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The importance of spectral and temporal properties in species and call recognition in a neotropical treefrog with a complex vocal repertoire

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Abstract. *Hyla microcephala* males use both single and multi-note advertisement and aggressive calls. Aggressive call introductory notes are more variable and have higher pulse repetition rates than those of advertisement calls. In two-choice experiments, female *H. microcephala* preferred synthetic conspecific advertisement calls to synthetic calls with pulse repetition rates characteristic of *H. ebraccata* and *H. phlebodes* advertisement calls and conspecific aggressive calls. Additional experiments indicated that spectral cues are also sufficient for species discrimination, but temporal information may be more important. Secondary notes of both advertisement and aggressive calls have pulse repetition rates similar to primary notes of advertisement calls. During vocal interactions, males add secondary notes to both advertisement and aggressive calls, and females preferred such complex calls to single-note calls. Hence, males can continue to give calls which will attract females even during aggressive interactions.

The importance of spectral and temporal features of anuran calls for species recognition has been studied for over 30 years (Bogert 1960; Blair 1964; Littlejohn 1977). However, many workers have simply described differences between vocalizations of sympatric species and assumed that these are important for mate choice by females (Fouquette 1960; Duellman 1967; Hodl 1977; Duellman & Pyles 1983) or have demonstrated that females are capable of discriminating conspecific from heterospecific calls in two-choice tests (Littlejohn & Michaud 1959; Blair 1964; Wells 1977). However, some characteristics of heterospecific calls may not be important for species discrimination (Straughan 1975; Gerhardt 1978a). Therefore, if we are to understand the evolution of call structure and reproductive isolation, it is necessary to employ carefully designed experiments to identify the relevant call properties. By using synthetic calls in female choice experiments, a technique that has been refined by workers such as Loftus-Hills & Littlejohn (1971) and particularly Gerhardt (1981a, b), it has been possible to vary signal elements and thereby dissect out those features important for species discrimination. These studies have shown that call components critical to species recognition may differ between pairs of species (Gerhardt 1981a, b, 1982). Usually either spectral (Gerhardt 1974, 1981a, b) or fine-scale temporal features such as pulse repetition rate (Loftus-Hills & Littlejohn 1971; Straughan 1975; Gerhardt 1978a) are important for species recognition.

Three neotropical hylid frogs, *Hyla microcephala*, *H. ebraccata* and *H. phlebodes*, breed in the same habitats in central Panama, with males of different species often calling within a few centimetres of one another (Schwartz & Wells 1984a, b, 1985). However, heterospecific pairs are almost never found in amplexus (Fouquette 1960; personal observations), suggesting that calls contain information mediating pre-mating isolation. The vocal repertoires of these species are very similar, and interspecific acoustic interactions between males occur frequently (Schwartz & Wells 1983a, b, 1984a, b, 1985). Males have a complex vocal repertoire (sensu Rand & Ryan 1981) and give multi-part advertisement and aggressive calls consisting of a buzz-like primary note often followed by shorter secondary click notes. Both the primary and secondary notes are composed of trains of pulses.

Fouquette (1960) described some temporal and spectral differences in the calls of these species and concluded that these differences maintained reproductive isolation. However, he did not present acoustic stimuli to females, so his conclusions are unsubstantiated. Moreover, his analysis of call structure did not include pulse repetition rate, which accounts for most of the interspecific differences in temporal structure of advertisement calls. This feature also differentiates aggressive calls from advertisement calls in all three species, with aggressive calls always having significantly higher pulse repetition rates (Schwartz & Wells 1984a).

In this study, I conducted experiments with synthetic vocalizations to identify features of *H. microcephala* calls that allow females to distinguish between conspecific and heterospecific calls, and between advertisement and aggressive calls of their own species. A previous analysis of call structure suggested that females could use either spectral or temporal cues to discriminate conspecific from heterospecific advertisement calls (Schwartz & Wells 1984a). Although the calls of *H. microcephala*, *H. ebraccata* and *H. phlebodes* exhibit considerable frequency overlap near 3 kHz, *H. microcephala* calls have a second band of energy centred at 6 kHz which is absent in the other species' calls (see sonagrams in Schwartz & Wells 1984a). Pulse repetition rates of advertisement calls show little intraspecific variation and are significantly higher in *H. microcephala* than in the other two species. Aggressive calls of *H. microcephala*, *H. ebraccata* and *H. phlebodes* show considerable intraspecific variation and also extensive overlap in pulse repetition rate among species (Schwartz & Wells 1984a). Therefore, an additional goal of the study was to assess the attractiveness of aggressive calls to female *H. microcephala*, both inherently and relative to advertisement calls. Because other experiments (Schwartz 1986) demonstrated that addition of secondary notes enhances the attractiveness of advertisement calls, I investigated whether the same was true for aggressive calls. Finally, I examined the fine temporal structure of secondary notes from advertisement and aggressive calls. These data were compared with pulse repetition rates in the primary notes of both types of calls.

METHODS

Study Area

The experiments described below were conducted during July and August 1984 and 1985. The study site was a flooded meadow in Gamboa, Panama, close to the Panama Canal (Schwartz & Wells 1984a). *H. microcephala*, *H. ebraccata* and *H. phlebodes* breed here in dense choruses during the rainy season, and males establish calling sites on vegetation in or adjacent to pools of water. Most calling occurs between 1930 and 2400 hours.

Analysis of Calls

The duration and number of pulses in the primary and secondary notes of advertisement and aggressive calls of four *H. microcephala* males were measured using a Tektronix 5111 storage oscilloscope. These data were used to calculate pulse repetition rates (pulses/s) in each note. Because *H. microcephala* secondary notes are composed of two discrete pulse trains (Fig. 1B), pulse rates were calculated for these elements individually. Sample sizes given for secondary notes equal the number of sub-units. The calls were recorded during playback experiments conducted in 1981 and 1982. Data were analysed using non-parametric statistics (Noether 1976).

Female Choice Experiments

Most choice stimuli were generated on a custom-built sound synthesizer described in Gerhardt (1974, 1978b). Synthetic signals were band-pass-filtered with a Krohn-Hite 3550 filter to reduce any harmonic distortions and recorded on a ReVox A77 tape-recorder. A three-note aggressive call was created by adding two recorded natural secondary notes to a synthetic one-note aggressive call. This approach was taken because the biphasic structure of secondary notes in *H. microcephala* calls made them impossible to synthesize using the above methods without degradation of the signal quality. These recordings were subsequently copied onto cassettes using a Uher 4200 Report Stereo IC tape-recorder and Sony TC-FX4 cassette tape-deck. The call rate was 10/min per channel; this is close to the median calling rate of male *H. microcephala* in the field (Schwartz & Wells 1985). Calls used in two-choice discrimination tests were alternated between channels every 3 s.

Both two-choice and single stimulus female choice experiments were performed in a darkened apartment in Gamboa at natural field temperatures (about 26°C) between 2230 and 0300 hours. Two Realistic Minimus 0·3 speakers (amplitude-frequency response: ±3 dB, 1·0–12·0 kHz) driven by a Marantz PMD 360 stereo cassette tape-recorder were placed 1·60 m apart at opposite corners of an arena delimited by uniformly coloured 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 the movements of the experimenter. A 25-W red bulb suspended 1 m above the centre of the arena provided illumination. Playback intensities for each speaker were regulated by separate Realistic L-pads. For two-choice tests, playback intensities were equalized at the female release point at 90 ± 1 dB (peak Sound Pressure Level (SPL); dB re 20 μPa), unless noted as otherwise, using a Gen Rad 1982 precision sound level meter set for flat weighting and held 2·5 cm above the floor. For most tests employing a single speaker, playback intensities at the release point were adjusted to 85 dB SPL. The intensities at the release point correspond to a *H. microcephala* male calling approximately 3·2 m (90 dB SPL) or 5·7 m (85 dB SPL) away (modal peak SPL = 106 dB at 50 cm; Schwartz & Wells 1984a).

Females were captured in amplexus between 2230 and 0100 hours and transported to the arena in individual plastic food boxes. Each female was placed 1·70 m from the speakers near the centre of the arena. The box lid was replaced with a piece of cardboard which could be lifted off the box with a string from outside the arena. The lid was lifted off the box 1 min after stimulus playbacks were started. A positive response was scored if a female approached to within 10 cm of one speaker within 10 min; in the two-choice experiments most females moved directly toward a speaker and either made contact or hopped to the curtain directly behind it. In the tests with just one sound source, females were given 10 min to give a positive response. If she did not approach the speaker, her response was recorded as negative.

RESULTS

Pulse Repetition Rates of Call Elements

The distributions of pulse repetition rates of primary and secondary notes of *H. microcephala* advertisement and aggressive calls are shown in Fig. 1. The pulse repetition rate of aggressive call secondary notes (median = 250 pulses/s, $N = 4$ males) was significantly lower than that of aggressive call primary notes (median = 379 pulses/s, $N = 4$ males; $P < 0.001$, two-tailed Mann–Whitney U-test) for each male recorded and was very similar to that of advertisement call primary notes (median = 235 pulses/s, $N = 4$ males). There was no significant difference between the pulse rates of aggressive and advertisement call secondary notes (median = 250 pulses/s). The previously published (Schwartz & Wells 1985) median value for pulse repetition rates of aggressive call primary notes is slightly lower than that reported here. This difference occurred because only calls with at least two secondary notes were included in the current sample. In *H. microcephala*, primary note duration is negatively correlated with the number of notes, and calls with long primary notes often have lower pulse repetition rates than those with short primary notes (Schwartz & Wells 1984a, 1985).

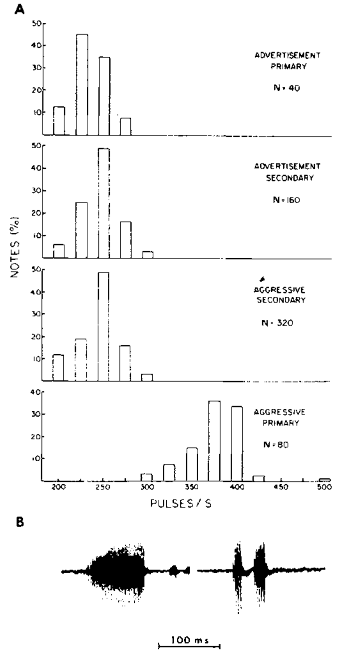

Figure 1. (A) Distributions of pulse repetition rates in primary and secondary notes of *H. microcephala* advertisement and aggressive calls. For the biphasic secondary notes, sample sizes give twice the actual number of notes. Equal numbers of notes were measured for each of four males. There was no significant difference in secondary note pulse repetition rate among males. (B) Oscillograms of a *H. microcephala* aggressive call primary note and the first secondary note showing the different pulse repetition rates. Horizontal bar shows time scale.

Importance of Pulse Repetition Rate

To assess the importance of pulse repetition rate in species discrimination, female *H. microcephala*

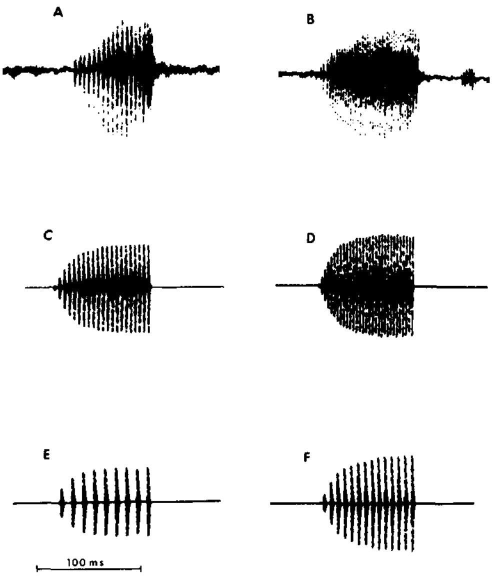

Figure 2. Oscillograms of natural *H. microcephala* calls and synthetic stimuli presented to females. (A) Natural advertisement call. (B) Natural aggressive call. (C) 225 pulses/s synthetic call. (D) 325 pulses/s synthetic call. (E) 95 pulses/s synthetic call. (F) 150 pulses/s synthetic call. Horizontal bar shows time scale.

were given a choice between a synthetic one-note conspecific advertisement call (225 pulses/s) and calls with pulse repetition rates characteristic of *H. ebraccata* (95 pulses/s) and *H. phlebodes* (150 pulses/s) advertisement calls. They were also given a choice between the first stimulus and a synthetic one-note conspecific aggressive call (325 pulses/s) at equal intensities of 90 dB SPL and unequal intensities of 85 and 90 dB SPL, respectively. The pulse repetition rates in synthesized calls were close to the median values in large samples of natural calls (Schwartz & Wells 1984a, b, 1985). These stimuli were identical in all other temporal features (duration = 90 ms; rise time = 45 ms; duty cycle = 0·5) and were similar in form to both *H. microcephala* advertisement calls and short aggressive calls (Fig. 2). Spectrally, the calls were similar to those of *H. microcephala*; two components of equal relative amplitude were centred at 3 kHz and 6 kHz, each with a power bandwidth of 400 Hz.

The call with a pulse rate characteristic of conspecific advertisement calls was strongly preferred to calls with pulse rates characteristic of heterospecific advertisement calls. Females also preferred the synthetic conspecific advertisement call to the synthetic conspecific aggressive call when playback intensities were equalized. However, they showed no preference when the intensity of the advertisement call was lowered 5 dB SPL (Table I). In single-speaker presentations, all five females tested at 90 dB SPL found the synthetic aggressive call attractive. At 85 dB SPL most females failed to approach the speaker and simply wandered around the arena, a significant difference ($G = 4{\cdot}53$, $P < 0{\cdot}05$, Table II). When given a choice between the synthetic one-note advertisement call and the three-note aggressive call, females demonstrated a significant preference for the aggressive call (Table I). Females did not show a side bias in any experiment.

In spite of these results, it was not clear whether females could use only the temporal information present in a natural chorus of conspecific and heterospecific males to identify a conspecific mate. For example, if auditory sensitivity in female *H. microcephala* is finely tuned around 6 kHz, then the pulse repetition rate of *H. ebraccata* and *H.*

Table I. Results of two-choice playback experiments with *H. microcephala* females

No. of females choosing		*P*
225 Pulses/s	95 Pulses/s	
8	0	0·008
225 Pulses/s	150 Pulses/s	
9	0	0·004
225 Pulses/s	325 Pulses/s	
9	1	0·022
225 Pulses/s	325 Pulses/s	
85 dB	90 dB	
7	7	NS
225 Pulses/s	325 Pulses/s	
1-note	3-note	
1	8	0·040
Normal	High attenuated	
13	4	0·050
Low attenuated	High attenuated	
8	0	0·008
Normal	Low attenuated	
1	8	0·040

Pulse rates are characteristic of the following calls:
225 Pulses/s = *H. microcephala* advertisement call;
95 Pulses/s = *H. ebraccata* advertisement call;
150 Pulses/s = *H. phlebodes* advertisement call;
325 Pulses/s = *H. microcephala* aggressive call;
P values are for two-tailed binomial tests.

Table II. Responses of female *H. microcephala* in single-speaker tests

Test	Stimulus	Positive	Negative	*P*
1	225 Pulses/s 3 kHz	6	0	<0·001*
2	95 Pulses/s 3 kHz	0	5	<0·01†
3	95 Pulses/s 6 kHz	0	5	<0·01†
4	325 Pulses/s 85 dB	3	7	<0·05‡
5	325 Pulses/s 90 dB	5	0	<0·001*

* *P* value for two-tailed binomial test. Expected probability for a positive result equals angle subtended by speaker face at the release point divided by 360 degrees.

† *G*-test of independence of responses to those during test 1.

‡ *G*-test of independence of responses to those during test 5.

phlebodes calls would be irrelevant because these calls have most of their energy near 3 kHz. To evaluate this possibility, I presented six females with synthetic calls with a pulse rate of 225 pulses/s, but with only the 3 kHz spectral component, in a single-speaker experiment. All six females responded by hopping directly to the speaker, most within 5 min (Table II). This shows that females can detect calls at 85 dB SPL near the dominant frequency of heterospecific calls. Therefore, they could use pulse repetition rate as a property of these calls to discriminate between the three species in the chorus. When presented with a 3 kHz synthetic call with a pulse repetition rate characteristic of *H. ebraccata* advertisement calls (95 pulses/s), females did not approach the speaker, a significant difference ($G=8{\cdot}47$, $P<0{\cdot}01$) from the previous experiment.

Importance of Frequency Characters

In a second series of tests, females were presented with calls having different spectral characteristics. They were first given a choice between the synthetic conspecific advertisement call and a call in which the 6 kHz component had been selectively attenuated by 10 dB relative to the 3 kHz component. A significant number of females preferred the normal call, although the discrimination was not as clear as when pulse repetition rate alone was varied (Table I). This result could be explained if females find the 6 kHz component more attractive than the 3 kHz component, or if a normal call, with both spectral components, is preferred over a call with just one component. Additional results support the first hypothesis rather than the second. In one experiment, females were given a choice between calls in which either the high or low frequency band had been selectively attenuated by 10 dB. All subjects preferred calls with peak energy centred at 6 kHz. When a normal call was alternated with a call deficient in energy at 3 kHz (−10 dB), most females chose the latter (Table I).

In a final single-speaker test, females were exposed to calls with the preferred spectral component (6 kHz) and the *H. ebraccata* pulse repetition rate (95 pulses/s). None of the five frogs tested approached the speaker, a significant difference from the complementary experiment with the preferred pulse repetition rate and the heterospecific dominant frequency ($G=8{\cdot}47$, $P<0{\cdot}01$).

DISCUSSION

The data demonstrate that *H. microcephala* females can use pulse repetition rate to discriminate conspecific from heterospecific calls. Other studies of hylid frogs have also demonstrated the importance of this temporal feature in species recognition (Loftus-Hills & Littlejohn 1971; Straughan 1975; Gerhardt 1978a). In the absence of temporal differences, spectral information can be used. However, single-speaker experiments suggest that the temporal information is more important. A call with the conspecific pulse repetition rate, but lacking energy at 6 kHz, was sufficient to attract females; a 6 kHz call with a pulse repetition rate of 95 pulses/s was not. Additional experiments are required to determine the degree to which females can discern fine differences in pulse repetition rate. It is possible, for example, that a 6 kHz, 150 pulses/s call would elicit phonotaxis. Females in a natural chorus would not have to choose between calls such as those used in the single-speaker tests. However, because of increased excess attenuation of high frequencies caused by scattering, atmospheric absorption and ground impedance (Wiley & Richards 1982) they might perceive calls similar to the 3 kHz, 225 pulses/s stimulus at some distance from conspecific males. Therefore, a failure to orient toward a call with appropriate temporal features, but deficient in energy at 6 kHz, could be disadvantageous. In *H. cinerea*, another species with a bimodal call spectrum, females do not detect deficiencies in the relative amplitude of the high frequency component at low sound pressure levels (Gerhardt 1976, 1981b).

The discrimination in a two-choice test against synthetic calls with a pulse repetition rate of conspecific aggressive calls may have occurred because heterospecific aggressive calls have similar pulse repetition rates. However, in spite of the serious consequences of pairing with a male of the wrong species, female *H. microcephala* found synthetic conspecific aggressive calls inherently attractive at 90 dB SPL. In a natural chorus it would not matter whether aggressive calls are absolutely or only relatively unattractive. *H. microcephala* males form dense aggregations, and gravid females in the chorus would usually be exposed to both advertisement and aggressive calls simultaneously. In addition, at close range, spectral information would be available to supplement temporal information.

Female discrimination experiments using advertisement and aggressive calls have been conducted with only two other species of frog. Oldham & Gerhardt (1975) found that female *H. cinerea* preferred advertisement calls over the conspecific aggressive call, but the conspecific aggressive call was preferred to the advertisement call of *H. gratiosa*. In this case, the *H. cinerea* aggressive call is not similar to calls of sympatric heterospecifics. The unpulsed advertisement call may be preferred simply because the pulsed aggressive call is very different in gross temporal structure. Wells & Bard (in press), working with *H. ebraccata*, also found that females discriminate against synthetic aggressive calls in favour of advertisement calls.

The level of discrimination of pulse repetition rate demonstrated by female *H. microcephala* contrasts sharply with the behaviour of males. Playback experiments and observations of natural interactions indicated that males are responsive to both conspecific and heterospecific vocalizations encompassing a wide range of pulse repetition rates (Schwartz & Wells 1985). Whether this behavioural dichotomy between the sexes reflects an underlying difference in peripheral or central processing of acoustic signals is unknown. Such a phenomenon has been reported only in *Eleutherodactylus coqui*, in which differential frequency tuning in the peripheral auditory system occurs in males and females (Narins & Capranica 1976). Recent work has indicated that neurons sensitive to different rates of amplitude modulation exist in the midbrain of certain species of frogs (Capranica & Rose 1983; Rose & Capranica 1983, 1984; Walkowiak 1984) suggesting that neurophysiological studies of *H. microcephala* could yield fascinating results.

Data from a female choice experiment indicate that male *H. microcephala* can counteract the relatively unattractive pulse repetition rate of aggressive call primary notes by adding secondary notes to their calls. Aggressive call secondary notes have pulse repetition rates similar to those of advertisement calls, and addition of secondary notes also enhances the attractiveness of advertisement calls (Schwartz 1986). Therefore, it is likely that a male can convey an aggressive message to a competing male and simultaneously continue to attract potential mates (Wells & Schwartz 1984). A similar degree of communicative sophistication may occur in *H. ebraccata*, where female preference for a synthetic advertisement call was eliminated when two secondary notes were added to a synthetic aggressive call (Wells & Bard, in press). A functional dichotomy in the components of biphasic calls is also known in *Eleutherodactylus coqui* of Puerto Rico (Narins & Capranica 1976, 1978) and in the Australian leptodactylid, *Geocrinia victoriana* (Littlejohn & Harrison 1985). In both species, the introductory notes of advertisement calls are important in male–male interactions, while females respond to the secondary notes.

Aggressive calls of *H. microcephala* males are graded; males lengthened their primary notes as the distance between competitors decreased (personal observation) or as call playback intensity increased (Schwartz & Wells 1985). In conjunction with changes in the duration of primary notes of aggressive calls are changes in the number of accompanying secondary notes. Aggressive calls with long primary notes tend to have few secondary notes (Schwartz & Wells 1985). This pattern in call structure could reflect some physical limit on the total duration (primary plus secondaries) of calls which males can give. However, because males occasionally give aggressive calls with long primary notes and many secondary notes, this explanation is unlikely. Alternatively, the behaviour may relate to the chances a male has of successfully attracting a mate. While engaged in close range aggressive interactions, it might not be advantageous to give calls that are attractive to females, since competing males could easily intercept potential mates. With increasing separation of competitors, there should be a corresponding increase in the advantage of adding secondary notes to calls.

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