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VOCAL BEHAVIOR OF THE NEOTROPICAL TREEFROG *HYLA PHLEBODES*

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ABSTRACT: We investigated the vocal behavior of *Hyla phlebodes* in central Panama by recording natural interactions between males and conducting playback experiments using conspecific and heterospecific calls. The vocal repertoire of *H. phlebodes* is very similar to that of *H. ebraccata* and *H. microcephala*, two sympatric species abundant at our study site. Males employ both advertisement and aggressive calls which consist of a buzz-like introductory note often followed by secondary click notes. The introductory notes of advertisement calls are relatively stereotyped, showing little variation in temporal characteristics, but those of aggressive calls are quite variable. 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 in some cases. Males often added many secondary notes to calls that were interrupted by calls of other males. Because of the temporal structure of multi-note calls and the timing of male responses, there was little interference between notes in long overlapping calls of two individuals. *H. phlebodes* only rarely gave aggressive calls during playback tests using conspecific or heterospecific calls. However, when males did respond, they gave aggressive calls with longer introductory notes to stimuli presented at high intensities than to those presented at lower intensity. The number of secondary notes in aggressive calls was negatively correlated with introductory note duration.

Key words: Amphibia; Anura; Hylidae; Communication; Vocalization; Behavior

THE vocal behavior of male frogs is influenced by interactions with other males in a chorus (Wells, 1977*a*,*b*). They may use advertisement and aggressive calls (Littlejohn, 1977) or calls of varying complexity (Arak, 1983*a*; Ramer et al., 1983; Rand and Ryan, 1981; Wells and Schwartz, 1984*a*) under different circumstances, and they may shift the timing of their calls in response to those of other individuals (Awbrey, 1978; Lemon, 1971; Lemon and Struger, 1980; Littlejohn and Martin, 1969; Rosen and Lemon, 1974; Schwartz and Wells, 1983*a*,*b*, 1984*a*,*b*; Wells and Schwartz, 1984*a*; Zelick and Narins, 1982, 1983). These kinds of responses may improve a male's ability to transmit information in a noisy environment (Greenfield and Shaw, 1983; Narins, 1982; Schwartz and Wells, 1983*a*,*b*; Zelick and Narins, 1982) and enhance his ability to attract mates (Arak, 1983*b*; Ryan, 1983; Wells and Schwartz, 1984*a*).

H. phlebodes is a neotropical treefrog with an elaborate vocal repertoire. Males call in choruses during the rainy season and use both advertisement and aggressive calls. These consist of an introductory note frequently accompanied by shorter secondary notes. The introductory notes of aggressive calls have higher pulse repetition rates and are more variable in pulse repetition rate, rise time and duration than those of advertisement calls (Schwartz and Wells, 1984*a*). The communication system of *H. phlebodes* is very similar to that of two sympatric species, *H. ebraccata* and *H. microcephala*. There is extensive overlap in the frequency spectra of these species' calls and considerable overlap in microhabitat choice by calling males (Fouquette, 1960). Aggressive calls of these hylids are more similar than are their advertisement calls and are used in interspecific interactions (Schwartz and Wells, 1984*a*).

We describe the results of playback experiments with *H. phlebodes* using advertisement and aggressive calls of *H. phlebodes*, *H. ebraccata* and *H. microcephala*. We also recorded natural intra- and interspecific vocal interactions. Since work on *H. ebraccata* revealed that males use similar vocal behavior during interactions with both conspecific and heterospecific males (Schwartz and Wells, 1984*a*), we

TABLE 1.—Characteristics of stimulus calls presented to *H. phlebodes* males. Durations, rise times, and pulse repetition rates are for the introductory 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. phlebodes, H. microcephala* or *H. ebraccata*), 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 85, 90 and 100 dB SPL is given in the last column.

		Introductory note					
Stimulus	Type	Duration (ms)	Rise time (ms)	Pulse rate (pulses/s)	Notes	Dominant frequency (Hz)	*n*
PAD3	Adv	94	52	159	3	3560	9, 12, 8
PAG2	Agg	150	52	300 (380)	2	3600	7, 10, 7
PAGL	Agg	366	144	153 (320)	1	4000	6, 7, 7
MAD1	Adv	100	54	210	1	2960, 5920	3, 5, 3
MAD3	Adv	104	56	221	3	2960, 6000	6, 8, 6
MAGL	Agg	480	16	227 (320)	2	2680, 5680	7, 8, 6
EAD1	Adv	188	92	96	1	3000	2, 6, 2
EAD3	Adv	200	172	95	3	3080	8, 12, 8
EAG3	Agg	150	88	365 (400)	3	3160	3, 7, 1
EAGL	Agg	416	352	222 (260)	2	2960	8, 12, 7

wanted to investigate the possibility that *H. phlebodes* behaves the same way. Our analysis of recordings focused on shifts in the timing and complexity of calls and the level of aggressive calling. Responses of both *H. ebraccata* and *H. microcephala* included changes of these kinds, and observations of male *H. phlebodes* indicated that their vocal behavior is also quite sensitive to the calls of other frogs.

MATERIALS AND METHODS

Study Area

We conducted our field work during June, July and August of 1980, 1981 and 1982. Our study site is a flooded meadow in Gamboa, Panama, near the Panama Canal. During the rainy season, frogs are abundant in and near ditches and pools of water scattered throughout the area. *H. phlebodes* calls almost exclusively from perches in grass 1.0–2.0 m high along the field border, while *H. ebraccata* and *H. microcephala* also are common in the vegetation 0–2.0 m high near pools. We conducted playback experiments and recorded natural interactions between 1930 h and 2330 h, since calling usually subsided by midnight. In the 3 yr of the study, temperature and humidity showed little variation from night to night ($\bar{x} = 26$ C, 95%), and temperatures rarely changed by more than 1 C during our work each evening (Schwartz and Wells, 1984*a*). Therefore, we were able to avoid the complications imposed by temperature related changes in temporal properties of anuran calls (Gerhardt, 1982; Schneider, 1977) often encountered by workers in the temperate zone.

Playback Experiments

Responses of *H. phlebodes* males to the calls of conspecifics, *H. ebraccata* and *H. microcephala* were determined by playing recorded natural vocalizations to individual calling males. We tried to work with relatively isolated frogs and sometimes removed neighboring conspecific and heterospecific males before beginning a test. The characteristics of stimulus calls are shown in Table 1. 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. phlebodes*. The same natural playback stimuli were used in our work with *H. ebraccata* (Schwartz and Wells, 1984*a*; Wells and Schwartz, 1984*a,b*) and *H. microcephala* (Schwartz and Wells, 1984*b*). We recorded each frog for 1.0 min before stimulus presentations began, and usually for 1.0 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.

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 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 of 85, 90 and 100 dB SPL. Usually, order of presentation was from lowest to highest intensity. The modal SPL of *H. phlebodes* calls was 103 dB at 50 cm in front of the frogs (Schwartz and Wells, 1984*a*), so these playback intensities are roughly equivalent to separations between males of 400, 220 and 70 cm.

Tape recordings were analyzed with a Tektronix 5111 storage oscilloscope. For each test, we determined the types of calls given and time (±80 ms) from the onset of the stimulus to each response. The durations of call notes were measured to the nearest 8 ms. Dominant frequencies of calls were determined with a Uniscan model 4500 spectrum analyzer (Unigon Industries). We have presented more extensive data on the durations, rise times, pulse repetition rates, and frequency spectra of calls of *H. phlebodes*, *H. ebraccata* and *H. microcephala* elsewhere (Schwartz and Wells, 1983*a*).

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). In all tests, $\alpha = 0.05$ was considered significant. When one-tailed tests were used, it was because observations of natural interactions indicated that males increased calling rate, multi-note calls, and aggressive calls in response to the calls of other males.

RESULTS

Vocal Repertoire

The calls of *H. phlebodes* have a dominant frequency of almost 4 kHz ($\bar{x} = 3708$ Hz, CV = 4.9, $n = 50$). Advertisement call introductory notes have a median duration of 68 ms (range = 42–94, $n = 50$), and a median pulse repetition rate of 164/s (range = 147–192, $n = 50$). Median duration and pulse repetition rate of aggressive call introductory notes are 282 ms (range = 46–752, $n = 106$) and 247 pulses/s (range = 101–409, $n = 106$). Secondary click notes of both advertisement and aggressive calls have a median duration of 38 ms (range = 24–56, $n = 218$). Oscillograms of representative calls are shown in Fig. 1.

Calling Rate

Calling rates of *H. phlebodes* males ranged from 5–22 calls/min (median = 13) during no-stimulus periods. Median calling rates were elevated slightly during presentation of all playback stimuli (pooled volumes) except the conspecific aggressive calls. However, the increase was statistically significant only for conspecific and

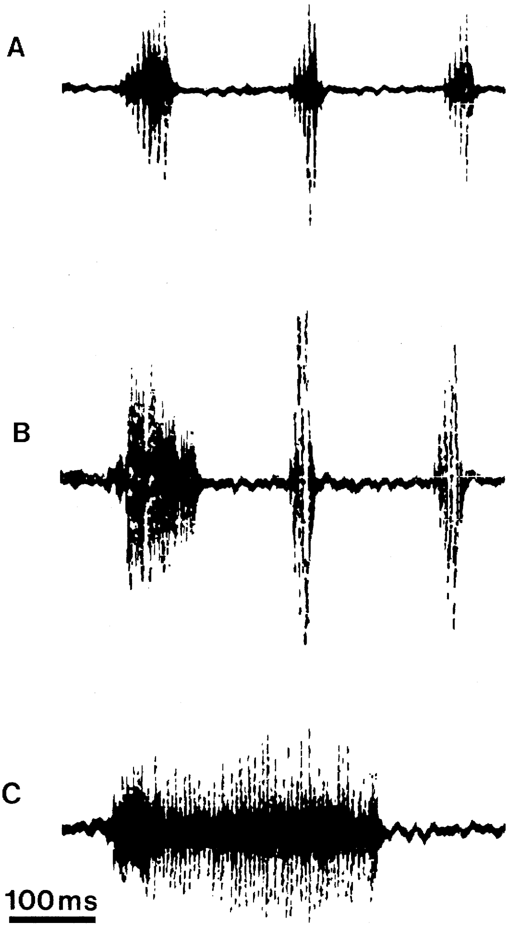

FIG. 1.—Oscillograms of a three-note advertisement call (A), and aggressive calls with short (B) and long (C) introductory notes. Note the higher pulse repetition rate of the aggressive calls.

H. ebraccata advertisement calls (one-tailed Wilcoxon matched-pairs signed-ranks test, $P = 0.013$, 0.001, respectively) (Table 2). Calling rate was not significantly influenced by playback intensity for any stimulus (Kruskal-Wallis ANOVA, $P > 0.1$ for all tests).

Timing of Responses

H. phlebodes males gave synchronized responses (defined as any call falling within 1.0 s of stimulus onset) to both conspecific and heterospecific calls. Seventy percent of first advertisement calls given by males in response to playbacks of all stimulus calls were synchronized (modal response latency = 400 ms, median = 560 ms, $n = 3819$). First aggressive call responses had greater delay times than advertisement calls (mode = 880 ms, median = 2400 ms, $n = 111$) (two-tailed Wilcoxon rank sum test, $P < 0.0001$) and only 13% were given synchronously. The percent of stimulus calls followed by a synchronized response was defined as the percent synchrony. The *H. ebraccata* one-note advertisement call at 90 dB SPL elicited the lowest percent synchrony (median = 28%), while the conspecific advertisement call at 90 dB elicited the highest percent synchrony (median = 93%). While synchrony was generally high to all conspecific calls, 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 parameters (introductory note duration, proportional rise time, pulse repetition rate, and number of notes) as independent variables explained only 23% of the total variation in percent synchrony.

During natural interactions with conspecific and heterospecific males, *H. phlebodes* also gave synchronized responses. Modal and median latencies to the first response were 240 and 320 ms during interactions with conspecifics ($n = 319$ calls, six males), 240 and 400 ms during interactions with *H. ebraccata* ($n = 88$ calls, two males), and 320 and 320 ms during an interaction with *H. microcephala* ($n = 36$ calls, one male). Many calls overlapped during these interactions, but individual notes usually did not (Fig. 2). In a sample of 62 overlapped conspecific calls, there was no overlap of notes in 58 cases, overlap of some notes in two, and overlap of all notes in two. Notes seldom overlapped mainly because inter-note intervals ($\bar{x} = 156$ ms, SD = 22.2, $n = 221$) are longer than either introductory ($\bar{x} = 68$ ms) or secondary ($\bar{x} = 38$ ms) notes of advertise-

TABLE 2.—Calling rates (calls/min) of *H. phlebodes* males during no-stimulus periods (Nst) and playbacks 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	Nst	PAD3	PAG2	PAGL	MAD1	MAD3	MAGL	EAD1	EAD3	EAG2	EAGL
1	12.0	15.6	13.2	13.8	—	9.6	13.2	—	—	10.8	—
2	13.2	13.2	12.6	13.2	—	6.6	7.8	—	22.8	—	20.4
3	18.0	28.8	17.4	18.0	—	13.2	16.8	—	19.2	—	17.4
4	11.4	15.6	—	—	—	—	—	—	18.0	—	12.0
5	22.2	—	21.6	19.8	—	23.4	24.6	—	24.0	—	18.6
6	9.6	16.2	10.2	7.8	—	—	—	—	17.4	—	16.2
7	10.2	12.0	8.4	9.0	—	—	—	—	23.4	—	12.6
8	13.8	18.0	13.8	7.2	18.6	18.6	19.8	—	—	—	—
9	18.6	—	—	—	10.2	—	—	22.2	24.0	21.6	14.4
10	15.0	9.0	—	—	15.0	16.2	19.2	21.6	15.6	16.8	15.6
11	7.2	11.4	—	—	—	—	8.4	14.4	16.8	13.8	10.2
12	13.8	15.0	12.6	—	12.0	9.0	14.4	13.8	14.4	14.4	16.2
13	13.2	15.0	12.6	—	22.2	20.4	24.0	10.8	16.2	9.0	4.2
14	4.8	20.4	16.2	—	—	—	—	9.6	10.2	8.4	8.4
Median	13.2	15.3	12.9	13.2	15.0	14.7	16.8	14.1	17.7	13.8	15.0
P		0.013	NS	NS	NS	NS	NS	NS	0.001	NS	NS

ment calls. Males did not lengthen the intervals between notes when their calls overlapped those of other males.

Multi-note Calling

The number of notes per call and the proportion of calls with more than one note were used as measures of multi-note calling. During the no-stimulus periods, 38% of all calls given by males were multi-note calls (range = 15–61%). Males significantly increased the proportion of multi-note calls in response to the *H. ebraccata* short aggressive call, the *H. microcephala* three-note advertisement call, and all conspecific stimuli (*G*-test, $P < 0.01$, responses pooled for different males) (Table 3). If only synchronized responses are considered, significant increases occurred for all stimuli except the *H. ebraccata* and *H. microcephala* one-note advertisement calls (*G*-test, $P < 0.01$). The proportion of multi-note calls was significantly lower for non-synchronized than synchronized responses for eight of 10 stimuli (Table 3).

When latencies to the first response are broken into six 1.0 s intervals, there are significant differences in number of notes per call (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 responses than in those with greater delay times (nonparametric multiple comparisons, Noether, 1976; $P < 0.05$) (Fig. 3). When the entire 6 s post-stimulus time period is considered, males significantly increased the number of notes per call only in response to two conspecific stimuli (one-sided Wilcoxon matched-pairs signed-ranks test, $P < 0.01$ for both tests). However, when only synchronized responses are considered, males gave significantly more notes per call to eight of 10 stimuli (one-tailed Wilcoxon matched-pairs signed-ranks test, $P < 0.05$), including all conspecific calls.

Occasionally stimulus calls were broadcast as a frog was giving a call. Interrupted calls had more notes than non-interrupted calls for all playback stimuli (one-sided Mann-Whitney *U*-test, $P < 0.01$) (Fig. 4). This could be due to the addition of click notes to interrupted calls, an increased chance that long calls would be interrupt-

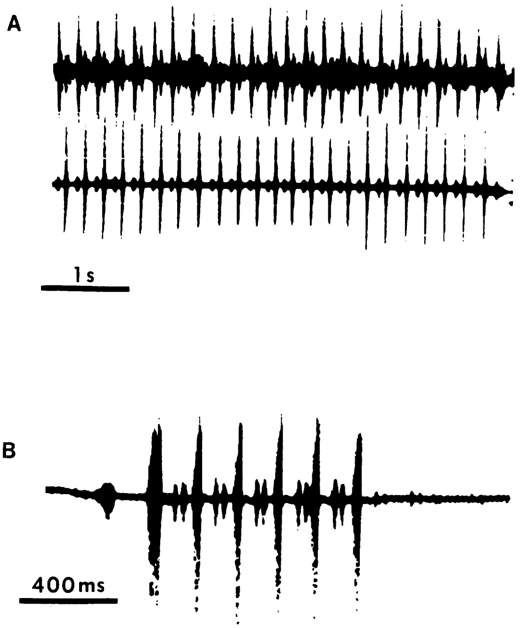

FIG. 2.—(A) Oscillogram of overlapping long multi-note advertisement calls of two *H. phlebodes*. (B) Oscillogram of a six-note advertisement call response by a *H. phlebodes* to a six-note *H. microcephala* advertisement call.

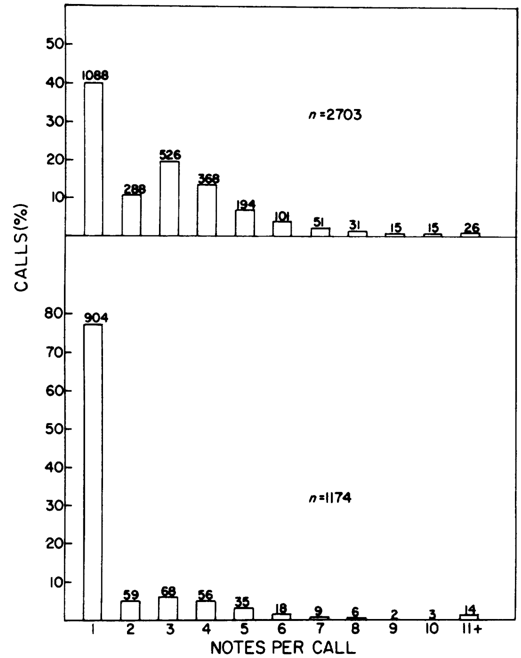

FIG. 3.—Distribution of number of notes in synchronized (above) and non-synchronized (below) first responses (responses to all stimuli are pooled).

ed, or both. The probability that calls would be interrupted was a function of their duration and frequency of occurrence. We calculated an expected frequency distribution of interrupted calls with different numbers of notes; when this distribution was compared with the actual distribution of interrupted calls, we found that males gave more notes in interrupted calls than expected by chance (data pooled for all stimuli; one-sided Mann-Whitney *U*-test, $P < 0.01$).

In natural interactions, male vocal behavior was similar to that during playback experiments. In three pairwise encounters between conspecifics (lasting a total of 10.5 min), all six frogs gave more notes in synchronized responses than non-synchronized responses. This result was significant

TABLE 3.—Proportion of multi-note calls given during no-stimulus periods (Nst) 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.

	PAD3	PAG2	PAGL	MAD1	MAD3	MAGL	EAD1	EAD3	EAG2	EAGL
Nst	0.34	0.36	0.34	0.46	0.38	0.38	0.44	0.38	0.42	0.38
All	0.56*	0.54*	0.44*	0.49	0.51*	0.38	0.46	0.41	0.55*	0.39
Syn	0.69*	0.64*	0.59*	0.52	0.66*	0.55*	0.54	0.47*	0.60*	0.59*
Nsyn	0.41†	0.43†	0.35†	0.48	0.42†	0.30†	0.43	0.38†	0.49†	0.32†

All vs. Nst or Syn vs. Nst: * $P < 0.05$.
Nsyn vs. Syn: † $P < 0.05$.

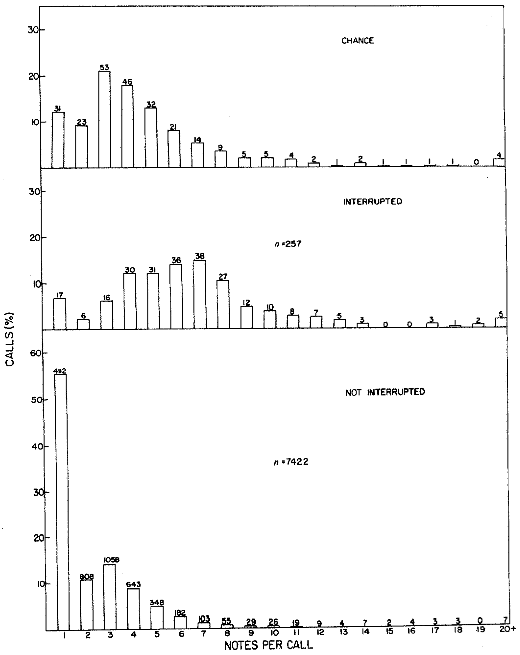

FIG. 4.—Number of notes in interrupted and non-interrupted calls. Also shown is the expected distribution based on chance alone (see text). Data are pooled for all males. Sample sizes are given above each bar.

for three males (one-tailed Wilcoxon rank sum test, $P < 0.02$). In one of the two interactions recorded with a *H. ebraccata* and another with a *H. microcephala*, *H. phlebodes* males behaved the same way. In the three conspecific interactions, there was a positive correlation between the number of notes in synchronized calls given by the two males (Spearman rank correlation, $r_s = 0.39$, $P < 0.0001$). This correlation was due largely to the tendency of males to add secondary notes to calls that were interrupted. Two frogs frequently produced a long series of alternating call notes (Fig. 2A). The number of notes in overlapping calls was highly correlated for three of the six males (r_s = 0.87, 0.93, 0.95; $P < 0.01$ for each male); correlations were positive for the remaining three, but not significant.

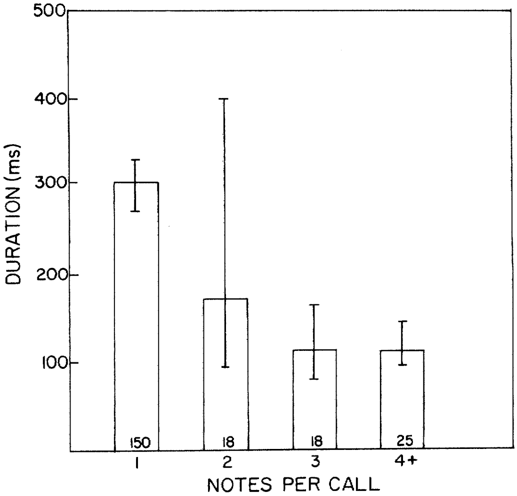

FIG. 5.—Durations of the introductory notes of aggressive calls with different numbers of notes. Data are presented as medians with approximate 95% confidence intervals. Sample sizes are given at the bottom of each bar.

Aggressive Call Responses

H. phlebodes males rarely gave aggressive calls during playback tests. The only stimulus that elicited a significant response in the proportion of aggressive calls was the conspecific advertisement call at 100 dB SPL (one-tailed Wilcoxon matched-pairs signed-ranks test, $P < 0.004$) (median proportion of aggressive calls among males tested = 0.36, range = 0.06–0.83). The median proportion of aggressive calls for each of the other stimulus presentations and during no-stimulus periods was 0.00. At 100 dB SPL, aggressive calls were given by eight males to the conspecific advertisement call, by three males to the short conspecific aggressive call, by one male to the long conspecific aggressive call, and by two males to the long *H. ebraccata* aggressive call.

Aggressive calls of *H. phlebodes* varied considerably in introductory note duration, pulse repetition rate, and rise time. Long calls had lower pulse repetition rates and slower proportional rise times than short calls (Schwartz and Wells, 1984*a*). There also was a low but significant neg-

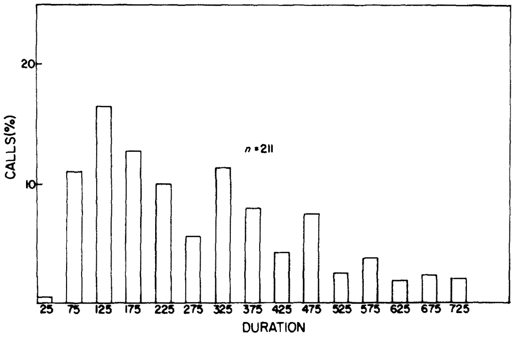

FIG. 6.—Durations of the introductory notes of aggressive calls given by males ($n = 23$) during all no-stimulus periods, playback tests, and natural interactions.

ative correlation between introductory note duration and the number of secondary click notes in a call ($r = -0.39$, $P < 0.0001$; correlation coefficients obtained for 13 frogs were judged homogenous; $\chi^2 = 7.56$, $P > 0.5$ and a combined estimate was obtained using the z-transformation, Sokal and Rohlf, 1969) (Fig. 5). The duration of introductory notes of aggressive calls ranged from 48–928 ms (median = 248) (Fig. 6). Males gave aggressive calls with significantly longer introductory notes to stimuli presented at high intensity than at low intensity (two-tailed Wilcoxon rank sum test, $P < 0.0001$) (Fig. 7). Long aggressive calls predominated in a 95 s agonistic encounter between two males about 45 cm apart; introductory note durations were 104–704 ms ($\bar{x} = 336$, SD = 140, $n = 26$).

DISCUSSION

Our work with *H. phlebodes* shows that males modify their calling behavior in response to the vocalizations of both conspecific and heterospecific males. These changes involve both the type and timing of calls and are similar to behavior observed in *H. ebraccata* and *H. microcephala* males (Schwartz and Wells, 1984*a*,*b*; Wells and Schwartz, 1984*a*,*b*). We believe this similarity is largely a reflection of the common problems that individuals of these and other chorusing species share in effectively communicating in a noisy environment (Greenfield and Shaw, 1983).

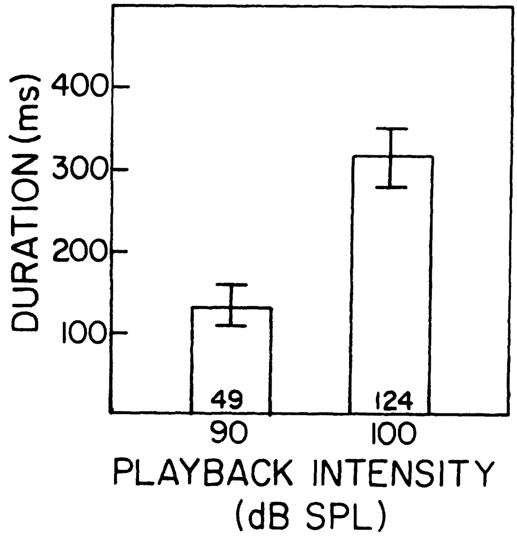

FIG. 7.—Durations of aggressive call introductory notes given to all conspecific stimuli at different playback intensities. Data are presented as medians with approximate 95% confidence intervals. Sample sizes are given at the bottom of each bar. Significance levels are for a Kruskal-Wallis ANOVA.

Calling Rates

Many species of chorusing frogs elevate calling rate in response to the vocalizations of other individuals (Lemon, 1971; Passmore, 1978; Ramer et al., 1983; Rosen and Lemon, 1974; Schwartz and Wells, 1984*a*,*b*; Wells, 1977*a*). *H. phlebodes* males increased calling rates significantly only to two stimuli, and in neither case were these elevations dramatic. During playback experiments, changes in calling rate were largely a product of *H. phlebodes* males responding with synchronized calls to individual vocalizations in the stimulus broadcasts. Since calling rates of all but three males were higher during the no-stimulus periods than the broadcast rate of stimulus calls, our results are not surprising. The three individuals with no-stimulus calling rates below 10 calls/min did increase their call frequency during 17 out of 18 stimulus presentations to which they were exposed. *H. ebraccata* and *H. microcephala* often elevated calling rates in response to calls of other males, and we speculate that males with high calling rates may be preferred or more easily located by females.

Timing of Responses

A common response of *H. phlebodes* males to conspecific and heterospecific stimuli was synchrony of their advertisement calls. This also was true for *H. ebraccata* and *H. microcephala*. In the case of *H. ebraccata*, stimulus duration explained most of the variation in percent synchrony to natural and synthetic calls (Schwartz and Wells, 1984*a*). However, multiple linear regression failed to identify a call feature that strongly influences this response in *H. phlebodes*. Results were similar to data for *H. microcephala*. All call stimuli presented to these two species were longer than the median duration of the introductory notes of their advertisement calls. This was not so for playbacks to *H. ebraccata* males. We suspect that duration might explain variation in synchrony by *H. microcephala* and *H. phlebodes* to stimuli shorter than those used in this study.

The temporal association between vocalizations of different individuals has been studied in many species. Alternation or synchronization of signals is common in anurans (Awbrey, 1978; Lemon, 1971; Lemon and Struger, 1980; Loftus-Hills, 1974; Passmore, 1978; Rosen and Lemon, 1974; Schwartz and Wells, 1983*a*, 1984*a*,*b*; Zelick and Narins, 1982), birds (Gochfeldt, 1978; Hultsch and Todt, 1982; Todt, 1970; Wasserman, 1977) and insects (Alexander, 1975; Greenfield and Shaw, 1983; Otte, 1977) and have been interpreted as mechanisms to reduce acoustic interference. In *H. phlebodes*, call synchrony probably functions in a similar way. If responses are timed so that introductory notes fall either after or in intervals between the notes of a neighbor's calls, then individual notes rarely overlap. Because inter-note intervals are much longer than notes, acoustic interference of this kind is unlikely even for long multi-note calls. In *H. microcephala*, call notes of interacting males also rarely overlap. However, in this species, males further reduce the chance of acoustic interference by lengthening the intervals between notes in overlapping calls, a response we did not observe in *H. phlebodes*. In *H. ebraccata*, synchronized responses to multi-note calls frequently result in masking of secondary notes of one male by the introductory notes of another. This occurs because advertisement call introductory notes are longer than inter-note intervals and males do not lengthen the intervals between notes (Wells and Schwartz, 1984*a*).

Synchronizing could benefit male *H. phlebodes* if females have difficulty detecting overlapped calls or locating their source. Males could benefit for the same reason by synchronizing to certain heterospecific vocalizations. For example, we recently demonstrated that female *H. ebraccata* discriminate against conspecific calls that are overlapped by either a background chorus or individual calls of *H. microcephala* (Schwartz and Wells, 1983*b*, 1984*a*). However, we suspect that synchrony by *H. phlebodes* males to heterospecific calls occurs primarily because these are similar to conspecific calls.

Multi-note Calling

H. phlebodes tend to add notes to calls that are interrupted or given immediately after the calls of conspecific and heterospecific males. In intraspecific interactions, this behavior frequently results in a pair of frogs producing overlapping calls of 15 or more notes (Fig. 2A). Males often appeared to add notes on a one by one basis, stimulated by individual notes in the other frog's calls. The behavior of *H. microcephala* is similar (Schwartz and Wells, 1984*b*). In one vocal exchange between *H. microcephala* and a *H. phlebodes*, males alternated individual call notes (Fig. 2B). In contrast, *H. ebraccata* rarely produces long multi-note calls, and interspecific vocal exchanges like these were not recorded.

Increases in call complexity during

acoustic interactions between males occur in many species of anurans (Arak, 1983*a*; Ramer et al., 1983; Rand and Ryan, 1981; Tuttle and Ryan, 1982; Wells and Schwartz, 1984*a*). Arak (1983*a*) reported that male *Philautus leucorhinus*, a Sri Lankan rhacophorid treefrog, respond to the multi-note calls of conspecifics by producing calls with equal numbers of notes. During the initial phase of vocal interactions, the number of notes per call usually increases, leading to the production of calls with up to eight notes. However, unlike *H. phlebodes* and *H. microcephala*, which often overlap calls, males of this species consistently alternate calls. Males of the Central American hylid *Smilisca sila* are also more likely to give complex calls in response to multi-note than single-note calls (Tuttle and Ryan, 1982).

The advantage to male *H. phlebodes* in adding notes to calls remains to be investigated. Rand and Ryan (1981) and Littlejohn and Harrison (1981) demonstrated that female *Physalaemus pustulosus* and *Geocrinia victoriana* prefer complex to simple calls in two-choice tests, and we obtained the same result with *H. ebraccata* (Wells and Schwartz, 1984*a*). Complex calls might allow females to assess "male quality" (Ryan, 1983) or to locate males more easily in a noisy chorus (Wells and Schwartz, 1984*a*) because highly stereotyped repetitious calls would provide maximum contrast with continuous background noise (Wiley, 1983). Data from the natural interactions suggest that long calls elicit long responses in *H. phlebodes* males. This could reflect a preference by females for males that produce either the longest call or the call that ends last. Such a preference might also explain production of long chains of notes in overlapping calls of interacting males. We believe the similar responses of males to heterospecific calls is due to the temporal and spectral similarity of these calls to their own.

Aggressive Calls

We observed relatively few aggressive interactions in *H. phlebodes* and hence recorded small samples of aggressive calls. During playback experiments, only one stimulus presentation effectively elicited aggressive calls from males: the conspecific advertisement call at 100 dB SPL. The dearth of natural agonistic encounters was due to the low density of calling males in our study site. On most nights, no more than three or four *H. phlebodes* were calling. The poor response to broadcasts of conspecific aggressive calls could have been due to our playback sequence. Usually, we presented advertisement calls before aggressive calls, since this corresponded to the natural sequence of events during interactions between males. The weaker response to aggressive calls might reflect habituation to the playbacks.

The gradual increase in the duration of introductory notes of aggressive calls in response to progressively louder stimuli, along with a drop in number of notes in long calls, is similar to the behavior of both *H. ebraccata* (Wells and Schwartz, 1984*b*) and *H. microcephala* (Schwartz and Wells, 1984*b*). Aggressive calls also show continuous variation in pulse repetition rate and rise time. These changes in aggressive calls suggest that *H. phlebodes* has a graded signaling system. However, more data are needed from playback experiments and natural encounters to test this prediction. We do not know how the temporal variation is perceived by males. Longer aggressive calls might signal a higher level of aggressive motivation. Alternatively, by trading aggressive calls, males might assess the physical strength of opponents (Wells and Schwartz, 1984*b*). A number of anuran species use one type of aggressive call in close-range encounters ("encounter calls") and another during less intimate interactions ("territorial calls," Littlejohn, 1977). Variation in *H. phlebodes* aggressive calls is such that their categorization as either "encounter" or "territorial" calls would be inappropriate. Arak (1983*a*) and Pengilley (1971) described aggressive calls in *Philautus leucorhinus* and Australian *Pseudophryne* which seem to be graded as well. Temporal variation appears continuous, and longer calls are given in closer interactions than shorter calls.

Aggressive calls of *H. microcephala, H. ebraccata* and *H. phlebodes* are more similar to one another in temporal structure than are their advertisement calls. *H. ebraccata* males respond to both conspecific aggressive calls and those of *H. microcephala* and *H. phlebodes* by giving high proportions of aggressive calls (Schwartz and Wells, 1984*a*). Male *H. microcephala* frequently interact aggressively with male *H. ebraccata,* although they do not exhibit strong responses to playbacks of heterospecific calls (Schwartz and Wells, 1984*b*). *H. phlebodes* gave relatively few aggressive calls to heterospecific calls, although some occasionally elicited aggressive responses. However, from our limited observations of aggressive interactions in this species, we cannot say whether interspecific agonistic encounters are a common occurrence. Observations in a population of higher density are needed to determine this.

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