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Interspecific acoustic interactions of the neotropical treefrog *Hyla ebraccata*

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Summary. *Hyla ebraccata, H. microcephala* and *H. phlebodes* commonly occur together in Panama. The three species have calls exhibiting broad frequency overlap and call during the same season and time of day from similar microhabitats, frequently in close proximity. The vocal repertoires of the three species are structurally and functionally similar. All employ multi-part advertisement and aggressive calls which consist of a primary note followed by a variable number of clicks. *H. ebraccata* males often responded to heterospecific calls with multi-note synchronized responses, and calls with primary notes greater than 150–200 ms were most effective in eliciting synchrony. Playback experiments with synthetic 1-note advertisement calls of different durations and both synthetic 1-note advertisement calls and 200 ms tones of different frequencies demonstrated that *H. ebraccata* males will synchronize with stimuli which are similar in frequency and duration to conspecific calls. Data from a two-choice experiment with female *H. ebraccata* demonstrate that calls of individual *H. microcephala* can reduce the attractiveness of a *H. ebraccata* male's calls if primary notes overlap. By synchronizing response calls to those of *H. microcephala*, a *H. ebraccata* may reduce the chances that his calls are rendered less attractive to potential mates.

Aggressive calls of these species are graded and are characterized by higher pulse repetition rates and often longer durations than advertisement calls. *H. ebraccata* males respond to aggressive calls of *H. microcephala* and *H. phlebodes* as they do to their own calls. Heterospecific aggressive interactions probably occur because the species interfere acoustically. Our results demonstrate that *H. ebraccata* males behave in ways which enhance their ability to communicate in a noisy assemblage of conspecific and heterospecific males.

Introduction

Interspecific territoriality has been reported in a number of taxa, although most studies have focussed on birds (Cody 1974; Murray 1981) and fishes (Myrberg and Thresher 1974; Ebersole 1977). In areas where several species of frogs breed synchronously, interspecific agonistic encounters and exchange of acoustic signals between species may occur. There has been considerable research on species isolating mechanisms (Littlejohn 1977; Gerhardt 1981a, b, 1982), intraspecific territoriality, and agonistic behavior in anurans (Wells 1977). There also have been reports of spatial shifts by males (Wiewandt 1969; Allan 1973; Whitney and Krebs 1975) or temporal adjustments in their calling (Rosen and Lemon 1974; Loftus-Hills 1974; Awbrey 1978; Narins and Capranica 1978; Lemon and Struger 1980) in response to conspecific vocalizations. However, very little work has been done to document interspecific behavioral interactions. At least three kinds of interactions may occur: (1) choruses of some species may inhibit calling by another species or cause a shift in calling to reduce acoustic interference (Littlejohn and Martin 1969; Schwartz and Wells 1983a, b); (2) males of one species may respond to individual calls of another species by changing the timing of calls or the type of calls given (Passmore 1978; Brzoska 1982; MacNally 1982; Zelick and Narins 1982); (3) males may engage in interspecific aggressive encounters.

Littlejohn (1977) hypothesized that aggressive vocalizations might be utilized interspecifically if they shared similar features, and a small but growing body of information suggests that he was correct. Brief accounts of natural aggressive encounters between males of different species are available for Puerto Rican and Australian leptodactylids (Drewry 1970; Pengilley 1971), Pana-

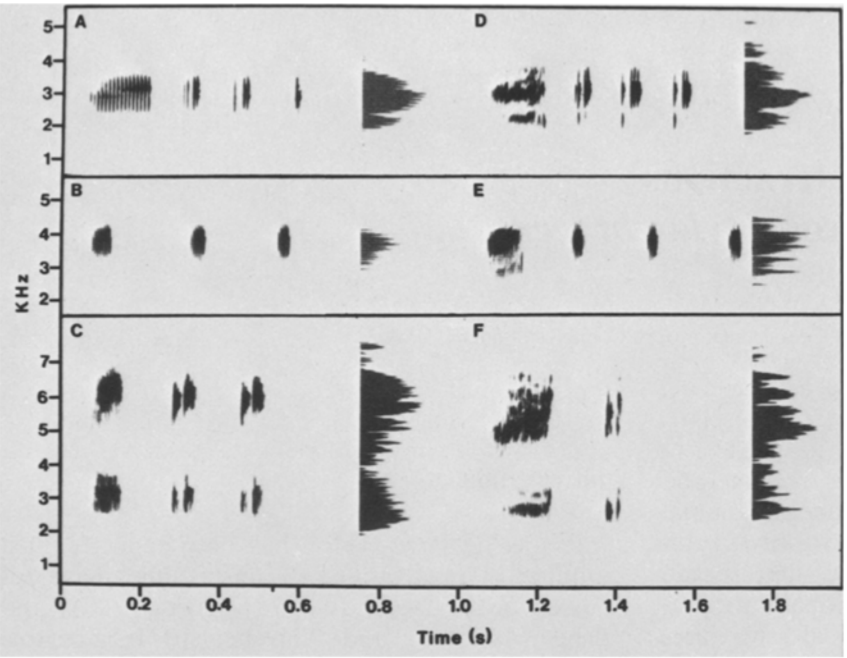

Fig. 1 A–F. Sonagrams of representative calls of *H. ebraccata* (*top*), *H. phlebodes* (*middle*), and *H. microcephala* (*bottom*) (wide band 300 Hz filter).
A–C Advertisement calls with secondary click notes.
D–F Aggressive calls with short primary notes given in response to playbacks of conspecific calls.
Sections, shown to the right of each call, were taken at the approximate midpoints of the primary notes. These show relative amplitude of energy at different frequencies

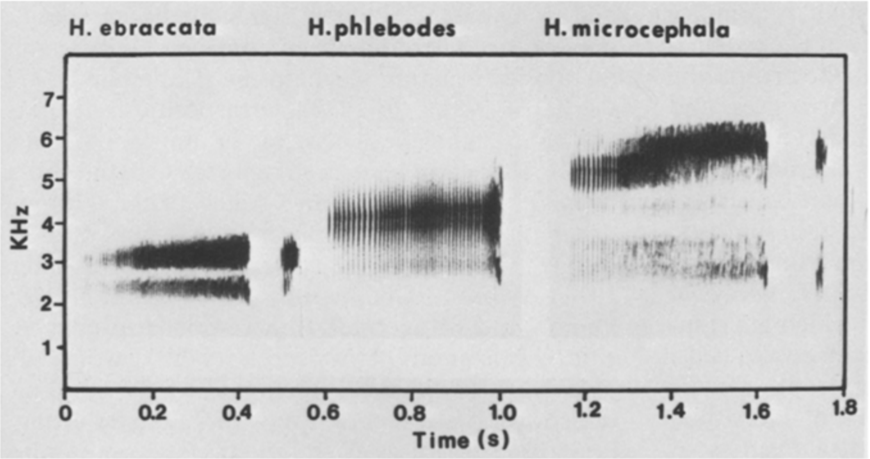

Fig. 2. Long aggressive calls of *H. ebraccata*, *H. phlebodes*, and *H. microcephala* given during close-range agonistic encounters (wide band 300 Hz filter)

manian dendrobatids (Wells 1980), and both European and South American hylids (Paillette 1970; Cardoso 1981). In most of these cases, aggressive calls of the interacting species are very similar. Additional data come from experimental work. MacNally (1982) reported that Australian *Ranidella signifera* occasionally gave aggressive call responses to playbacks of *R. parinsignifera* advertisement calls. Male European water frogs of the *Rana esculenta* complex (*R. lessonae*, *R. ridibunda*, and their hybrid, *R. esculenta*) gave aggressive calls in response to playback of the aggressive calls of all three phenotypes (Brzoska 1982). Playback of calls of *Bufo valliceps* above 80 dB were sufficient to elicit chuckle calling by *Rana berlandieri* in Texas (Gambs and Littlejohn 1979). The chuckle calls of this species seem to be aggressive vocalizations.

For several years, we have been investigating the vocal communication of three treefrogs, *Hyla ebraccata*, *H. microcephala*, and *H. phlebodes*. These species are sympatric throughout much of Central America (Fouquette 1960; Savage and Heyer 1969; Duellman 1970). In central Panama, these frogs are particularly common in disturbed areas and call in dense choruses during the rainy season. In our primary study site, there is extensive overlap in microhabitat choice by calling males, and it is common to find individuals within 50 cm of heterospecifics. The three species have rather elaborate and similar vocal repertoires, and there is considerable spectral overlap in their calls (Figs. 1, 2). All have multi-part advertisement calls and aggressive calls consisting of a primary note followed by a variable number of clicks (Fouquette 1960; Duellman 1970; Wells and Greer 1981; Wells and Schwartz 1984b). Aggressive calls of all three species have higher pulse repetition rates than the advertisement calls and sound remarkably similar. Males give mainly single-note advertisement calls when isolated from other calling males; they respond to conspecific calls by increasing the proportion of multi-note and aggressive calls (Wells and Greer 1981; Wells and Schwartz 1984a; Schwartz and Wells, in preparation). Advertisement call responses often are synchronized, following the onset of other males' calls by less than 1 s. Males of each species respond to each others' calls, and we have shown that choruses of both *H. microcephala* and *H. phlebodes* can inhibit calling by *H. ebraccata* (Schwartz and Wells 1983a, b).

This paper focusses on the extent and biological importance of the vocal responses of *Hyla ebraccata* to calls of individual *H. microcephala* and *H. phlebodes*. Our goal was to determine whether vocal responses observed in intraspecific communication occur in similar contexts at the interspecific level. Specifically, we asked the following questions: (1) To what extent does the timing of responses to heterospecific vocalizations affect the ability of a male *H. ebraccata* to communicate in a noisy chorus? (2) Are aggressive calls used at both the interspecific and intraspecific levels in similar ways? (3) What are the temporal and spectral characteristics of heterospecific vocalizations which elicit responses from *H. ebraccata*?

Materials and methods

Study area. Field work was conducted during June, July, and August of 1980, 1981 and 1982. Our study site is a flooded meadow in Gamboa, Panama, close to the Panama Canal. *H. phlebodes* calls almost exclusively from perches in grass of intermediate height (1–2 m) along the meadow border, while *H. ebraccata* and *H. microcephala* also are common in shorter vegetation in or near the pools of water found elsewhere in the study area. Recordings and playback experiments were done between 19,30 and 23,30 h. Temperatures ranged from 22.5 to 27.4° C ($\bar{x} = 25.3$, SD = 1.0, $n = 134$ nights). Temperatures rarely changed by more than 1° C during our work. Relative humidity ranged from 86 to 100% ($\bar{x} = 95.5$, SD = 2.8).

Analysis of calls. The durations, rise times (time until a call reaches its maximum amplitude), and pulse repetition rates of the primary notes of over 680 *H. ebraccata, H. microcephala,* and *H. phlebodes* advertisement and aggressive calls were measured using a Tektronix 5111 storage oscilloscope. These calls were recorded during natural interactions between males and during a variety of playback experiments. Because pulse repetition rates vary throughout aggressive calls, we also measured this call parameter at the beginning, middle, and end of these vocalizations (segments examined were 50 ms in duration for calls over 200 ms and 25 ms in duration for calls less than 200 ms). Pulse repetition rate is relatively constant throughout advertisement calls of the three species. These data were analyzed using nonparametric ANOVA and cluster analysis (SAS Institute, Cary, NC, 1979) to determine the degree of similarity within and between species. The dominant frequency of calls was determined with a Uniscan Model 4500 spectrum analyzer (Unigon Industries). We analyzed five calls per male for 20 *H. ebraccata*, 10 *H. microcephala*, and 10 *H. phlebodes* males. For *H. microcephala* calls, we determined the dominant frequency of both upper and lower frequency bands. Sonagrams of vocalizations were made on a Kay 7029 A Sona-Graph for illustrative purposes.

Playback experiments with natural calls. Responses of *H. ebraccata* males to the calls of conspecifics, *H. microcephala*, and *H. phlebodes* were determined by playing prerecorded natural vocalizations to individual calling males. We chose males which were calling in isolation or we removed neighboring individuals which could interact with our subjects. The characteristics of the stimuli we used are shown in Table 1. Each stimulus tape consisted of 20 recordings of the same call, at a rate of 10 calls/min; this approximated the spontaneous call rate of *H. ebraccata* (Wells and Schwartz 1984a). 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.

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 1562 A sound level calibrator. We measured Peak SPL at 1 m with a random incidence microphone. Sound pressure levels are expressed in dB SPL (dB re 20 μPa). Calls were presented at intensities ranging from 85–100 dB SPL. Usually, order of presentation was from lowest to highest intensity since loud calls tended to inhibit calling, elicit aggressive calls, or induce retreat. The playback intensities were similar to those encountered by *H. ebraccata* in the field (Table 2) and allowed us to assess the effect of distance between males on their interactions.

For analysis of playback experiments, a visual record of each playback test was obtained using a Heath SR 206 two-channel strip chart recorder. For each test, we determined the types of calls given and time (to the nearest 0.5 s) from the onset of the stimulus to each response. We used the *G*-test (Sokal and Rohlf 1969) to test for independence of type of response calls and stimulus conditions; Wilcoxon matched-pairs signed-ranks tests (Siegel 1956) were used to compare calling rates during stimulus and no-stimulus periods. We assessed the importance of individual call parameters in explaining variation in synchronous and aggressive responses with multiple linear regression (Draper and Smith 1981).

Table 1. Parameters of stimulus calls presented to *H. ebraccata* males. Durations, rise times, and pulse repetition rates are for the primary note of the calls only. Numbers in parentheses are peak pulse repetition rates of aggressive calls. Dominant frequency of both the lower and upper spectral bands are shown for the *H. microcephala* calls. The first letter of the call stimulus abbreviations identify the species, and the number gives the number of notes in the call. The letter *L* indicates a call of long duration

Call stimulus	Type	Primary note duration (ms)	Rise time (ms)	Pulse rate (pulses/s)	Notes	Dominant frequency (Hz)
EAD1	Adv	188	92	96	1	3,000
EAD3	Adv	200	172	95	3	3,080
EAG3	Agg	150	88	365 (400)	3	3,160
EAGL	Agg	416	352	222 (260)	2	2,960
MAD1	Adv	100	54	210	1	2,960, 5,920
MAD3	Adv	104	56	221	3	2,960, 6,000
MAGL	Agg	480	16	227 (320)	2	2,680, 5,680
PAD3	Adv	94	52	159	3	3,560
PAG2	Agg	150	52	300 (380)	2	3,600
PAGL	Agg	366	144	153 (320)	1	4,000

Table 2. Sound pressure levels of *H. ebraccata, H. microcephala,* and *H. phlebodes* males calling in the field. Measurements were made at 0°, 50 cm in front of the frogs except for *H. phlebodes*. For that species, measurements at 0° and 90° were similar and were pooled. Also shown are the distances at which a frog calling at the modal SPL would have an SPL equal to each of the four playback intensities used in the experiments. These values were calculated assuming attenuation due only to spherical spread

Species	Modal SPL	Range	Number of		Distance (cm) at intensity (dB SPL)			
			males	calls	85	90	95	100
H. ebraccata	100	96–105	12	163	283	159	89	50
H. microcephala	106	101–109	12	178	566	317	178	100
H. phlebodes	103	101–105	5	83	400	224	126	71

Playback experiments with synthetic stimuli. Unless otherwise noted the type and arrangement of equipment in the field and the calibration of playback intensities were the same in these experiments as those using natural calls. Tones and synthetic calls were produced on a custom-built sound synthesizer as described in Gerhardt (1974, 1978). An oscilloscope was used to compare pulses and rise times of natural and synthetic calls. Synthetic signals were band-pass filtered with a Krohn-Hite 3550 filter and recorded on a ReVox A77 or a Nagra S tape recorder at a rate of 10 per min.

We presented two sets of synthetic stimuli to *H. ebraccata* males. The first was a set of 1-note advertisement calls (95 pulses/s, 3 kHz) which were 50–600 ms long. The second was a set of 200 ms 1-note calls and 200 ms tones with dominant frequencies of 1–6 kHz. Because background noise levels varied from night to night, we determined the playback intensity of these stimuli for each frog individually. In these tests, the stimulus most similar to the conspecific advertisement call was presented first, with the playback intensity adjusted to the level which elicted a maximum rate of synchrony. This intensity (usually 85 or 90 dB SPL) was used for all other stimuli presented to the same male. Order of presentation of the stimuli was varied for different males. Delay times from stimulus onset to first advertisement call response were measured to the nearest 8 ms on the Tektronix oscilloscope.

Female choice experiments. Female choice experiments were performed in a darkened apartment in Gamboa at natural field temperatures (about 26° C) between 22,30 and 03,00 h. Two Heppner mid-range horn speakers (amplitude-frequency response: ±4 dB, 1.1–10.5 kHz) driven by a Uher stereo tape recorder and mounted on wooden baffles were placed 2.8 m apart at opposite ends of an arena delimited by uniformly colored blankets. Large brown cushions were placed along the wall behind each speaker to minimize the reflection of sound. The arena was approximately 3 m long, 1.6 m wide, and 1 m high. It served to shield test animals from extraneous light and movements of the experimenters, but it did not restrain the movements of the frogs. The only light was provided by a 25 W red bulb suspended 1 m above the center of the arena.

Females were captured in amplexus between 22,30 and 01,00 h and transported to the arena in individual plastic food boxes. Each female was placed in the center of the arena in the box. The lid was replaced with a piece of cardboard which could be lifted off the box with a string from outside the arena. Most females remained immobile when placed in the arena, so testing began within 1 min. After stimulus playbacks were started, the lid was carefully lifted off the box. A positive response was scored if a female approached to within 10 cm of one speaker; most females moved directly toward a speaker and made contact with it. If a female hopped onto the arena walls or showed extensive undirected wandering, her response was scored as an escape. Females exhibiting this behavior were tested one more time later in the evening. All females showing a positive response did so within 8 min; females that failed to respond within 10 min were removed and retested later.

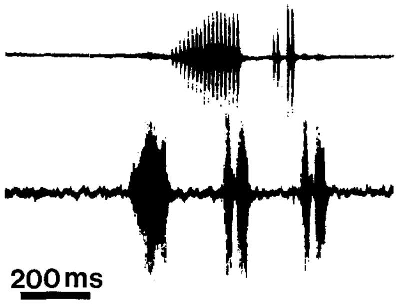

Fig. 3. Oscillogram of a *H. ebraccata* response call to a 3-note *H. microcephala* advertisement stimulus call. Note that the primary note of the synchronized response call falls between the first two notes of the stimulus call

Thirty-six female *H. ebraccata* were given a choice between a synthetic one-note advertisement call (184 ms long) overlapped by the 105 ms primary note of a natural 3-note *H. microcephala* advertisement call and a synthetic call falling between the primary note and the first click note of the same *H. microcephala* call. The temporal arrangement of the second pair of calls is similar to that often resulting from a synchronized response of *H. ebraccata* to calls of *H. microcephala* (Fig. 3). We were interested in the significance of this behavior in the field and designed the experiment to determine whether masking by the primary note of a *H. microcephala* call could render a *H. ebraccata* call less attractive to females than one which was not overlapped.

The choice stimuli were made by recording the synthetic *H. ebraccata* call and natural *H. microcephala* call on separate tracks of the same tape using the two Uher tape recorders and a patch cord. The timing relationship was checked with the Tektronix oscilloscope. Each of the two stimuli (overlapped and non-overlapped calls) was then re-recorded on a separate single track of a tape loop so that they alternated every 6 s. This tape loop was used to record the final tape we played to the females. We used a Nagra E tape recorder linked to a Uher 4200 Report Monitor to create the tape loop and final stimulus tape. The relative intensity of the calls of each species was the same in each stimulus (as determined with the oscilloscope). The *H. microcephala* call was approximately 3 dB greater than the *H. ebraccata* call. The modal sound pressure level (Peak SPL) of the advertisement call of a *H. microcephala* male is 106 dB at 50 cm. Since this is 6 dB greater than the advertisement call of a male *H. ebraccata* at the same distance, our choice of relative call intensities is reasonable.

Playback intensities for each speaker were regulated by separate Realistic L-pads and were equalized at 90 dB (±1 dB) (Peak SPL) using the Gen Rad sound level meter held 2.5 cm above the floor. For both stimuli, the meter (set at Peak SPL) measured the intensity of the click notes of the *H. microcephala* call since these had a greater amplitude than the primary note. Therefore, at the center of the arena, the intensities of the synthetic *H. ebraccata* call in the two stimuli were identical.

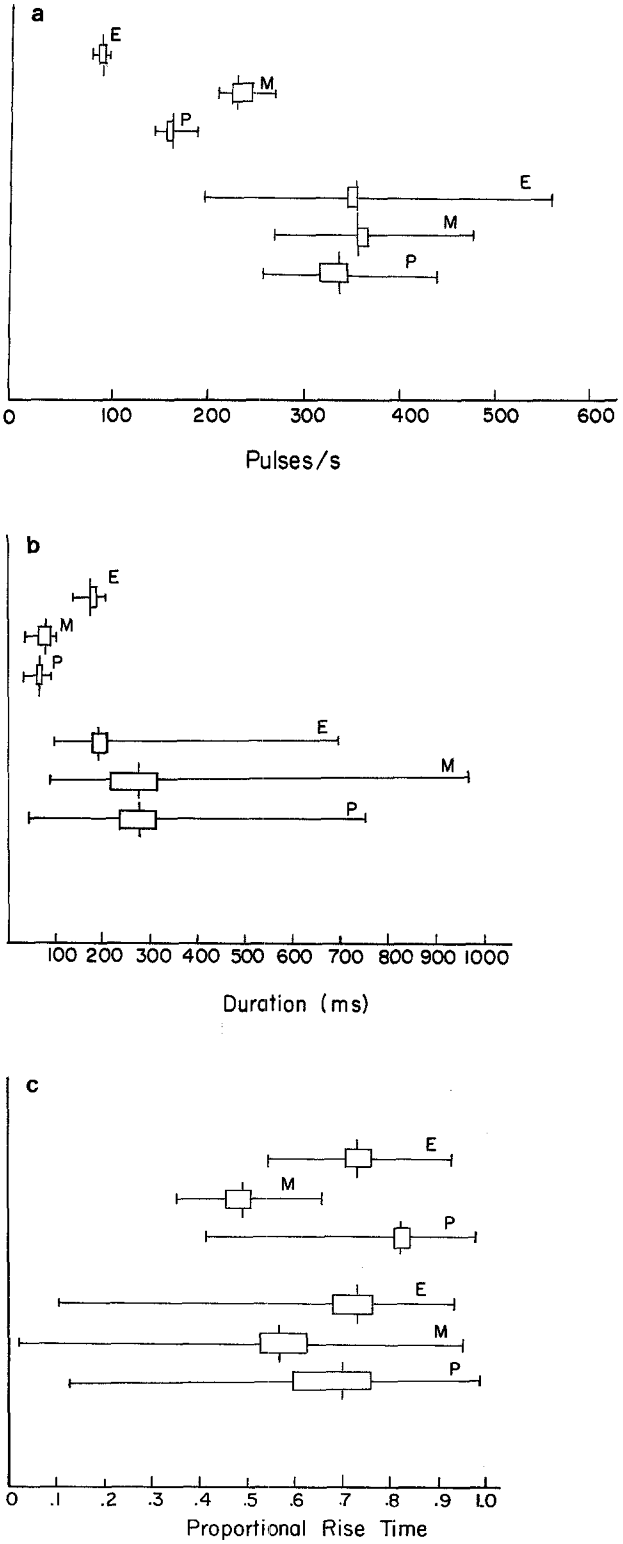

Fig. 4a–c. Medians (*vertical lines*), approximate 95% confidence intervals (*boxes*), and ranges (*horizontal lines*) for three temporal parameters of advertisement (*upper*) and aggressive (*lower*) calls. **a** Pulse repetition rates. **b** Durations. **c** Proportional rise times. *E H. ebraccata; M H. microcephala; P H. phlebodes*. Sample sizes: advertisement calls – E = 50, M = 40, P = 50; aggressive calls – E = 156, M = 280, P = 106

Results

Features of natural calls

The calls of *H. ebraccata* have a dominant frequency of approximately 3 kHz ($\bar{x} = 3{,}129$ Hz, CV = 4.9, $n = 100$) and those of *H. phlebodes* nearly 4 kHz ($\bar{x} = 3{,}708$ Hz, CV = 6.7, $n = 50$). *H. microce-*

phala calls have energy distributed in one band centered at almost 3 kHz ($\bar{x}=2{,}941$ Hz, CV $=8.2$, $n=50$) and another near 6 kHz ($\bar{x}=5{,}773$ Hz, CV $=5.8$, $n=50$).

The pulse repetition rates, proportional rise times (rise time/total duration) and durations of the primary notes of calls of *H. ebraccata, H. microcephala,* and *H. phlebodes* are shown in Fig. 4. The advertisement calls show very little variation in pulse repetition rate and duration within species. However, there is considerable variation among species for all three call parameters. The three species' advertisement calls differ significantly in pulse repetition rate (Kruskal-Wallis ANOVA, $P<0.01$). *H. ebraccata* advertisement calls are significantly longer than those of *H. microcephala* or *H. phlebodes* (Mann-Whitney *U*-test, $P<0.01$ for both tests). *H. microcephala* calls have proportionately faster rise times than those of *H. ebraccata* or *H. phlebodes* (Mann-Whitney *U*-test, $P<0.01$ for both tests).

The aggressive calls of each species have significantly higher pulse repetition rates than their advertisement calls (Mann-Whitney *U*-test, $P<0.01$ for all tests). Each species employs a spectrum of aggressive vocalizations. While there is relatively little variation in the durations of advertisement calls within each species, aggressive calls span a wide range of durations (Fig. 4b). Long aggressive calls take proportionally longer to reach their maximum amplitude (*H. ebraccata*: $r_s=0.34$, $P<0.0001$; *H. microcephala*: $r_s=0.62$, $P<0.0001$; *H. phlebodes*: $r_s=0.68$, $P<0.0001$) and have lower maximum pulse repetition rates (*H. ebraccata*: $r_s=-0.61$, $P<0.0001$; *H. microcephala*: $r_s=-0.50$, $P<0.0001$; *H. phlebodes*: $r_s=-0.48$, $P<0.0001$) than short aggressive calls.

During natural intraspecific interactions, the propinquity of males influences the nature of their aggressive calls. Males of the three species defend calling sites and use predominantly long aggressive calls during wrestling bouts and vocal encounters with close opponents (closer than approx. 1 m). Short aggressive calls predominate in interactions between males further away (Wells and Schwartz 1984b). To substantiate this, we examined a subset of the data. We classified aggressive calls given during three intraspecific interactions between pairs of males near to one another (*H. microcephala* separated by 15 cm, *H. phlebodes* separated by 45 cm, and *H. ebraccata* fighting) and in response to playback of conspecific calls at 100 dB SPL or greater (a few playbacks were made at 105 dB) as those from close-range encounters. Aggressive calls given during no-stimulus periods (presumably in response to another distant male in the field) and in response to playbacks of calls at or below 95 dB SPL were classified as those from long-range encounters. The medians of the three temporal call parameters are plotted for advertisement calls and these two categories of aggressive calls in Fig. 5. Cluster analysis (SAS Cluster procedure) grouped advertisement calls, close-range aggressive calls and long-range aggressive calls into three distinct clusters. Conspecific calls were less similar to one another than were heterospecific calls in the same category. The average standardized Euclidean distances between call medians were: 0.599 for advertisement calls, 0.263 for close-range aggressive calls, and 0.284 for long-range aggressive calls. This shows that aggressive calls of *H. ebraccata, H. microcephala,* and *H. phlebodes* are more similar to one another than are their advertisement calls.

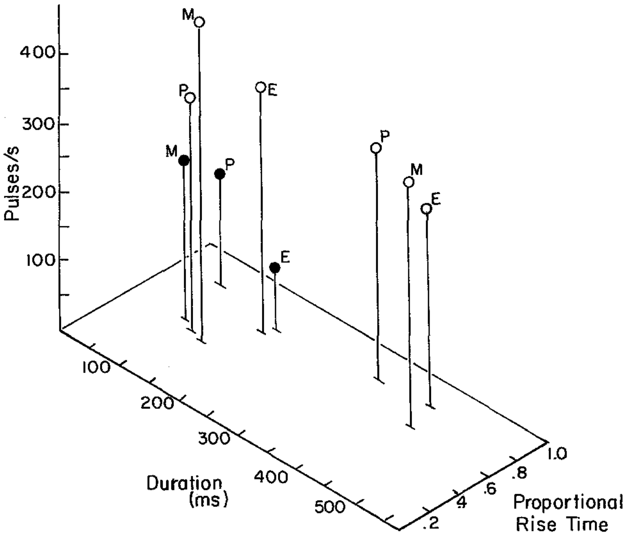

Fig. 5. Median values of three temporal call parameters for different categories of *H. ebraccata (E)*, *H. microcephala* (*M*), and *H. phlebodes* (P) vocalizations. *Black circles*: advertisement calls; *open circles*: aggressive calls from long-range encounters (*on the left*) and from close-range encounters (*on the right*). Original sample sizes: *black* – E = 50, M = 40, P = 50, *open left* – E = 86, M = 19, P = 10, *open right* – E = 26, M = 59, P = 61

Advertisement call responses

Multi-note calling. H. ebraccata responded to all heterospecific stimulus calls except the three-note *H. phlebodes* advertisement call by giving a higher proportion of multi-note calls than during the no-stimulus periods (Table 3). Their response to conspecific calls was similar (Wells and Greer 1981; Wells and Schwartz 1984a). The *H. microcephala* long aggressive call and the *H. phlebodes* short aggressive call elicited a significantly greater proportion of multi-note responses than any of the other

Table 3. Single-note and multi-note calls given by *H. ebraccata* males during different playback conditions. Independence of response call type and playback conditions (stimulus or no-stimulus (*NS*)) was tested with a *G*-test. Responses of all males at all playback intensities were pooled. $G > 3.84$, $P < 0.05$

Stimulus	Single-note % (*n*)	Multi-note % (*n*)	*G*
NS	46 (1298)	54 (1552)	
MAD1	26 (287)	74 (804)	125.11
MAD3	38 (393)	62 (629)	15.19
MAGL	20 (278)	80 (1104)	271.10
PAD3	42 (662)	58 (900)	1.83
PAG2	19 (280)	81 (1178)	169.31
PAGL	38 (323)	62 (530)	12.17

Table 4. Median callrates (*CPM*) of *H. ebraccata* males during presentation of heterospecific stimulus calls at 85, 90, 95 and 100 dB SPL and during no-stimulus periods (*NS*). Stimuli were *H. microcephala* and *H. phlebodes* calls. Significance levels are for one-tailed Wilcoxon signed-ranks tests of elevated callrates during call playback relative to no-stimulus periods. The number of frogs tested is shown in parentheses

Call stimuli	Intensity			
	85 dB	90 dB	95 dB	100 dB
MAD1	12.58 (11)**	12.19 (11)*	12.07 (7)	7.46 (11)
NS	11.00	11.00	10.40	10.40
MAD3	13.01 (10)*	12.12 (11)	11.61 (6)*	6.87 (11)
NS	11.00	10.93	9.83	10.67
MAGL	11.40 (11)**	11.86 (13)**	10.86 (11)*	11.99 (8)
NS	7.80	9.33	7.80	10.31
PAD3	9.70 (16)	9.83 (16)*	10.61 (13)*	9.13 (14)
NS	9.10	9.77	8.59	9.77
PAG2	12.59 (14)	11.23 (14)	10.73 (10)*	11.75 (10)
NS	10.32	10.32	9.10	10.67
PAGL	12.05 (10)	11.99 (10)*	8.09 (1)	11.80 (10)
NS	10.74	10.74	9.35	10.74

* $P < 0.05$, ** $P < 0.01$

heterospecific calls (*G*-Test, $P < 0.05$ for all tests). For all experimental conditions, the modal number of notes in these multi-note calls was two, as it is in playbacks of conspecific advertisement calls (Wells and Schwartz 1984a).

Calling rate. H. ebraccata responded to playback of conspecific calls by increasing calling rates (Wells and Greer 1981; Wells and Schwartz 1984a). Median calling rates also were elevated during presentation of most heterospecific calls relative to no-stimulus periods (Table 4). However, the increase was statistically significant only for 11 of the 24 stimulus – volume combinations presented (one-tailed Wilcoxon signed-ranks test). At 100 dB, none of the stimuli significantly elevated calling rates; in fact, calling rate was significantly reduced during playback of both one-note and three-note *H. microcephala* advertisement calls ($P < 0.01$).

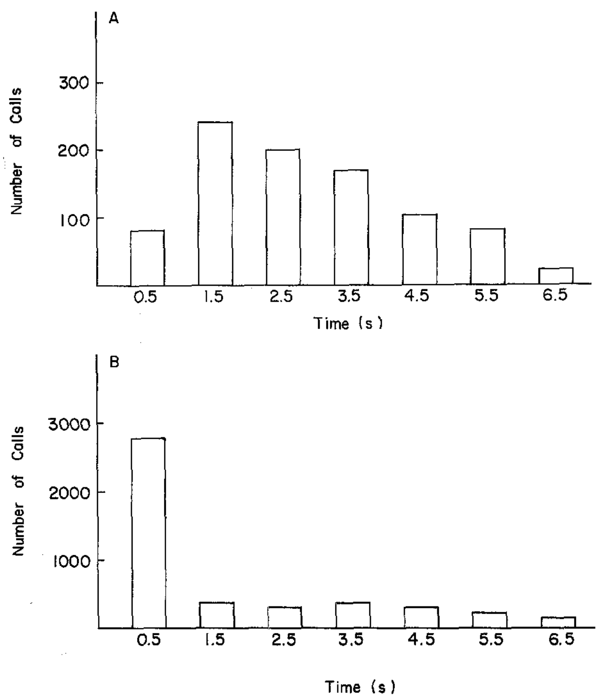

Fig. 6. Latencies to the first aggressive (**A**) or advertisement (**B**) call response of *H. ebraccata* males following the initiation of heterospecific stimulus calls

Synchronized responses. H. ebraccata males respond to conspecific calls by giving synchronized advertisement call responses (Wells and Schwartz 1984a). These were defined as any calls falling within 1 s of the beginning of a stimulus. Most first advertisement calls given by males in response to heterospecific stimulus calls also were synchronized, but aggressive calls were not (Fig. 6). The percent of stimulus calls which were followed by such a synchronized response was defined as the percent synchrony. For each stimulus call type, we determined the playback intensity at which each frog exhibited the maximum level of synchrony. The means and 95% confidence intervals of maximum percent synchrony are shown in Table 5. The data are presented this way because, for a particular stimulus, percent synchrony was not uniform across all playback intensities for a given frog. Often calls at high intensity partially inhibited calling or elicited a greater proportion of aggressive calls (Wells and Schwartz 1984b). In addition, as playback intensity of some stimuli (*H. microcephala* advertisement calls) increased, males shifted from synchronizing to alternating their advertisement call responses.

Table 5. Mean percent synchrony and 95% confidence intervals of *H. ebraccata* males to conspecific and heterospecific stimulus calls

Call stimuli	Percent synchrony	Number of frogs
EAD1	77.2 ± 10.8	13
EAD3	82.5 ± 9.9	10
EAG3	63.3 ± 8.9	10
EAGL	79.1 ± 12.9	10
MAD1	68.9 ± 11.9	11
MAD3	53.4 ± 13.1	11
MAGL	90.1 ± 8.8	14
PAD3	36.9 ± 8.1	17
PAG2	81.7 ± 8.5	14
PAGL	68.2 ± 19.9	10

Table 6. Summary of multiple regression ANOVA of percent synchrony to natural stimulus calls by *H. ebraccata*

Step	Source of variation	*df*	*F*[a]	*P*	Multiple R	Increase in R
1	Log (duration)	1,115	28.72	0.0001	0.333	0.333
2	Duration	1,114	18.12	0.0001	0.404	0.071
3	Rise time[b]	1,113	8.83	0.0036	0.444	0.040
4	Notes	1,112	10.35	0.0017	0.481	0.037
5	Pulse rate	1,111	3.49	0.0643	0.496	0.014
6	Dominant frequency	1,110	2.77	0.0986	0.508	0.012

[a] Values associated with Type II sums of squares

[b] Rise time expressed as a proportion of total call duration

To account for the variation in percent synchrony to conspecific and heterospecific calls, we performed a multiple linear regression (SAS Stepwise procedure) using the dominant frequency and temporal parameters of these stimuli as independent variables. The temporal variables were log duration, duration, proportional rise time, pulse repetition rate, and number of notes. All variables but pulse repetition rate and dominant frequency significantly reduced the error sums of squares when added to the model (Table 6). The model with the four remaining independent variables accounted for 48 % of the total variance. Log duration accounted for 69% of the variance explained by this model.

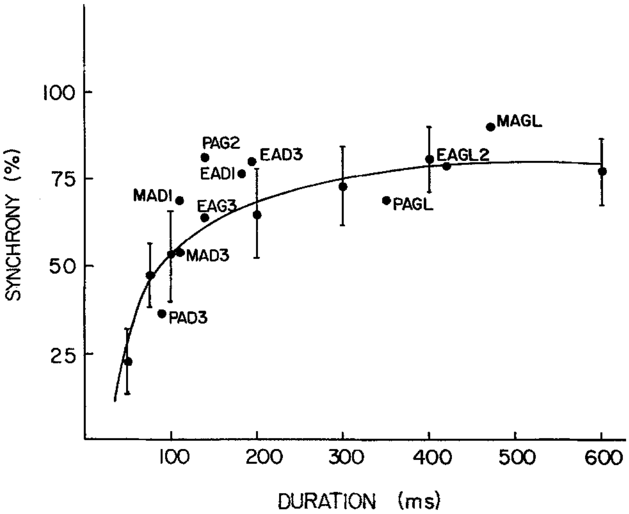

Fig. 7. The percent of synthetic advertisement calls of 50–600 ms duration which *H. ebraccata* males ($n=11$) answered within 1 s (percent synchrony). Data are presented as means with 95% confidence intervals. The curve for these data was drawn by hand. Also shown are the durations and mean percent synchrony of males for the natural stimulus calls. Call abbreviations are explained in Table 1

Variable duration synthetic calls. To more accurately assess the effect of call duration on synchrony, we presented 11 males with synthetic 1-note advertisement calls of 50, 75, 100, 200, 300, 400, and 600 ms duration. Figure 7 shows the mean percent synchrony of *H. ebraccata* males to these stimuli, together with durations and mean percent synchrony for natural stimulus calls. There was a good correspondence between points from the two data sets. Percent synchrony was low for short stimuli, but increased very rapidly with duration up to about 200 ms and then increased more slowly. Modal response latencies were 140–200 ms, although the variance in response latency increased with stimulus duration (Wells and Schwartz 1984a). These results, together with those from the multiple linear regression analysis using natural calls, indicate that the low response to certain heterospecific calls was due primarily to their short duration.

Variable frequency calls and tones. Although calls of the three hylids exhibit considerable frequency overlap, there are spectral differences among the species. In addition, other species of anurans in the study area have calls which lack the discrete pulse structure of the calls of these hylids and cover a range of frequencies. To determine the range of call frequencies to which *H. ebraccata* is vocally responsive, 200 ms synthetic advertisement calls of 1, 2, 3, 4, 5, and 6 kHz were presented to 10 males. The same animals were presented with 200 ms tones of these frequencies to assess the importance of fine temporal structure of vocalizations and of frequency-temporal structure interaction in eliciting synchronized responses. Delay times from stimulus onset to first advertisement call were ranked (all delay times over 1 s received the same rank). These data were analyzed using the SAS

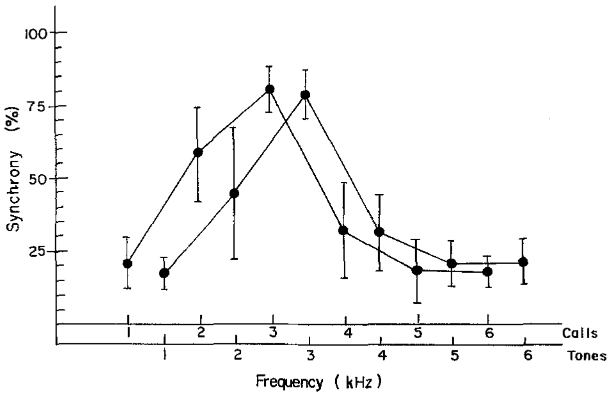

Fig. 8. The percent of synthetic advertisement calls and tones of 1–6 kHz which *H. ebraccata* males answered within 1 s (percent synchrony). Data are presented as means with 95% confidence intervals (*vertical lines*)

Institute General Linear Models Varcomp procedure. Frequency and type of stimulus (synthetic call or tone) were fixed effects and the frogs were a random effect.

Ranked delay times differed significantly only among frequencies ($P<0.01$), and there was a significant frog × frequency × stimulus type interaction effect ($P<0.01$). Delay times were significantly lower for the 3 kHz stimuli than for those of all other frequencies (Tukey's studentized range test, $P<0.05$). The percentage of synchronized responses peaked at 3 kHz (Fig. 8).

Female choice experiment

Twenty-nine of the 36 female *H. ebraccata* we tested responded positively by moving to a speaker. Twenty-two of these approached the speaker broadcasting synthetic conspecific single-note advertisement calls which were not overlapped by the primary note of a 3-note *H. microcephala* advertisement call (two-tailed binomial test, $P=0.0096$). Choice of calls was independent of speaker position ($G=0.09$, $P>0.50$).

Aggressive call responses

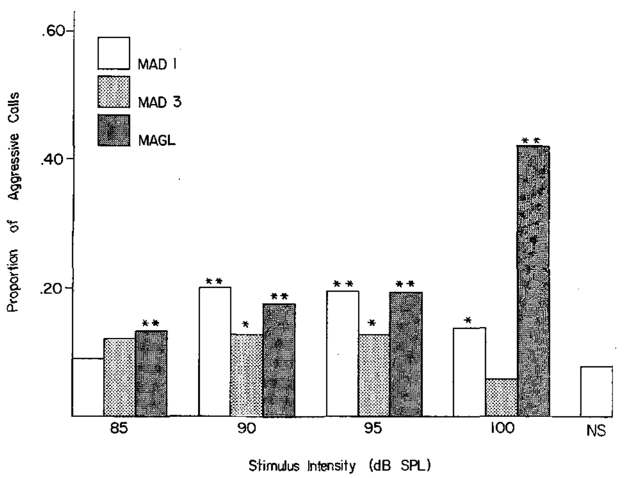

Fig. 9. Proportion of aggressive calls given by *H. ebraccata* males to *H. microcephala* 1-note advertisement (*MAD 1*), 3-note advertisement (*MAD 3*), and long aggressive calls (*MAGL*) at 4 playback intensities. Also shown is the proportion of aggressive calls given during the no-stimulus periods (data pooled for all males). Significance levels for comparisons between stimulus types are given in the text. *Asterisks* indicate a significant difference between calls given to stimuli and during the no-stimulus periods (*$P<0.05$, **$P<0.01$, G-test)

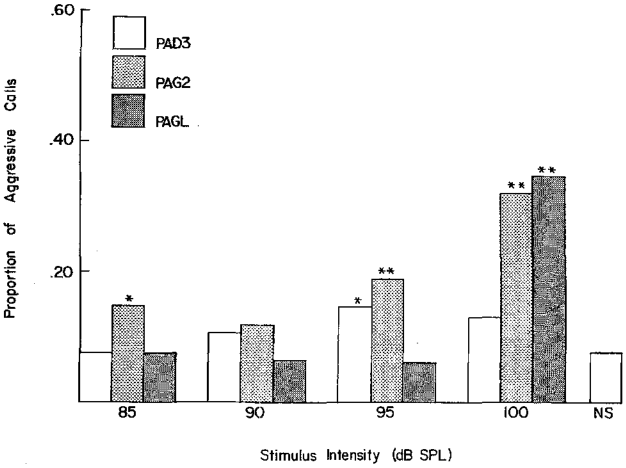

Fig. 10. Proportion of aggressive calls given by *H. ebraccata* males to *H. phlebodes* 3-note advertisement (*PAD 3*), 2-note short aggressive (*PAG 2*), and long aggressive calls (*PAGL*) at 4 playback intensities. Also shown is the proportion of aggressive calls given during the no-stimulus periods (data pooled for all males). Significance levels for comparisons between stimulus types are given in the text. *Asterisks* indicate a significant difference between calls given to stimuli and during the no-stimulus periods (*$P<0.05$, **$P<0.01$, G-test)

At most playback intensities *H. microcephala* advertisement and aggressive calls elicited a significantly higher proportion of aggressive calls from *H. ebraccata* males than were given during no-stimulus periods (Fig. 9). This was true for *H. phlebodes* calls only at high playback intensities (Fig. 10). At high playback intensity (100 dB SPL), *H. ebraccata* responded to the aggressive vocalizations of *H. microcephala* and *H. phlebodes* with a significantly higher proportion of aggressive calls than to the advertisement calls of these species (Figs. 9, 10) (*H. microcephala* calls: $G=80.4$, $P<0.01$; *H. phlebodes* calls: $G=41.6$, $P<0.01$). This was not true at the lower intensities. *H. ebraccata* gave proportionately more aggressive calls to long conspecific aggressive calls than long aggressive calls of the other species (Fig. 11) (*H. microcephala* calls: $G=23.3$, $P<0.01$; *H. phlebodes* calls:

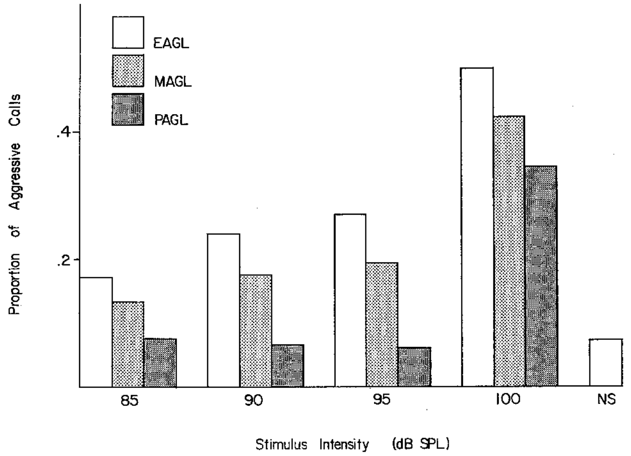

Fig. 11. Proportion of aggressive calls given by *H. ebraccata* males to conspecific (*EAGL*) and heterospecific long aggressive calls (*MAGL*, *PAGL*) at 5 playback intensities. Also shown is the proportion of aggressive calls given during the no-stimulus periods (data pooled for all males)

Table 7. Summary of multiple regression analysis of variance of data on proportion of aggressive calls given by *H. ebraccata* to natural stimulus calls presented at 100 dB SPL

Step	Source of variation	*df*	*F*[a]	*P*	Multiple R	Increase in R
1	Peak pulse rate	1,83	18.28	0.0001	0.183	0.183
2	Rise time[b]	1,82	6.52	0.0126	0.248	0.065
3	Frequency	1,81	2.50	0.1181	0.263	0.015
4	Duration	1,80	2.24	0.1381	0.277	0.014
5	Notes	1,79	0.87	0.3550	0.285	0.011

[a] Values associated with Type II sums of squares
[b] Rise time expressed as a proportion of total call duration

$G = 50.3$, $P < 0.01$; pooled over all volumes). The proportion of aggressive calls given in response to *H. microcephala* calls was significantly greater than to *H. phlebodes* calls ($G = 8.52$, $P < 0.01$).

To account for the variation in aggressive calling to conspecific and heterospecific calls, we performed a multiple linear regression (SAS stepwise procedure) using the dominant frequency and temporal parameters of these stimuli as independent variables. The temporal variables were duration, proportional rise time, peak pulse repetition rate, and number of notes. The dependent variable was the proportion of responses which were aggressive calls. Only pulse repetition rate and proportional rise time had an *F*-statistic significant at the $P < 0.05$ level. Peak pulse repetition rate accounted for most of the variation explained by the model (Table 7).

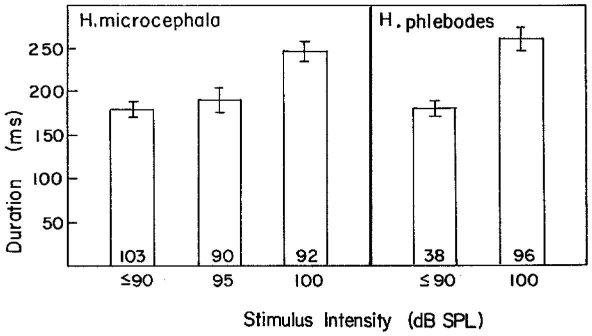

Fig. 12. Primary note durations of aggressive calls given by *H. ebraccata* males to playback of *H. microcephala* and *H. phlebodes* long aggressive calls at different intensities. Responses at 85 and 90 dB SPL were not significantly different and were pooled. Data are presented as means and 95% confidence intervals. The number of response calls measured is shown at the base of each column

Aggressive calls of *H. ebraccata* are graded; there is a negative relation between the mean duration of calls used in agonistic encounters and the distance between males (Wells and Schwartz 1984b). *H. ebraccata* males gave longer aggressive calls in response to playbacks of heterospecific aggressive calls at high intensity than low intensity (Fig. 12). Duration of aggressive call responses to long heterospecific aggressive calls was significantly correlated with playback intensity (*H. microcephala* calls: $r_s = 0.45$, $P < 0.0001$; *H. phlebodes* calls: $r_s = 0.64$, $P < 0.0001$). During natural vocal interactions with heterospecifics, *H. ebraccata* also gives mainly long aggressive calls during close-range encounters. In a 150 s recording of a wrestling match between a *H. ebraccata* and *H. microcephala*, the modal duration of *H. ebraccata* aggressive calls was nearly 300 ms ($\bar{x} = 377$, $SD = 109$, range = 184–608, $n = 45$).

Discussion

Our results demonstrate that *H. ebraccata* males are behaviorally responsive to a range of acoustic stimuli they commonly encounter in the field. Conspecific (Wells and Schwartz 1984a, b) and heterospecific calls elicit a predictable pattern of vocal activity. We believe some of the responses to heterospecific males are functionally similar to responses to conspecific males because they facilitate mate attraction, advertisement of position, and aggressive interactions in a complex acoustic environment. Playback experiments with natural and synthetic stimuli have identified features of calls which are important in effecting various vocal responses in *H. ebraccata*.

Calling rates

H. ebraccata males frequently exhibited elevated calling rates during exposure to both conspecific and heterospecific calls. Similar patterns of call stimulation have been reported for repetitively signalling insects (Jones 1966; Smith 1973; Aiken 1982) and other species of frogs (Wells 1977; Narins and Capranica 1978; Passmore 1978; Walkowiak and Brzoska 1982). In part, elevated calling rates resulted from synchrony to the recorded stimulus calls, which we presented at a rate of 10 per min. We do not believe increasing calling rate, per se, has any adaptive significance at the heterospecific level exclusive of that discussed below for synchronizing behavior. Playback of calls at 100 dB reduced or failed to significantly raise calling rates, indicating that some active inhibition may have occurred as well. This may result from the tendency of *H. ebraccata* males to reduce calling when exposed to high noise levels such as those occurring near *H. microcephala* choruses (Schwartz and Wells 1983a).

Synchronized and multi-note calls

H. ebraccata will synchronize with acoustic stimuli over a range of frequencies. Peak responsiveness occurs at the dominant frequency of this species' calls. Temporal organization of the stimulus into pulses, as occurs in the natural calls, is not required for a strong response; tones and synthetic calls were equally effective in eliciting synchronized responses. These frogs also will synchronize to 200 ms filtered noise bursts centered at 3 kHz (Wells and Schwartz 1984a).

During vocal interactions, *H. ebraccata* males frequently synchronize their advertisement call responses (modal delay times of 140–200 ms) to calls of conspecific males (Wells and Schwartz 1984a). Usually these responses are 2-note calls, although in very dense choruses, males may rapidly alternate 1-note calls. Experiments with female *H. ebraccata* demonstrated that by displaying this stereotyped behavior, males increase their relative attractiveness to females. In two-choice tests, female *H. ebraccata* failed to show any preference for either leader or follower 1-note calls, but preferred a 3-note follower to a 1-note leader. In addition, females were given a choice between 2-note calls arranged so that the primary note of the second call overlapped the click note of the first. Females preferred the call in which the click note was not obscured (Wells and Schwartz 1984a). These data suggest that males effectively mask the click notes of competitors by synchronizing their responses to other males' calls. Synchronizing response calls to those of a competitor also may reduce the likelihood that he will respond. Narins (1982) found that *H. ebraccata* males rarely answer stimuli delivered less than 210 ms after the onset of their own calls.

H. ebraccata males often responded to heterospecific calls with multi-note synchronized responses. Since male *H. ebraccata* do not compete with male *H. microcephala* or *H. phlebodes* for mates, it is unlikely that they behave this way to mask click notes or reduce the number of responses by heterospecifics. Alexander (1975) suggested that when individuals synchronize or alternate calls with heterospecifics, it may be an incidental effect of synchronizing to their own calls. We believe *H. ebraccata* males respond to heterospecific calls because certain calls are spectrally and temporally similar to conspecific calls. Playback experiments with stimuli of variable duration and frequency support this hypothesis. If a *H. ebraccata* male is presented with calls which equal or exceed conspecific advertisement calls in duration and fall in a frequency range of 2–4 kHz, he probably will answer them with synchronized calls. If the calls are very loud (100 dB SPL or greater), his responses may not be synchronized. Instead, he may give delayed aggressive calls or alternating advertisement calls.

Data from the choice experiment with *H. ebraccata* females demonstrated that calls of individual *H. microcephala* can influence the attractiveness of a *H. ebraccata* male's calls. In a previous experiment, we showed that female *H. ebraccata* will choose a call which is not overlapped by a background chorus of *H. microcephala* over a call which is overlapped (Schwartz and Wells 1983b). By synchronizing responses to calls of *H. microcephala*, a *H. ebraccata* male may reduce the chance that his calls will be overlapped and rendered less attractive to females. Therefore, at the interspecific level, there appears to be an adaptive advantage to the generalized synchronizing behavior exhibited by males. Nevertheless, we suspect that this is a fortuitous consequence of behavior selected for at the intraspecific level.

A number of taxa of acoustically active organisms adjust the timing of their signals in response to those of conspecifics (Alexander 1975; Wasserman 1977; Awbrey 1978; Passmore 1978; Lemon and Struger 1980; Hultsch and Todt 1982; Narins 1982; Tuttle and Ryan 1982). In many cases, the putative advantage of this behavior is preservation of signal integrity through reduction of acoustic interference. When there is insufficient spatial separation between heterospecific individuals using similar signals, males may make fine scale modifications in the timing of calls, perhaps to minimize acoustic jamming. This has been reported among insects (Samways and Broughton 1976; Latimer 1981), birds (Ficken et al. 1974) and frogs (Littlejohn and Martin 1969; Passmore 1978; Schwartz and Wells 1983a, b). The synchronizing behavior of *H. ebraccata* evidently operates at both the intraspecific and interspecific levels to improve signal transmission in a noisy environment.

Aggressive calls

H. ebraccata, H. microcephala, and *H. phlebodes* have vocal repertoires which are structurally and functionally similar. *H. ebraccata* males respond to the aggressive calls of *H. microcephala* and *H. phlebodes* as they do to their own. When exposed to these calls during experimental playbacks or natural interactions, males responded with a high proportion of aggressive calls. Aggressive calls are graded; males use longer calls during close range vocal interactions and during physical encounters. Shorter calls are used more frequently in interactions among more distant animals. During close conspecific or heterospecific aggressive interactions, one frog may attack his opponent. The males typically wrestle and continue to trade long aggressive calls until one hops away (usually within 1 min). The animals may resume aggressive calling and combat if they remain close together. We have observed nine such encounters between *H. ebraccata* males, seven between *H. microcephala* males, and 11 between *H. ebraccata* and *H. microcephala*. We also witnessed a close-range aggressive vocal interaction between a pair of *H. phlebodes*. Male frogs probably attack heterospecifics calling nearby because they represent an important source of acoustic interference which may impair a male's ability to attract females.

Aggressive calls of the three species are more similar in peak pulse repetition rate, proportional rise time, and duration than are their advertisement calls. Together with high spectral overlap, this structural similarity explains the facility with which aggressive calls are used interspecifically. Pulse repetition rate is the feature which best distinguishes the advertisement calls of the three species from both conspecific and heterospecific aggressive calls (Fig. 4a). In a playback experiment using synthetic calls which varied in pulse repetition rate and rise time, we found that high pulse repetition rate was the feature of aggressive calls which was most important in eliciting aggressive call responses from *H. ebraccata* males (Wells and Schwartz 1984b).

The advertisement calls of *H. microcephala* have pulse repetition rates which are higher than those of *H. ebraccata* or *H. phlebodes* and which fall within the 95% confidence interval for the median peak pulse repetition rate of *H. ebraccata* aggressive calls. However, playbacks of *H. microcephala* advertisement calls did not elicit a proportion of aggressive calls comparable to aggressive call stimuli. Three factors may account for this. First, while the pulse repetition rate of the *H. microcephala* advertisement call is high, it falls near the lower limit for *H. ebraccata* aggressive calls. Second, *H. microcephala* advertisement calls are only half as long as the shortest *H. ebraccata* aggressive calls, so they may not be recognized as aggressive calls. Third, *H. microcephala* calls have most of their energy distributed in two bands, one centered at 6 kHz and another at 3 kHz. Therefore the relative amplitude of a *H. microcephala* call between 2.5 and 3.5 kHz is less than that of a *H. ebraccata* call if the two calls are equal in intensity. Since *H. ebraccata* demonstrated peak responsiveness to synthetic calls and tones in this frequency range, it is likely that, at equal playback intensities a *H. ebraccata* call would be perceived by males of this species as a more intense vocalization than a *H. microcephala* call. If this is true, then presentation of *H. microcephala* advertisement calls to *H. ebraccata* at intensities greater than those employed here could elicit an aggressive response similar to that observed with aggressive call stimuli.

Natural selection may favor the evolution of interspecific territoriality and aggression if some common resource is contested (Orians and Willson 1964; Cody 1974; Ebersole 1977; Walters 1979; Ortiz and Jenssen 1982). Some researchers believe that selection has favored the convergence of signals used during agonistic encounters (Cody 1974) or other types of interspecific social interactions (Moynihan 1968). Other workers disagree (Gochfeld 1979; Murray 1976; but see Murray 1981). Our work is relevant since it demonstrates that different species of frogs which compete acoustically also interact aggressively and react to one another's aggressive calls.

Unfortunately, we do not have data which adequately demonstrate whether natural selection favored the convergence of aggressive signals among the three species to facilitate their interspecific use (Brown 1977). Among species like *H. ebraccata, H. microcephala* and *H. phlebodes* which compete intensively for space in the acoustic environment, such selection could be strong. The fact that advertisement calls of these hylids are less similar than their aggressive calls, particularly in pulse repetition rate, suggests that "character convergence" may have occured. However, the phylogenetic affinity of *H. microcephala* and *H. phlebodes*, both of which are members of the *H. microcephala* species group (Duellman 1970), could partly explain this pattern. Other species in the group which are not sympatric, such as *H. minuta*, also have very similar aggressive calls (Cardoso 1981; Wells, unpublished). Character displacement (Blair 1974) of advertisement calls, but not of aggressive calls, also is a viable hypothesis. Evidently, females have no difficulty identifying conspecific advertisement calls correctly. We have obsverved hundreds of individuals in amplexus, but we have never seen a heterospecific pair (see also Fouquette 1960). Finally, random drift or evolution of the advertisement calls of *H. ebraccata, H. microcephala*, and *H. phlebodes* in different selective environments could be responsible for some of their differences.

Our results demonstrate the behavioral versatility of *H. ebraccata* males. *H. microcephala* and *H. phlebodes* can be significant sources of acoustic interference for this species. However, *H. ebraccata* can enhance its ability to communicate under the less than ideal conditions of its breeding habitat in a number of ways. Males can improve the effectiveness of their signaling by avoiding calling during the chorusing of other species (Schwartz and Wells 1983a, b), shifting the timing of their calls in response to individual calls, and driving heterospecific males away from calling sites. We suspect that future work will show that interspecific interactions very similar to those reported here occur between individuals of many species of chorusing frogs.

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