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Author(s): Kentwood D. Wells and Joshua J. Schwartz

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

by

KENTWOOD D. WELLS and JOSHUA J. SCHWARTZ<sup>1</sup>)

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

(With 7 Figures)

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## Introduction

Males of many species of frogs defend their calling sites against conspecific males (WELLS, 1977). In most cases, aggressive behavior is accompanied by one or more kinds of vocalizations distinct from the advertisement call. We refer to these as aggressive calls. The purpose of this study was to investigate the ways in which the aggressive calls of a neotropical treefrog, *Hyla ebraccata*, are used in agonistic encounters, document the range of variation in temporal characteristics of the calls, and determine which characteristics are important in eliciting aggressive responses from males.

Usually the functions of anuran aggressive calls have been inferred from the contexts in which the calls occur (*e. g.*, CAPRANICA, 1968; EMLÉN, 1968; PENGILLEY, 1971; PIERCE & RALIN, 1972; WELLS, 1978, 1980; FELLERS, 1979; KLUGE, 1981; ODENDAAL *et al.*, 1983). However, experimental studies have shown that playbacks of either advertisement or aggressive calls may cause males to stop calling, give increased numbers of aggressive calls, make aggressive advances toward speakers, or retreat, with the response depending on the intensity of the stimulus (EMLÉN, 1968; WIEWANDT, 1969; ALLAN, 1973; ROSEN & LEMON, 1974; PASSMORE, 1978; WELLS, 1978; GAMBS & LITTLEJOHN, 1979; WHITNEY, 1980;

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BRZOSKA, 1982; BRZOSKA *et al.*, 1982; PERRILL *et al.*, 1982; ROBERTSON, 1982; TELFORD, 1982; RAMER *et al.*, 1983).

The advertisement calls of *H. ebraccata* consist of buzz-like introductory notes which may be given alone or followed by one or more secondary click notes. Males give mostly single-note calls when calling alone, but respond to the calls of other males by increasing the proportion of both multi-note and aggressive calls (WELLS & GREER, 1981; WELLS & SCHWARTZ, 1984). Aggressive calls have higher pulse repetition rates than advertisement calls and often are much longer. They may be given with one or more secondary click notes (Fig. 1). FOUQUETTE (1960) originally described these as "abnormal" calls because their functional significance was not understood. In a preliminary study (WELLS & GREER, 1981), two types of aggressive calls were described. Those with short introductory notes were given mainly when males were some distance apart, whereas those with long introductory notes were given mainly in close-range interactions. In the present study, we show that these calls actually represent ends of a continuum which may constitute a functionally graded signaling system.

## 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, close to the Panama Canal. Male frogs called from elevated perches in vegetation or from the ground near pools of water and usually were about 1-2 m apart. We did field work between 1930 and 2330 hours, after which calling usually subsided. 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 on any given night. Relative humidity ranged from 86 to 100% ( $\bar{x}$  = 95.5, SD = 2.8). This climatic stability allowed us to ignore temperature-related changes in temporal features of calls in our experiments.

### 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. 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  $\pm 3$  dB from 1.1 to 14.5 kHz. We positioned the speaker so there was little or no vegetation between the speaker and the test frog. 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  $\mu$ Pa) at 1 m with a random incidence microphone. 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 (the modal intensity of calls measured in the field was 100 dB at 50 cm in front of the frogs; WELLS & SCHWARTZ, 1984).

### Playbacks of natural calls.

We made stimulus tapes of natural calls by 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 ( $x = 11.3$ ,  $N = 60$ ). Four natural call stimuli were used: a single-note advertisement call (stimulus A), a three-note advertisement call (stimulus B), a three-note aggressive call with a short introductory note (stimulus C), and a two-note aggressive call with a long introductory note (stimulus D). Temporal features of these calls are given in Table 1. Stimulus A and B are illustrated in WELLS & SCHWARTZ (1984); stimulus C and D resemble calls shown in Fig. 1A and C. Twelve males were tested with stimulus A, and 11 of these also were tested with stimulus B. Ten males were tested with both stimulus C and D; four of these had been tested with stimulus A and B, while the other six were different males. When more than one stimulus was presented to the same male, all presentations were made within a 2-h period.

TABLE 1. Temporal characteristics and dominant frequencies of natural call stimuli presented to males in playback experiments

Stimulus	Type	Notes	Duration* (ms)	Pulse rate* (Pulses/s)	Rise time* (ms)	Frequency (Hz)
A	Adv	1	188	96	92	3000
B	Adv	3	200	95	172	3080
C	Agg	3	150	365	88	3160
D	Agg	2	416	222	352	2960

\*) Measured for introductory notes only.

In playback experiments with natural call stimuli, each male was recorded for 1 min without a stimulus tape, or until he had given at least 10 calls. Two-minute stimulus playbacks were then interspersed with 1-min no-stimulus periods until each stimulus had been presented at several intensities. Because loud playbacks sometimes caused males to stop calling and retreat, stimuli usually were presented in order of increasing intensity. In some cases, 100 dB playbacks were done first, followed by 85, 90, and 95 dB. The change in playback order did not appear to affect male responses, but sample sizes for 100 dB playbacks were too small to test this statistically. Because we did not find significant differences in calling behavior during no-stimulus periods, these were pooled for each male and used as a control for comparison with calling during stimulus presentations.

### Playbacks of synthetic stimuli.

Synthetic calls were used to investigate the importance of pulse repetition rate and rise time (time from call onset to maximum amplitude) in eliciting aggressive call responses. Synthetic calls were produced on a sound synthesizer described in GERHARDT (1974, 1978a). These were band-pass filtered with a Krohn-Hite 3550 filter to remove any harmonic distortion produced by the synthesizer and then recorded on a ReVox A77 tape recorder at a rate of 10 calls/min. Four synthetic stimuli were used: fast pulse/fast rise time (FPFR), fast pulse/slow rise time (FPSR), slow pulse/fast rise time (SPFR), and slow pulse/slow rise time (SPSR). All calls were 300 ms long, approximately the length of an average aggressive call. Pulse rates were 95 pulses/s for slow pulse calls and 240 pulses/s for fast pulse calls, corresponding to rates for natural advertisement and aggressive calls respectively. Rise times were 125 ms for fast rise calls and 300 ms for slow rise calls.

Because background noise levels varied from night to night, playback intensities for synthetic stimuli had to be adjusted for each frog. If playback intensities were too low, males would give synchronized advertisement calls within 1.0 s of stimulus onset, but would not give aggressive calls. If playback intensities were too high, males would give nothing but aggressive calls to all stimuli. In most experiments, playbacks were started at 90 dB. If a male synchronized with all stimuli but gave very few aggressive calls, the intensity was raised to 95 dB. If he gave mostly aggressive calls to stimuli at 90 dB, the intensity was lowered to 85 dB. All stimuli presented to the same individual were played at the same intensity. Order of presentation was randomized. In these experiments, we compared responses to different stimulus tapes, but we did not compare calling behavior with and without stimulus tapes. 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. However, 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.

#### Analysis of recordings.

The number of advertisement and aggressive calls given during no-stimulus and stimulus periods was determined by listening to the tape or by making a visual record on a Heath SR 206 two-channel strip-chart recorder. We used a Tektronix 5111 storage oscilloscope to measure call note durations ( $\pm 8$  ms), pulse repetition rates, and rise times. Data were analyzed by computer with SAS statistical packages (SAS Institute, Inc., Cary, N.C., 1982), following standard parametric (SOKAL & ROHLF, 1969) and non-parametric (SIEGEL, 1956) techniques.

## Results

### Temporal characteristics of aggressive calls.

The advertisement calls of *H. ebraccata* are highly stereotyped, with little variation within or among individuals in dominant frequency, introductory note duration, pulse repetition rate, and rise time (WELLS & SCHWARTZ, 1984). Although the dominant frequencies of aggressive calls are similar to those of advertisement calls (about 3 kHz; WELLS & GREER, 1981), aggressive calls are much more variable in all temporal characteristics (Table 2). While nearly all introductory notes of advertisement calls are less than 210 ms long (WELLS & SCHWARTZ, 1984), aggressive call introductory notes range from 120 to 664 ms. In a sample of 156 aggressive calls recorded from 10 males, rise time was positively correlated with introductory note duration ( $r_s = 0.34$ ,  $p < 0.0001$ ), while pulse repetition rate was negatively correlated with note duration ( $r_s = -0.61$ ,  $p < 0.0001$ ). Examples of calls with different durations, pulse rates, and rise times, all recorded from the same individual on the same night, are shown in Fig. 1.

The number and type of click notes in aggressive calls also was related to the duration of the introductory note. In general, as the duration of the introductory note increased, the number of click notes in a call decreased

TABLE 2. Comparison of temporal characteristics of advertisement and aggressive calls of *H. ebraccata*

Temporal feature	Advertisement calls				Aggressive calls			
	N <sub>F</sub>	N <sub>C</sub>	Mean	CV	N <sub>F</sub>	N <sub>C</sub>	Mean	CV
Duration (ms)	11	1622	178 (96-240)	12	—*)	576	280 (120-664)	38
Pulse rate (Pulses/s)	8	574	94 (85-110)	6	10	156	291 (157-461)	21
Rise time (ms)	5	50	131 (100-156)	10	10	156	179 (36-640)	60
Prop. rise time	5	50	0.73 (0.54-0.92)	10	10	156	0.70 (0.11-0.93)	22

\*) Aggressive call durations from recordings of natural interactions only. Number of individual males not known.

N<sub>F</sub> = number of frogs. N<sub>C</sub> = number of calls. CV = coefficient of variation. Prop. rise time = rise time expressed as a proportion of call duration. Ranges are in parentheses.

(Fig. 2;  $P = 0.0001$ , Kruskal-Wallis ANOVA). Nearly all three and four-note calls had short introductory notes, but one-note calls ranged from very short to very long. The click notes of advertisement calls were nearly always biphasic, with a pause of a few milliseconds between two groups of pulses (see oscillograms in WELLS & SCHWARTZ, 1984). Click notes of aggressive calls were either biphasic or monophasic (Fig. 1). The number of pulses in either type of click note was inversely related to the duration of the introductory note (Fig. 3;  $P = 0.0001$ , Kruskal-Wallis ANOVA).

The distribution of introductory note durations for aggressive calls recorded during natural encounters is continuous, without clear breaks between distinct types of calls. The calls form a graded series exhibiting gradual change in introductory note duration, pulse rate, rise time, and number and duration of click notes (Fig. 1). In natural interactions between males, the duration of the introductory note increased as the distance between males decreased (Fig. 4;  $P = 0.0001$ ; Kruskal-Wallis ANOVA). Calls given during very close range encounters (< 15 cm) had introductory notes over twice as long, on average, as calls given in long-range interactions (> 120 cm). In addition, as the distance between males decreased, there was a gradual shift from aggressive calls with mostly three or four notes to calls with only one or two notes. This shift was statistically significant (G-test of independence comparing proportions of calls with 1, 2, or 3-4 notes,  $G = 122.01$ , 4 df,  $p < 0.001$ ). In our

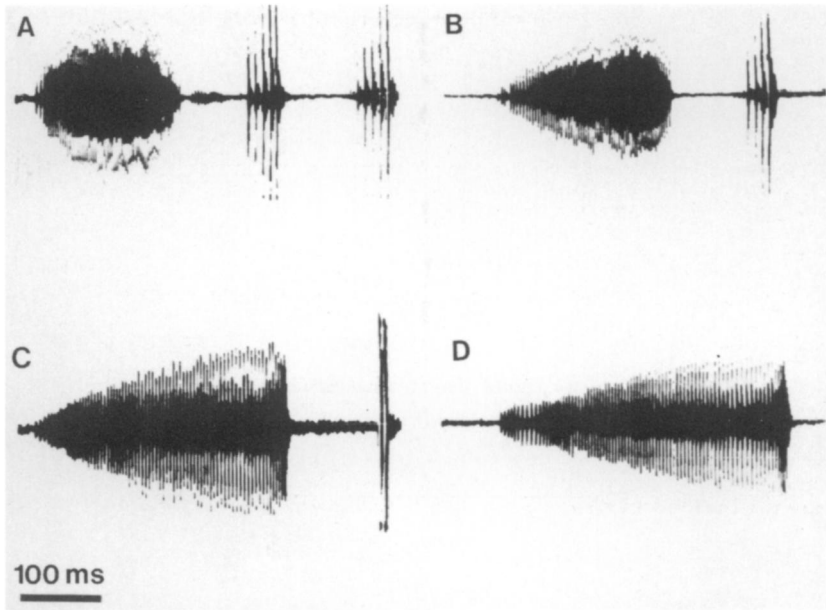


Fig. 1. Oscillograms of four aggressive calls given by the same individual on the same night. A) 3-note call with short introductory note. B) 2-note call with intermediate introductory note. C) 2-note call with long introductory note and short click. D) 1-note long call. Pulse repetition rates decrease with increasing call duration, while rise times increase. In playback experiments, stimulus C was similar to (A); stimulus D was similar to (C).

playback experiments, we used the proportion of aggressive calls, the duration of introductory notes, and the number of notes per call as behavioral assays of the level of aggressiveness in a male's response.

#### Responses to natural call stimuli.

Most advertisement calls given in response to call playbacks are closely synchronized with the stimulus (WELLS & SCHWARTZ, 1984), but aggressive call responses are not (Table 3). There were six 1.0 s periods between stimulus calls, so the proportion of calls expected to fall within 1.0 s of the stimulus if calls were given at random is 16.7%. When responses to all four natural call stimuli were pooled, 63% of advertisement calls ( $N = 2630$ ) fell in the first 1.0 s ( $\chi^2 = 3368$ ,  $P < 0.001$ ), but only 17.3% of aggressive calls ( $N = 730$ ) fell in that period ( $\chi^2 = 0.13$ ,  $P > 0.70$ ).

Males gave significantly more aggressive calls during playbacks of all stimulus tapes than during no-stimulus periods (Fig. 5). The proportion

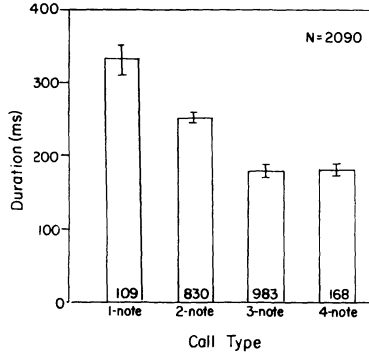


Fig. 2. Duration of introductory notes of aggressive calls in relation to the number of notes in the call. Bars show means  $\pm$  2 SE. Sample sizes are given at the bottom of each bar.

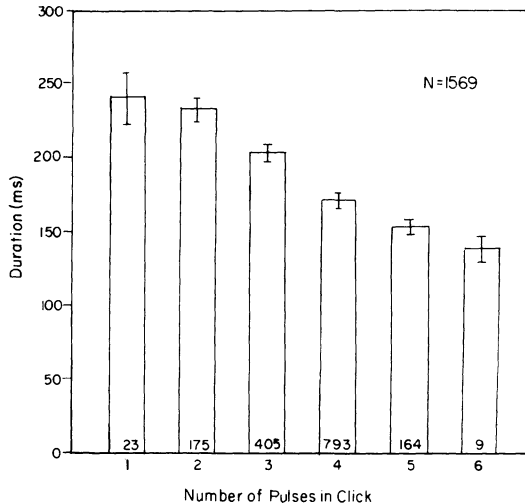


Fig. 3. Duration of introductory notes of aggressive calls in relation to the number of pulses in click notes. When a call had click notes with different numbers of pulses, the click with the largest number of pulses was used. Bars show means  $\pm$  2 SE. Sample sizes are given at the bottom of each bar.

of aggressive calls increased with increasing playback intensity for all stimuli, but the increase was statistically significant only for stimulus B (one-tailed Wilcoxon matched-pairs signed-ranks test, 90 vs 95 dB,  $P < 0.05$ ) and stimulus C (Friedman two-way ANOVA,  $\chi^2 = 9.00$ , 3 df,  $P < 0.05$ ). When responses of all males to playback intensities of 90-100 dB were pooled, there were significant differences in the proportion of ag-



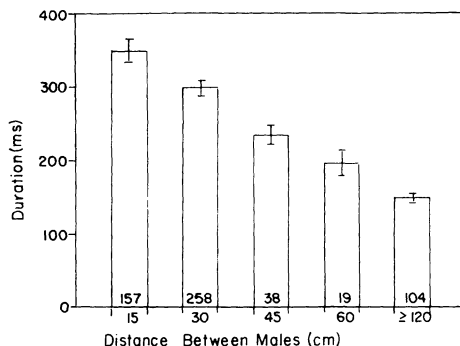


Fig. 4. Duration of introductory notes of aggressive calls given in natural interactions in relation to the distance between males. Bars show means  $\pm$  2 SE. Sample sizes are given at the bottom of each bar.

gressive calls given to different stimuli ( $G = 309.09$ , 3 df,  $P < 0.001$ ), with much higher proportions being given to the aggressive call stimuli.

There was a significant increase in the duration of aggressive call introductory notes with increasing playback intensity in response to stimulus A, C, and D (Kruskal-Wallis ANOVA,  $P = 0.0001$  for all tests), but not to stimulus B ( $P = 0.245$ ) (Fig. 6). The frogs almost never gave aggressive calls with introductory notes longer than 200 ms in response to advertisement call stimuli, but responses to aggressive calls sometimes exceeded 350 ms in length. A playback intensity of 100 dB was equivalent

TABLE 3. Proportion of advertisement and aggressive calls given within 1.0 s of the onset of a stimulus call in response to playbacks of advertisement calls (stimulus A, B) and aggressive calls (stimulus C, D)

Stimulus	$N_F$	$N_C$	Advertisement	$N_C$	Aggressive	P
A	12	1070	0.54 (0.24-0.98)	233	0.08 (0.00-0.29)	0.001
B	7	470	0.82 (0.39-1.00)	65	0.00 (0.00-0.58)	0.014
C	9	368	0.73 (0.40-0.92)	224	0.30 (0.06-0.50)	0.004
D	9	722	0.73 (0.61-0.94)	208	0.11 (0.00-0.27)	0.004

Data are presented as median proportions for all males responding to playbacks at 85-95 dB SPL. Ranges are given in parentheses.  $N_F$  = number of frogs.  $N_C$  = number of calls. P values are for one-tailed Wilcoxon matched-pairs signed-ranks tests.

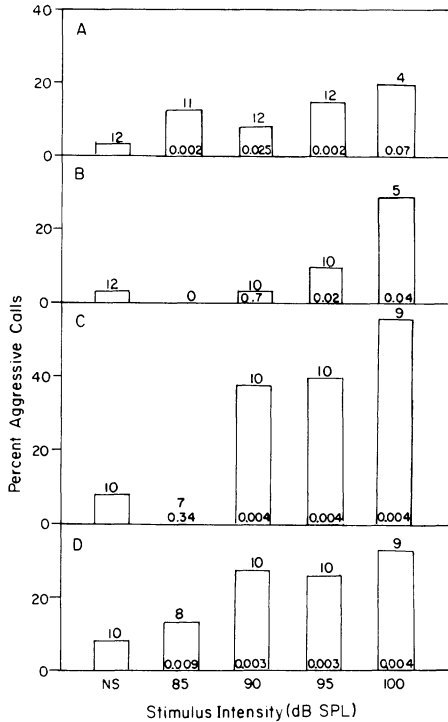


Fig. 5. Percent aggressive calls given in response to the four natural call stimuli at different playback intensities. Data show the number of aggressive calls given during stimulus presentations expressed as a percent of total calls given. Bars show median values for all males. Numbers at tops of bars show number of males tested. P values at bottom of each column are for one-tailed Wilcoxon matched-pairs signed-ranks tests comparing percent of aggressive calls during stimulus presentations with no-stimulus (NS) periods.

to a separation between males of about 50 cm. The mean duration of aggressive calls given in response to stimulus C and D at this intensity (200-210 ms) was similar to that predicted from data on natural aggressive interactions (Fig. 4).

Males gave virtually no single-note aggressive calls in response to advertisement calls, and 80% of the responses had three or four notes. In contrast, males gave substantial numbers of one and two-note calls in response to aggressive call stimuli. When responses of all males at 90-100 dB were pooled, there were significant differences among stimuli in the proportion of 3- or 4-note calls ( $G = 78.56$ , 3 df,  $P < 0.001$ ). There was no significant difference between stimulus A and B ( $G = 2.87$ , 1 df,  $P > 0.05$ ), but a significantly higher proportion of 3- or 4-note calls was given to stimulus D than to stimulus C ( $G = 24.20$ , 1 df,  $P < 0.001$ ).

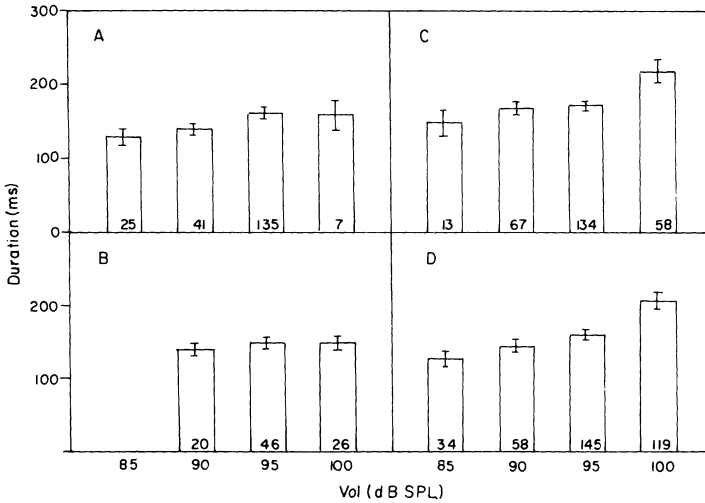


Fig. 6. Duration of the introductory notes of aggressive calls given in response to the four natural call stimuli at different playback intensities. Bars shows means  $\pm$  2 SE, with data pooled for all males. Sample sizes are given at the bottom of each bar.

Responses to synthetic call stimuli.

Thirteen males were presented with the four synthetic stimuli differing in pulse repetition rate and rise time. The temporal characteristics of the fast pulse/ slow rise stimulus (FPSR) most closely resembled a long aggressive call, fast pulse/fast rise (FPFR) resembled a short aggressive call, slow pulse/fast rise (SPFR) resembled an advertisement call, and slow pulse/slow rise (SPSR) was not very similar to any natural call, although the pulse rate was the same as that of an advertisement call. Males gave much higher proportions of aggressive call responses to calls with fast pulse rates than those with slow pulse rates (Fig. 7). A Friedman two-way ANOVA showed significant differences in the proportion of aggressive calls given to the different stimuli ( $\chi^2 = 14.91$ , 3 df,  $P < 0.01$ ). Order of stimulus presentation did not affect the proportion of aggressive calls (Friedman two-way ANOVA,  $\chi^2 = 1.11$ , 3 df,  $P > 0.70$ ). Males gave a significantly higher proportion of aggressive calls to FPSR than to FPFR (1-tailed Wilcoxon test,  $P = 0.03$ ), but there was no difference in the proportion of aggressive calls given to the two slow pulse stimuli ( $P = 0.16$ ).

The introductory notes of aggressive calls given in response to fast pulse calls were longer than those given to slow pulse calls. A Kruskal-Wallis ANOVA using pooled data for all frogs showed significant dif-

ferences in note duration among the four stimuli ( $P = 0.0001$ ). A nested parametric ANOVA with individual frogs entered as a random variable showed significant heterogeneity among individuals ( $F_{1,43} = 8.65$ ,  $P = 0.0001$ ). However, when the mean square term for individual frogs was used as an error term, there still was a significant effect of stimulus type ( $F_{1,3} = 8.68$ ,  $P = 0.0001$ ). Of the calls given in response to the fast pulse stimuli, 45-50% were over 250 ms long, whereas 95-100% of the calls given to the slow pulse stimuli were less than 250 ms long.

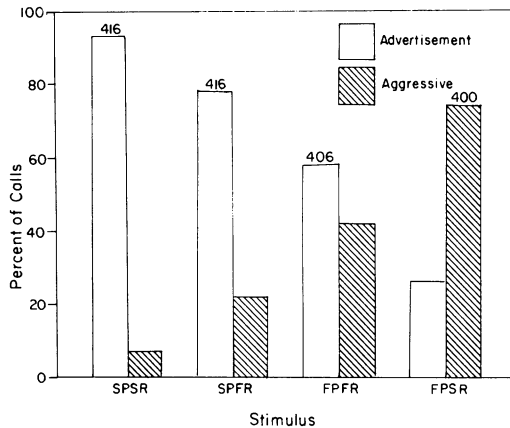


Fig. 7. Percent advertisement and aggressive calls given to the four synthetic stimuli. Bars show median values for 13 males. Total number of calls given in response to each stimulus is shown at the tops of the bars.

Males gave almost no single-note aggressive calls in response to any of the synthetic stimuli. Probably this was because these stimuli were played only at moderate intensities (85-90 dB). Responses to the two slow pulse stimuli were identical, with about 80% of the calls having three or four notes. These results were similar to those obtained with playbacks of natural advertisement calls. In contrast, more than 50% of the aggressive calls given to fast pulse stimuli were two-note calls. A Friedman two-way ANOVA using the seven males that gave aggressive calls to all stimuli showed significant differences among stimuli in the proportion of calls with three or more notes ( $\chi^2 = 14.66$ , 3 df,  $P < 0.01$ ). A G-test using pooled data for all 13 individuals produced the same result ( $G = 77.21$ , 3 df,  $P < 0.001$ ).

## Discussion

Aggression and changes in calling behavior.

Although male *H. ebraccata* sometimes engage in physical combat for possession of calling sites, spacing appears to be maintained mainly by vocal interactions. Fights occurred infrequently, and we never observed a male making aggressive approaches to a speaker during a playback experiment, as has been reported in other species (EMLEN, 1968; WIEWANDT, 1969; WELLS, 1978; GAMBS & LITTLEJOHN, 1979; WHITNEY, 1980; BRZOSKA, 1982; BRZOSKA *et al.*, 1982; RAMER *et al.*, 1983). A relatively low level of physical aggression seems to be characteristic of many hylids which maintain regular spacing in choruses but do not necessarily defend fixed territories night after night (FELLERS, 1979). In contrast, fighting seems to be more frequent, more prolonged, and more violent in anurans which defend resources such as oviposition sites (EMLEN, 1968; WIEWANDT, 1969; WELLS, 1978; HOWARD, 1978; KLUGE, 1981).

Our playback experiments with natural calls showed that males will give aggressive calls in response to both advertisement and aggressive calls, but aggressive calls were more effective in eliciting such responses. WHITNEY (1980) and PERRILL *et al.* (1982) reported that *H. regilla* and *H. cinerea* gave more aggressive calls to aggressive call stimuli, but in neither case was the difference statistically significant. GAMBS & LITTLEJOHN (1979) reported that male *Rana berlandieri* gave slightly higher proportions of aggressive calls to playbacks of advertisement calls than to aggressive calls, but sample sizes were too small for statistical comparisons. In the Australian leptodactylid *Uperoleia rugosa* (ROBERTSON, 1982) and in several European ranids (BRZOSKA, 1982), playbacks of both advertisement and aggressive calls elicited aggressive calls from males, but aggressive calls did so at a significantly lower playback intensity.

As we increased playback intensity, males gave higher proportions of aggressive calls, especially to aggressive call stimuli. This was expected, since increasing playback intensity mimics the approach of a neighboring male. Similar results were obtained by BRZOSKA *et al.* (1982) with *H. arborea savignyi* in Israel, by TELFORD (1982) with two species of *Hyperolius* in Africa, and by ROBERTSON (1982) with *Uperoleia rugosa*. Several studies have shown that spacing in frogs is related to the sound pressure level of neighboring males' calls (FELLERS, 1979; BRZOSKA *et al.*, 1982; ROBERTSON, 1982; WILCZYNSKI *et al.*, 1982). When the intensity of a neighbor's calls exceeds that expected at normal inter-male distances, a male often

switches from advertisement to aggressive calls. In some species, this tends to be an all-or-none response, with males switching from all advertisement calls to all aggressive calls (GAMBS & LITTLEJOHN, 1979; ROBERTSON, 1982; TELFORD, 1982; J. BRZOSKA, personal communication). In contrast, *H. ebraccata* males showed a more graded response, gradually increasing not only the proportion of aggressive calls, but also the duration of their introductory notes. Hence it was impossible to define a threshold at which males switch from advertisement to aggressive calling (*e.g.*, BRZOSKA, 1982).

### Critical features of aggressive calls.

Since it is pulse repetition rate which best distinguishes aggressive calls of *H. ebraccata* from advertisement calls (Table 2), we predicted that pulse rate would be most important in enabling a male to identify a call as an advertisement or aggressive call. Our playback experiments with synthetic calls supported this hypothesis; calls with fast pulse rates were much more effective in eliciting aggressive responses than those with slow pulse rates. Rise time also was important if calls had fast pulse rates, but not if pulse rates were slow.

We have not yet tested the responses of females to aggressive calls. We predict that calls with fast pulse rates may be somewhat attractive to females, but probably less so than those with slow pulse rates characteristic of advertisement calls. OLDHAM & GERHARDT (1975) found that female *H. cinerea* preferred aggressive calls of their own species to advertisement calls of *H. gratiosa*, but preferred conspecific advertisement calls over aggressive calls. By adding clicks to aggressive calls, a male *H. ebraccata* may be able to give female-attracting signals while simultaneously giving an aggressive signal to other males. We have found that advertisement calls with click notes are more attractive to females than single-note calls (WELLS & SCHWARTZ, 1984). It is particularly interesting that the most common type of aggressive call given in long-range interactions was a three-note call, whereas the most common type of advertisement call given in natural choruses or in response to playbacks was a two-note call (WELLS & SCHWARTZ, 1984). We speculate that males may compensate for a less attractive introductory note in aggressive calls by giving additional click notes. We plan to test this hypothesis in the future with playback experiments using synthetic vocalizations.

### Discrete *vs* graded signals.

The advertisement and aggressive calls of *H. ebraccata* are easily distinguished from one another, but it was not possible to identify distinct long-range and short-range aggressive calls, as originally expected (WELLS & GREER, 1981). Instead, the calls form a graded series exhibiting continuous variation in introductory note duration, pulse repetition rate, rise time, number of click notes, and duration of click notes. Our recordings of natural aggressive encounters showed that this variation is a function of the distance between interacting males, and hence the intensity of neighboring males' calls. We were able to confirm this experimentally by playing calls to males at different intensities. The changes in temporal features of calls given in response to playbacks closely paralleled those observed in natural encounters. Because of the graded nature of these calls, use of the terms "territorial calls" and "encounter calls" to distinguish long-range and short-range signals (LITTLEJOHN, 1977) is inappropriate for this species.

A major difficulty in interpreting a signaling system which appears to be graded is that we usually do not know how the animals perceive different signal variants. A signaling system may appear to vary continuously, but may be perceived categorically by the animals (GREEN, 1975; CHENEY & SEYFARTH, 1982). Alternatively, signals which appear to be distinct may be interpreted by the animals as functionally identical (GREEN & MARLER, 1979). Our experiments showed that males can distinguish between calls differing in gross temporal structure (pulse rate and rise time), and that they respond in a predictable manner to calls presented at different intensities. However, we have not tested their ability to discriminate between fine degrees of variation in call duration, pulse rate, or rise time within the range of natural aggressive calls. We do not know, for example, whether males will give longer aggressive calls as the duration of stimulus calls increases, independent of call intensity; in natural encounters, both call duration and call intensity increase as the distance between males decreases. Therefore, we cannot say at this point whether males give graded responses to graded changes in temporal structure.

The only direct test of the ability of frogs to discriminate among calls varying continuously in temporal structure is GERHARDT's (1978b) work with *H. cinerea*. He found that females could discriminate between sounds with only slight differences in temporal structure, and they appeared to process these sounds in a continuous rather than a categorical fashion.

Hence female *H. cinerea* have the ability to process information in a graded signaling system, even though that species has only discrete signals in its repertoire. Therefore, it seems likely that *H. ebraccata* can do so as well.

There have been few detailed quantitative analyses of the aggressive calls of other species of frogs, so it is not clear how widespread graded aggressive calls are in anurans. Our data on *H. microcephala* and *H. phlebodes*, although less complete than for *H. ebraccata*, indicate that these species also have graded aggressive calls, with introductory notes increasing in duration with decreasing distance between males (SCHWARTZ & WELLS, 1984 and unpublished data). Other frogs may have similar systems. For example, in the Sri Lankan rhacophorid *Philautus leucorhinus* (ARAK, 1983a) and Australian leptodactylids of the genus *Pseudophryne* (PENGILLEY, 1971), males have both long and short aggressive calls. The calls are structurally very similar and either overlap or nearly overlap in duration, suggesting that they are part of a continuously graded system. In both species, the longest calls are given in the closest or most intense encounters.

The function of graded aggressive calls in *H. ebraccata* remains obscure. One possibility is that graded calls indicate increasing levels of aggressive motivation or signal an increasing probability that a male will attack an opponent (MORTON, 1982). However, several authors have argued that an animal should not give reliable information about its motivation or the probability that it will attack an opponent (DAWKINS & KREBS, 1978; CLUTTON-BROCK & ALBON, 1980). Instead, aggressive signals might be used to advertise the size, vigor, or fighting ability of an individual. Many aggressive encounters would involve a prolonged and gradually escalating exchange of signals in which each individual attempted to assess the qualities of its opponent. Only when opponents were evenly matched would actual fighting occur (PARKER, 1974; MAYNARD SMITH & PARKER, 1976; RIECHERT, 1978; CLUTTON-BROCK & ALBON, 1980). Apparent assessment of body size of opponents based on the pitch of the call has been reported for several anurans (DAVIES & HALLIDAY, 1978; ROBERTSON, 1982; ARAK, 1983b; RAMER *et al.*, 1983), but assessment based on temporal features of calls has not been demonstrated. In the case of *H. ebraccata*, the ability to sustain production of very long aggressive calls might be related to the size or vigor of an individual. This hypothesis is purely speculative at this point, but we hope to test it in the future by comparing the duration of call notes and the persistence of aggressive calling in winners and losers of natural aggressive encounters.



## Summary

We studied the aggressive calls of *Hyla ebraccata* in Panama by recording natural interactions in the field and by playing recordings of natural and synthetic calls to males. Aggressive calls of this species had higher pulse repetition rates than advertisement calls and often were much longer. Aggressive calls also were much more variable in introductory note duration, pulse rate, rise time, and the number and structure of click notes. Pulse repetition rate was negatively correlated with the duration of the introductory note, as were the number of click notes in the call and the number of pulses in each click. In natural encounters, the duration of introductory notes increased as the distance between interacting males decreased. Males gave aggressive calls in response to playbacks of both advertisement and aggressive calls, but aggressive calls were much more effective in eliciting such responses. The proportion of aggressive calls and the duration of introductory notes generally increased with increasing playback intensity. Playbacks of synthetic calls which varied in pulse repetition rate and rise time showed that a high pulse repetition rate was the most important feature in eliciting aggressive responses from males, but rise time also was important when calls had fast pulse rates. The aggressive calls of this species appear to be a graded signaling system, the first to be documented in amphibians.

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