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Intra- and Interspecific Vocal Behavior of the Neotropical Treefrog *Hyla microcephala*

JOSHUA J. SCHWARTZ AND KENTWOOD D. WELLS

The vocal communication of *Hyla microcephala* was studied in central Panama. We recorded natural interactions between males and conducted playback experiments using conspecific and heterospecific calls. Males employ both advertisement and aggressive calls which consist of a buzz-like introductory note often followed by secondary click notes. Advertisement calls show little variation in temporal features, whereas aggressive calls are quite variable. Playback of both conspecific advertisement calls and aggressive calls at high intensity elicited a significant increase in aggressive calling. Males increased the duration of aggressive call introductory notes in response to increasing playback intensity. Aggressive calls with long introductory notes were also used during close vocal or physical encounters with both conspecific males and *H. ebraccata*. In most cases, playback of heterospecific calls were ineffective in eliciting increased aggressive calling. Males synchronized and often added click notes to advertisement calls in response to conspecific and heterospecific calls. Call playbacks also elicited an increase in calling rate. When interrupted, males often abruptly terminated calls or added secondary notes to them. Males typically alternate individual notes in overlapping calls. Internote intervals in overlapping multi-note calls are longer than those in non-overlapping calls, reducing the probability of note overlap.

ACOUSTICALLY signaling animals which call in dense choruses are faced with two major problems: 1) intense competition among males to attract mates, and 2) acoustic interference from the calls of both conspecific and heterospecific males which reduce an individual's ability to broadcast his calls effectively (Alexander, 1975; Greenfield and Shaw, 1983; Schwartz and Wells, 1983a, b, 1984a). Male frogs exhibit several adaptations which probably make their calls more conspicuous in a noisy chorus and thereby increase their chances of attracting mates. These include increasing the rate of calling, increasing the complexity of calls by adding notes to them, and shifting the timing of calls to avoid overlap with those of neighbors (Loftus-Hills, 1974; Awbrey, 1978; Lemon and Struger, 1980; Narins, 1982; Zelick and Narins, 1982, 1983; Ramer et al., 1983). In addition, males usually maintain some minimum distance between themselves and neighboring males in the chorus and employ aggressive vocalizations to repel intruders (Wells, 1977a; Wilczynski et al., 1982; Arak, 1983).

Although many frogs have relatively simple vocal repertoires consisting of single-note advertisement and aggressive calls, some neotropical hylid frogs have elaborate repertoires of complex multi-note advertisement and aggressive calls (Fouquette, 1960; Duellman, 1970; Wells, 1977b). One such species is *Hyla microcephala*, a common frog in ponds and flooded fields throughout much of Central America. This species calls in very dense choruses during the rainy season. Males usually do not call independently, but respond to the calls of both conspecific males and those of other species in the chorus. In our study area in Panama, *H. microcephala* is found in the same microhabitats as *H. ebraccata* and *H. phlebodes*, and males of the three species often are found calling within 50 cm of one another. The calls of these species exhibit considerable spectral overlap, and their vocal repertoires are functionally and structurally very similar (Schwartz and Wells, 1984a). Advertisement calls are stereotyped, showing little variation in primary note duration or pulse repetition rate. Aggressive calls of all three species have higher pulse repetition rates than advertisement calls and are highly variable in pulse repetition rate, rise time, and duration (Schwartz and Wells, 1984a).

This paper is part of a comparative study of vocal communication in these three species. Previous work showed that *H. ebraccata* and *H. phlebodes* males increase calling rates and the

TABLE 1. FEATURES OF STIMULUS CALLS PRESENTED TO *H. microcephala* MALES. Durations, rise times and pulse repetition rates are for the primary note of the calls only. Pulse repetition rates of aggressive calls are given as mean values, with peak values in parentheses. Dominant frequency of both the lower and upper spectral bands are shown for *H. microcephala* calls. The first letter of each stimulus abbreviation identifies the species (*H. microcephala, H. ebraccata* or *H. phlebodes*), and the number gives the number of notes in the call. The letter L indicates a call of long duration. Number of males tested at 90, 95, 100 and 105 dB SPL is given in the last column.

Call stimulus	Type	Primary note duration (ms)	Rise time (ms)	Pulse rate (pulses/s)	Notes	Dominant frequency (Hz)	Sample sizes
MAD1	Adv	100	54	210	1	2,960, 5,920	(7, 6, 4, 0)
MAD3	Adv	104	56	221	3	2,960, 6,000	(9, 8, 7, 0)
MAGL	Agg	480	16	227 (320)	2	2,680, 5,680	(11, 10, 10, 8)
EAD1	Adv	188	92	96	1	3,000	(5, 4, 4, 0)
EAD3	Adv	200	172	95	3	3,080	(11, 11, 8, 0)
EAG2	Agg	150	88	365 (400)	3	3,160	(5, 4, 4, 0)
EAGL	Agg	416	352	222 (260)	2	2,960	(11, 10, 10, 9)
PAD3	Adv	94	52	159	3	3,560	(6, 5, 4, 0)
PAGL	Agg	366	144	153 (320)	1	4,000	(5, 5, 5, 5)

complexity of advertisement calls in response to both conspecific and heterospecific calls (Schwartz and Wells, 1984a, b; Wells and Schwartz, 1984a). *H. ebraccata* males give increased numbers of aggressive calls in response to loud playbacks of both conspecific and heterospecific calls and are especially responsive to aggressive calls of *H. microcephala* (Schwartz and Wells, 1984a; Wells and Schwartz, 1984b). However, calling by *H. ebraccata* males can be inhibited by loud choruses of *H. microcephala* (Schwartz and Wells, 1983a, b). In this paper we describe the vocal behavior of *H. microcephala* and quantify the responses of males to playbacks of conspecific advertisement and aggressive calls and those of *H. ebraccata* and *H. phlebodes.* We show that *H. microcephala* males respond to calls of other individuals in ways which probably reduce acoustic interference and thereby enhance their ability to communicate in a noisy environment. We also show that despite similarities in the vocal repertoires of all three species, some aspects of the temporal patterning of calling in *H. microcephala* differ in important ways from the behavior of the other species, particularly *H. ebraccata.*

MATERIALS AND METHODS

Study area.—Field work was conducted during June, July and Aug. 1980, 1981 and 1982. Our study site is a flooded meadow in Gamboa, Panama, near the Panama Canal. Fourteen species of frogs call and breed at this site during the rainy season. *H. microcephala, H. ebraccata* and *H. phlebodes* are particularly abundant in vegetation 0–2 m high near ditches and pools of water scattered throughout the area. We did field work between 1930 and 2330 hrs, because calling usually subsided by midnight. Temperature and humidity showed little nightly variation, averaging about 26 C and 95% (Schwartz and Wells, 1984a). Temperatures rarely changed by more than 1 C during our work each night. This climatic stability was a great advantage in our experimental work, because it allowed us to ignore temperature related changes in temporal properties of calls (Schneider, 1977; Gerhardt, 1982) and auditory sensitivity (Hubl and Schneider, 1979) which often are very important in studies of temperate zone anurans.

Playback experiments.—Responses of *H. microcephala* males to the calls of conspecifics, *H. ebraccata* and *H. phlebodes* were determined by playing prerecorded natural vocalizations to individual calling males. Stimuli were representative advertisement and aggressive calls of each species (Table 1). The same stimuli were used in our work with *H. ebraccata* (Schwartz and Wells, 1984a; Wells and Schwartz, 1984a, b) and *H. phlebodes* (Schwartz and Wells, 1984b). Each stimulus tape consisted of 20 recordings of the same call, presented at a rate of 10 calls/min; this approximated the spontaneous call rate of *H. microcephala*. We recorded each frog for 1 min before stimulus presentations began, and usually for 1 min between successive presentations. These no-stimulus periods served as a control and allowed us to evaluate a male's response to a particular call type. Unless otherwise specified, data obtained during all no-stimulus periods were pooled for each frog. We tried to work with relatively isolated males and sometimes removed neighboring males before beginning a test. However, it often was impossible to maintain complete isolation because *H. microcephala* were very abundant, and initially undetected males sometimes began calling nearby during playback tests. Such individuals were removed as soon as possible.

Recordings were made on a Uher 4200 Report Stereo IC tape recorder with a Sennheiser MKE 802 microphone. Playbacks were made from another Uher recorder through a University 4401 horn speaker mounted on a wooden baffle and placed 1 m from the test animal. The amplitude-frequency response of this speaker was measured to be ±3 dB from 1.1–14.5 kHz. The two recorders were linked with a patch cord so that the frog's responses could be recorded on the right channel of the first Uher while the stimulus was recorded simultaneously on the left channel.

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 (dB SPL re 20 μPa) at 1 m with a random incidence microphone. These measurements were made near the study site in an area removed from the background noise of the chorus. Calls were presented at intensities ranging from 90–105 dB SPL. Usually, order of presentation was from lowest to highest intensity because frogs sometimes stopped calling or moved away if high intensity calls were presented first. The modal SPL of *H. microcephala* calls was 106 dB at 50 cm in front of the frogs (Schwartz and Wells, 1984a), so these playback intensities are equivalent to those generated by a male calling at the modal intensity at distances of about 320 to 60 cm (assuming attenuation due only to spherical spreading). The speaker was placed so there was little or no vegetation between the frog and the speaker, so the measured sound pressure levels were very close to the intensities perceived by our subjects. The order of presentation of different stimuli varied between males.

Tape recordings were analyzed on a Tektronix 5111 storage oscilloscope. For each playback test, we determined the types of calls given and time (±80 ms) from the onset of the stimulus to each response. Intervals between call notes and the durations of the introductory notes of aggressive calls were measured to the nearest 8.0 ms. Dominant frequencies of calls were determined with a Uniscan model 4500 spectrum analyzer (Unigon Industries). More extensive data on the durations, rise times, pulse repetition rates, and frequency spectra of calls of *H. microcephala, H. ebraccata* and *H. phlebodes* are presented in Schwartz and Wells (1984a).

We used mostly standard non-parametric techniques (Siegel, 1956) and the G-test (Sokal and Rohlf, 1969) to evaluate the responses of males to different stimulus conditions. Data obtained for all playback intensities were pooled when there were no significant differences among groups. We pooled results from all frogs when sample sizes were small. We assessed the importance of individual call parameters in explaining variation in synchronous responses with multiple linear regression (Draper and Smith, 1981).

RESULTS

Vocal repertoire.—Sonagrams of representative *H. microcephala* calls are given in Schwartz and Wells, 1984a. Calls of *H. microcephala* have energy concentrated in one band at almost 3 kHz ($\bar{x} = 2941$ Hz, CV = 8.2, N = 50 calls of 10 males) and another near 6 kHz ($\bar{x} = 5773$ Hz, CV = 5.8, N = 50 calls). The introductory notes of advertisement calls have a median duration of 84 ms (range = 34–104, N = 40 calls of 4 males), and a median pulse repetition rate of 235 per sec (range = 214–274, N = 40 calls). Median duration and pulse repetition rate of aggressive call introductory notes are 280 ms (range = 72–1,248, N = 810 calls of 12 males) and 321 pulses/s (range = 128–433, N = 185 calls of 5 males) respectively. Secondary notes are usually biphasic (Fig. 7) and have a median duration of 64 ms (range = 48–88, N = 318 notes of 2 males).

Calling rate.—Calling rates of *H. microcephala* males ranged from 5 to 32 calls per min (median = 9) during the initial no-stimulus periods. Median calling rates were elevated during presentation of all playback stimuli (pooled volumes) compared to the initial no-stimulus pe-

TABLE 2. CALLING RATES (CALLS/MIN) OF *H. microcephala* MALES DURING THE INITIAL NO-STIMULUS PERIODS (INS) AND DURING PLAYBACK OF CONSPECIFIC AND HETEROSPECIFIC CALLS. Calling rates did not differ significantly among playback intensities for any stimulus (Kruskal-Wallis ANOVA, $P > 0.05$) and results for all volumes are pooled. *P* values are for one-tailed Wilcoxon matched-pairs signed-ranks tests comparing no-stimulus with stimulus periods.

		Stimulus								
Frog	INS	MAD1	MAD3	MAGL	EAD1	EAD3	EAG2	EAGL	PAD3	PAGL
1	15.6	10.8	8.4	8.4	15.0	15.0	14.4	13.8	—	—
2	4.8	8.4	8.4	13.2	13.2	19.2	19.2	22.2	20.4	22.8
3	9.0	10.8	—	14.4	11.4	12.0	14.4	16.8	—	13.2
4	7.8	12.6	21.0	15.6	9.6	12.0	14.4	17.4	26.4	—
5	18.6	10.2	3.6	15.0	—	17.4	—	18.6	—	—
6	31.8	33.6	32.4	32.4	—	35.4	—	27.0	32.4	33.0
7	8.4	—	16.2	21.6	—	13.2	—	15.0	—	—
8	25.2	—	15.6	21.0	—	31.8	—	25.8	26.4	28.8
9	22.2	—	19.2	17.4	—	23.4	—	22.8	22.8	22.8
10	6.0	—	11.4	20.4	—	20.4	—	19.8	—	—
11	9.6	11.4	4.8	21.0	13.2	14.4	16.8	16.8	11.4	—
Median	9.0	10.8	13.5	17.4	13.2	17.1	14.4	18.6	24.6	22.8
P		NS	NS	NS	NS	<.005	NS	<.024	.016	.031

riods (Table 2). However, the increase was statistically significant only for four heterospecific stimuli (one-tailed Wilcoxon matched-pairs signed-ranks test). In general, males with high initial calling rates did not further increase calling rates in response to stimulus playbacks. There was no significant change in calling rate with increasing playback intensity for any stimulus (Kruskal-Wallis ANOVA). For 7 of the 11 males tested, there was an elevation in calling rate during no-stimulus periods following stimulus playbacks relative to the calling in the initial no-stimulus period (range = 13–32 calls per min, median = 15). This significant increase (one-tailed Wilcoxon matched-pairs signed-ranks test, $P < 0.024$) was probably a continuation of the increase in calling elicited by stimulus presentation.

Aggressive call responses.—Males gave a significantly higher proportion of aggressive calls in response to the long conspecific aggressive call at 90, 95, 100 and 105 dB SPL than during the no-stimulus periods (Fig. 1). At 100 dB, this was also true for the conspecific 3-note advertisement call. Males gave a significantly higher proportion of aggressive calls to the long conspecific aggressive call than to the 1-note or 3-note conspecific advertisement calls at 90 dB ($P = 0.008$, N = 7 and $P = 0.031$, N = 9 respectively, one-tailed Wilcoxon matched-pairs signed-ranks test).

The only heterospecific stimulus which elicited a significant increase in the proportion of aggressive calls by *H. microcephala* males was the 1-note *H. ebraccata* advertisement call at 90 dB (one-tailed Wilcoxon matched-pairs signed-ranks test, $P = 0.03$, N = 11). In general, the response to heterospecific calls was weaker than

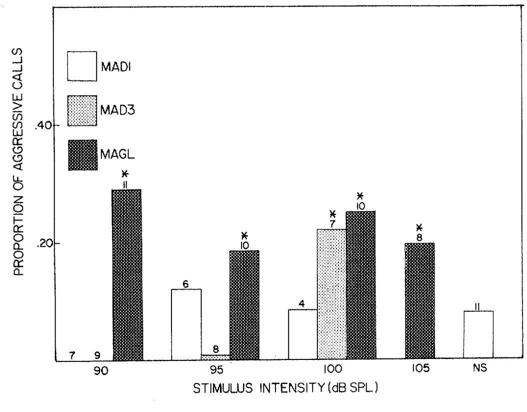

Fig. 1. Proportion of aggressive calls given by *H. microcephala* males to conspecific 1-note advertisement calls (MAD1), 3-note advertisement calls (MAD3) and long aggressive calls (MAGL) at 4 playback intensities. The number of males tested is given above each bar. Asterisks indicate a significant difference between calls given to stimuli and during the no-stimulus periods (one-tailed Wilcoxon matched-pairs signed-ranks test, * $P < 0.05$).

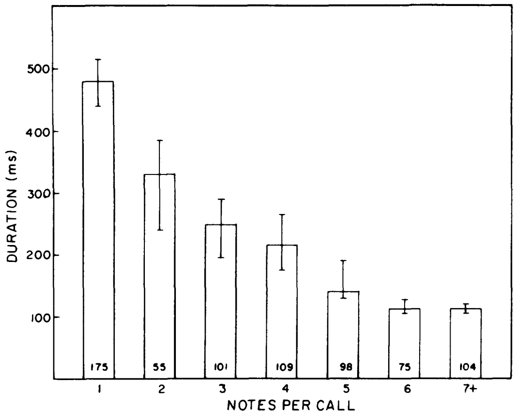

Fig. 2. Durations of the introductory notes of aggressive calls with different numbers of notes. Data are presented as medians with approximate 95% confidence intervals. Sample sizes are given at the bottom of each bar.

to the conspecific calls. Males gave a significantly higher proportion of aggressive calls to the conspecific long aggressive call than to either the *H. ebraccata* long aggressive call (one-tailed Wilcoxon matched-pairs signed-ranks test, $P < 0.05$) or *H. phlebodes* long aggressive call (G-test, $P < 0.01$, using pooled responses of all frogs) at 90, 95, 100 and 105 dB SPL.

Aggressive calls of *H. microcephala* exhibit wide variation in introductory note duration, pulse repetition rate, and rise time. Long calls have lower pulse repetition rates and slower proportional rise times than short calls (Schwartz and Wells, 1984a). There also is a significant negative correlation between introductory note duration and the number of secondary click notes in a call ($r = -.63, P < 0.0001$; correlation coefficients obtained for nine frogs were judged homogenous; $\chi^2 = 11.2, P > 0.1$ and a combined estimate was obtained using the z-transformation, Sokal and Rohlf, 1969) (Fig. 2). The distribution of introductory note durations is relatively smooth, lacking discontinuities (Fig. 3). This suggests that calls with long and short introductory notes do not constitute two distinct types of aggressive calls. During playback of all conspecific stimuli, the duration of the introductory notes of aggressive call responses increased with increasing playback intensity (Fig. 4) (Kruskal-Wallis ANOVA, $P < 0.0001$). There was also significant heterogeneity in note duration among frogs (Kruskal-Wallis ANOVA,

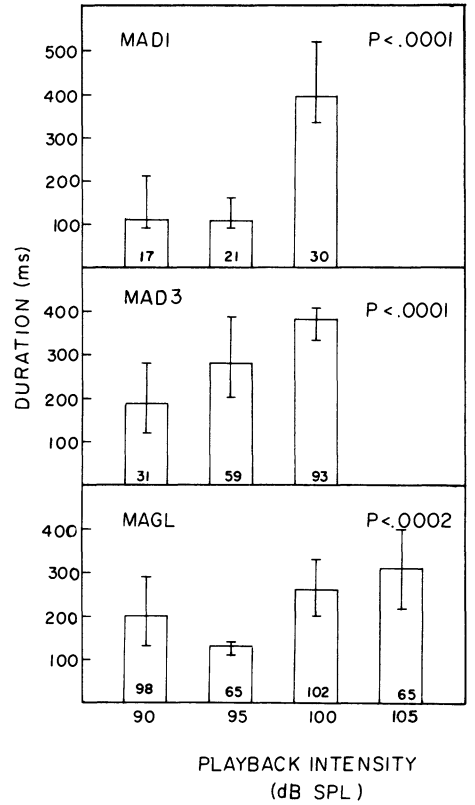

Fig. 4. Durations of aggressive call introductory notes given to conspecific 1-note advertisement calls (MAD1), 3-note advertisement calls (MAD3) and long aggressive calls (MAGL) at different playback intensities. Data are presented as medians with approximate 95% confidence intervals. Sample sizes are given at the bottom of each bar. Significance levels indicate heterogeneity in duration among playback intensities (Kruskal-Wallis ANOVA).

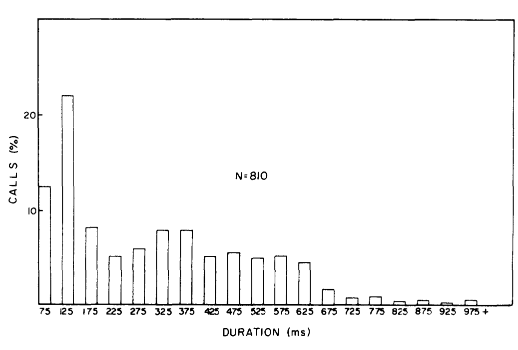

Fig. 3. Durations of all aggressive call introductory notes given by males ($N = 14$) recorded in this study.

TABLE 3. PROPORTION OF MULTI-NOTE CALLS GIVEN DURING NO-STIMULUS PERIODS (NS) AND DURING PLAYBACK OF CONSPECIFIC AND HETEROSPECIFIC CALLS. The G-test was used to compare numbers of multi-note calls and single note calls given during stimulus periods and no-stimulus periods. We also compared proportions of synchronized and non-synchronized calls which were multi-note calls. All = all responses, Syn = synchronized responses, Nsyn = non-synchronized responses.

	MAD1	MAD3	MAGL	EAD1	EAD3	EAG2	EAGL	PAD3	PAGL
NS	0.84	0.79	0.80	0.82	0.80	0.82	0.80	0.82	0.83
All	0.85	0.82*	0.79	0.89*	0.82*	0.85	0.81	0.84	0.82
Syn	0.88	0.87*	0.90*	0.89	0.86*	0.85	0.88*	0.85	0.92*
Nsyn	0.76	0.84+	0.80+	0.90	0.90	0.81	0.84+	0.80	0.79+

All vs NS or Syn vs NS: * $P < 0.05$.
Nsyn vs Syn: + $P < 0.05$.

$P < 0.05$). At all four playback intensities, the duration of aggressive call introductory notes was significantly greater than those given during no-stimulus periods (two-tailed Mann-Whitney U-test, $P < 0.03$ for each volume).

Most aggressive calls given during close-range agonistic encounters also had long introductory notes. During a 110 s vocal exchange between conspecifics about 15 cm apart, note durations were 60–1,248 ms ($\bar{x} = 526$, SD = 246, N = 49). In a 150 s recording of a wrestling match between a *H. ebraccata* and a *H. microcephala* male, the duration of the introductory notes of most *H. microcephala* aggressive calls was nearly 600 ms ($\bar{x} = 593$, SD = 143, range = 208–816, N = 43).

Multi-note calling.—We calculated two measures of the level of multi-note calling: the proportion of multi-note calls and the number of notes per call. During no-stimulus periods, most males gave a high proportion of multi-note calls ($\bar{x} = .80$, range = .49–.89, N = 4,286). There was a weak tendency to increase the proportion of multi-note calls in response to some of the stimulus calls (Table 3). This increase was significant only for the *H. ebraccata* advertisement calls and 3-note *H. microcephala* advertisement call when all responses are included (G-test, $P < 0.05$). If only calls given within 1.0 s of stimulus onset are considered (operationally defined as synchronized responses), significant increases occurred in response to five of nine playback stimuli, including two of three conspecific calls (Table 3).

When latencies to the first response are broken into six 1.0 s intervals, there are significant differences among these groups in number of call notes (Kruskal-Wallis ANOVA, $P < 0.0001$; data pooled for all stimuli). For both conspecific and heterospecific stimuli, the number of notes was greater in synchronized first responses than in those with delay times greater than 3.0 s (nonparametric multiple comparisons, Noether, 1976; $P < 0.05$) (Fig. 5). When the entire 6.0 s post-stimulus time period is considered, there was no significant increase in the number of notes per call for any stimulus relative to no-stimulus periods (one-tailed Wilcoxon matched-pairs signed-ranks test). However, males gave significantly more notes per call in synchronized responses to the conspecific long aggressive call, the *H. ebraccata* long aggressive, and the 3-note *H. ebraccata* advertisement call than during no-stimulus periods (one-tailed Wilcoxon matched-pairs signed-ranks test, $P < 0.05$).

During playback tests, some stimulus calls were broadcast while a subject was giving a call. Calls which were interrupted had more notes than those which were not (Fig. 6), and this difference was significant for each of the playback stimuli (one-tailed Mann-Whitney U-test, $P < 0.05$, pooled volumes). This could be because males add notes to interrupted calls, or because long calls with many notes are more likely to be interrupted. The probability that calls with a particular number of notes would be interrupted is a function of their duration and their frequency of occurrence. We calculated a frequency distribution of interrupted calls with different numbers of notes based on this chance expectation and compared it with the actual distribution of interrupted calls. We found that males gave more notes in interrupted calls than expected by chance alone (data pooled for all stimuli; one-tailed Mann-Whitney U-test, $P < 0.01$).

Calls also elicited multi-note responses during pairwise natural interactions. All six frogs we recorded gave a higher proportion of multi-

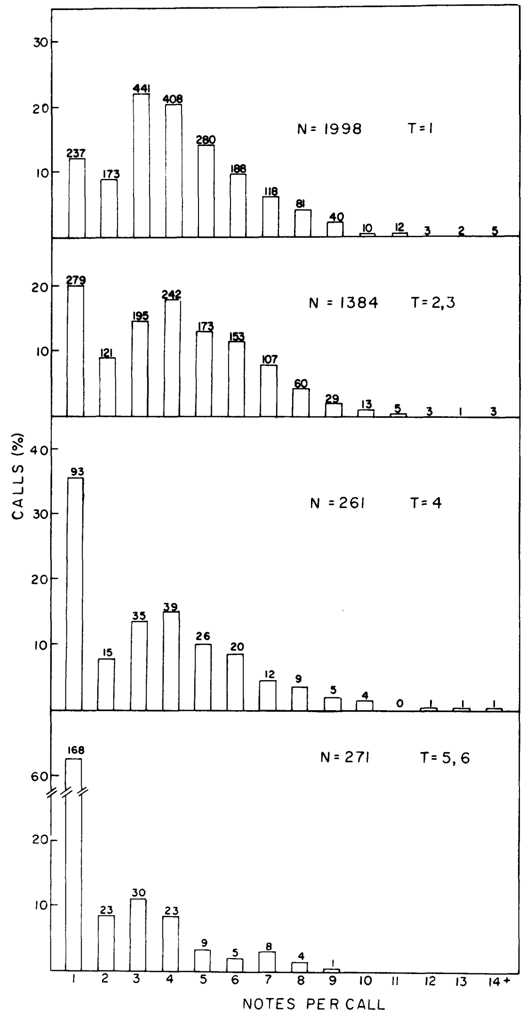

Fig. 5. Distributions of number of notes in first response calls given in six sequential 1 s latency intervals (T = 1–6) (responses to all stimuli are pooled). Number of notes in calls given in the second and third (T = 2, 3) and fifth and sixth (T = 5, 6) intervals were not significantly different and are pooled (non-parametric multiple comparisons, $P > 0.05$; Noether, 1976).

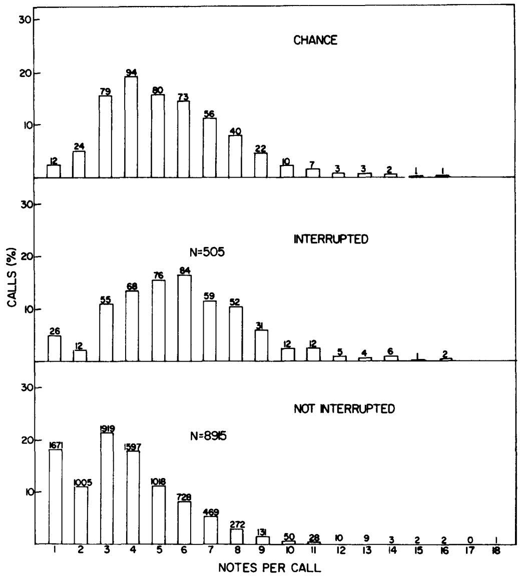

Fig. 6. Distributions of number of notes in calls which were or were not interrupted by playback of a stimulus call. Also shown is the distribution generated assuming the frequency of interruption was based on chance alone (see text). Data pooled for all males. Sample sizes are given above each bar.

note calls in synchronized than in non-synchronized responses (one-tailed sign test, $P = 0.016$), and four males gave significantly more notes per call in synchronized responses (one-tailed Mann-Whitney U-test, $P < 0.05$ for each male).

Timing of responses.—*H. microcephala* males respond to many conspecific and heterospecific calls by giving synchronized advertisement call responses (calls within 1.0 s of stimulus onset). Fifty-three % of first advertisement calls given by males in response to playback of all stimulus calls were synchronized (modal response latency = 400 ms, median = 960 ms, N = 3,511). First aggressive call responses had greater delay times than advertisement calls (mode = 1,200 ms, median = 2,400 ms, N = 812) (Mann-Whitney U-test, $P < 0.0001$) and only 18% were given synchronously. The percent of stimulus calls followed by a synchronized response was defined as the percent synchrony. The *H. ebraccata* 1-note advertisement call at 90 dB SPL and the *H. microcephala* long aggressive call at 100 dB elicited the lowest percent synchrony (median = 25%). The *H. microcephala* 3-note advertisement call at 95 dB elicited the highest percent synchrony (median = 70%). However, variation in percent synchrony was not strongly influenced by variation in the characteristics of the stimuli. Multiple linear regression (SAS Stepwise procedure, SAS Institute, Cary, N.C., 1979) using playback intensity, dominant frequency, and temporal characteristics (duration, proportional rise time, pulse repetition rate, and number of notes) as independent variables ex-

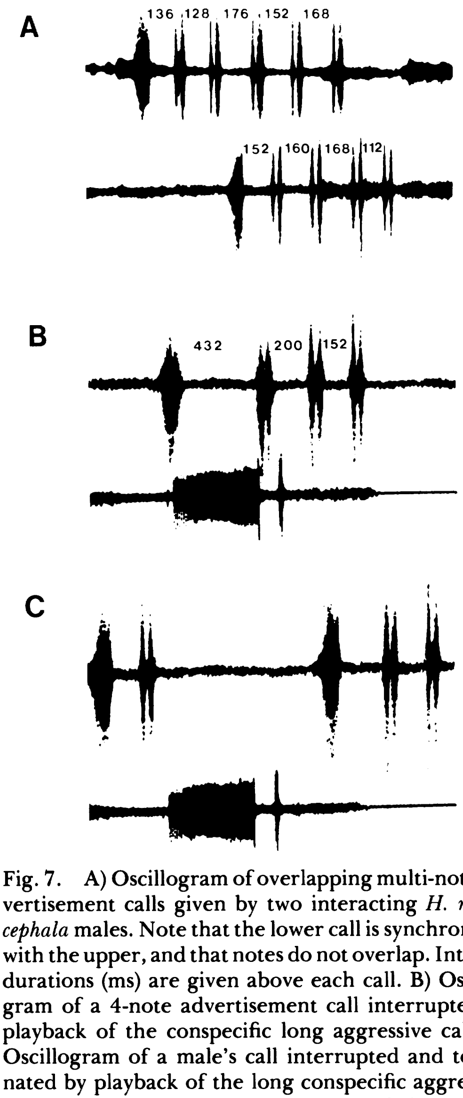

Fig. 7. A) Oscillogram of overlapping multi-note advertisement calls given by two interacting *H. microcephala* males. Note that the lower call is synchronized with the upper, and that notes do not overlap. Interval durations (ms) are given above each call. B) Oscillogram of a 4-note advertisement call interrupted by playback of the conspecific long aggressive call. C) Oscillogram of a male's call interrupted and terminated by playback of the long conspecific aggressive call. A second, synchronized, response follows.

TABLE 4. CONSEQUENCES OF INTERRUPTION OF *H. microcephala* CALLS BY STIMULUS CALLS. Individual calls were terminated (T1), terminated and followed by a new call less than 1 s after the stimulus call was initiated (T2), or showed an increase in inter-note intervals (I). The total number of interrupted calls and the percent which showed one of these changes also is given.

Stimulus	T1	T2	I	Total	Percent
MAD1	2	0	8	36	27.8
MAD3	2	3	1	51	11.8
MAGL	49	50	21	150	80.0
EAD1	0	0	0	36	00.0
EAD3	10	5	3	85	21.2
EAG2	0	0	0	60	00.0
EAGL	15	11	1	126	21.4
PAD3	6	5	1	58	20.7
PAGL	17	16	4	79	46.8

plained only 13% of the total variance in percent synchrony.

During natural interactions, many calls overlapped temporally, but usually the individual notes of these calls did not (Fig. 7A). In a sample of 100 instances of overlapped calls, there was no overlap of notes in 74 cases, overlap of some notes in 16, and overlap of all notes in only 10. In part, this was because the intervals between notes are longer than introductory or secondary notes of advertisement calls. For example, in one natural interaction introductory notes averaged 91 ms (SD = 11, N = 92), secondary notes averaged 62 ms (SD = 6, N = 318), and the intervals between notes in uninterrupted calls averaged 127 ms (SD = 15, N = 127). Males further reduce the likelihood of note overlap by lengthening inter-note intervals when the note of another frog falls within an interval (Fig. 7A, B). In the above interaction, intervals interrupted by notes of another frog averaged 169 ms (SD = 13, N = 203), a significant increase (t-test, $P < 0.0001$). When a male was interrupted by a stimulus call during playback tests, he sometimes terminated his call or terminated the call and started another one immediately after the end of the stimulus (Fig. 7C). The long aggressive calls of *H. microcephala* and *H. phlebodes* were the most effective in eliciting these changes in timing (Table 4); the former was significantly more effective than all other stimuli (G-test, $P < 0.01$ for all comparisons).

DISCUSSION

Results of this study indicate that *H. microcephala* males change both the types of calls and their temporal patterning in response to conspecific and heterospecific calls. We suspect that much of the behavior we described evolved to enhance the ability of males to communicate in an environment replete with sources of acoustic interference. It is not surprising that there are many similar examples of modifications in calling behavior among chorusing frogs and insects

(Greenfield and Shaw, 1983; Schwartz and Wells, 1984a, b; Wells and Schwartz, 1984a, b).

Calling rates.—Some males increased calling rates during exposure to both conspecific and heterospecific calls, but the response was not as strong as that of *H. ebraccata* males (Wells and Schwartz, 1984a; Schwartz and Wells, 1984a). Because many *H. microcephala* males were not completely isolated from conspecifics, calling rates of most males were high when we initiated playback experiments. Most males that showed no increase in calling rate had initial rates higher than the 10 calls per min of the stimulus tape (Table 2). Elevation of calling rate is a common phonoresponse among chorusing anurans (Wells and Schwartz, 1984a) and may result from responses to individual calls of other males or a more general stimulation of calling by the chorus as a whole. Both explanations probably apply to *H. microcephala.* Males synchronize to individual calls and also are stimulated by distant choruses. Females of some species prefer males with high calling rates (Sullivan, 1982, 1983; Arak, 1983), and a more repetitive call also may be easier to locate in a noisy chorus (Wells and Schwartz, 1984a). *H. microcephala* males give a rapid series of single-note calls when a female is detected nearby, perhaps because this makes the male more conspicuous (Wells and Schwartz, 1984a).

Aggressive calls.—Clearly, conspecific aggressive calls are perceived by *H. microcephala* males as signals distinct from advertisement calls. Males gave the strongest aggressive response to playbacks of the conspecific aggressive call, and advertisement calls failed to elicit a high proportion of aggressive calls except at high intensities. Males of a number of anuran species respond to playbacks of conspecific calls in a similar way (see references in Wells and Schwartz, 1984b). The increase in the duration of aggressive call introductory notes in response to loud stimuli, coupled with a decrease in number of notes in long calls, is very similar to the behavior of both *H. ebraccata* (Wells and Schwartz, 1984b) and *H. phlebodes* (Schwartz and Wells, 1984b). These species all appear to have graded aggressive calls. Graded signals are common in birds and mammals (Morton, 1982) but have not been previously reported in amphibians. How *H. microcephala* males actually perceive graded changes in temporal characteristics of calls has yet to be determined. If fine scale temporal changes in these signals correlate with fine scale changes in their perception, then this would constitute a truly graded communication system (Green and Marler, 1979; Maier, 1982). The duration of introductory notes could signal a male's level of aggressive motivation, or it could be a measure of resource holding potential (size, strength, vigor) (Wells and Schwartz, 1984b).

In general, *H. microcephala* gave relatively few aggressive calls in response to the broadcast of either *H. ebraccata* or *H. phlebodes* calls. This is surprising because males engage in interspecific aggressive encounters with *H. ebraccata,* and aggressive calls are used in these interactions. Furthermore, aggressive calls of *H. microcephala, H. ebraccata* and *H. phlebodes* are more similar to one another in temporal characteristics than are their advertisement calls. *H. ebraccata* males readily respond to both conspecific aggressive calls and those of *H. microcephala* and *H. phlebodes* by giving high proportions of aggressive calls (Schwartz and Wells, 1984a; Wells and Schwartz, 1984b). It may be that heterospecific calls must be louder than intensities used in our experiments before *H. microcephala* males will shift to aggressive calling. *H. ebraccata* and *H. phlebodes* calls have energy concentrated below the upper spectral component of *H. microcephala* calls (see sonagrams in Schwartz and Wells, 1984a). If the peak in sensitivity of the auditory system of male *H. microcephala* is shifted away from the dominant frequencies of the heterospecific calls, this could explain the weak response elicited during playbacks. *H. microcephala* males also call in dense aggregations and may be more tolerant of loud calls of other frogs. Most of the 11 interspecific encounters we witnessed involved wrestling, so males were exchanging aggressive calls at very close range.

Multi-note calling.—*H. microcephala* males increased the proportion of multi-note calls in response to some stimuli. Again, a stronger response might have occurred had calling *H. microcephala* been less numerous in our study area. The male which exhibited the greatest increase in multi-note calling during stimulus broadcasts was well isolated from all other males and was tested on an exceptionally quiet night. He had given mostly single-note calls before stimuli were presented.

The strength of this response appeared to be related to its temporal relationship to the stimulus call. Stimuli which interrupted a male's calls elicited the greatest increase in number of notes per call, and synchronized responses had a higher proportion of multi-note calls and more notes per call than non-synchronized responses. This suggests that the neural mechanism responsible for the behavior has a rapidly decaying sensitivity. In terms of the dynamics of chorus activity, the net effect may be that males only increase call complexity in response to the vocal activity of nearby individuals with whom they are interacting closely.

Both *H. ebraccata* (Schwartz and Wells, 1984a; Wells and Schwartz, 1984a) and *H. phlebodes* (Schwartz and Wells, 1984b) add secondary notes to their calls in response to the calls of conspecific and heterospecific males. However, *H. ebraccata* males seldom give calls with more than three notes, while *H. phlebodes* commonly give calls with up to 25 notes. In this respect, the behavior of *H. microcephala* is more similar to *H. phlebodes,* the species to which it is more closely related (Duellman, 1970). Males of a number of other species of anurans also add notes to their calls in response to conspecific vocalizations (Littlejohn and Harrison, 1981; Rand and Ryan, 1981; Tuttle and Ryan, 1982; Ramer et al., 1983). Females prefer more complex multi-note calls in three species (Littlejohn and Harrison, 1981; Rand and Ryan, 1981; Wells and Schwartz, 1984a). Such calls may be most easily detected against the continuous background noise of a chorus (Wells and Schwartz, 1984a). We suspect that *H. microcephala* females will show a similar preference for multi-note calls, but their responses have yet to be tested.

Timing of responses.—The most common response of *H. microcephala* males to both conspecific and heterospecific stimuli was to give synchronized advertisement calls. In our study of *H. ebraccata,* we showed that stimulus duration explained most of the variation in percent synchrony to natural and synthetic calls (Schwartz and Wells, 1984a). In contrast, multiple linear regression failed to identify a call parameter which strongly influences this response in *H. microcephala.* We believe, nevertheless, that call duration also is important for *H. microcephala.* In *H. ebraccata,* percent synchrony increased in an asymptotic fashion when plotted against stimulus duration. Synchrony was poor to short calls, but increased rapidly as duration rose to 200 ms and then leveled off. The median duration of the introductory notes of *H. ebraccata* advertisement calls was 180 ms, while in *H. microcephala* it was 82 ms (Schwartz and Wells, 1984a). All call stimuli presented to *H. microcephala* were longer than 82 ms (Table 1). Therefore, if the functional response is similar to that of *H. ebraccata,* the importance of stimulus duration would be undetectable in our data. We believe that playback of synthetic stimuli shorter than the *H. microcephala* advertisement call would underscore the significance of this temporal feature.

Perhaps the most fascinating aspect of the vocal behavior of *H. microcephala* is the way males respond to calls which overlap temporally with their own. During vocal interactions, males usually alternate individual notes of their calls. Males of many species of frogs alternate individual calls (Lemon, 1971; Rosen and Lemon, 1974; Passmore, 1978), but *H. microcephala* is one of the few species in which alternation of individual notes within calls has been demonstrated. This behavior is similar to that of *H. phlebodes,* which also gives calls with inter-note intervals much longer than notes (Schwartz and Wells, 1984b). In contrast, this is not true of *H. ebraccata* calls. Advertisement call introductory notes of this species are longer than inter-note intervals, and synchronized responses to multi-note calls frequently result in masking of secondary notes of one male by the introductory note of another (Wells and Schwartz, 1984a).

Recent work indicates that frogs are capable of making rapid adjustments in calling behavior. For example, Zelick and Narins (1983) found that male *Eleutherodactylus coqui* and *E. portoricensis* could call selectively during very brief periods in which background noise level was reduced. *H. microcephala* males can make very precise changes in the timing of individual notes in their calls. Males lengthen the interval between notes when the note of another male falls within it, and calls may be abruptly terminated if they are interrupted. The time scale in which these shifts occur is very brief. The increase in interval duration appears to occur only in those intervals which are interrupted. Therefore, the response must decay rapidly, and a pair of interacting males will display mutual note-by-note inhibition. Surprisingly, lengthening of inter-note intervals does not occur in the long overlapping calls of interacting *H. phlebodes* (Schwartz and Wells, 1984b).

It would be interesting to know how this response is influenced by the duration and intensity of the interrupting stimulus. For example, the strength of the response might be sensitive to stimulus duration, as is the synchronizing response of *H. ebraccata.* In our playback experiments, calls were most likely to be terminated if interrupted by very long calls. For example, 66% of calls interrupted by the conspecific long aggressive call were terminated, as were 42% of calls interrupted by the long *H. phlebodes* aggressive call. The magnitude of the response also might be affected by the delay time between the notes of interacting males. In some species, the capacity of a male to respond is related to the temporal relationship between a stimulus and a male's preceding call (Loftus-Hills, 1974; Lemon and Struger, 1980; Narins, 1982). In the models formulated by Loftus-Hills and Narins, a male is refractory to call stimulation immediately following the initiation of his call. Lengthening of inter-note intervals by *H. microcephala* also could depend on the precise timing of the stimulus call relative to a refractory period. This will be investigated in the future with playbacks of synthetic calls.

H. microcephala males display a spectrum of phonoresponses which may improve their ability to transmit information in a noisy environment. These include synchronization of call notes, termination of interrupted calls, lengthening of inter-note intervals, and addition of secondary notes to calls. Other chorusing species display behavior which presumably yields the same results (Littlejohn and Martin, 1969; Alexander, 1975; Awbrey, 1978; Narins, 1982; Zelick and Narins, 1982, 1983; Greenfield and Shaw, 1983; Schwartz and Wells, 1983a, b). For example, many species of chorusing insects increase the intervals between calls (or chirps) while duetting (e.g., Jones, 1966; Latimer, 1981), resulting in a pattern of repeated acoustic units similar to the alternating notes of *H. microcephala* calls. Results presented here constitute the first example of lengthening inter-note intervals in anurans.

In addition to the fine scale changes in the calling behavior of individual males within a chorus, the overall acoustic output of groups of *H. microcephala* changes over time. Choruses are cyclical, producing fluctuating levels of background noise. In over 2 hrs of recordings of chorus activity, the duration of 259 calling bouts ranged from 1.5 s to 78.0 s ($\bar{x} = 17.3$, SD = 11.9), interrupted with quiet periods of 1.5 s to 58.5 s ($\bar{x} = 10.2$, SD = 9.5) (Schwartz and Wells, 1983a). This pattern of group calling, termed "unison bout singing," has been reported in a number of orthopteran species (Greenfield and Shaw, 1983). What causes males to temporarily stop calling is currently a mystery. One possibility is that males stop calling when background noise reaches an intensity which makes communication impossible. If so, cycling of choruses would be a manifestation of another behavior by individuals which reduces the effects of acoustic interference.

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