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Male Calling Behavior and Female Choice in the Neotropical Treefrog *Hyla microcephala*

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With 4 figures

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Abstract

The effect of stimulus call complexity and calling rate on the vocal responses of males and female mate choice was studied in *Hyla microcephala* in Panama. Males increased the number of notes in their calls in response to increases in stimulus call complexity during both playback of 1 to 8-note advertisement calls and during natural interactions. However, precise matching of the number of notes in stimuli and responses did not occur consistently. Males also increased calling rates if stimuli were presented above prestimulus rates. Two-stimulus choice experiments demonstrated that females prefer both higher calling rates and greater call complexity, indicating that the ways males change their vocal behavior during interactions increases their attractiveness to potential mates. Tests in which the relative intensity of a high and low rate stimulus was varied indicated that females prefer stimuli with higher total sound energy. In a natural chorus, it is likely that females simply approach males giving the most conspicuous calls.

Introduction

Research on the vocal behavior of anuran amphibians has demonstrated that in many species signal production by males is a dynamic process. Chorusing males may change the timing, structural complexity, frequency, temporal characteristics, and rate of their calls in response to changes in their social and acoustic environment (LITTLEJOHN 1977; WELLS 1977a, b; NARINS, pers. comm.). For example, in *Physalaemus pustulosus* (RAND & RYAN 1981), *Philautus leucorhinus* (ARAK 1983a), and *Hyla ebraccata* (WELLS & SCHWARTZ 1984), males add secondary notes to their calls in response to calls of neighboring males. Changes in vocalizations have been hypothesized to enhance the ability of males to communicate in a noisy environment (SCHWARTZ & WELLS 1983a, b, 1985; ZELICK &

NARINS 1982, 1983) or to increase the attractiveness of males' calls to potential mates relative to those of competitors (RAND & RYAN 1981; WELLS & SCHWARTZ 1984). In most cases, empirical work to determine how specific alterations in male calling behavior influence females has not been completed.

This paper is an extension of previous work conducted on the neotropical treefrog *Hyla microcephala* (SCHWARTZ & WELLS 1985). The species is found in ponds and flooded sites in Central America (DUELLMAN 1970). Males have a complex vocal repertoire which includes single and multi-note advertisement and aggressive calls. Both introductory and secondary notes are composed of pulse trains, although the latter are biphasic and shorter than the buzz-like introductory notes (see sonagrams in SCHWARTZ & WELLS 1984a). Playback experiments established that males add secondary notes to calls in response to those of other males (SCHWARTZ & WELLS 1985). Increases in call complexity were most dramatic when stimulus and response calls were closely coupled in time, or when a calling male was interrupted by a stimulus call. During pairwise natural interactions, males frequently alternate individual notes in long overlapping calls. Other call-mediated alterations in vocal behavior include possible elevation of calling rate, shifts in the timing of calls and the duration of inter-note intervals, and increases in aggressive calling.

In this study, I examined more closely the effect of stimulus call complexity and calling rate on the vocal responses of males. I also conducted female choice experiments to evaluate how certain call mediated shifts in male vocal behavior might influence mate choice. In *Hyla ebraccata*, another Central American treefrog with a similar vocal repertoire, advertisement calls with secondary notes are preferred by females over single-note calls (WELLS & SCHWARTZ 1984). If this is true for *H. microcephala*, then males may attempt to match the complexity of a competitor's calls (ARAK 1983a), or outsignal a competitor by giving calls with more notes. Since stimulus calls used in previous experiments had at most three notes (SCHWARTZ & WELLS 1985), it was not possible to test these hypotheses rigorously with the old data. In this study, a stimulus tape incorporating calls with up to eight notes was used in a field playback experiment and supplemented with data recorded in natural interactions. Male shifts in calling rate also were reexamined since previous tests showed that elevations generally occurred only if an animal's baseline calling rate was lower than that of the stimulus. As a result, data were insufficient to demonstrate a significant response to conspecific calls. The experiment described below was designed to overcome this problem by presenting males with a range of stimulus calling rates, including those higher than naturally given. Female choice experiments were used to assess the significance of multi-note calling and elevation of calling rate. The consequences of aggressive calling and fine-scale shifts in the timing of notes for mate choice are discussed in SCHWARTZ (1987, in prep.).

Materials and Procedures

Study Area

The experiments described below were conducted during July and August of 1984 and 1985. Natural vocal interactions were recorded during the same months in 1982 and 1985. The study site is a

flooded meadow in Gamboa, Panama, close to the Panama Canal (SCHWARTZ & WELLS 1984a). *H. microcephala* breed here in dense choruses during the rainy season, and males establish calling sites on vegetation in or near water. Most calling occurs between 19.30 and 24.00 h.

Recordings and Playback Experiments

Stereo recordings of natural interactions among males were made in 1982 using a Uher 4200 Report IC tape recorder, a Sennheiser MKE 802 microphone and a Uher M517 microphone. In 1985, I used a Marrantz PMD 360 tape recorder and Realistic 33-1062 and Akai ADM-8 microphones.

A stimulus tape of 100 randomly arranged 1, 2, 4, 6, and 8-note *H. microcephala* advertisement calls was used to test the response of males to different levels of call complexity. The tape was prepared by making a tape loop of an 8-note call, previously recorded at 19 cm/s, such that the call was repeated every 6 s. 10 calls/min approximates the spontaneous call rate of *H. microcephala* (SCHWARTZ & WELLS 1985). Using two Uher 4200 Report Stereo IC tape recorders linked with a patch cord, I played the tape loop at 4.7 cm/s and selectively deleted secondary notes from the 8-note call (by turning the record level dial to zero) to produce the other call types. Each type of call was recorded a total of 20 times on the stimulus tape (10 min duration when played at 19 cm/s). The frequency response of the Uher 4200 at 4.7 cm/s was sufficient to ensure that spectral quality of the random calls was not sacrificed. Stimulus calls were re-recorded onto a cassette tape and played in the field with a Marrantz PMD 360 tape recorder. Males also were presented with a single-note synthetic advertisement call at 10, 20 and 30 calls/min. Playbacks at each rate were for 2 min, and the order of presentation was randomized.

I recorded each male for 1 or 2 min prior to each stimulus presentation. This served as a control and allowed me to determine baseline levels of calling rate and multi-note calling for each subject. I tried to select males which were relatively isolated from other calling frogs, or removed neighboring males before each test. However, because of the large numbers of *H. microcephala* in my study area it was rarely possible to maintain this isolation. Two Marrantz PMD 360 tape recorders were used to present the stimuli and record responses of the males. One recorder drove a University 4401 horn speaker mounted on a wooden baffle and placed 1 m from the frog. The amplitude-frequency response of this speaker was measured to be ± 3 dB from 1.1 to 14.5 kHz. The animal's responses were recorded on one channel using a Realistic 33-1062 directional microphone, and the stimuli were recorded on the other channel via 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. I measured Peak SPL (dB SPL re 20 μ Pa) at 1 m with a random incidence microphone. The measurements were made in an area close to the study site but removed from the background noise of the anuran assemblage. The stimulus calls were usually presented at 90 dB SPL. However, on quiet nights when playbacks at this intensity elicited many aggressive calls (SCHWARTZ & WELLS 1985), stimulus intensity was set at 85 dB SPL. The speaker was positioned so that there was little or no vegetation between it and the frog. Therefore, the measured sound pressure levels were very close to the intensities at the position of a male and corresponded to a *H. microcephala* calling at the modal intensity (peak SPL) at distances of either 3.2 (90 dB) or 5.7 m (85 dB) (SCHWARTZ & WELLS 1985).

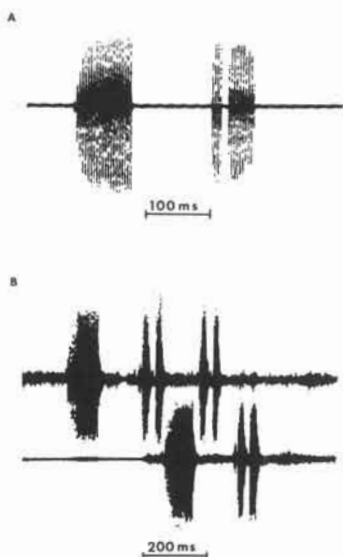
Analysis of Calls

The tape recordings were analyzed on a Tektronix 5111 storage oscilloscope. For each playback test, I determined the types of calls given and, for the 1 to 8-note presentations, the time (± 80 ms) from the onset of each stimulus to each response. Data were analyzed using standard non-parametric statistics available under SAS (SAS Institute, Inc., Cary, N. C.) unless assumptions of parametric tests were satisfied.

Female Choice Experiments

Three two-stimulus discrimination tests were conducted with female *H. microcephala* to assess the significance of multi-note calling. All stimuli were presented at a rate of 10 calls/min. In the first experiment, females were presented with alternating single-note and two-note advertisement calls (Fig. 1 A). Here the time delay in call onset from one speaker to call onset from the other was 3 s. In the second experiment, females were presented with single-note advertisement calls in a leader-

Fig. 1: Oscillograms of some of the stimuli presented to *H. microcephala* females in two-choice tests. (A) 2-note synthetic advertisement call. (B) Overlapping natural multi-note advertisement calls. Synthetic calls had a pulse repetition rate of 225 pulses/s, primary note duration of 90 ms, rise time of 45 ms, and a duty cycle of 0.5. Calls had two spectral components (power bandwidth = 400 Hz) of equal relative amplitude centered at 3 and 6 kHz



follower arrangement. The follower calls were broadcast 200 ms after the onset of each leader call. The temporal arrangement mimicked the stereotypic short latency responses of *H. microcephala* males to conspecific calls (SCHWARTZ & WELLS 1985). This experiment served primarily as a control for a third test with overlapping three and two-note calls which also had a leader-follower arrangement (Fig. 1 B). This stimulus mimicked a natural pairwise interaction with two males alternating notes in overlapping calls. The experiment was designed to test whether females could distinguish the number of notes in overlapping calls.

A final series of choice tests was conducted to determine whether females could discriminate among calling rates, and, if so, identify the basis of the behavior. On one channel of the stimulus tape, synthetic single-note calls were recorded at a rate of 10 calls/min. On the other channel, calls were recorded at twice this rate. Calls on the fast stimulus channel fell 1.5 s before and 1.5 s after each call on the slow stimulus channel. A preference for calls at 20/min could be explained by the increased number of calls per unit time, or the increase in total sound energy concomitant with an elevation in calling rate. To distinguish between these alternatives, calls at the two rates were presented at three relative intensities. These were: equal intensities (90 dB SPL), equal sound energy (10 calls/min: 90 dB, 20 calls/min: 87 dB), and unequal sound energy and unequal intensities (10 calls/min: 90 dB, 20 calls/min: 84 dB). A drop of 3 dB SPL corresponds to a halving of sound intensity (sound energy per unit time).

Most stimuli were produced with a custom-built sound synthesizer described in GERHARDT (1978). Synthetic signals were band-pass filtered with a Krohn-Hite 3550 filter to reduce harmonic distortions and recorded on a ReVox A77 tape recorder. The stimulus tape of overlapping two- and three-note calls was created using a recording of a natural three-note call, with the last note erased to form the two-note call. Each call was recorded on a separate channel of a tape loop, and the timing relationship between notes and relative amplitude were checked with a storage oscilloscope. All stimulus tapes were subsequently copied onto cassette tapes.

Female choice experiments were performed in a darkened apartment in Gamboa at about 26 °C between 22.30 and 03.00 h. Two Realistic Minimus 0.3 speakers (amplitude-frequency response: +/- 3 dB, 1.0–12.0 kHz) driven by a Marrantz PMD 360 stereo cassette tape recorder were placed 1.6 m apart at opposite corners of an arena delimited by uniformly colored blankets. Large cushions were placed along the wall facing the speakers to reduce the reflection of sound. The arena was 3.35 m long, 1.70 m wide, and 1 m high and shielded test animals from extraneous light and movements of the experimenter. A 25-W red bulb suspended 1 m above the center of the arena provided illumination. Playback intensities for each speaker were regulated by separate Realistic L-pads and, except for

the final two experiments described above, intensities were equalized at 90 dB \pm 1 dB (Peak SPL; dB re 20 μ Pa) at the female release point using a Gen Rad 1982 precision sound level meter.

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 1.7 m from the speakers near the center of the

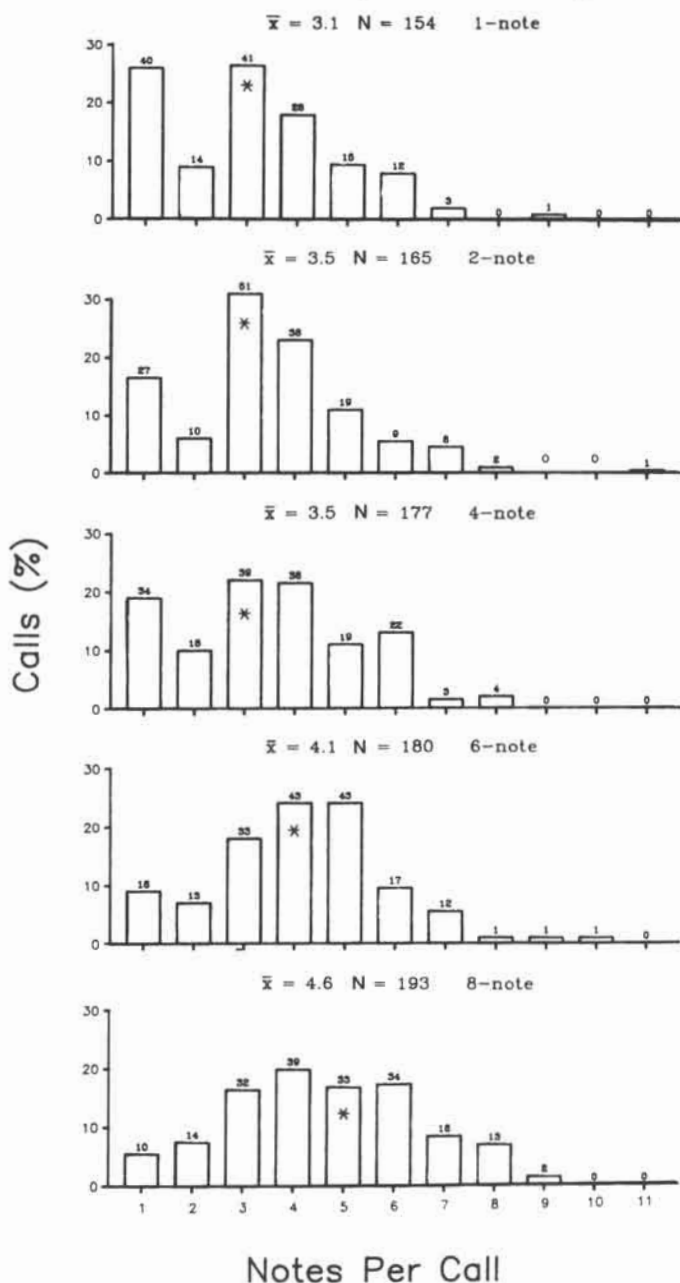
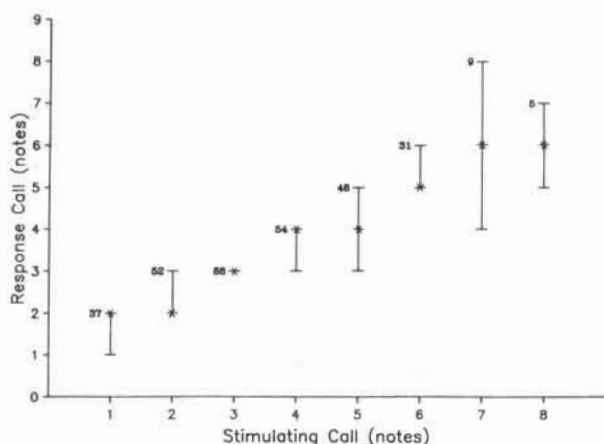


Fig. 2: Distributions of number of notes in first response calls of 10 males to 1, 2, 4, 6, and 8-note natural advertisement calls. Number of calls is given above each bar. Asterisks indicate median values

Fig. 3: Number of notes in first response calls of four males to calls of differing complexity during natural interactions with conspecifics. Data are presented as medians with approximate 95 % confidence intervals. Number of calls is shown by each interval; $r_s = .66$, $p < .0001$



arena. One min after stimulus playbacks were started, the lid was carefully lifted off the box with a string from outside the arena. A positive response was scored if a female approached to within 10 cm of a speaker within 10 min; most females moved directly toward a speaker and either made contact or hopped to the curtain directly behind it.

Results

Male Vocal Behavior

Call Complexity and Calling Rate

There are two obvious ways a male calling at constant intensity might increase the attractiveness of his calls relative to those of competitors. He could increase their rate of production and he could add secondary notes to them. Therefore, in the analysis of male responses, I considered differences in calling rate, call complexity and a quantity dependent upon these two — the total number of notes given in responses to stimulus calls.

1 to 8-Note Stimuli

During the no-stimulus periods, males gave predominantly multi-note calls (mode and median = 3 notes/call) and called at an average rate of 12.4 calls/min ($M = 12.3$). The high level of multi-note calling during these periods indicates that males were responding to calls from the background chorus (SCHWARTZ & WELLS 1985). Therefore, as one measure of call complexity, I compared the number of notes in the first response to each stimulus call. First responses were less likely to be responses given to other males in the chorus than were subsequent calls. An ANOVA on these data ranked by frog revealed significant heterogeneity in number of notes among first responses given to the five types of stimulus calls ($F_{4,864} = 20.4$, $p < 0.0001$). In general, call complexity increased with stimulus complexity. There were low, but significant, correlations between the number of notes in stimuli and first responses for nine of the 10 frogs tested ($r_s = .23-.55$, $p < 0.01$). However, frogs usually did not match the number of notes in stimulus calls precisely (Fig. 2). As the number of notes in stimulus calls increased, males

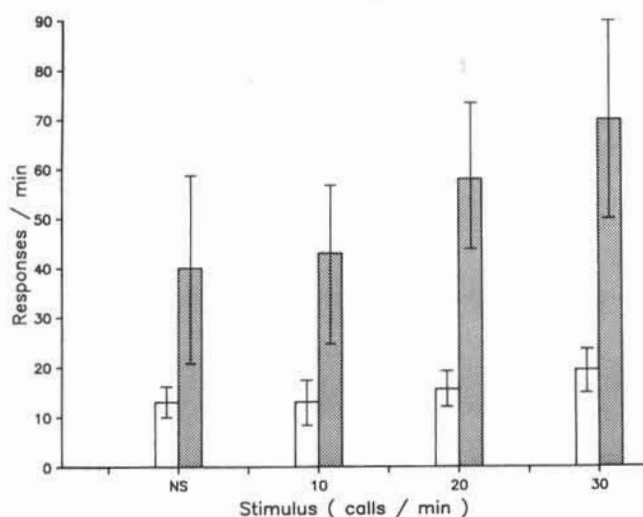


Fig. 4: Call rate (open) and note rate (stippled) of 9 males prior to (NS) and during playback of 1-note synthetic advertisement calls at three call rates. Data are presented as means with 95 % confidence intervals

were more likely to answer. In addition, both calling rate and the number of notes delivered in all response calls increased with stimulus call complexity (Tables 1, 2).

During natural interactions, there was a closer correspondence between number of notes in the calls of interacting individuals than I obtained during playback experiments (Fig. 3). Nevertheless, in most instances, males still did not match calls precisely.

Table 1: Calling rates (calls/min) of *H. microcephala* males during the initial no-stimulus periods (INS) and during playback of 1 to 8-note stimulus calls

Frog	INS	Stimulus				
		1	2	4	6	8
1	21.5	23.5	20.0	24.0	24.0	24.5
2	1.5	7.5	8.0	11.5	10.0	13.5
3	10.1	11.5	10.0	13.5	16.5	15.0
4	12.1	12.0	12.5	16.5	17.0	18.5
5	13.9	15.0	20.0	16.0	17.0	18.5
6	19.0	18.5	21.5	18.5	21.5	24.0
7	12.5	17.5	17.5	19.5	22.5	22.0
8	8.2	11.5	15.5	16.0	14.0	15.5
9	10.2	12.0	13.5	18.0	18.0	21.0
10	14.5	7.0	7.5	13.5	12.5	13.5
Mean	12.4	13.6	14.6	16.7	17.3	18.6
Median	12.3	12.0	14.5	16.3	17.0	18.5
Calls	236	272	292	334	346	372
p		n.s.	*	**	**	**

p values are for one-tailed Wilcoxon matched-pairs signed-ranks tests comparing no-stimulus with stimulus periods. * $p < 0.05$, ** $p < 0.01$

Table 2: Total number of notes given by *H. microcephala* males in response to each stimulus call of 1 to 8 notes. Both means and (medians) are shown

Frog	Stimulus				
	1	2	4	6	8
1	9.35 (8.0)	9.00 (7.5)	10.50 (13.0)	11.20 (11.5)	11.20 (11.0)
2	2.45 (0.0)	3.40 (2.5)	4.00 (2.0)	5.30 (5.0)	6.80 (6.0)
3	5.15 (4.5)	5.40 (3.5)	5.40 (3.5)	9.25 (9.5)	8.95 (8.0)
4	3.85 (3.0)	4.45 (4.0)	5.25 (2.5)	4.85 (4.0)	7.60 (7.0)
5	5.35 (5.5)	6.95 (7.0)	6.35 (6.0)	6.70 (6.5)	8.70 (8.0)
6	7.20 (7.5)	7.40 (7.0)	7.30 (7.5)	8.60 (8.0)	10.60 (10.0)
7	5.70 (6.0)	5.35 (5.0)	7.65 (8.0)	8.05 (9.0)	8.25 (9.0)
8	3.60 (3.5)	5.40 (5.5)	4.90 (4.5)	5.75 (4.5)	6.65 (6.5)
9	3.45 (3.0)	4.20 (3.0)	5.50 (6.0)	6.05 (6.0)	7.50 (8.0)
10	1.40 (1.0)	1.55 (1.0)	3.10 (3.0)	3.70 (4.0)	5.15 (5.0)
All frogs	4.75 (4.0)	5.31 (4.5)	5.99 (6.0)	6.94 (6.0)	8.14 (8.0)

$\chi^2 = 32.8$, d.f. = 4, $p < 0.0001$, Friedman test

Variable Call Rate Stimuli

Males ($N = 9$) increased both calling rate and number of notes per min with increasing stimulus rate (Fig. 4, two-way ANOVA, $F_{3,24} = 17.4$, 28.3, $p < 0.001$), although the lowest rate failed to elicit significant increases above no-stimulus levels (Tukey's studentized range test, overall $p = 0.05$). Average number of notes per call increased slightly during playback of 20 and 30 calls/min stimuli, but the change was not significant (two-way ANOVA).

Table 3: Results of two-choice playback experiments with *H. microcephala* females. p values are for a two-tailed binomial test

No. of females choosing:		No. tested	p
1-note call	2-note call		
0	9	12	0.004
3-note leader	2-note follower		
11	2	14	0.022
1-note leader	1-note follower		
10	6	20	0.454
10 calls/min	20 calls/min		
0	9	9	0.004
10 calls/min	20 calls/min (-3 dB)		
8	10	21	0.814
10 calls/min	20 calls/min (-6 dB)		
18	7	25	0.044

Female Choice Experiments

Results of the female choice experiments are presented in Table 3. All 9 females responding in the test using alternating single and two-note calls chose the multi-note calls. Females also discriminated in favor of a three-note call which was overlapped by a follower two-note call. The control test using leader and follower single note calls demonstrated that it is unlikely this preference was based on the temporal arrangement of these two multi-note calls. Females did not show a significant preference for a leader or a follower single-note call. In these and all other experiments, animals demonstrated no side bias.

At 90 dB SPL, female *H. microcephala* displayed an unanimous preference for the higher of the two call rates. When sound energy from the two speakers was equalized by dropping the 20 calls/min source 3 dB SPL, the result was significantly different ($G = 4.50$, $p < 0.05$), and this preference disappeared. Dropping the intensity of the calls at the high rate another 3 dB SPL reversed the preference in favor of the lower call rate.

Discussion

This study has clarified the relationship between certain changes which occur during male-male vocal interactions in the chorus and the behavior of female *H. microcephala*. Modifications made by males in call complexity and calling rate increase their attractiveness to females and suggest that competition among males to broadcast the most conspicuous signals is intense.

The results of tests using 1 to 8-note calls indicate that there is a trend in the direction of increased complexity of first responses as stimulus note number increased. A closer match with the stimulus occurred if the measure of complexity was total notes given in responses to each call. Although this quantity was also influenced by the time delay between stimulus calls, the result is probably reliable because calling rate in the stimulus was close to the natural average. A much better fit between stimulus call and response call complexity occurred during the natural interactions. During such interactions, males reduce the chance of note interference by lengthening inter-note intervals in overlapping calls (SCHWARTZ & WELLS 1985). The invariant temporal structure of recorded stimulus calls may have impaired both the ability of males to interdigitate notes with those of the stimulus and to match call complexity.

Males also demonstrated an ability to adjust their calling behavior in response to changes in stimulus rate. As suggested from data in SCHWARTZ & WELLS (1985), stimulus rates higher than baseline levels elicited significant increases in vocalizations. However, most males failed to match or exceed the rates of 20 or 30 calls/min. Nevertheless, they more than compensated for their lower calling rate with a delivery rate of individual notes higher than present in the stimuli. In anurans, metabolic cost appears to rise with calling effort (BUCHER et al. 1982; TAIGEN & WELLS 1985; TAIGEN et al. 1985; WELLS & TAIGEN 1986). Therefore, male frogs may increase levels of this energetically demanding activity only when changes in the local acoustic environment require it.

In two-stimulus tests, female *H. microcephala* prefer calls with secondary notes to those without them. Moreover, discrimination of note number is possible when calls overlap with notes interdigitating — as they frequently do in a natural chorus. There are similar data demonstrating a female preference for complex calls for *H. ebraccata* (WELLS & SCHWARTZ 1984), *Physalaemus pustulosus* (RAND & RYAN 1981), and *Geocrinia victoriana* (LITTLEJOHN & HARRISON 1985). However, it is not known whether the sensitivity to number of notes is as acute as that demonstrated by *H. microcephala*; females of these other species were not given a choice between overlapped multi-note calls which differed by only a single note.

Why do females of these species prefer more complex calls? It seems likely that the behavior is simply a manifestation of a passive (sensu PARKER 1982; ARAK 1983b) response to calls containing a larger number of attractive elements or more energy in the appropriate frequency range; i.e., the most distinctive or conspicuous signals. Multi-note calls, consisting of a series of identical subunits with rapid rise and fall times, would be well suited for communication in the noisy acoustic environment of a natural anuran chorus (RICHARDS & WILEY 1980; WILEY & RICHARDS 1982; WELLS & SCHWARTZ 1984). Active female choice, perhaps to select a mate of superior fitness, seems to be a less viable hypothesis. In male *H. microcephala* (SCHWARTZ & WELLS 1985), *H. ebraccata* (WELLS & SCHWARTZ 1984), and *Physalaemus pustulosus* (RAND & RYAN 1981; pers. obs.), there is little variation among individuals in the tendency to add secondary notes to calls in response to those of other males.

A reanalysis of data obtained previously (SCHWARTZ & WELLS 1984a) indicates that significant variation in call intensity exists among male *H. microcephala* (Kruskal-Wallis test, chi-square approximation, $\chi^2 = 132.9$, d.f. = 11, $p < 0.0001$). Median intensities of 12 males ranged from 100.5 to 107.8 dB SPL at 50 cm directly in front of the frog ($N = 178$ calls). The extent to which individual males can modify the intensity of their calls is not clear. It would be particularly interesting to couple sound level measurements with playbacks of calls to determine whether facultative adjustment of this parameter to the competitive regime occurs. Calling rates among males also show considerable variation (Table 1), although to a large extent this is a function of the acoustic milieu in the vicinity of individuals (SCHWARTZ & WELLS 1985). Additionally, individual males increase calling rates dramatically when a female is detected nearby (SCHWARTZ & WELLS 1985).

The importance of calling rate and call intensity in mate attraction is underscored by results of tests in which these parameters were varied. The data indicate that the total sound energy received by the female is particularly critical; the way this quantity is maximized may be irrelevant. This conclusion is similar to that reached by AIKEN (1982), who varied both rate and intensity of calls in female choice experiments with corixid bugs. Therefore, it may have general validity for chorusing organisms and may explain, at the proximate level, why females of other anuran species prefer high calling rates (WHITNEY & KREBS 1975; SULLIVAN 1982, 1983; FORESTER & CZARNOWSKI 1985; WELLS & BARD in prep.).

The results presented here demonstrate that, all else being equal, a male *H. microcephala* which calls more loudly or more frequently than nearby competitors should have an advantage in attracting mates. However, in a natural habitat all else is rarely equal. Female *H. microcephala* entering a chorus are confronted with a dense assemblage of calling males in a structurally complex environment. Males are located at a variety of perch heights, and different densities of vegetation will affect the attenuation of their calls (WILEY & RICHARDS 1982; BRENOWITZ et al. 1984; WELLS & SCHWARTZ 1982). Moreover, the ability of females to discriminate among call types may be reduced as the number of sound sources (GERHARDT 1982) and background noise levels increase (EHRET & GERHARDT 1980; SCHWARTZ & WELLS 1984a, b; WELLS & SCHWARTZ 1984). Therefore, while natural selection has resulted in calling behavior which may improve the chances of mating success over long periods of time, on any given night a male's ability to attract a female may depend to a large degree on chance.

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Literature Cited

- AIKEN, R. B., 1982: Effects of group density on call rate, phonokinesis, and mating success in *Palmacorixa nana* (Heteroptera: Corixidae). *Can. J. Zool.* **60**, 1665—1672.
- ARAK, A., 1983a: Vocal interactions, call matching and territoriality in a Sri Lankan treefrog, *Philautus leucorhinus* (Rhacophoridae). *Anim. Behav.* **31**, 292—302.
- , 1983b: Sexual selection by male-male competition in natterjack toad choruses. *Nature* **306**, 261—262.
- BRENOWITZ, E. A., W. WILCZYNSKI, & H. H. ZAKON, 1984: Acoustic communication in spring peepers: Environmental and behavioral aspects. *J. Comp. Physiol.* **155**, 585—592.
- BUCHER, T. L., M. J. RYAN, & G. A. BARTHOLOMEW, 1982: Oxygen consumption during resting, calling, and nest building in the frog *Physalaemus pustulosus*. *Physiol. Zool.* **55**, 10—22.
- DUELLMAN, W. E., 1970: The Hylid Frogs of Middle America. Univ. Kansas Mus. Nat. Hist. Monogr. **1**.
- EHRET, G., & H. C. GERHARDT, 1980: Auditory masking and effects of noise on responses of the green treefrog (*Hyla cinerea*) to synthetic mating calls. *J. Comp. Physiol.* **141**, 13—18.
- FORESTER, D. C., & R. CZARNOWSKI, 1985: Sexual selection in the spring peeper, *Hyla crucifer* (Amphibia, Anura): role of the advertisement call. *Behaviour* **92**, 112—128.
- GERHARDT, H. C., 1978: Mating call recognition in the green treefrog (*Hyla cinerea*): the significance of some fine-temporal properties. *J. Exp. Biol.* **74**, 59—73.
- , 1982: Sound pattern recognition in some North American treefrogs (Anura: Hylidae): implications for mate choice. *Amer. Zool.* **22**, 581—595.
- LITTLEJOHN, M. J., 1977: Long-range acoustic communication in anurans: an integrated and evolutionary approach. In: *The Reproductive Biology of Amphibians*. (TAYLOR, D. H., & S. I. GUTTMAN, eds.) Plenum Press, New York, pp. 263—294.
- , & P. A. HARRISON, 1985: The functional significance of the diphasic advertisement call of *Geocrinia victoriana* (Anura: Leptodactylidae). *Behav. Ecol. Sociobiol.* **16**, 363—373.

- PARKER, G. A., 1982: Phenotype-limited evolutionarily stable strategies. In: Current Problems in Sociobiology. (Kings College Sociobiology Group, ed.) Cambridge Univ. Press, Cambridge, pp. 173—201.
- RAND, A. S., & M. J. RYAN, 1981: The adaptive significance of a complex vocal repertoire in a neotropical frog. *Z. Tierpsychol.* 57, 209—214.
- RICHARDS, D. G., & R. H. WILEY, 1980: Reverberations and amplitude fluctuations in the propagation of sound in a forest: Implications for animal communication. *Am. Nat.* 115, 381—399.
- SCHWARTZ, J., 1987: The importance of spectral and temporal features in species and call recognition in a neotropical treefrog with a complex vocal repertoire. *Anim. Behav.*, in press.
- , & K. D. WELLS, 1983a: An experimental study of acoustic interference between two species of neotropical treefrogs. *Anim. Behav.* 31, 181—190.
- , & —, 1983b: The influence of background noise on the behavior of a neotropical treefrog, *Hyla ebraccata*. *Herpetologica* 39, 121—129.
- , & —, 1984a: Interspecific acoustic interactions of the neotropical treefrog *Hyla ebraccata*. *Behav. Ecol. Sociobiol.* 14, 211—224.
- , & —, 1984b: Vocal behavior of the neotropical treefrog *Hyla phlebodes*. *Herpetologica* 40, 452—463.
- , & —, 1985: Intra- and interspecific vocal behavior of the neotropical treefrog *Hyla microcephala*. *Copeia* 1985, 27—38.
- SULLIVAN, B. K., 1982: Sexual selection in Woodhouse's toad (*Bufo woodhousei*). I. Chorus organization. *Anim. Behav.* 30, 680—686.
- , 1983: Sexual selection in Woodhouse's toad (*Bufo woodhousei*). II. Female choice. *Anim. Behav.* 31, 1011—1017.
- TAIGEN, T. L., & K. D. WELLS, 1985: Energetics of vocalization by an anuran amphibian (*Hyla versicolor*). *J. Comp. Physiol.* 155, 163—170.
- , —, & R. L. MARSH, 1985: The enzymatic basis of high metabolic rates in calling frogs. *Phys. Zoo.* 58, 719—726.
- WELLS, K. D., 1977a: The social behaviour of anuran amphibians. *Anim. Behav.* 25, 666—693.
- , 1977b: The courtship of frogs. In: The Reproductive Biology of Amphibians. (TAYLOR, D. H., & S. I. GUTTMAN, eds.) Plenum Press, New York, pp. 233—262.
- , & J. J. SCHWARTZ, 1982: The effect of vegetation on the propagation of calls in the neotropical frog *Centrolenella fleischmanni*. *Herpetologica* 38, 449—455.
- , & —, 1984: Vocal communication in a neotropical treefrog, *Hyla ebraccata*: Advertisement calls. *Anim. Behav.* 32, 405—420.
- , & T. L. TAIGEN, 1986: The effect of social interactions on calling energetics in the gray treefrog (*Hyla versicolor*). *Behav. Ecol. Sociobiol.* 19, 9—18.
- WHITNEY, C. L., & J. R. KREBS, 1975: Mate selection in Pacific tree frogs. *Nature* 225, 325—326.
- WILEY, R. H., & D. G. RICHARDS, 1982: Adaptations for acoustic communication in birds: sound transmission and signal detection. In: Acoustic Communication in Birds. Vol. 1. (KROODSMA, D. E., & E. H. MILLER, eds.) Acad. Press, New York, pp. 132—176.
- ZELICK, R. D., & P. M. NARINS, 1982: Analysis of acoustically evoked call suppression behavior in a neotropical treefrog. *Anim. Behav.* 30, 728—733.
- , & —, 1983: Intensity discrimination and the precision of call timing in two species of neotropical treefrogs. *J. Comp. Physiol.* 153, 403—412.

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