic call experiments). This placed the beginning of most responses near the end of a one-note stimulus, but responses usually overlapped the click notes of multi-note stimuli (Fig. 3A, B).

For both stimuli, the number of synchronized responses increased with increasing playback

intensity, but it declined at 100 dB for stimulus A (Fig. 4). There was no difference in the number of synchronized responses to stimuli A and B at 90 dB ($P = 0.509$) or 95 dB ($P = 0.07$; two-tailed Wilcoxon tests). For both stimuli, the most common synchronized response was a two-note call (Fig. 5). There was no significant difference in the proportion of one-note ($P = 0.258$), two-note ($P = 0.604$), or three- or four-note ($P = 0.194$) calls given to the two stimulus tapes (two-tailed Wilcoxon tests).

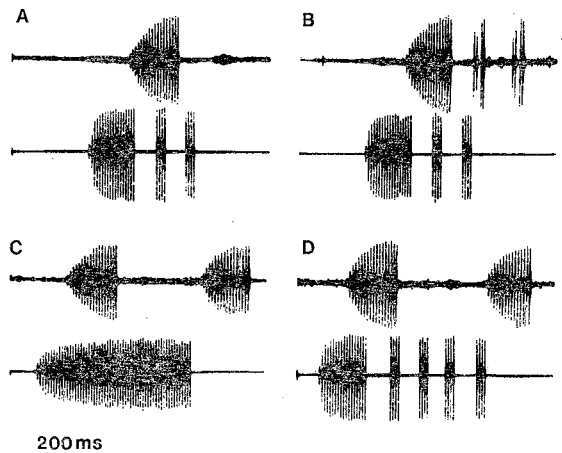


Fig. 3. Synchronized responses to synthetic advertisement calls. The stimulus is on the bottom in each panel, the response on top. (A) One-note response to three-note call. (B) Three-note response to three-note call. Note overlap of responses with click notes of stimulus. (C) Double-call response to 600-ms synthetic call. The interval between responses was 338 ms. (D) Double-call response to four-click synthetic call. The interval between responses was 363 ms. Horizontal bar shows time scale.

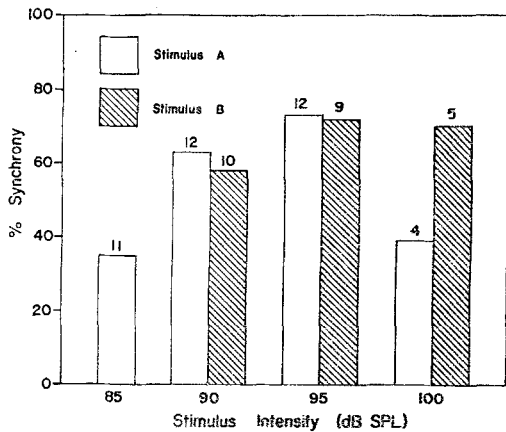


Fig. 4. Percentage synchrony to stimuli A and B. Percentage synchrony was the proportion of stimulus calls out of the total presented (usually 20) which elicited a response within 1.0 s of stimulus onset. Bars show median values. Numbers above each bar show the number of frogs tested.

Responses of Males to Synthetic Stimuli

Methods

In our presentations of synthetic stimuli to males, we were concerned with comparing responses to different stimuli with each other, but not with calling behaviour during no-stimulus periods. Therefore, we recorded the test male during an initial 1-min no-stimulus period to ensure that he was calling at a normal rate, but we did not record the male between stimulus presentations. If the male gave a substantial number of aggressive calls or stopped calling during a stimulus presentation, he was allowed to resume normal calling before testing began again.

Because background noise levels varied from night to night, playback intensities had to be adjusted for each frog. If playback intensities were too low, males would not synchronize with the tape. If playback intensities were too high, males would give aggressive calls to virtually any stimulus. In most experiments, playbacks were started at 90 dB SPL. If a male gave mostly aggressive calls, the intensity was lowered to 85 dB. If a male gave very few synchronized responses, the intensity was raised to 95 dB. On very quiet nights, some males gave aggressive calls almost exclusively, even at low playback intensities. In those cases, testing was discontinued.

In all tests, the stimulus most similar to a natural advertisement call was played first and used as a standard against which other stimuli

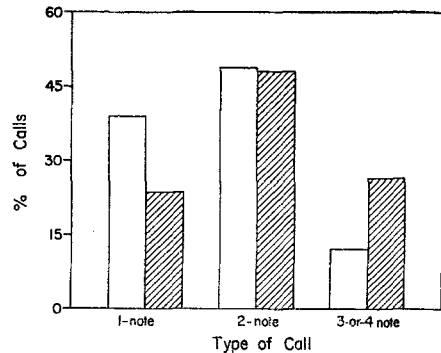


Fig. 5. Types of advertisement calls given as synchronized responses to stimulus A (open bars) and stimulus B (diagonal lines). Data for playbacks at 90–100 dB are pooled. The data include only those males ($N=9$) which were tested with both stimuli. Bars show median proportions of each call type.

were compared. Once the playback intensity had been set for the standard stimulus, the same volume was used for all other stimuli presented to the same male. The goal was to find the intensity at which the standard call elicited the maximum rate of synchrony and then compare that with responses to other stimuli. When more than two stimuli were presented, the order of presentation was varied.

Pulsed Versus Unpulsed Signals

To determine whether the pulses characteristic of natural calls were necessary to elicit synchronized responses, we presented males with three types of synthetic stimuli: (1) 200-ms pulsed calls with a dominant frequency of 3 kHz and a pulse repetition rate of 95 pulses/s, (2) 200-ms 3-kHz pure tones, and (3) 200-ms bursts of filtered noise centred at 3 kHz with a one-third-octave nominal bandwidth. Because pure tones concentrated energy into a narrower frequency band than calls, we reduced playback intensities of tones by 5 dB below those used for calls; otherwise, males gave mostly aggressive calls to the tones instead of synchronizing with them. This adjustment was purely operational: we did not attempt to adjust the stimuli to precisely equal energy levels.

Both pure tones and filtered noise were as effective as pulsed calls in eliciting synchronized responses (tones: $P=0.80$; noise: $P=0.31$; two-tailed Wilcoxon tests). The three types of synthetic stimuli elicited an average of 12–14 synchronized responses (60–70%), equivalent to responses elicited by the natural calls at 90 dB or

above (Fig. 4). In another experiment (Schwartz & Wells 1984), we presented males with pure tones and pulsed calls at a range of dominant frequencies from 1 to 6 kHz; those at 3 kHz, near the dominant frequency of natural calls, elicited the highest rates of synchronized responses. In general, we have found that males will synchronize their calls to virtually any sound with energy in the appropriate frequency range.

Variation in Call Duration and Number of Click Notes

These experiments were designed to determine (1) whether calls of different durations elicit different numbers of synchronized responses, (2) whether the timing of male responses is independent of stimulus duration, and (3) whether males increase the number of click notes in their calls in response to increasing stimulus duration or increasing numbers of click notes. Males would be expected to increase the number of click notes in their calls if they attempted to match the calls of their neighbours (Arak 1983a) or to out-signal their competitors (Wells & Greer 1981; Arak 1983a).

Methods. The first set of stimulus tapes consisted of single-note calls similar to those presented in the previous experiment (3 kHz, 95 pulses/s), but varying in duration from 50 to 600 ms. This encompassed a range from less than the duration of a typical click note to more than the duration of most long aggressive calls (Wells & Greer 1981; Wells & Schwartz, unpublished data). These stimuli varied in rise time, because the rise time of a natural call note is longer than the duration of the shortest synthetic stimulus. However, we have found that rise time did not affect the number of synchronized responses and had only minor effects on timing of responses (Wells & Schwartz, unpublished data).

The second stimulus set consisted of calls with a 200-ms introductory note and 1, 2, 4 or 6 click notes. Males frequently give calls with one or two click notes, but seldom with four or six. The same males were presented with both sets of stimuli. In all tests, the 200-ms single-note call was the standard call used to adjust playback volumes and was always presented first. The order in which the other stimuli were presented was randomized, but all single-note calls were presented before the calls with variable numbers of clicks.

Variable duration. Males synchronized poorly to calls of very short duration, but calls more than 200–300 ms long were equally effective in

eliciting synchronized responses (Fig. 6). In experiments described in more detail elsewhere (Schwartz & Wells, in press), we found that much of the variation in responses of male *H. ebraccata* to playbacks of heterospecific calls could be explained by differences in call duration.

When data for all frogs were pooled, latencies to first advertisement call response increased significantly with increasing stimulus duration (Kruskal–Wallis ANOVA, $P < 0.0001$). This also was true for nine of 11 individual frogs. Friedman two-way analyses of variance using median and modal latencies for each individual showed a significant effect of stimulus duration (medians: $\chi^2 = 49.02$, 6 *df*, $P < 0.001$; modes: $\chi^2 = 17.54$, 6 *df*, $P < 0.01$). This was due mainly to differences between the extremes of stimulus durations: responses to intermediate durations were very similar. Modal latencies for all frogs combined showed very little change, with most responses coming within 140–200 ms (Fig. 7). This indicates that males tend to give most of their responses at a relatively fixed interval after the beginning of a stimulus. However, if a male misses synchronizing with the beginning of a call, a response apparently can be triggered by later pulses in the call.

Some males gave a second synchronized response 432–736 ms ($\bar{X} = 612$ ms, $N = 25$) after the onset of the first response (Fig. 3C). These double-call responses were given only to long stimuli and apparently occurred because the stimulus continued after the male's initial response. Generally, double-call responses occurred when the initial response latency was very

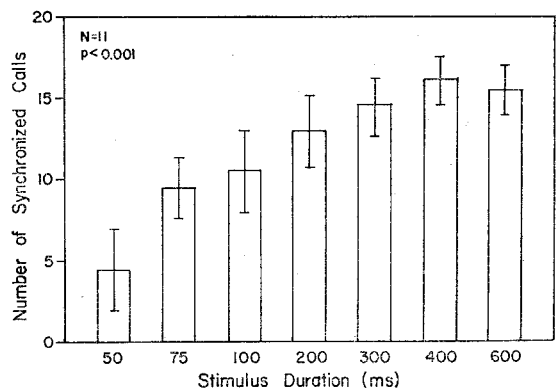


Fig. 6. Number of synchronized responses (out of a possible 20) to synthetic calls of different durations. Data for 11 males are included. Bars show means \pm 2 SE. P is for a Friedman two-way ANOVA (6 *df*).

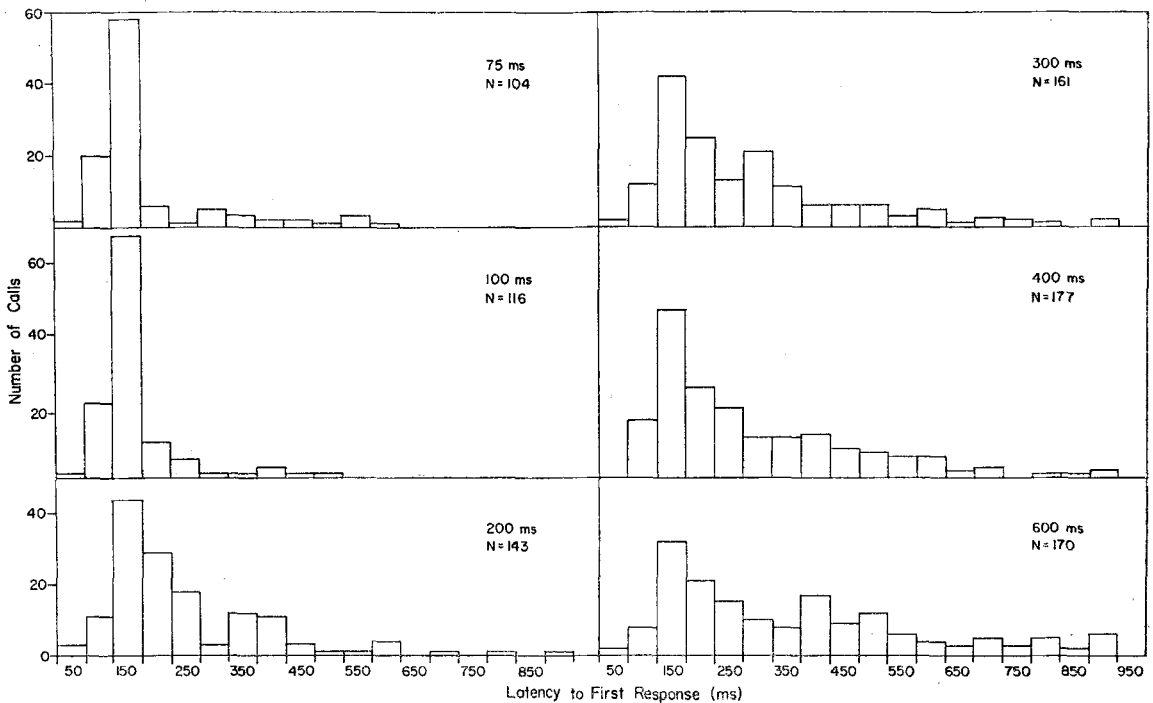


Fig. 7. Latencies to first advertisement call responses to synthetic calls of different durations, measured in 50-ms intervals. Numbers on the abscissa are mid-points for each bar. Data for 11 males are pooled. Only calls given with 1.0 s of stimulus onset are included. N = number of calls. The 50-ms stimulus elicited very low numbers of synchronized calls from all males and has been omitted.

short. Initial latencies for double-call responses to the 600-ms stimulus (median = 144 ms, $N = 25$) were significantly shorter than those for single-call responses to the same stimulus (median = 336 ms, $N = 105$; Mann-Whitney U -test, $P = 0$).

There was no tendency for males to increase the proportion of multi-note calls as the duration of stimulus calls increased. Two-note calls were the most common responses to stimuli of all durations except 600 ms; males gave mostly single-note calls to that stimulus (Fig. 8). Thus, the hypothesis that males might increase call duration in response to longer stimuli is not supported, and the results for 600-ms playbacks suggest that very long stimuli may inhibit the production of click notes.

Variable numbers of click notes. The results of playbacks of calls with variable numbers of click notes were similar to those for the variable-duration playbacks. However, in this experiment the introductory notes of all calls were the same length (200 ms), and the frogs gave an average of 14–15 synchronized responses (70–75%) to all stimuli. The responses to different stimuli were

not significantly different (Friedman two-way ANOVA, $\chi^2 = 1.29$, 4 df , $P > 0.7$). Combined data for all frogs showed a significant increase in response latency with increasing number of click notes (Kruskal-Wallis ANOVA, $P < 0.0001$), but this was true for only two of 10 individual frogs. Again, modal response latencies showed virtually no change (Fig. 9). A Friedman two-way ANOVA using median and modal latencies for each individual showed no significant effect of number of click notes (medians: $\chi^2 = 6.51$, 3 df , $P > 0.05$; modes: $\chi^2 = 4.59$, 3 df , $P > 0.2$). However, there were distinct secondary peaks in response latencies at the times expected if males were synchronizing to click notes (Fig. 9). Hence, if a male misses synchronizing with the beginning of a stimulus, he may synchronize with any one of the clicks.

As in the previous experiment, some males gave double-call responses, but only to very long stimuli (four-click and six-click calls; Fig. 3D). These calls are outside the range of conspecific call durations normally encountered by males in the field, but they are within the range of some

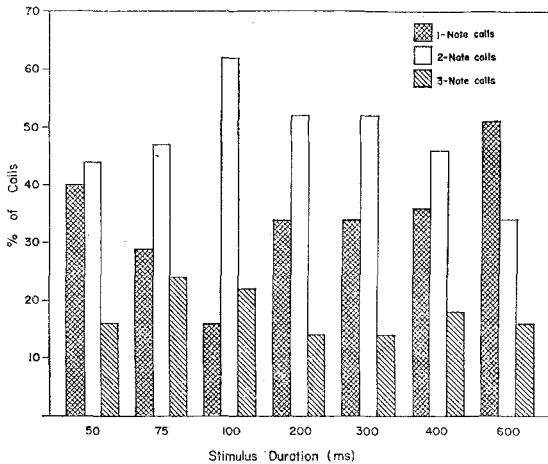


Fig. 8. Types of advertisement calls given as synchronized responses to synthetic calls of different durations. Bars give pooled mean proportions of each call type for 11 males. Data for 922 calls are included.

calls of *H. microcephala* and *H. phlebodes*, to which male *H. ebraccata* also respond (Schwartz & Wells 1984). Latencies to the first response were significantly shorter for double-call responses to four- or six-click stimuli (median = 160 ms, $N=52$) than for single-call responses (median = 240, $N=242$; Mann-Whitney U -test, $P=0$). Again, males gave double-call responses when the stimulus continued past the end of their first calls.

Males showed no tendency to increase the number of click notes in their calls as the number of click notes in the stimulus increased, and again, the most common response to all stimuli was a two-note call (Fig. 10). Hence, there is no evidence that males adjust their responses to try to out-signal competitors, nor is there any evidence of call matching. This is consistent with the results of natural call playback experiments, which showed no differences in responses to single-note and three-note calls.

Female Choice Experiments

Experiment 1

Since males typically respond to other males' calls by adding click notes to their calls, we presented females with alternating single-note and three-note calls from speakers at opposite ends of the test arena. Each speaker produced calls at a rate of 10 calls/min, and the delay from the onset of each call to the onset of the other was 3 s. Females clearly preferred the three-note calls

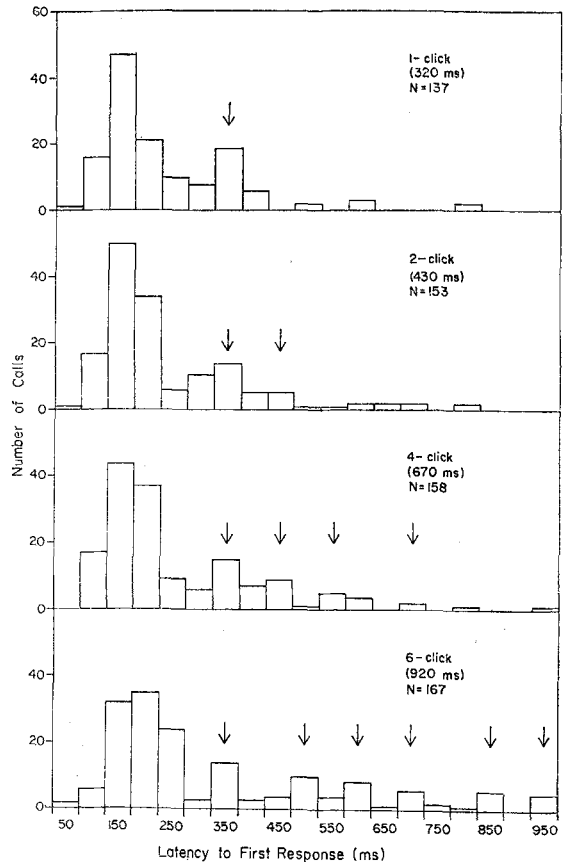


Fig. 9. Latencies to first advertisement call response to synthetic calls with different numbers of click notes. Data as in Fig. 7. The total duration of each stimulus is given in parentheses. Arrows indicate synchronized responses to click notes.

(Table II). Call preference was independent of the speaker position ($G=1.23$, $P>0.2$).

Experiment 2

In experiment 2, females were presented with the same calls as in the first experiment, but with the three-note call following immediately after the single-note call (Fig. 11A). This simulated a male responding to a single-note call with a synchronized three-note call. In this experiment and in experiments 3 and 4, the two speakers were in opposite corners of one end of the test arena, as described in the methods section. Again, females preferred the three-note call (Table II), and call preference was independent of the speaker position ($G=0.58$, $P>0.3$).

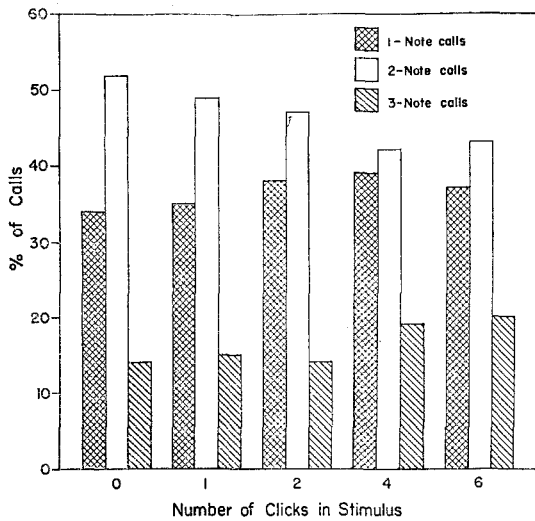


Fig. 10. Types of advertisement calls given as synchronized responses to synthetic calls with different numbers of click notes. Bars give pooled mean proportions of each call type for 11 males. Data for 621 calls are included.

Experiment 3

Since males time their responses to other males' calls so that the introductory note of the response often overlaps with one or more click notes of the leading call, we presented females with two-note calls from each speaker in a leader-follower arrangement, with the introductory note of the second call completely overlapping the click note of the first call (Fig. 11B). If the second call masks the click note of the first, then females should go to the second call, since it would have a more distinctive click note.

This was precisely the behaviour observed (Table II), and call preference was independent of the speaker position ($G=0$, $P=1.0$).

Experiment 4

In the last experiment, we presented females with a choice of two single-note calls in the same leader-follower timing relationship used in experiment 3. This experiment served as a control for experiments 2 and 3 by testing for a preference for the leading versus the following call when the two calls are the same. This is important, because the results of experiments 2 and 3 could be explained by a tendency of females to go to the second call. However, females exhibited no such preference in this experiment (Table II); again, call preference was independent of the speaker position ($G=0.12$, $P>0.8$).

Discussion

Our results show that male *H. ebraccata* respond to conspecific calls by modifying their advertisement calling in two ways: (1) they synchronize their responses to the calls of nearby males, and (2) they add click notes to their calls. Virtually any sound in the appropriate frequency range will trigger this response. A male does not necessarily wait for the end of a call before beginning his response; most responses are given at a relatively fixed time (140–200 ms) after the onset of a stimulus. Our experiments with natural and synthetic calls showed that males tend to give similar responses to all stimuli, regardless of their duration or complexity. These results are not surprising, given the timing of a male's responses. Since a male often begins his own call before the stimulus has ended, he cannot anticipate the

Table II. Results of Two-choice Playback Experiments with *H. ebraccata* Females

Experiment	Stimuli	N_T	N_R	Number of females choosing:		P
1	Alternated 1 and 3-note calls	44	40	1-note call 12	3-note call 28	0.018
2	1-note leader, 3-note follower	25	15	1-note call 2	3-note call 13	0.008
3	Masked and masking 2-note calls	21	15	Masked call (leader) 3	Masking call (follower) 12	0.036
4	1-note leader and follower calls	26	19	Leader call 11	Follower call 8	0.648

P values are for two-tailed binomial tests.
 N_T = number of females tested.
 N_R = number of females responding.

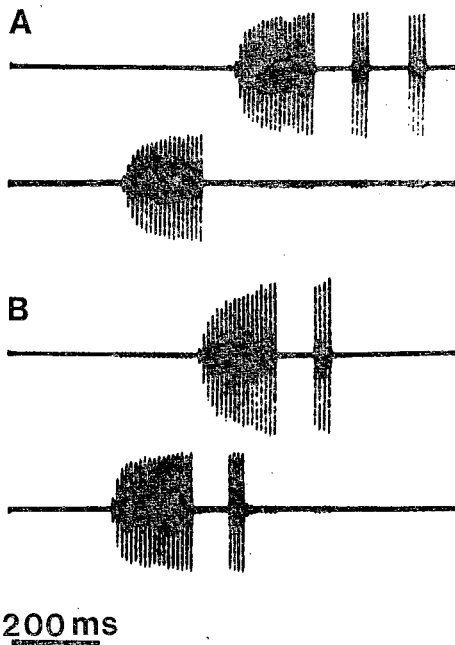


Fig. 11. Timing relationships of stimulus calls used in two-choice playback experiments with females. (A) One-note leader and three-note follower used in experiment 2. The delay from the onset of the first call to the onset of the second call was 250 ms. (B) Overlapping two-note calls used in experiment 3. The delay from the onset of the first call to the onset of the second call was 200 ms. Horizontal bar gives time scale.

length of the stimulus or the number of click notes it will contain. However in a natural chorus, males give mostly one- or two-note calls with introductory notes 150–200 ms long. Hence, if a male starts his responses 140–200 ms after the onset of another male's calls, most of his calls will not overlap the introductory notes of his neighbours' calls. If he adds click notes to his own calls, these generally will fall after the end of the neighbour's calls (Fig. 3B).

The results of our playback experiments with females showed that females approach calls with click notes in preference to single-note calls in a two-choice test, regardless of whether the calls are presented in alternation or with the one-note call leading and the three-note call following. However, there was no preference for leading or following calls when the calls were identical. When a male overlaps the click notes of another male's call with the introductory note of his own call, he effectively reduces the attractiveness of the neighbour's calls, apparently by partially masking the notes most attractive to females.

Presumably his advantage is increased if he also adds click notes to his own call. The implications of these results for female choice in natural choruses will be discussed in more detail below.

Functional Interpretations and Comparisons with Other Species

Changes in calling rate. Many features of the vocal behaviour of *H. ebraccata* are characteristic of chorusing frogs in general and, indeed, of most acoustically signalling animals. For example, males of many species call at faster rates in choruses than in isolation (Emlen 1968; Rosen & Lemon 1974; Garton & Brandon 1975; Passmore 1977, 1978; Wells 1977b, 1978). This probably is true of most chorusing frogs, although increases in calling rates have been demonstrated experimentally for only a few species (Lemon 1971; Ramer et al. 1983). In some species which do not normally call in dense choruses, males show little or no response to playbacks of conspecific calls (Dubois 1977; Greer & Wells 1980). In *H. ebraccata*, increased calling rates were largely a consequence of males responding to individual calls in the stimulus sequence. Males that failed to increase their calling rates or showed little change almost always had initial calling rates which matched or exceeded that of the stimulus tape (see also Wells & Greer 1981). We have not yet tested the responses of females to calls presented at different rates, but a preference for higher calling rates has been demonstrated for *Bufo woodhousei* (Sullivan 1982) and *Hyla cinerea* (H. C. Gerhardt, personal communication). The fact that male *H. ebraccata* give a rapid series of single-note calls when females are nearby suggests that females of this species might show a similar preference for high calling rates. By responding to each call given by a neighbouring frog, a male ensures that a competitor will not enjoy a large advantage in mate attraction simply because he calls at a faster rate.

Changes in number of call notes. A second vocal response which *H. ebraccata* shares with other anurans is the addition of secondary notes to the advertisement call when other males are calling nearby. This also occurs in *Hyla microcephala*, *H. phlebodes* (Schwartz & Wells, in preparation) and *H. minuta* (Wells, unpublished data). It probably is characteristic of many other species in the *H. microcephala* and *H. leucophyllata* species groups, all of which have complex multi-note calls (Duellman 1970, 1978; Cardoso 1981).

Similar behaviour has been reported in frogs from various families around the world, including a Central American leptodactylid, *Physalaemus pustulosus* (Rand & Ryan 1981), a Central American hylid, *Smilisca sila* (Tuttle & Ryan 1982), a rhacophorid treefrog, *Philautus leucorhinus*, from Sri Lanka (Arak 1983a), and the North American green frog, *Rana clamitans* (Ramer et al. 1983). Complex multi-note calls also are characteristic of the North American bullfrog, *R. catesbeiana* (Capranica 1968), African ranids of the genus *Ptychadena* (Passmore 1977, 1978), and some hyperoliid frogs (Schjötz 1967), but these species have not been studied experimentally. In *Smilisca*, males give more multi-note calls in response to multi-note stimuli than to single-note calls, and in *Philautus*, males usually match numbers of call notes with their neighbours. The behaviour of these species contrasts with that of *H. ebraccata*, which shows no tendency to give more multi-note responses to multi-note stimuli. In *Physalaemus*, females preferred complex calls with 'chuck' notes to simple 'whine' calls in two-choice experiments, a result which parallels our results for *H. ebraccata*. The responses of females have not been tested in the other species.

There seems to have been convergent evolution of complex multi-note calls in chorusing frogs from several different families, but the advantage of complex calls is still not clear. In *Smilisca*, the production of multi-note calls facilitates overlapping of calls by neighbouring males. This results in a synchronous burst of calling which is confusing to predatory bats (Tuttle & Ryan 1982). On the other hand, production of complex calls by *Physalaemus* males increases the risk of bat predation (Ryan et al. 1982). Unfortunately, we have no information on the risk of predation for *H. ebraccata*, so we cannot even speculate on how it might have affected the evolution of this species' calls.

Complex multi-note calls could be a product of sexual selection (Arak 1983b). Rand & Ryan (1981) and Ryan (1983) suggested that female *Physalaemus* prefer complex calls because the secondary chuck note contains information about male body size. This cannot be a general explanation, because in the other species the frequency spectra, and hence potential information about male body size, are the same in simple and complex calls. Females might prefer long or complex calls because they provide information about the genetic quality of the male, or because the females' male offspring would produce

especially attractive calls (Arak 1983b; Ryan 1983). We originally hypothesized that males would attempt to out-signal competitors by producing calls which matched or exceeded those of their neighbours in number of notes, as has been suggested for *Philautus leucorhinus* (Arak 1983a). However, our experiments with natural and synthetic calls clearly showed that males do not behave this way. Furthermore, we have found no evidence of consistent individual variation in the complexity of calls given by males in a chorus. Our data do not strongly support the sexual selection hypothesis, but it cannot be completely ruled out.

An alternative explanation relates to the ability of females to perceive calls in a noisy environment. Females entering a chorus are generally confronted with a nearly continuous din of background noise which will tend to obscure the calls of individual males (Ehret & Gerhardt 1980). This noise may be derived from the calls of conspecifics, calls of other species of frogs (Schwartz & Wells 1983a, b), insect sounds, wind, or moving vegetation. Calls consisting of highly stereotyped, repetitive notes with very rapid amplitude transitions, such as a series of click-like notes, are most likely to contrast with continuous background noise undergoing random amplitude fluctuations (Schleidt 1973; Green & Marler 1979; Richards & Wiley 1980). This may make it easier for females to detect and locate calling males in a noisy environment. A similar explanation has been proposed for the evolution of click-like calls in frogs calling near noisy waterfalls (Dubois 1977).

Timing of vocal responses. In many frogs (Lemon 1971; Loftus-Hills 1971, 1974; Rosen & Lemon 1974; Wells 1977a; Awbrey 1978; Narins & Capranica 1978; Lemon & Struger 1980; Narins 1982), insects (Alexander 1975; Otte 1977; Greenfield & Shaw 1983), and birds (Todt 1970; Wasserman 1977; Gochfeldt 1978; Hultsch & Todt 1982) males call or sing at some relatively fixed time interval after the calls or songs of their neighbours. Depending on the precise timing of the response, this has been termed antiphonal calling, call alternation, or synchrony. As in other papers on frog calls (Dubois 1977; Narins 1982; Tuttle & Ryan 1982), we use the term 'synchronized response' to describe calls given very shortly after the onset of another male's call. In the insect literature, the term 'synchrony' generally has been applied to situations in which individual call elements of

different males are precisely in phase (Otte 1977). This type of synchrony is unknown in frogs.

The timing of a male's responses often depends on where the stimulus falls in the male's calling period. In most species, males probably have a refractory period following the initiation of their own calls in which they will not respond to stimuli (Loftus-Hills 1974; Lemon & Struger 1980). In *H. ebraccata*, the behavioural refractory period is about 210 ms (Narins 1982). This means that the faster a male responds to another male's calls, the less likely the leading male is to respond with a second call of his own. However, in a natural chorus, there often will be a third male that responds to the second male's calls, a fourth male that responds to him, and so forth. The result will be a nearly continuous bout of calling by all males in the immediate area.

Call Interference

Most authors have suggested that timed vocal responses reduce acoustic interference between neighbouring males (Alexander 1975; Littlejohn 1977; Otte 1977; Wasserman 1977; Wells 1977a; Gochfeldt 1978; Hultsch & Todt 1982; Narins 1982; Zelick & Narins 1982). Greenfield (1983) suggested that males might attempt to call at the end of a bout to reduce acoustic interference from conspecifics. Acoustic interference could have two consequences: (1) a female might have difficulty localizing an individual male in the chorus, and (2) critical temporal features of the call may be obscured. Passmore & Telford (1981) found that female *Hyperolius marmoratus* could easily locate speakers broadcasting either simultaneous or temporally spaced calls. Since the calls broadcast simultaneously were exactly in phase, species-specific temporal patterns were not obscured. Therefore, their experiment did not address the second consequence of acoustic interference.

We have found that female *H. ebraccata* more readily approach unobscured calls than those overlapped by either individual calls or choruses of *H. microcephala* (Schwartz & Wells 1983b, in press). Presumably the heterospecific calls not only make the calls more difficult to hear, but they also obscure the temporal pattern of the calls. Overlapping of introductory notes of conspecific calls might have a similar effect, since it would be very rare for the calls of two males to be exactly in phase. However, Otte & Loftus-Hills (1979), working with grasshoppers (*Syrbula admirabilis*), found that females were equally attracted to calls of a single male and the calls of

two males which overlapped. Consequently, the extent to which overlap of similar call notes results in interference remains unclear.

Because *H. ebraccata* has multi-note calls, synchronized responses often overlap the click notes of other males. Some authors have suggested that frogs and insects may have evolved a strategy of interfering with the signals of other males (Otte 1974, 1977; Partridge & Krebs 1978; Otte & Loftus-Hills 1979). A counter-argument is that males which overlap similar call notes will experience equal interference and will derive no net benefit (Alexander 1975; Otte 1977; Wells 1977a). In *H. ebraccata*, long introductory notes are overlapped with short click notes, so the leading male suffers the greatest interference. It is not clear whether this represents an evolved interference strategy or is simply a fortuitous consequence of the timing of vocal responses. However, in nightingales (*Luscinia megarhynchos*) some males appear consistently to overlap the beginning of their songs with the end of other males' songs. Hultsch & Todt (1982) suggested that this might obscure features in the last part of the song which enable a female to locate a singing male, but this has not been tested experimentally.

Implications for Female Choice in Natural Choruses

One of the difficulties in interpreting the results of two-choice playback experiments with females is that the conditions in the test arena are very different from those in a natural chorus. Background noise levels are much higher in choruses, and females usually will be confronted with more than two calling males. Consequently, clear preferences for certain types of calls observed in a test arena may be obscured or erased in a real chorus (Gerhardt 1982). This raises the question of whether the vocal responses of males described in this paper actually have much effect on a female's choice of mates.

We believe that at least on nights of low to moderate calling activity, the adjustments in male calling behaviour described in this paper probably would enhance a male's ability to attract females. Females generally move into the chorus from the periphery of the field early in the evening (2000–2200 hours). Usually a female sits for several hours in an area where several males are calling. Eventually, the female orients toward a calling male and makes a relatively rapid approach, going into amplexus within a few seconds to a few minutes (see also Miyamoto

& Cane 1980a). In making her choice, a female probably is influenced only by a few males in her immediate vicinity, with other males in the chorus simply contributing to background noise. We have seen no evidence of females moving through large segments of a chorus in search of mates. Most unpaired females located early in the evening were found in amplexus in the same place a few hours later.

We suggest that males whose calls are most easily detected during the brief period when a female is choosing a mate will be the most successful. Since a male cannot predict when this will be, he should make his calls distinctive at all times by responding appropriately to the calls of near neighbours. Males may enhance their competitive position by aggressively excluding both conspecific (Wells & Greer 1981) and heterospecific males (Schwartz & Wells in press) from nearby calling sites. In addition, males that see an approaching female and switch to rapid 'courtship' calling may enjoy a slight edge over those that continue to call at the normal rate. Finally, in dense choruses, when vocal competition becomes very intense, some males may profit by switching to a satellite strategy and attempting to intercept females (Wells 1977a; Perrill et al. 1978, 1982; Miyamoto & Cane 1980b).

Other factors may affect a male's chances of obtaining a mate on a given night, including the intensity of the male's calls, the effect of his calling site on sound propagation (Wells & Schwartz 1982), and the proximity of heterospecific choruses which interfere with his calls (Schwartz & Wells 1983a, b). Mating success over an entire season also would be affected by such factors as the number of nights a male is in a chorus (Greer & Wells 1980; Woodward 1982; Ryan 1983) and the arrival schedule of females. Because of the size of our population and the difficulty of locating all mated pairs in our study area, it is not possible to obtain good data on individual mating success. Nevertheless, we believe this type of experimental study provides at least a first step in understanding the functional significance of complex vocal repertoires in anurans.

Acknowledgments

We thank the Smithsonian Tropical Research Institute for providing housing and logistic support, and A. Stanley Rand for helpful suggestions. Carl Gerhardt provided generous help in the production of synthetic signals. Peter Narins made helpful comments on the manuscript.

Financial support was provided by a National Science Foundation grant (BNS 8004516) to KDW, a short-term Smithsonian research fellowship to JJS, and a grant from the University of Connecticut Research Foundation.

REFERENCES

- Alexander, R. D. 1975. Natural selection and specialized chorusing behavior in acoustical insects. In: *Insects, Science, and Society* (Ed. by D. Pimentel), pp. 35-77. New York: Academic Press.
- Arak, A. 1983a. Vocal interactions, call matching and territoriality in a Sri Lankan treefrog, *Philautus leucorhinus* (Rhacophoridae). *Anim. Behav.*, **31**, 292-302.
- Arak, A. 1983b. Male-male competition and mate-choice in anuran amphibians. In: *Mate Choice* (Ed. by P. Bateson), pp. 181-210. Cambridge: Cambridge University Press.
- Awbrey, F. T. 1978. Social interaction among chorusing Pacific tree frogs, *Hyla regilla*. *Copeia*, **1978**, 208-214.
- Brzoska, J. 1982. Vocal response of male European water frogs (*Rana esculenta* complex) to mating and territorial calls. *Behav. Proc.*, **7**, 37-47.
- Capranica, R. R. 1968. The vocal repertoire of the bullfrog (*Rana catesbeiana*). *Behaviour*, **31**, 302-325.
- Cardoso, A. J. 1981. Organização espacial e temporal na reprodução e vida larvária em uma comunidade de hiledeos no sudeste do Brasil (Amphibia, Anura). M.S. thesis, Universidade Estadual de Campinas, Brasil.
- 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.
- Duellman, W. E. 1970. *The Hylid Frogs of Middle America*. Lawrence: University of Kansas Museum of Natural History.
- Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Misc. Publ. Mus. Nat. Hist. Univ. Kansas*, **65**, 1-352.
- Ehret, G. & Gerhardt, H. C. 1980. Auditory masking and effects of noise on responses of the green treefrog (*Hyla cinerea*) to synthetic mating calls. *J. comp. Physiol.*, **141**, 13-18.
- Emlen, S. T. 1968. Territoriality in the bullfrog, *Rana catesbeiana*. *Copeia*, **1968**, 240-243.
- Gamb, R. D. & Littlejohn, M. J. 1979. Acoustic behavior of males of the Rio Grande leopard frog (*Rana berlandieri*): an experimental analysis through field playback trials. *Copeia*, **1979**, 643-650.
- Garton, J. S. & Brandon, R. A. 1975. Reproductive ecology of the green treefrog, *Hyla cinerea*, in southern Illinois (Anura: Hylidae). *Herpetologica*, **31**, 150-161.
- Gerhardt, H. C. 1974. The significance of some spectral features in mating call recognition in the green treefrog (*Hyla cinerea*). *J. exp. Biol.*, **61**, 229-241.
- Gerhardt, H. C. 1978. Mating call recognition in the green treefrog (*Hyla cinerea*): the significance of some fine-temporal properties. *J. exp. Biol.*, **74**, 59-73.
- Gerhardt, H. C. 1981a. Mating call recognition in the green treefrog (*Hyla cinerea*): importance of two

- frequency bands as a function of sound pressure level. *J. comp. Physiol.*, **144**, 9–16.
- Gerhardt, H. C. 1981b. Mating call recognition in the barking treefrog (*Hyla gratiosa*): responses to synthetic calls and comparisons with the green treefrog (*Hyla cinerea*). *J. comp. Physiol.*, **144**, 17–25.
- Gerhardt, H. C. 1982. Sound pattern recognition in some North American treefrogs (Anura: Hylidae): implications for mate choice. *Am. Zool.*, **22**, 581–595.
- Gochfeld, M. 1978. Intraspecific social stimulation and temporal displacement of song of the lesser skylark *Alauda gulgula*. *Z. Tierpsychol.*, **48**, 337–344.
- Green, S. & Marler, P. 1979. The analysis of animal communication. In: *Handbook of Behavioral Neurobiology*, Vol. 3 (Ed. by P. Marler & J. G. Vandenbergh), pp. 73–158. New York: Plenum Press.
- Greenfield, M. D. 1983. Unsynchronized chorusing in the coneheaded katydid *Neoconocephalus affinis* (Beauvois). *Anim. Behav.*, **31**, 102–112.
- Greenfield, M. D. & Shaw, K. C. 1983. Adaptive significance of chorusing with special reference to the Orthoptera. In: *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects* (Ed. by D. T. Gwynne & G. K. Morris), pp. 1–27. Boulder, Colorado: Westview Press.
- Greer, B. J. & Wells, K. D. 1980. Territorial and reproductive behavior of the tropical American frog *Centrolenella fleischmanni*. *Herpetologica*, **36**, 318–326.
- Hultsch, H. & Todt, D. 1982. Temporal performance roles during vocal interactions in nightingales (*Luscinia megarhynchos* B.). *Behav. Ecol. Sociobiol.*, **11**, 253–260.
- Lemon, R. E. 1971. Vocal communication of the frog *Eleutherodactylus martinicensis*. *Can. J. Zool.*, **49**, 211–217.
- Lemon, R. E. & Struger, J. 1980. Acoustic entrainment to randomly generated calls by the frog, *Hyla crucifer*. *J. acoust. Soc. Amer.*, **67**, 2090–2095.
- Littlejohn, M. J. 1977. Long-range acoustic communication in anurans: an integrated and evolutionary approach. In: *The Reproductive Biology of Amphibians* (Ed. by D. H. Taylor & S. I. Guttman), pp. 263–294. New York: Plenum Press.
- Loftus-Hills, J. J. 1971. Neural correlates of acoustic behaviour in the Australian bullfrog *Limnodynastes dorsalis* (Anura: Leptodactylidae). *Z. vergl. Physiol.*, **74**, 140–152.
- Loftus-Hills, J. J. 1974. Analysis of an acoustic pace-maker in Strecker's chorus frog, *Pseudacris streckeri* (Anura: Hylidae). *J. comp. Physiol.*, **90**, 75–87.
- Miyamoto, M. M. & Cane, J. H. 1980a. Notes on the reproductive behavior of a Costa Rican population of *Hyla ebraccata*. *Copeia*, **1980**, 928–930.
- Miyamoto, M. M. & Cane, J. H. 1980b. Behavioral observations of noncalling males in Costa Rican *Hyla ebraccata*. *Biotropica*, **12**, 225–227.
- Narins, P. M. 1982. Behavioral refractory period in neotropical treefrogs. *J. comp. Physiol.*, **148**, 337–344.
- Narins, P. M. & Capranica, R. R. 1978. Communicative significance of the two-note call of the treefrog *Eleutherodactylus coqui*. *J. comp. Physiol.*, **127**, 1–9.
- Otte, D. 1974. Effects and functions in the evolution of signaling systems. *Ann. Rev. Ecol. Syst.*, **5**, 385–417.
- Otte, D. 1977. Communication in Orthoptera. In: *How Animals Communicate* (Ed. by T. A. Sebeok), pp. 334–361. Bloomington: Indiana University Press.
- Otte, D. & Loftus-Hills, J. J. 1979. Chorusing in *Syrbula* (Orthoptera: Acrididae). Cooperation, interference competition, or concealment? *Entomol. News*, **90**, 159–165.
- Partridge, B. & Krebs, J. R. 1978. Tree frog choruses: a mixed evolutionarily stable strategy? *Anim. Behav.*, **26**, 959–963.
- Passmore, N. I. 1977. Mating calls and other vocalizations of five species of *Ptychadena* (Anura: Ranidae). *S. Afr. J. Sci.*, **73**, 212–214.
- Passmore, N. I. 1978. The vocalizations and aspects of the reproductive behaviour of the genus *Ptychadena* in South Africa. Ph.D. thesis, University of the Witwatersrand, Johannesburg.
- Passmore, N. I. & Telford, S. R. 1981. The effect of chorus organization on mate localization in the painted reed frog (*Hyperolius marmoratus*). *Behav. Ecol. Sociobiol.*, **9**, 291–293.
- Perrill, S. A., Gerhardt, H. C. & Daniel, R. 1978. Sexual parasitism in the green treefrog (*Hyla cinerea*). *Science, N.Y.*, **209**, 523–525.
- Perrill, S. A., Gerhardt, H. C. & Daniel, R. 1982. Mating strategy shifts in male green treefrogs (*Hyla cinerea*): an experimental study. *Anim. Behav.*, **30**, 43–48.
- Ramer, J. D., Janssen, T. A. & Hurst, C. J. 1983. Size-related variation in the advertisement call of *Rana clamitans* (Anura: Ranidae), and its effects on conspecific males. *Copeia*, **1983**, 141–155.
- Rand, A. S. & Ryan, M. J. 1981. The adaptive significance of a complex vocal repertoire in a neotropical frog. *Z. Tierpsychol.*, **57**, 209–214.
- Richards, D. G. & Wiley, R. H. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *Am. Nat.*, **115**, 381–399.
- Rosen, M. & Lemon, R. E. 1974. The vocal behavior of spring peepers, *Hyla crucifer*. *Copeia*, **1974**, 940–950.
- Ryan, M. J. 1980. Female mate choice in a neotropical frog. *Science, N.Y.*, **209**, 523–525.
- Ryan, M. J. 1983. Sexual selection and communication in a neotropical frog, *Physalaemus pustulosus*. *Evolution*, **37**, 261–272.
- Ryan, M. J., Tuttle, M. D. & Rand, A. S. 1982. Bat predation and sexual advertisement in a neotropical anuran. *Am. Nat.*, **119**, 136–139.
- Schiøtz, A. 1967. *The Treefrogs (Rhacophoridae) of West Africa*. Copenhagen: Bianco Lunos Bogtrykkeri.
- Schleidt, W. M. 1973. Tonic communication: continual effects of discrete signs in animal communication systems. *J. theoret. Biol.*, **42**, 359–386.
- Schwartz, J. J. & Wells, K. D. 1983a. An experimental study of acoustic interference between two species of neotropical treefrogs. *Anim. Behav.*, **31**, 181–190.
- Schwartz, J. J. & Wells, K. D. 1983b. The influence of background noise on the behaviour of a neotropical treefrog, *Hyla ebraccata*. *Herpetologica*, **39**, 121–129.
- Schwartz, J. J. & Wells, K. D. In press. Interspecific acoustic interactions of the neotropical treefrog *Hyla ebraccata*. *Behav. Ecol. Sociobiol.*
- Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.

- Sullivan B. K. 1982. Sexual selection in Woodhouse's toad (*Bufo woodhousei*) I. Chorus organization. *Anim. Behav.*, **30**, 680-686.
- Todt, D. 1970. Gesangliche Reaktionen der Amsel *Turdus merula* auf ihren experimentell reproduzierten Eigengesang. *Z. vergl. Physiol.*, **66**, 294-317.
- Tuttle, M. D. & Ryan, M. J. 1982. The role of synchronized calling, ambient light, and ambient noise in anti-bat-predator behavior of a treefrog. *Behav. Ecol. Sociobiol.*, **11**, 125-131.
- Wasserman, F. E. 1977. Intraspecific acoustical interference in the white-throated sparrow (*Zonotrichia albicollis*). *Anim. Behav.*, **25**, 949-952.
- Wells, K. D. 1977a. The social behaviour of anuran amphibians. *Anim. Behav.*, **25**, 666-693.
- Wells, K. D. 1977b. The courtship of frogs. In: *The Reproductive Biology of Amphibians* (Ed. by D. H. Taylor & S. I. Guttman), pp. 233-262. New York: Plenum Press.
- Wells, K. D. 1978. Territoriality in the green frog (*Rana clamitans*): vocalizations and agonistic behaviour. *Anim. Behav.*, **26**, 1051-1063.
- Wells, K. D. & Greer, B. J. 1981. Vocal responses to conspecific calls in a neotropical hylid frog, *Hyla ebraccata*. *Copeia*, **1981**, 615-624.
- Wells, K. D. & Schwartz, J. J. 1982. The effect of vegetation on the propagation of calls in the neotropical frog *Centrolenella fleischmanni*. *Herpetologica*, **38**, 449-455.
- Whitney, C. L. & Krebs, J. R. 1975. Mate selection in Pacific tree frogs, *Hyla regilla*. *Nature, Lond.*, **255**, 325-326.
- Woodward, B. 1982. Male persistence and mating success in Woodhouse's toad (*Bufo woodhousei*). *Ecology*, **63**, 583-585.
- Zelick, R. D. & Narins, P. M. 1982. Analysis of acoustically evoked call suppression behaviour in a neotropical treefrog. *Anim. Behav.*, **30**, 728-733.

(Received 18 April 1983; revised 8 August 1983;
MS. number: A4069)