

THE VOCAL REPERTOIRE OF HYLA CRUCIFER

by

Nancy Case Hurst

Thesis submitted to the Graduate Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

Biology

APPROVED:

T. A. Jenssen, Chairman

D. A. West

H. J. Heikkinen

November, 1982

Blacksburg, Virginia

ACKNOWLEDGEMENTS

I wish to thank the Virginia Polytechnic Institute and State University Biology Department for a grant which permitted this work. Both the Department and my committee, particularly my advisor, Dr. T. A. Jenssen, deserve my thanks for their patience, since my progress of necessity was slow. The cooperation of the Mechanical Engineering Department in the use of instrumentation was most appreciated. I am also greatly indebted to Dr. C. J. Hurst for his acoustical expertise and encouragement.

TABLE OF CONTENTS

	Acknowledgements.....	ii
I.	Introduction.....	1
II.	Literature Review.....	3
III.	Materials and Methods.....	14
IV.	Results.....	32
V.	Discussion.....	59
VI.	Conclusions.....	66
	Literature Cited.....	67
	Appendix.....	72
	Vita.....	74

I. INTRODUCTION

My study of Hyla crucifer calls has dealt mainly with amplitude and temporal relationships. The calls have a very narrow frequency range. It seems possible, therefore, that more information may be conveyed by amplitude patterns than by frequency patterns among these frogs.

Measurements of amplitude and temporal variables led to the discovery of a new call: the tapered call. The "peep", "trill" and "release call" (small-pulsed call) have been described in H. crucifer literature (Conant, 1958; Fellers, 1976; Noble, 1954; Oplinger, 1963; Wells, 1977; Wright and Wright, 1949). To my knowledge, the tapered call has never been described.

Most previous analyses of frog calls (such as Allan, 1973; Blair, 1958 a; Capranica, 1968; Gerhardt, 1973; Straughan, 1975; Sullivan, 1982; Wells, 1978) have been made with a Kay Sona-Graph which, while it gives an accurate idea of the frequency vs. time pattern of calls, gives very little information about amplitude. This instrument is well suited for the study of vocalizations with complicated frequency changes, but is not suitable for most frog calls where time and amplitude patterns are important. Capranica (1966,1968) and Gerhardt (1973,1974,1978) have used oscillographs extensively for the study of frog calls with

better results. Narins and Capranica (1977) employed a real time frequency analyzer having a digital display system with several filters. While their system had some advantages in the measurement of temporal relationships, it was cumbersome to use. I was able to use a digital processing oscilloscope with Fast Fourier Transform capability which enabled me to make fine, accurate measurements of temporal variables as well as frequencies.

II. LITERATURE REVIEW

Introduction

Early publications dealing with frog calls were mainly descriptive in nature. They rarely gave any quantitative data. Most of the work was summarized in a review by Bogert (1960). He proffered a tentative classification of frog calls, listing them as mating, release, territorial, "rain", distress, and warning calls. Later authors (McDiarmid and Adler, 1974; Wells, 1977) proposed to divide "mating" calls into two categories: advertisement and encounter, feeling that "mating" assigned too specific a function to the calls.

Efforts more recently have been made to deal with frog calling in a more quantitative fashion. The rest of this chapter will set forth the findings of various authors as they have approached the subject from the viewpoints of determining the characters used in species recognition and female attraction, the effects of temperature on calls and hearing, the amplitudes involved in calls; and more functionally, the roles of calls in territoriality and aggression and in calling ensembles and choruses.

Calls in Species Recognition

Efforts to determine the mechanisms of species recognition of frog calls were anecdotal until about

the middle of this century. The role of mating calls as isolating mechanisms among some Hylidae was investigated by Martof (1961). W. F. Blair (1958, 1959) expanded on the work of his father, A. F. Blair (1941), by using sonagrams to study the intraspecific and interspecific variation of frog calls within populations, and among closely related species in sympatry. He found that such sympatric species tend to exaggerate the differences between their calls in comparison with allopatric populations of the same species and went on to use calls as evidence of evolutionary relationships among anurans (1960, 1962).

Carrier frequency and pulse rate both seem to be important in species discrimination, one species or population often favoring one character over the other. Blair (1964) suggested that both variables are probably functions of the frog's body size and therefore inherent properties of a particular population, but in Bufo woodhousei australis, mean pulse rate and mean call duration are not significantly correlated with snout-vent length (SVL) (Sullivan, 1982). Only mean carrier frequency is correlated with body size (negatively).

Several authors have studied the role of pulse rate in species recognition. Two Australian species of Hyla (Loftus-Hills and Littlejohn, 1971 b) and two American Hyla species (Straughan, 1975) were found to be discriminating on pulse rate alone. The pulse rates of similarly calling species usually differ by a factor of two or more, with no

overlap in the ranges of variation (Littlejohn, 1977). Evidence from hybrids indicates that pulse rate is genetically controlled (Gerhardt, 1973).

Call frequency is the more important discriminating character for bull frogs, and one frequency band alone is not sufficient for species recognition. The bullfrog call possesses three frequency bands, a high one, a middle one and a low one. Both the high and low frequencies are necessary in species recognition (Capranica, 1966, 1968).

The brain-evoked responses of several species of Australian frogs to auditory stimuli are consistently bimodal (Loftus-Hills and Johnstone, 1970). Such bimodality probably indicates that the responses are the manifestations of outputs from the basilar and amphibian papillae of the anuran ear. Sensitivity to different frequencies in two bands by different species could act as a filter system enabling frogs to respond only to conspecifics in an environmental situation where many species were present at once, such as a mixed chorus (Loftus-Hills and Johnstone, 1970). In Acris crepitans individual neural fibers of the auditory nervous system are tuned to local dialects, most of the tuning being limited to the high frequency component of the call (Capranica, Frishkopf, and Nevo, 1974). Female Hyla cinerea choose conspecifics on the basis of bimodal frequency spectra but the low frequency peak alone is

effective as an attractant to the female if it is loud enough (Gerhardt, 1974).

A combination of carrier frequency and pulse rate may be necessary for discrimination between some species. H. cinerea and Hyla gratiosa have differing high frequency bands, although the separation of the ranges of the two bands was not complete. This could jeopardize species separation since the two species are frequently sympatric and breed at the same time. H. cinerea females are more attracted to calls that have a low frequency component. Both species' calls begin with a pulsatile segment, but this has proved more necessary for discrimination by H. gratiosa. Gerhardt (1981 a,b) suggested the following scenario: the low frequency component of calls attracts from a long distance; as females approach the chorus the high frequency portion becomes more important; within a short radius of individual callers females choose mates based on finer discrimination within the high frequency band and the presence or absence of the pulsatile segment.

Temperature Effects

The carrier frequencies of calls by H. cinerea males are not affected by temperature changes (Gerhardt and Mudry, 1980). The upper frequency bands did not change in individuals subjected to lower temperatures. An interesting side effect did emerge from this study: female H. cinerea

kept at low temperatures tended to prefer lower frequency calls. The calls of conspecifics did not change with the lower temperatures. However, the calls of H. gratiosa naturally are lower in frequency than those of H. cinerea. At low temperatures H. cinerea females tended to prefer H. gratiosa calls. Low temperatures, therefore, could be another factor in incomplete separation of these two species.

Call parameters which are determined by active physiological processes, such as call duration, pulse rate and call repetition rate are greatly influenced by temperature. Call duration is negatively correlated with temperature, while pulse rate and repetition rate are positively correlated (Littlejohn, 1977).

Amplitude

Sound pressure levels (SPL) of frog calls are also important in male to male encounters and in attracting females. Amplitude alone can change perception of a call and, therefore, must be carefully controlled (Wells and Greer, 1981). Loftus-Hills and Littlejohn (1971 a) measured sound pressure levels at 1 m and 50 cm from calling Australian frogs. Gerhardt (1975) published SPL values at measured distances for 21 species of North American frogs. Both papers mainly furnished data in efforts to supply a need noticed in playback experiments. Calls have different

meanings at different amplitudes. Louder calls are perceived as coming from a closer male, and therefore are more agonistic in context. The two papers differ over the matter of relative amplitudes produced by large and small species of frogs: Loftus-Hills and Littlejohn found that large species called more loudly than small, but Gerhardt did not find this to hold true.

Within the same call, differing amplitudes can convey differing messages, as in the case of Eleutherodactylus cogui (Narins and Hurley, 1982). The first "co-" portion of the call, having lower amplitude and frequency, is attractive to females, while the concluding "-qui" portion with its higher amplitude and frequency is repellant to other males.

Any description of animal calls requires an understanding of the physical constraints on the calls. Ground impedance is very important in the attenuation of high frequencies when the caller is close to the ground. The high frequency component is not affected so much when both caller and receiver are near water. When both receiver and caller are elevated, the amplitude is complicated by reflected sound being added to sound waves travelling in a direct path to the receiver. This can obscure differences between the calls of nearby males. The least affected situation is when either the receiver or caller is elevated

and the other is on the ground. In this case the path of the sound is likely to be most direct, with the least opportunity for absorption or reflection (Gerhardt, 1981 a).

Territoriality and Aggression

A debate exists over whether frogs, particularly prolonged breeders (such as H. crucifer), are truly territorial, or whether they call as a spacing mechanism. If territorial, just what are they defending? They may defend the areas around oviposition sites, calling perches or courtship areas, but they rarely, if ever, engage in physical combat over the possession of individual females (Wells, 1977).

The spacing of clusters of Rana clamitans males remains constant even when the cluster as a whole moves from place to place (Martof, 1953). Such spacing is not only an important method of energy conservation, but in very small species spacing may be necessary for females to find individual calling males. Among the Microhylidae which emit high frequency calls, orientation to sound is limited by the small size of the head. Phase differences between signals are ambiguous for frequencies with wave lengths greater than twice the distance between the ears receiving them. Separation of calling males is therefore very important to these little frogs (Nelson, 1973). Such a spacing call has been described in the Hyla versicolor complex (Pierce and

Ralin, 1972). Calling results in even spacing of male H. crucifer at low population densities, but the spacing breaks down and becomes random at high densities (Fellers, 1976). The calls of Dendrobates pumilio serve the dual functions of spacing males 2-3 m apart and attracting females (Bunnell, 1973).

The degree of territoriality to be found in Hyla regilla is debatable. Male H. regilla call more to attract females than to delimit territories, according to Brattstrom and Warren (1955). Later Allan (1973) reported that H. regilla gave a monophasic call in response to any sudden nearby movement and a trill which causes other males to move away from the area of the caller.

Fighting has been reported among H. crucifer males (Fellers, 1976). It appears to be temperature-dependent: at low temperatures when the calling rate is lower and the pauses between each male's call longer a fourth male is tolerated in a trio. However, at higher temperatures and faster calling rates, fighting breaks out when a fourth caller attempts to join the ensemble. Fighting also occurs when males are 10 cm or less apart.

Physalaemus pustulosus males frequently fight each other (Ryan, 1980). Rana clamitans occasionally engage in physical combat (Jenssen and Preston, 1968; Wells, 1978) after emitting a warning "growl" signal. Physical

encounters are also reported among Hyla faber (Lutz, 1960), among Dendrobates galendoi and Prostherapis panamensis (Duellman, 1966) and among Scaphiopus hammondi (Whitford, 1967).

Silent satellite males are often tolerated within the area defended by a calling male. Satellite males occur in several species: among H. crucifer (Fellers, 1976); among Physalaemus pustulosus (Ryan, 1980); and among H. cinerea, Hyla squirella and H. versicolor (Perrill, Gerhardt, and Daniel, 1978). Perrill, et. al. (1978) found that satellite males are waiting to intercept females. Sometimes satellite males actively pursue approaching females. When a calling male is removed from his position, some satellite males begin to call, but most simply leave the area.

Calling Ensembles

There has been some speculation that calling ensembles (duets, trios, quartets,) may be a manifestation of hierarchical order of dominance, but this has yet to be proven. Just what is a manifestation of dominance is also in question. Duellman (1967) mentioned "dominant individuals" in his description of neotropical anuran social orders. The dominant male of Engystomops pustulosus is the most successful breeder in a chorus of these frogs (Brattstrom, 1962). P. pustulosus males larger than the mean size of that population are more likely to acquire mates

(Ryan, 1980). Probably these larger males call with a lower frequency, in which case a lower frequency call might be considered dominant. Female Bufo woodhousei australis prefer males who call more frequently (Sullivan 1982), indicating that higher call rate could be a dominant character. Both of these observations deal with breeding success which may not parallel dominance in ensembles. This problem has not been studied adequately.

Attempts to sort out the mechanisms of the calling ensemble began with a description of Hyla crucifer choruses by Goin (1949). He used musical annotation to designate the carrier frequencies of each of the callers in a trio. Since then interest has switched to the timing of calls in an ensemble. A graphical presentation of the timing and call order of H. crucifer duets was developed by Rosen and Lemon (1974). Loftus-Hills (1974) proposed a model for the pacing of calls: a frog calls; a refractory period follows during which he cannot be induced to call again; an excitatory phase follows during which calling can be induced; an activation phase follows, during which, if another call does not induce calling by the frog investigated, that frog calls spontaneously. However, H. crucifer males are affected by stimulus calls occurring during the refractory period as well as during the excitatory period (Lemon and Struger, 1980). The frogs are not able to call until the refractory

time is complete, but the effect is to shorten the interval before the next call. The refractory period is a period of stimulus receptivity, but the frog is unable to call while it lasts. The stimulus effect of calls on male Hyla meridionalis is associated with the dilatory effect of the refractory period on a response (Paillette, 1976). Amplitude has an effect on overriding the pause between calls. However, once this occurs, the ensuing pause lasts longer.

Choruses

The chorus of prolonged breeders such as H. crucifer may be likened to the lek behavior found among birds (Wells, 1977). The chorus is made up of many ensembles of frogs occupying a suitable breeding area: usually a shallow swamp, temporary pond or ditch having emergent or shoreline vegetation which can serve as calling perches. The combined sound of many frogs calling at one time carries much farther than does the call of a single frog. This is particularly true of the smaller species of frogs with their high frequency calls. The watery area is analogous to the display ground of a bird lek, and the combined calling to combined visual displays.

III. MATERIALS AND METHODS

Field

I recorded 465 calls of 36 individual frogs in the field on five nights during the springs of 1977 and 1978. A Uher 4000 Report IC tape recorder was used with a Uher M514 microphone. This dynamic pressure type microphone had a nominally flat frequency response from 40 Hz to 14kHz. The tape recorder's frequency response was flat from 40 Hz to 20 kHz. I calibrated both tape recorder and microphone by comparing output from the Uher and its microphone with known sound levels determined using a Bruel and Kjaer type 4145 2.54 cm diameter capacitor microphone and a Bruel and Kjaer type 2204 precision sound level meter. The calibration measurements were made in an acoustically soft-walled room to avoid extraneous noise problems.

In the field I set the recording volume below zero on the VU meter so that the sound pressure peaks of the frog calls did not exceed the range of the recorder. During recording sessions the VU meter was carefully monitored to avoid saturation. I checked the resulting tapes with an oscilloscope to be sure that the signals were not clipped at each volume setting. All calls were recorded at the maximum volume setting which avoided clipping. I made recordings only on very still nights, since I found that rain and

particularly wind distorted the signals markedly.

All but 21 of the calls were made between 1900 and 2200 h in the field at three temporary ponds and a drainage ditch (Fig. 1). These were located in a meadow about 50 to 100 m from Tom's Creek near Longshop 14.5 km west of Blacksburg, Montgomery County, Virginia. The shores of the ponds and the ponds themselves were nearly bare of growing vegetation in March when the first recordings were made. At that time the frogs tended to call from the cover of hummocks of dead grasses and sedges. They were well hidden near the water line. As the season progressed and the air became warmer, the frogs were to be found progressively higher on the emergent vegetation and plants growing along the shores, closer to the water on cold nights and farther from it (up to 1.5 m) on warmer ones. The most frequent calling distance from the water ranged between 25 cm to 1 m. During April and May grasses, sedges, daffodils, and honeysuckle grew up and leafed out, furnishing calling perches.

Suitable evenings for recording were few due to rains and wind which interfered with recording, or periods of floods, drought and cold which decreased calling activity. The nights that were warm enough for much activity brought out large choruses of frogs which created too much background interference.



Fig. 1. Pond and ditch in Montgomery County, Virginia where most of the field work was done.

Twenty-one of the calls used in the analysis were recorded in a 30 x 76 x 30 cm aquarium in which there were five frogs.

Analysis of Recorded Calls

I analyzed all calls with a Norland 3001 Digital Processing Oscilloscope. The calls were captured in digital form using a 50 microsecond sample rate. The Norland memory is capable of holding 4096 samples, so it was possible to record a total call length of 204.8 ms. This was quite adequate for most calls, and longer calls could be recorded in sections. The Norland possesses a trigger mechanism which can be set to begin recording at predetermined delayed times. By using it I could measure the later portions of longer calls in a second playing of the same tape section, and could piece the sections together accurately.

The Norland Fast Fourier Transform (FFT) program transforms time domain samples gathered as above to the frequency domain, giving amplitude vs. frequency information. However, the FFT program can work with only 1024 data points, and requires 2048 memory locations to store the result. When the first 1024 points in the memory are used as input to the FFT program, the average frequencies in the first quarter of the recorded call are found. When the last 1024 points in the memory are used, the frequencies of the last quarter of the captured call are

calculated. All calls were "windowed" before analysis. This process reduces the amplitude of the call segment to zero near each end as required in the FFT procedure to eliminate spurious frequency information.

I measured seven variables for each call. These are defined in the following paragraphs.

Call Duration: Call duration was measured from the onset of the call to the end of the main body of the call (Fig. 2). Frequently there was a "tail" of varying length and very low amplitude which was not included in the measurement, since it was probably caused by residual energy or sound reflection.

Number of Pulses: The number of pulses was counted and the degree of amplitude modulation was found to vary considerably from a single pulse to 15 or 16 pulses. I considered a pulse to be a marked amplitude modulation. This involved some subjective judgement since the number of pulses in a call was not always distinct (Fig. 3).

Position of Maximum Amplitude: Each call was assigned to one of 6 categories which best expressed its amplitude configuration (Fig. 4). These were based on the position of maximum amplitude: (1) at the beginning of the call, (2) in the first half of the call, (3) even throughout the call, (4) in the middle of the call, (5) in the second half of the call, or (6) at the end of the call.

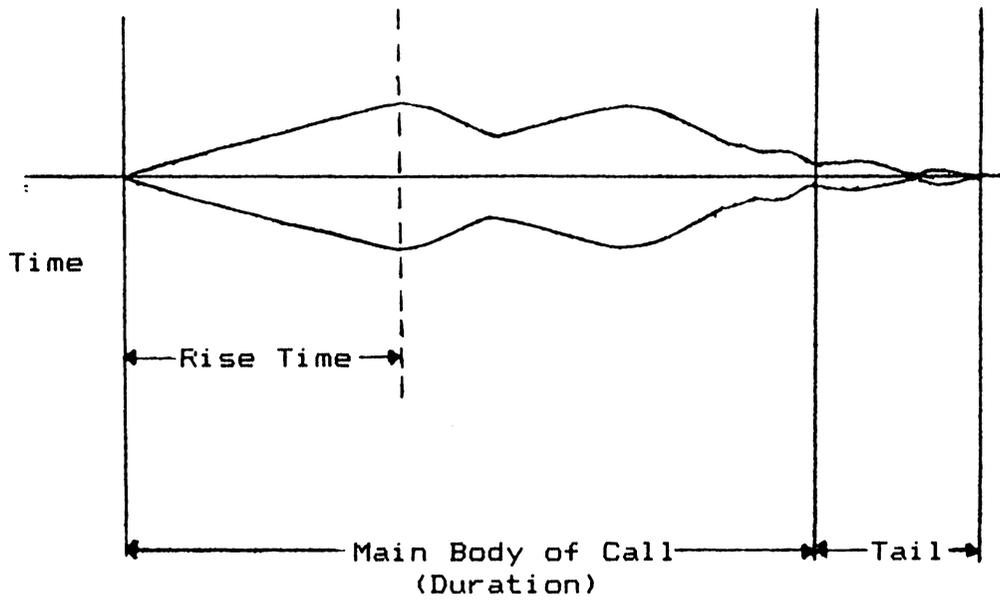


Fig. 2. Schematic drawing of the parts of a Hyla crucifer call in an amplitude vs. time trace.

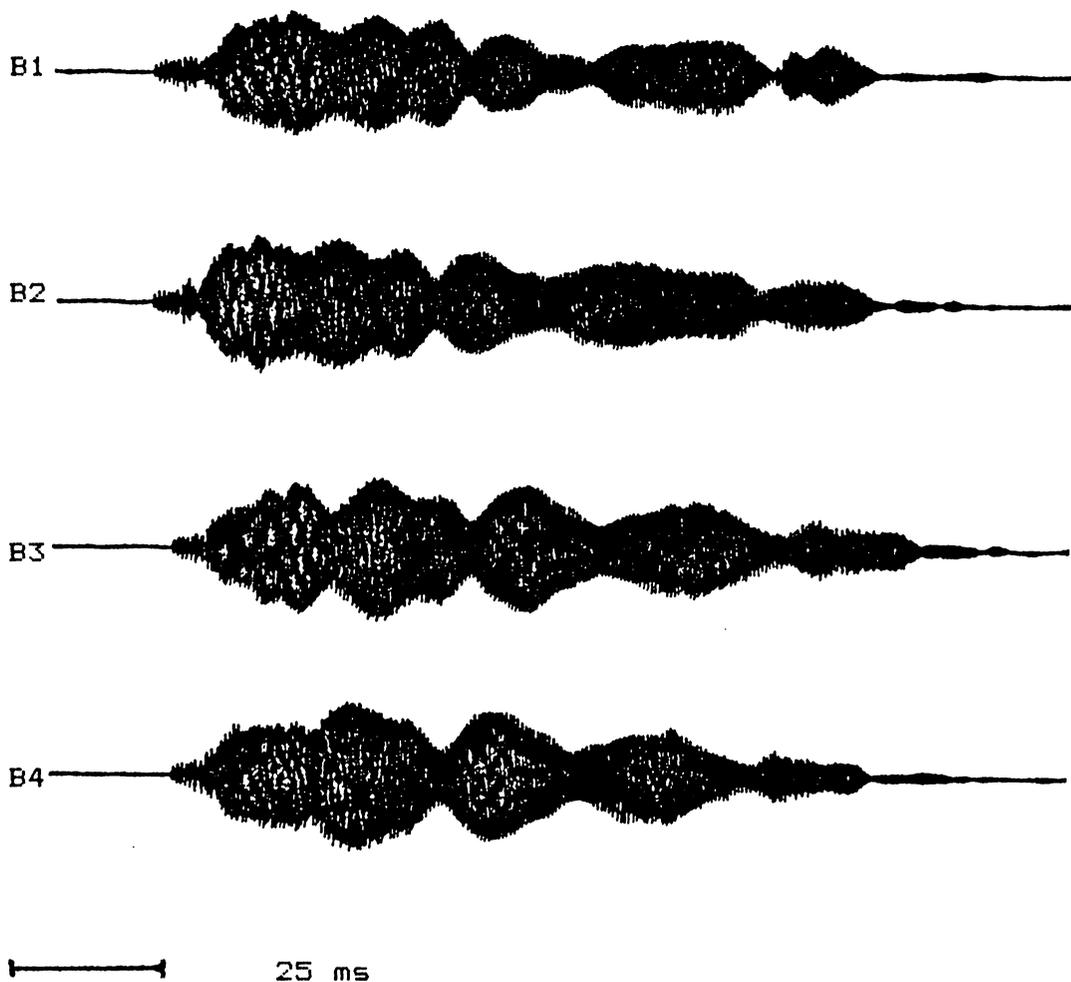


Fig. 3. Series of Hyla crucifer peeps illustrating the ambiguity of pulse numbers. B1 was counted as having 4 pulses, B2: 4, B3: 5, B4: 4.

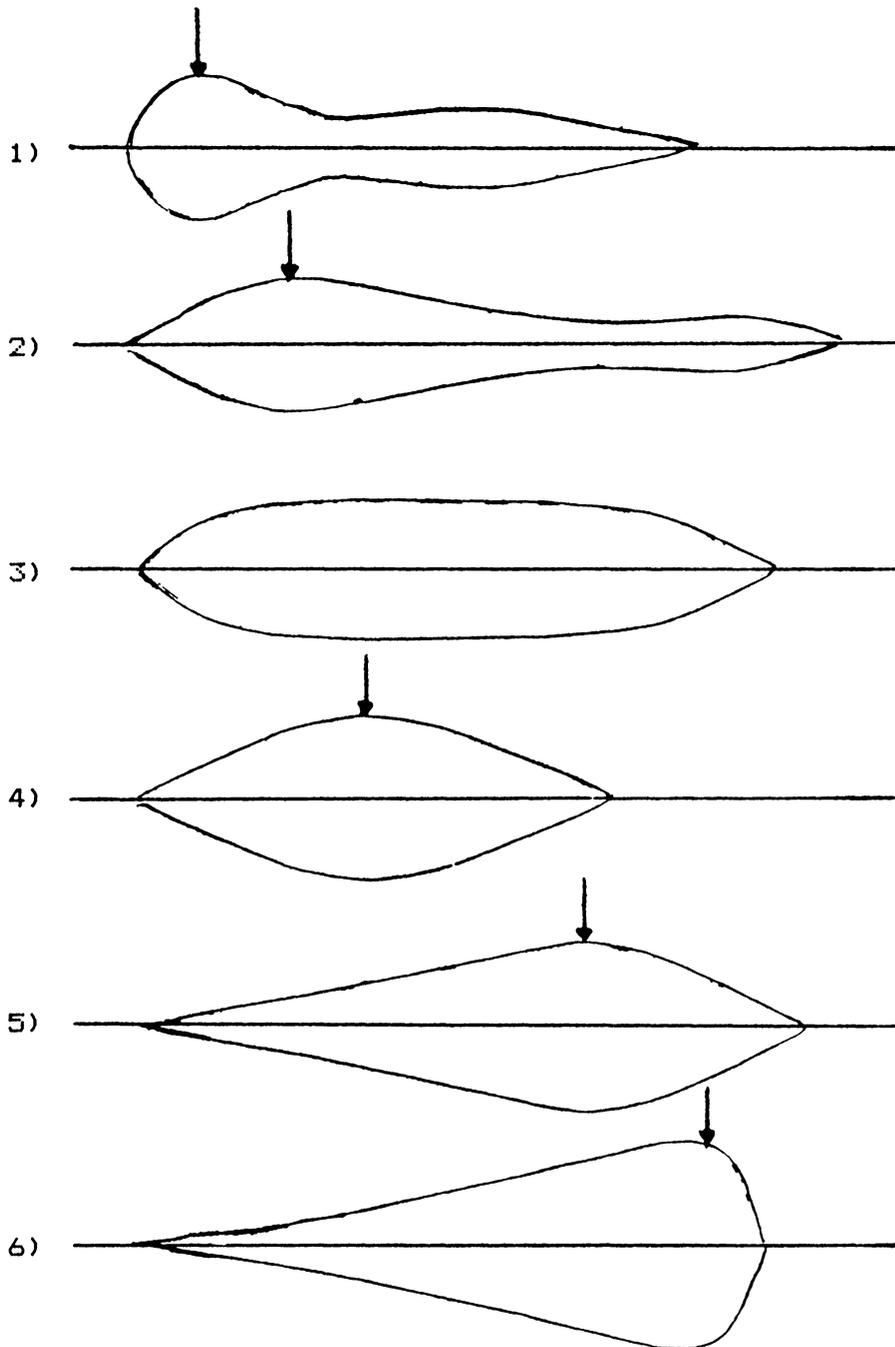


Fig. 4. Call envelopes showing configuration of position of maximum amplitude (arrow) in Hyla crucifer calls: 1) beginning of call, 2) first half of call, 3) even throughout call, 4) middle of call, 5) second half of call, and 6) end of call.

Initial Frequency and Sweep: I defined the initial frequency (kHz) as that calculated by the FFT program from the first 1024 points sampled in the call (in practice, the first 20-50 ms of the call). The final frequency I defined as that found from the last 1024 points (the last 20-50 ms). The sweep of the call was the change in frequency from the beginning to the end of the call, and was calculated by subtracting the initial frequency from the final frequency.

Rise Time: The rise time I defined as the elapsed time (ms) between the onset of the call and 90% of the maximum amplitude within the first pulse. This is consistent with standard engineering usage (Gannet, Day, Carter and Greer, 1972).

Interval Length: The interval length was the time (ms) since the previous call emitted by the same caller.

No attempt was made to measure the amplitude of the calls. Unless readings are taken right at the position of the caller, readings can vary widely due to interference and the natural reflectivity found within the environment (Gerhardt, 1975).

I classified each call into one of four call types: tapered call, peep, trill or small-pulsed call. This was purely a subjective categorization based on my perception of the sound of each call and visual inspection of its oscillogram. With some experience I was able to

discriminate among the four types in the field. The tapered call begins softly and progressively builds up to a higher frequency and amplitude. It sounds slightly tentative. The peep reaches its maximum amplitude early in the call and sounds more abrupt. The trill is a many-pulsed call and easily distinguished from the others, sounding much as its name indicates. The small-pulsed call is lower in frequency than all other calls and very low in amplitude. It, too, is quite distinctive, sounding more rasping than the other calls. I made traces of representative calls of each type using a Hewlett-Packard 7004 X-Y Recorder (Figs. 5 - 9).

Statistical Methods

The major statistical calculations were carried out by a stepwise discriminant analysis (Biomedical Computer Programs, BMDP7N, P-Series, Dixon and Brown, 1979). The first step of the program used the variable having the widest differences which, therefore, best discriminated among the call types. Each step thereafter used the variables in descending order of their discriminating power. The canonical correlations between the variables were also listed. Eigenvalues were computed for the between-groups sums of cross products and the pooled (within groups) sum of squares. These as well as coefficients for the canonical variables were listed in the output. The canonical variables resulting from the first two steps were used as

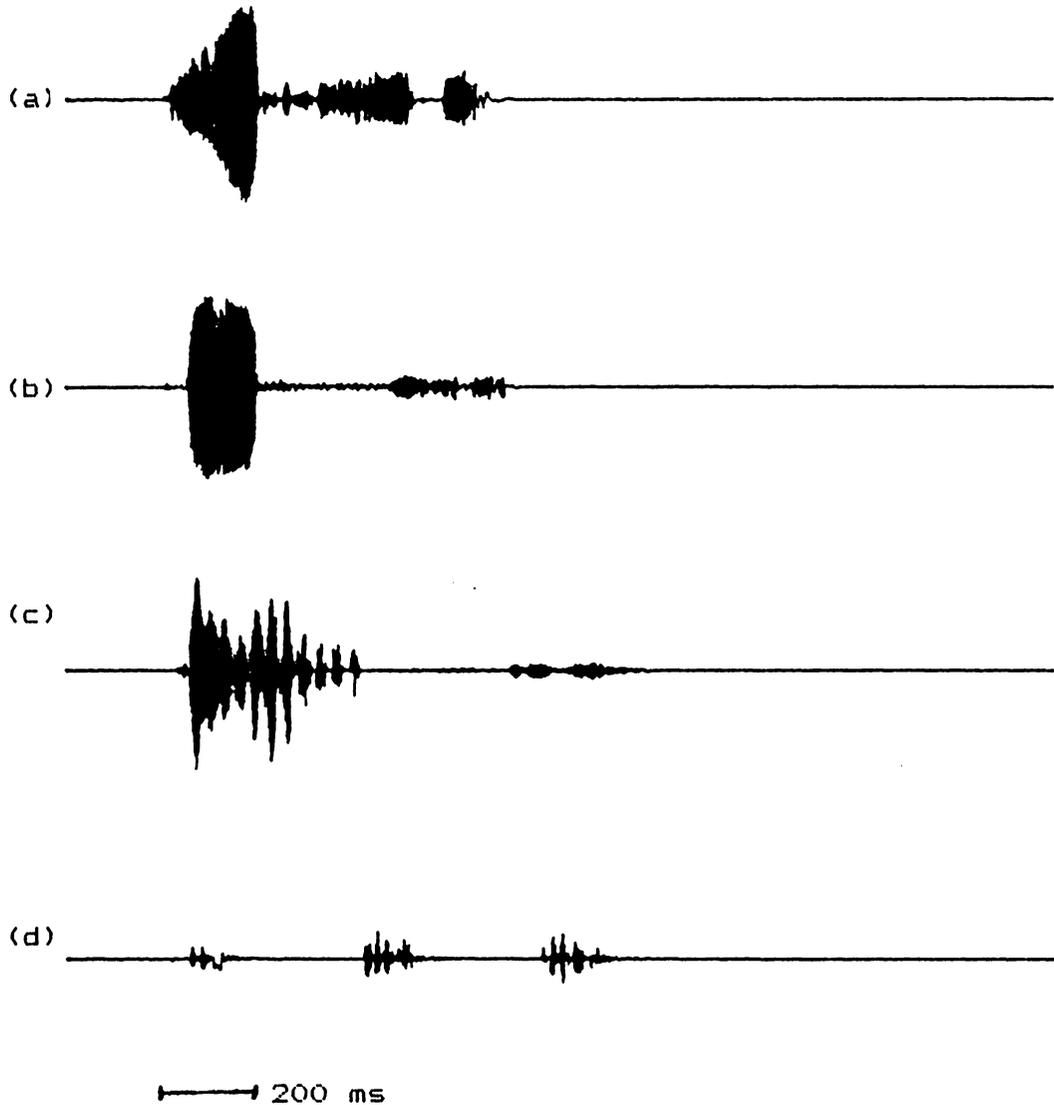


Fig. 5. Tracings of all four *Hyla crucifer* call types: a) tapered call, b) peep, c) trill, d) small-pulsed call. The time scale for all calls was the same and sample rate was 500 microseconds. Vertical axes indicate amplitude, horizontal: time.

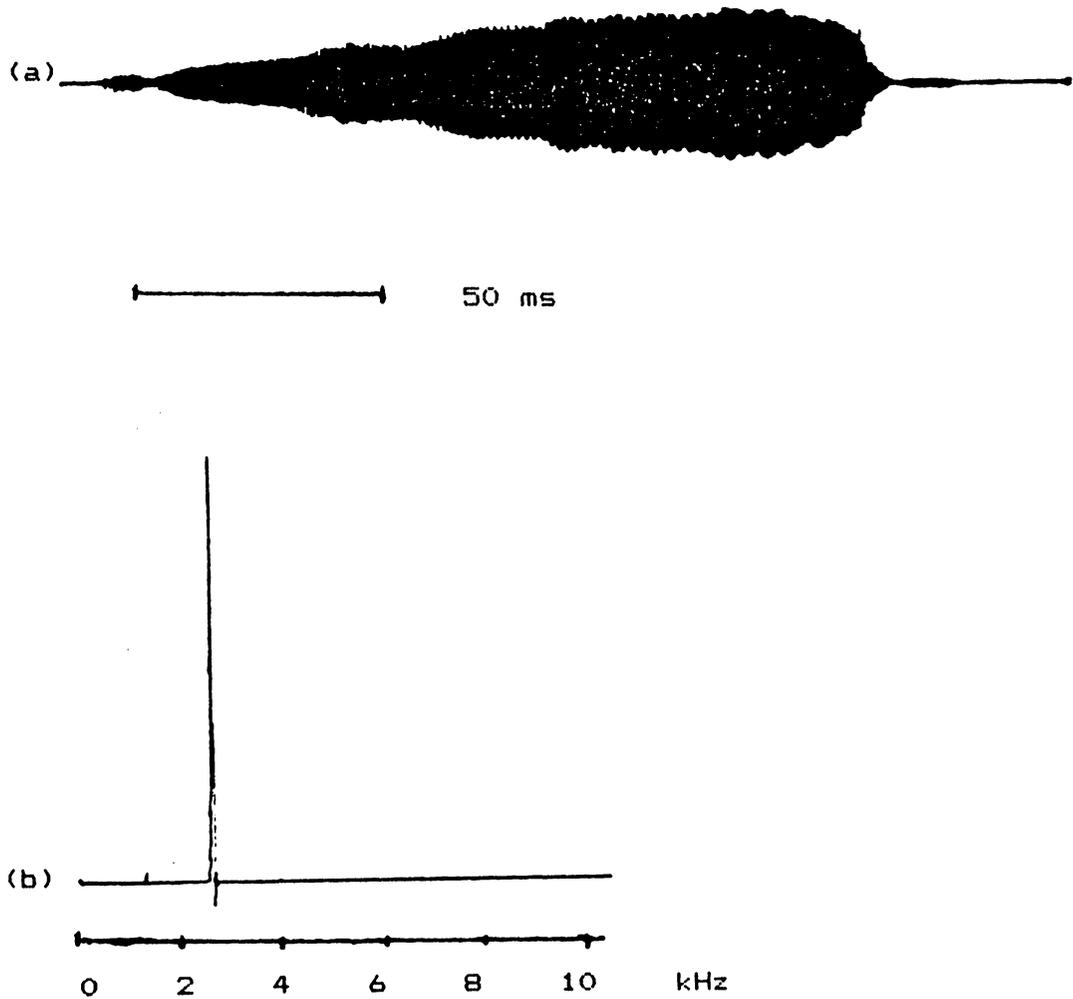


Fig. 6. (a) Amplitude vs. time trace of a *Hyla crucifer* tapered call and (b) its frequency analysis showing pure tone. Sample rate was 50 microseconds for call and frequency.

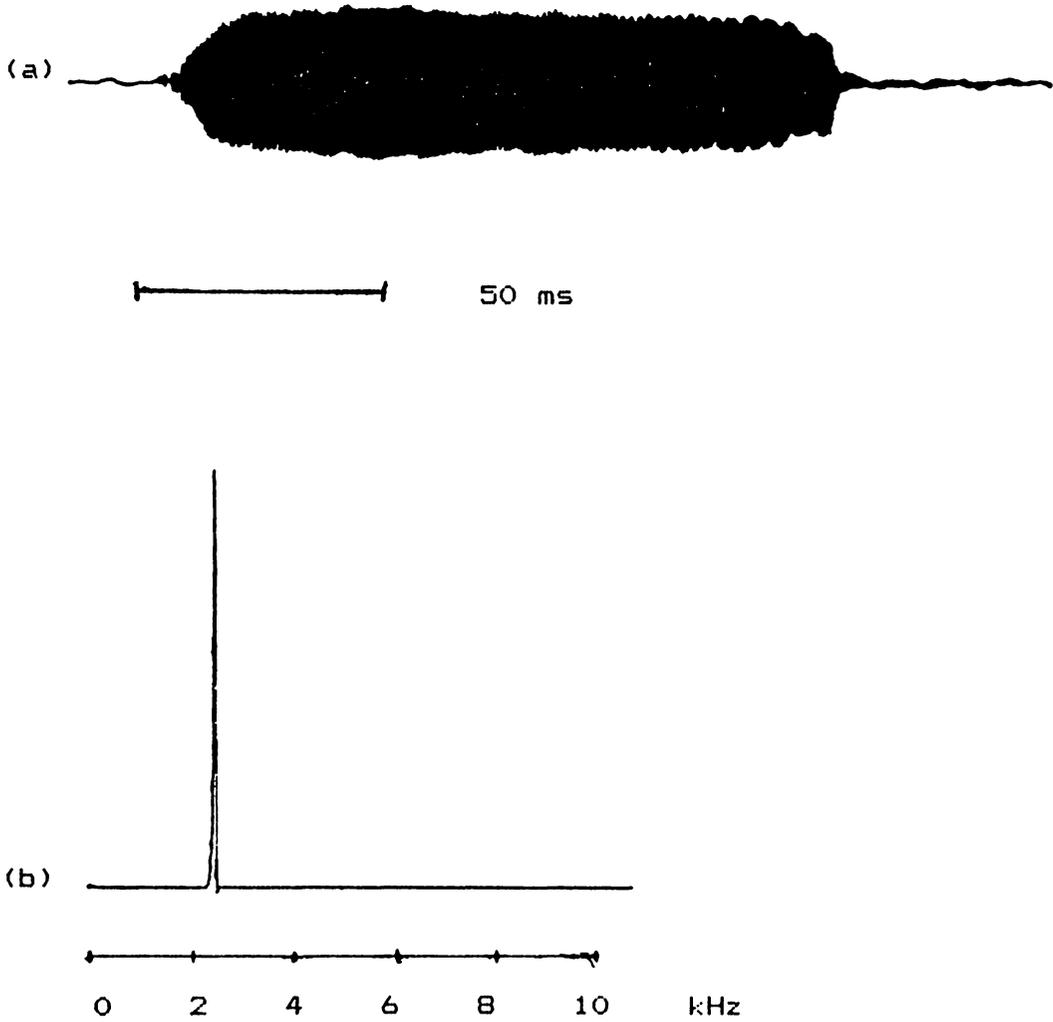


Fig. 7. (a) Amplitude vs. time trace of a Hyla crucifer peep and (b) its frequency analysis showing pure tone. Sample rate was 50 microseconds for call and frequency.

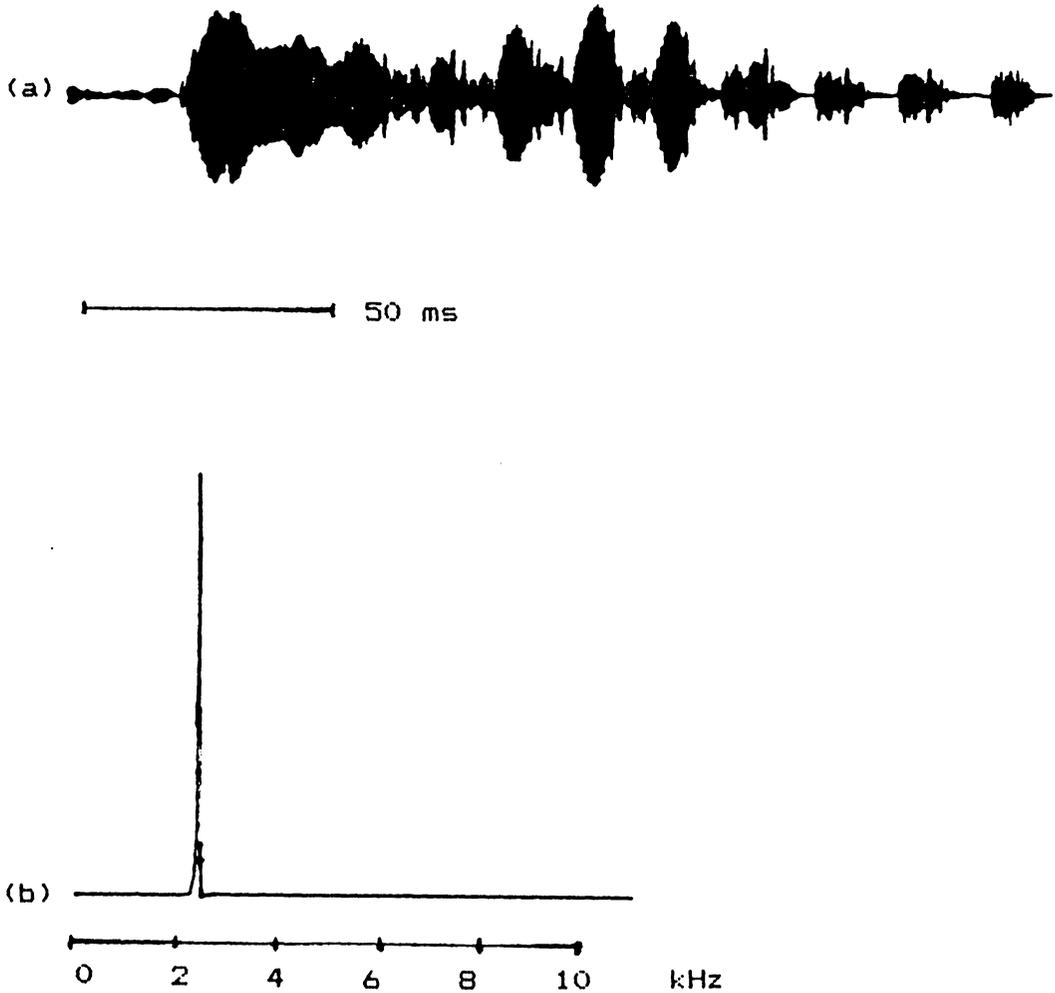


Fig. 8. (a) Amplitude vs. time trace of a Hyla crucifer trill and (b) its frequency analysis showing pure tone. Sample rates were 100 microseconds for call, 50 microseconds for frequency.

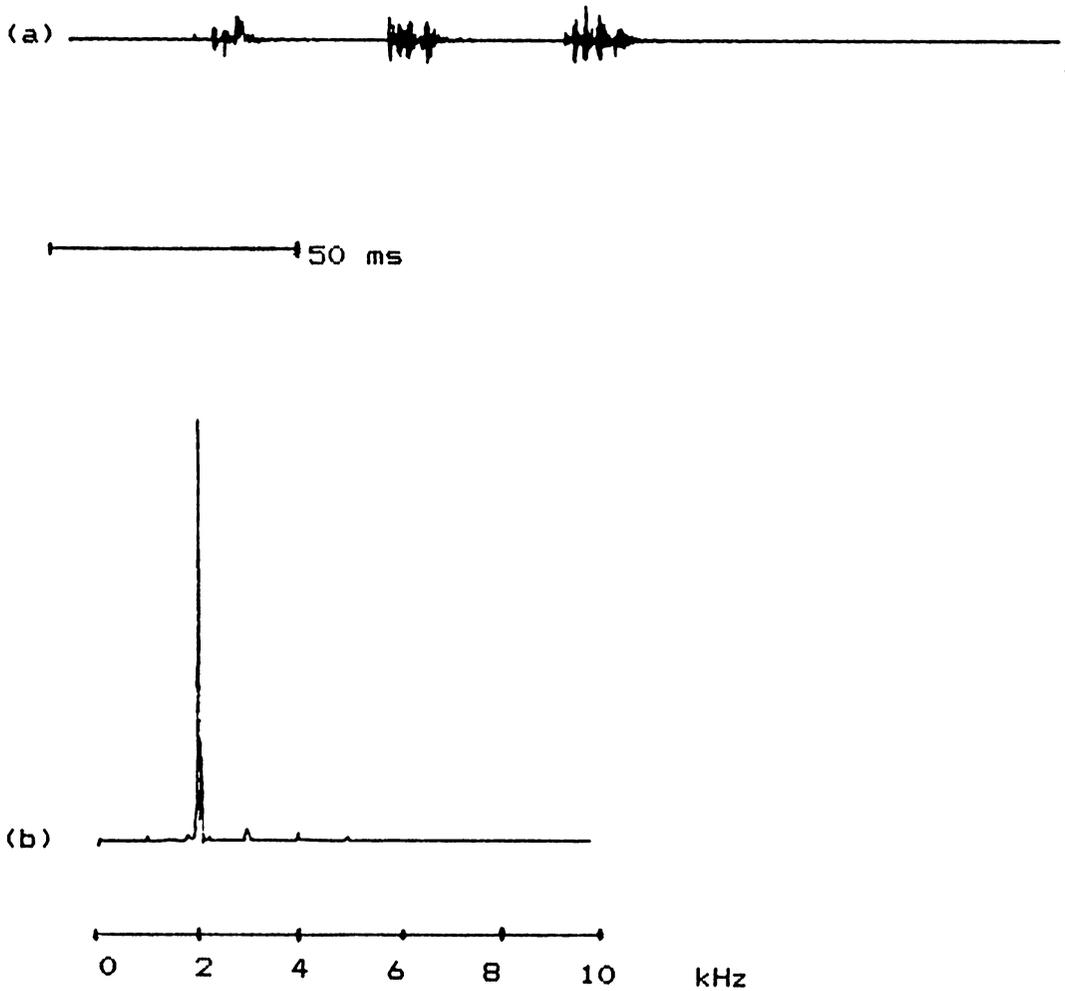


Fig. 9. (a) Amplitude vs. time trace of a Hyla crucifer small-pulsed call and (b) its frequency analysis showing evidence of some slight harmonics. Sample rates were 100 microseconds for call, 50 microseconds for frequency.

the axes in a scatter plot of the group means and all cases.

I tested each variable among the four call types for significant differences, using the Student-Newman-Keuls (SNK) procedure (Sokal and Rohlf, 1969). Then I calculated confidence limits for each set of significantly varying means, and plotted the results.

Context

I made a number of attempts to establish the context of the various calls. First was the construction of a large (1.22 m by 2.44 m by 0.61 m high) artificial habitat of plywood to provide the subjects with a large area so that naturally occurring spacing between calling males could be duplicated. It had an aerated artificial pond along its length with sand "banks" and artificial vegetation on either side. Along the inside of the enclosure were 61 cm (2 ft) square white acoustical panels to eliminate reverberation. Fluorescent lights along the top furnished enough illumination for video monitoring of any action. Unfortunately, once installed, frogs in pairs and in groups of up to 7 refused to call. I tried several modifications: playing tape loops of vigorously calling frogs and choruses; eliminating aeration equipment; replacing fluorescent lights with red lamps; halving the number of acoustical panels; darkening the walls with spray paint stippling; and as a last resort moving the whole tank out of the laboratory to

the front porch of a farmhouse located amid several populations of calling H. crucifer. Still only one frog called and there were no interactions.

In a second, more successful attempt, I placed pairs of frogs in a much smaller enclosure (30 by 76 by 30 cm) which contained 2 cm of water and sand banks. The enclosure had a 2.5 square cm column of open-celled polyurethane foam in one corner and a 2.5 cm thick layer of foam on one end wall to dampen reverberation. In this situation the frogs interacted. I videotaped these activities using a JVC QS2500 camera, Sanyo video recording system, and an Electro-Voice 635A dynamic microphone. The microphone was calibrated in a manner similar to that used for the Uher microphone. Three of the 23 pairs I studied were also recorded using the Uher tape recorder and its microphone. Unfortunately, these experiments were not useful for reasons presented in the Results section.

A third attempt was made to study context in a more natural setting. I constructed three "floating islands" of shallow 50 cm square platforms surmounted by hardware cloth cages roughly 40 cm high. These were placed in one of my study ponds. Each of these I tenanted with a recently captured male who was allowed a half hour adjustment period. Then I drew the island through the water toward a free-ranging, actively calling male. This experiment

literally ran afoul of weeds growing up in the water.

A last attempt involved playback experiments with tape loops of peeps and a 2.5 cm speaker. I extended the speaker on a boom toward a calling male in the field and noted the distance of the speaker from the caller at which he switched his type of call. Six trials yielded inconclusive results.

IV. RESULTS

Computer_Sorting_of_Calls

Four different calls were distinguished: a tapered call, a peep, a trill and a small-pulsed call. The discriminant analysis separated the call types into two distinct groups with less discrete separation of the two calls within each group (Fig 10). The tapered calls and peeps overlapped each other somewhat. The trills and small-pulsed calls were more completely separated, with the small-pulsed calls lying clearly above the trills.

The discriminant analysis found the number of pulses to be the best distinguishing variable, with duration, rise time, position of maximum amplitude, and initial frequency of progressively less importance. Sweep and interval length did not significantly contribute to the analysis, and so were not used by the discriminant analysis.

The Discriminant Analysis Program successfully classified nearly 93% of the calls (Table 1). The highest number of misclassifications occurred among the tapered calls (28.4%). The computer reclassified 25 of these as peeps, while four of the peeps were reclassified as tapered calls.

Rise time was the main characteristic determining the misclassification of peeps and tapered calls. All of the

OVERLAP OF DIFFERENT GROUPS IS INDICATED BY *

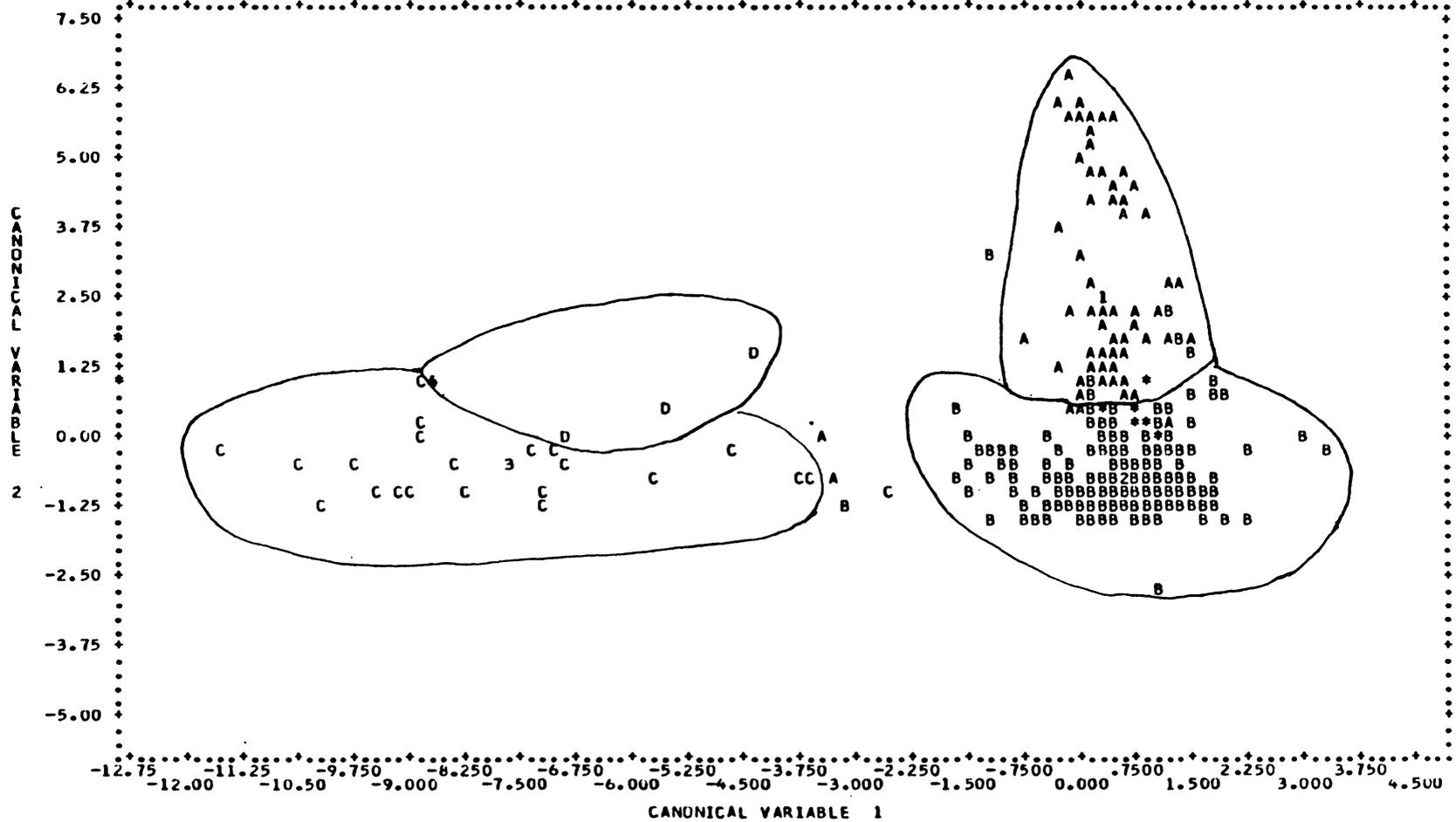


Fig. 10. Scatter plot produced by Stepwise Discriminant Analysis program for *Hyla crucifer* calls: A) tapered calls, B) peeps, C) trills, D) small-pulsed calls.

Table 1. Classification matrix of types of Hyla crucifer calls resulting from discriminant analysis program.

Group	Percentage Correct	Number of cases classified into Each Group			
		Tapered	Peep	Trill	Sm-Puls
Tapered Calls	71.6	63	25	0	0
Peeps	98.7	4	315	0	0
Trills	91.3	0	2	21	0
Small-pulsed	80.0	1	0	0	4
Totals	92.6	68	342	21	4

reclassified tapered calls had rise times on the short end of the range (≤ 49.20 ms), while the reclassified peeps had longer than usual rise times (≥ 53.65 ms). In addition, the position of maximum amplitude in 15 of the 25 tapered calls was either in the middle or spread evenly over the call, positions more characteristic of peeps.

Two trills were reclassified as peeps. This was due in both cases to the trills having relatively short durations and low number of pulses, making them more similar to peeps than trills.

The single small-pulsed call which was reclassified was the shortest of the five such calls sampled. Since the small-pulsed calls were separated from the rest of the calls in the second step of the discriminant analysis on the basis of overall length, this particular call with its length of 371.30 ms would have fit in any of the categories. It was later placed in the tapered call group as its rise time of 41.90 ms was relatively long.

Variables Distinguishing Among Calls

The durations of the four types of calls were all significantly different (SNK-test, $p \leq 0.05$; Fig. 11; Table 2). Peeps were the shortest calls ($\bar{X} = 135.83$ ms), while tapered calls were somewhat longer ($\bar{X} = 160.88$ ms). Both had similar distributions, but the tapered calls did not vary as widely as peeps (Fig. 12 a,b).

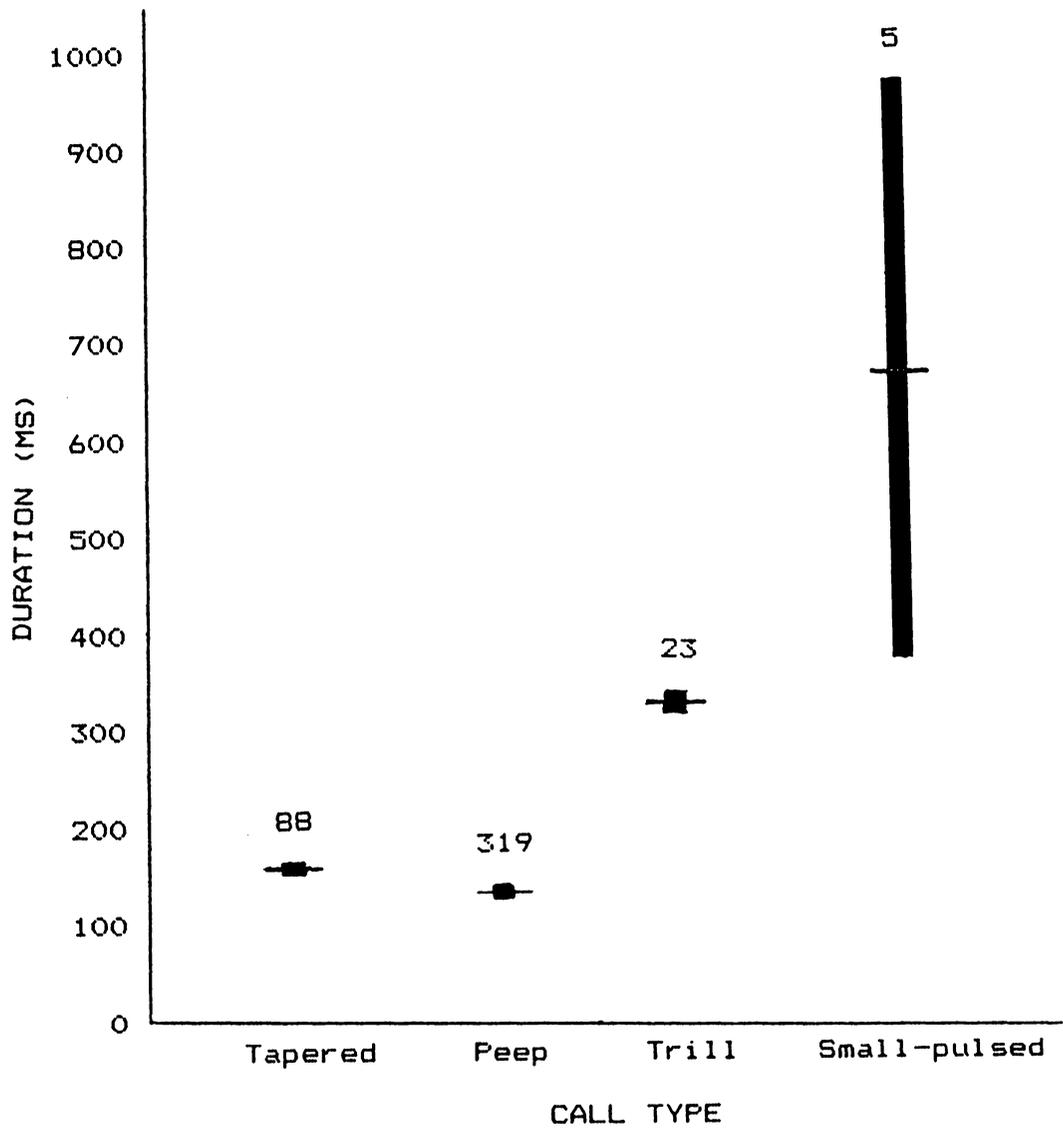
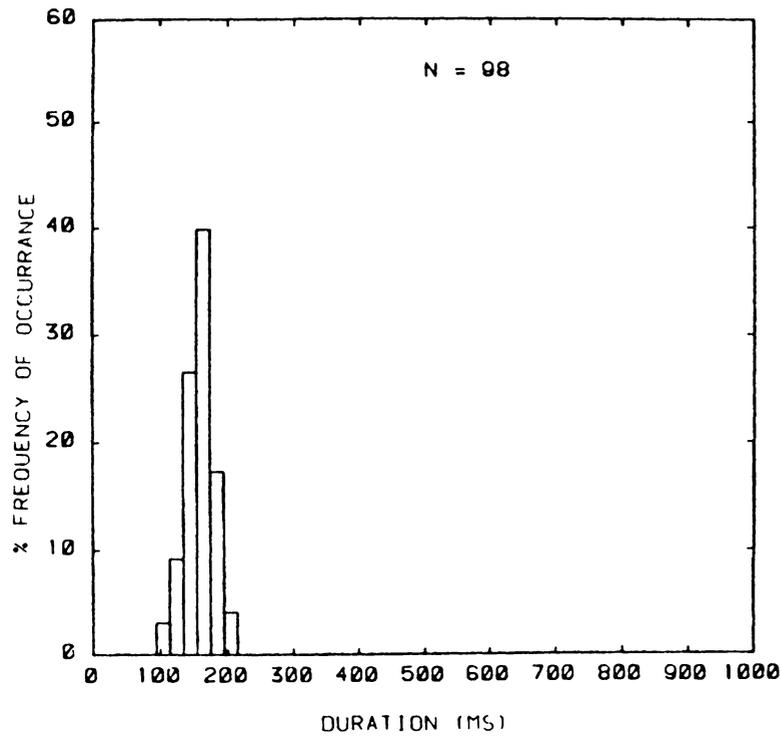


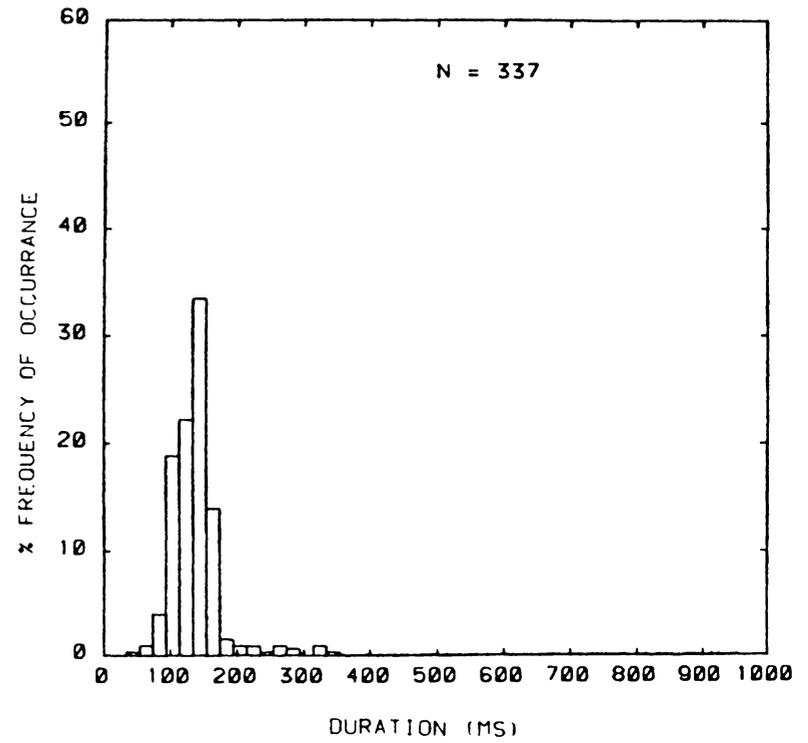
Fig. 11. Hyla crucifer call durations by call types. Means are indicated by horizontal lines; 95% confidence intervals by solid bars. Durations of all call types are significantly different ($p \leq 0.05$, SNK-test). Sample sizes appear over bars.

Table 2. Descriptive statistics for Variables of *Hyla crucifer* Call Types

Group	Tapered Calls	Peeps	Trills	Small-Pulsed
Duration (ms)				
mean	160.88	135.83	330.96	670.98
std. error	1.97	2.28	4.80	107.81
minimum	113.95	12.15	201.30	317.30
maximum	197.80	335.05	455.80	933.00
Number of Pulses				
mean	1.40	1.97	11.13	3.00
std. error	0.13	0.07	0.64	0.55
minimum	1	1	6	2
maximum	8	7	16	5
Rise Time (ms)				
mean	67.18	16.18	10.04	18.14
std. error	3.12	0.56	1.31	6.93
minimum	7.40	3.25	2.45	3.80
maximum	129.10	75.00	27.50	41.90
Position of Max. Amplitude				
mean	4.27	3.08	3.57	3.00
std. error	0.12	0.09	0.33	0.55
minimum	2	1	1	2
maximum	6	6	6	5
Initial Freq. (kHz)				
mean	2.609	2.622	2.577	2.200
std. error	0.007	0.015	0.029	0.176
minimum	2.461	2.285	2.275	1.701
maximum	2.852	3.066	2.959	2.651
Sweep (kHz)				
mean	0.227	0.207	0.277	0.082
std. error	0.005	0.018	0.022	0.032
minimum	0.098	0.039	0.010	0.022
maximum	0.430	0.469	0.604	0.178
Interval Lgth(ms)				
mean	820.06	970.19	3402.11	1325.20
std. error	32.93	56.85	1034.16	709.91
minimum	419.50	317.00	109.50	349.00
maximum	10230.0	12580.0	19105.0	4138.0



(a) tapered call



(b) peep

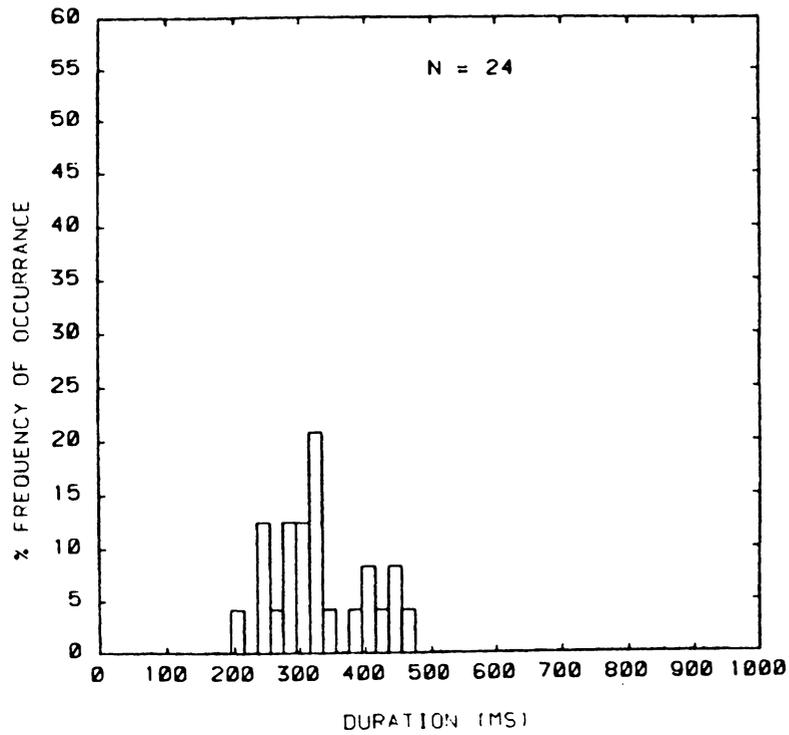
Fig. 12 a,b. Histograms comparing durations of Hyla crucifer call types. While the distribution of tapered calls is similar to that of peeps, its range is broader.

Trills ($\bar{X} = 330.96$ ms) and small-pulsed calls ($\bar{X} = 670.98$ ms) were the longest (Table 2), with distribution ranges of 200-475 ms and 350-900 ms, respectively (Fig. 12 c,d)

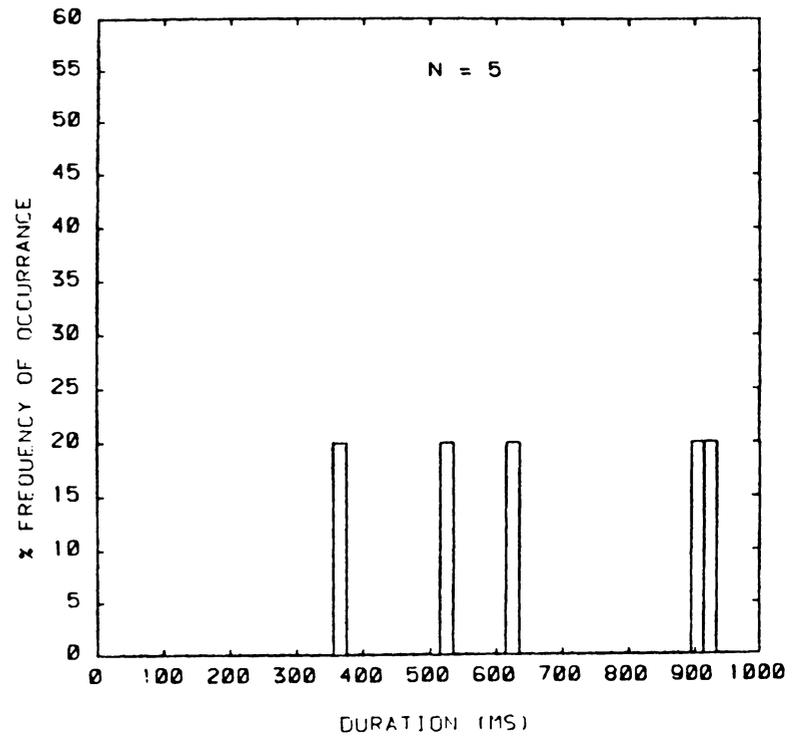
The mean number of pulses for the tapered call was slightly above one pulse per call ($\bar{X} = 1.40$) and the trill mean was just above 11 ($\bar{X} = 11.13$). Both were significant at the $p \leq 0.05$ level (SNK-test) (Table 2, Fig 13). The means for the peep and small-pulsed calls were not significantly different. Single-pulsed calls were most numerous among tapered calls; while trills were quite distinct in having a high, widely varying range of number of pulses (Fig. 14).

Rise time separated the tapered calls from the other types. Its mean ($\bar{X} = 67.18$ ms) (Table 2) differed significantly from the other three (SNK-test, Fig. 15) . It was about four times as long as the others. The rise time of tapered calls also had a much wider range than did other types of calls, (Fig. 16). Peeps and trills had similarly distributed rise times.

The initial frequency of small-pulsed calls ($\bar{X} = 2.2002$ kHz) was significantly lower (SNK-test) than that of other calls (Table 2, Fig. 17). This was readily noticed by the human observer. These calls sound like a short series of small rasps.



(c) trill



(d) small-pulsed call

Fig. 12 c,d. Histograms comparing durations of Hyla crucifer call types. Small pulsed calls are the longest calls.

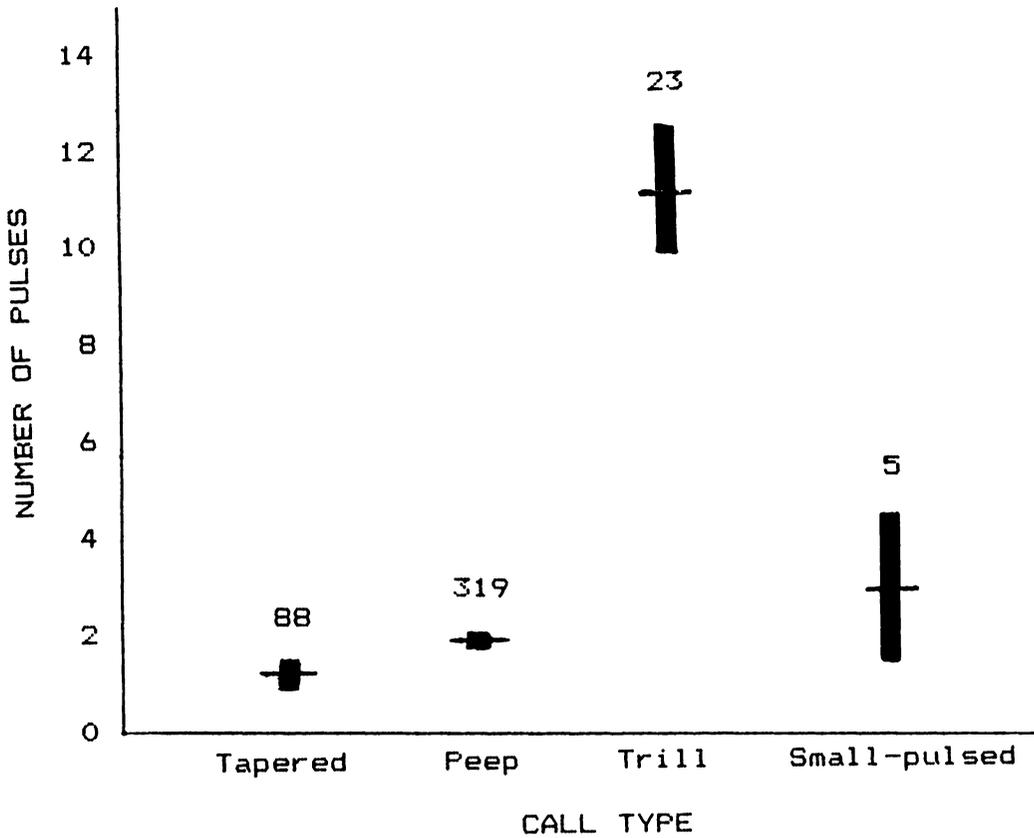
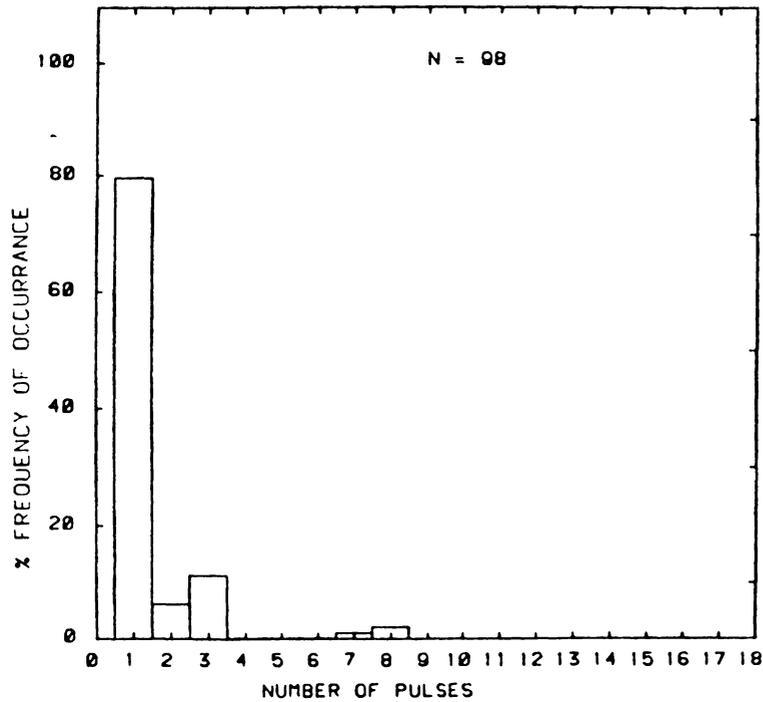
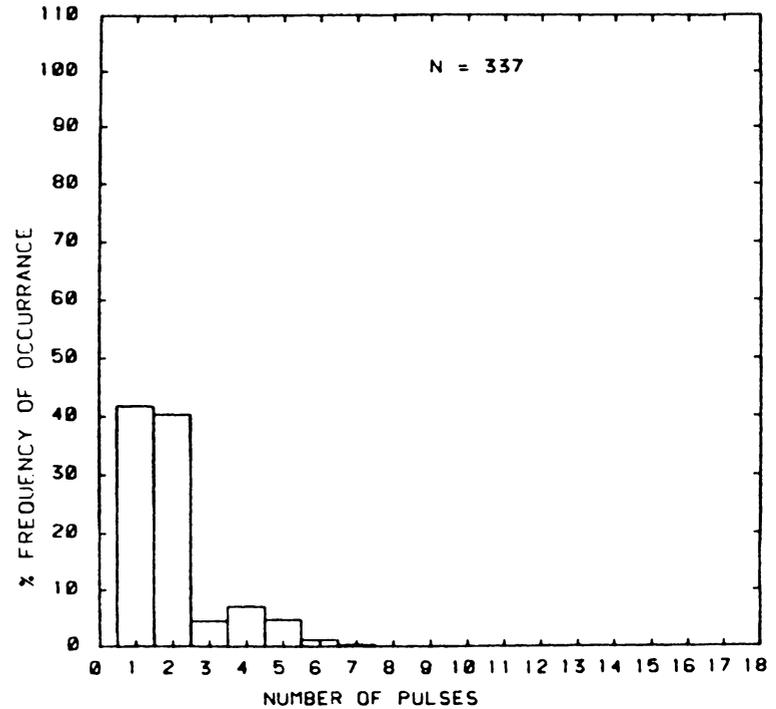


Fig. 13. Number of pulses found in four types of Hyla crucifer calls. Means are indicated by horizontal lines; 95% confidence intervals by solid bars. The tapered call and the trill are significantly different from the other calls in number of pulses ($p \leq 0.05$, SNK-test).

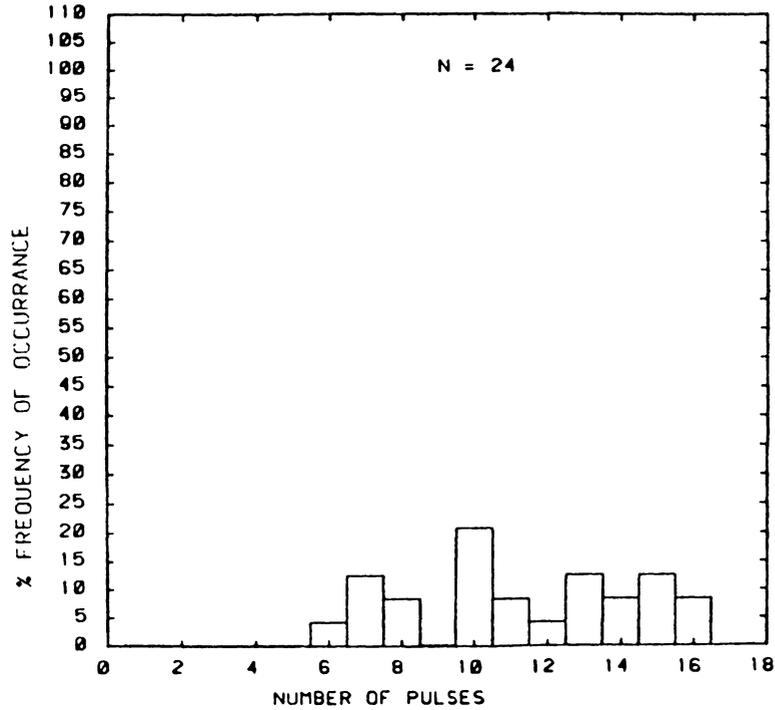


(a) tapered call

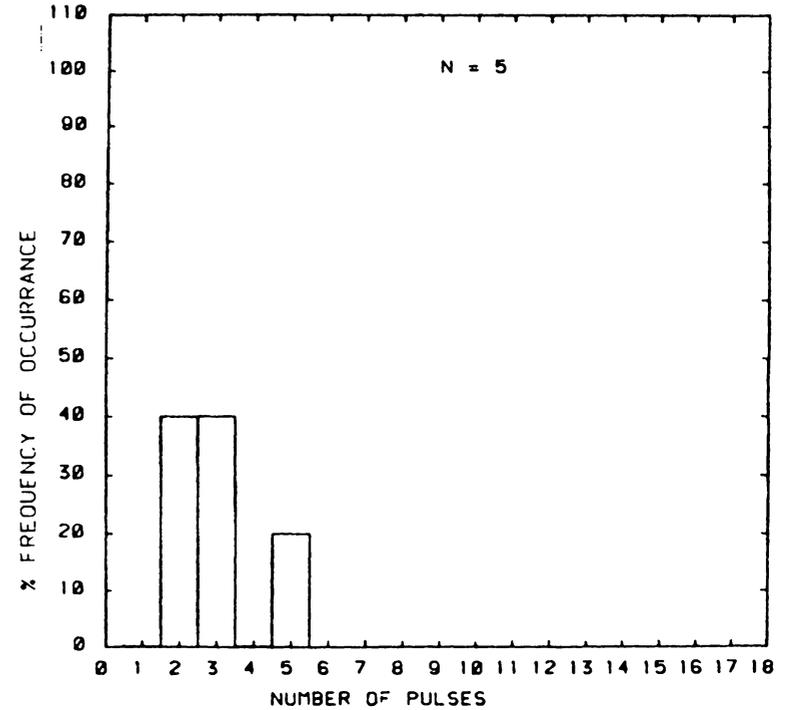


(b) peep

Fig. 14 a,b. Histograms comparing the number of pulses in Hyla crucifer call types. Tapered calls and peeps have similar numbers of pulses, but most tapered calls are single-pulsed.



(c) trill



(d) small-pulsed call

Fig. 14 c,d. Histograms comparing the number of pulses in Hyla crucifer call types. The number of pulses in trills is significantly different from that in other calls.

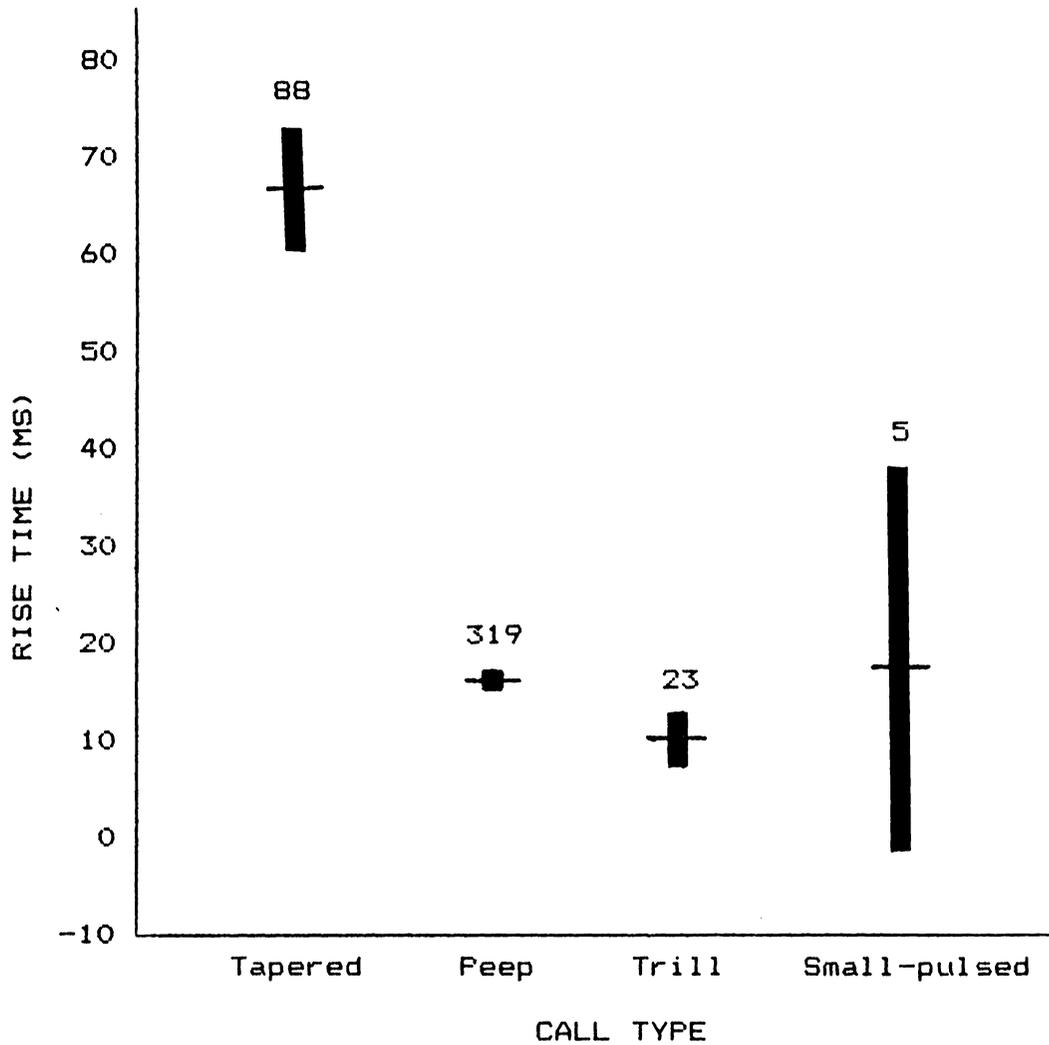
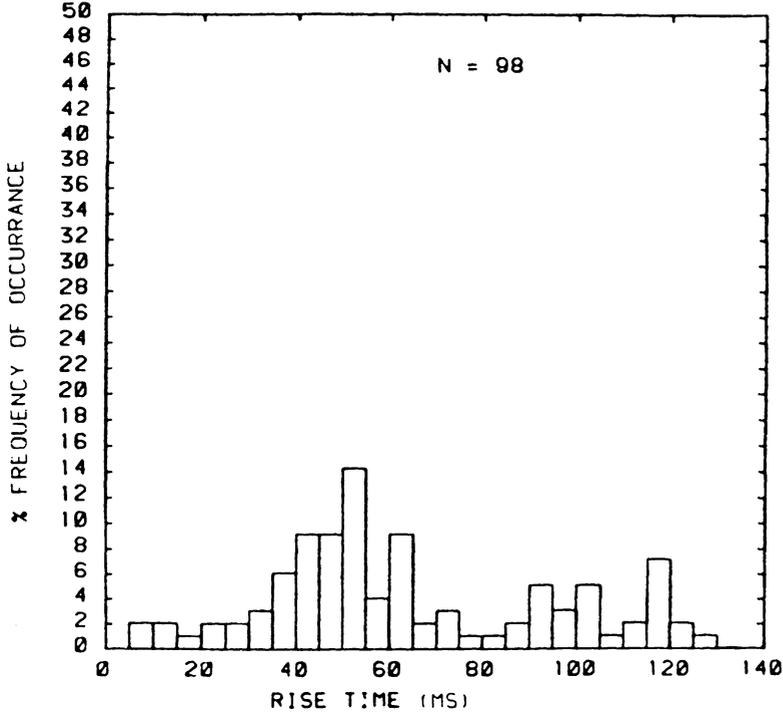
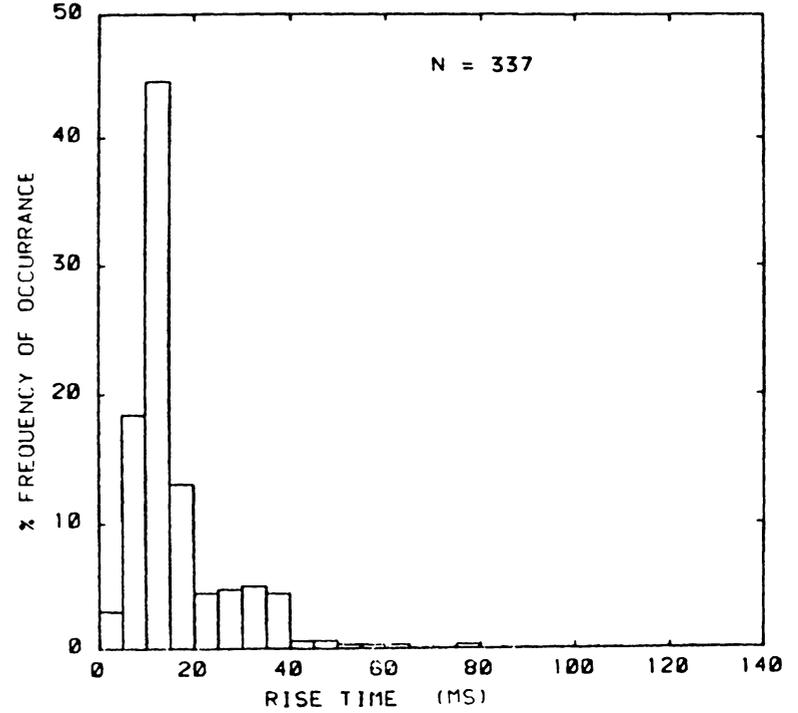


Fig. 15. Rise times of four types of *Hyla crucifer* calls. Means are indicated by horizontal lines; 95% confidence limits by solid bars. Only the tapered calls' rise time is significantly different ($p \leq 0.05$, SNK-test)

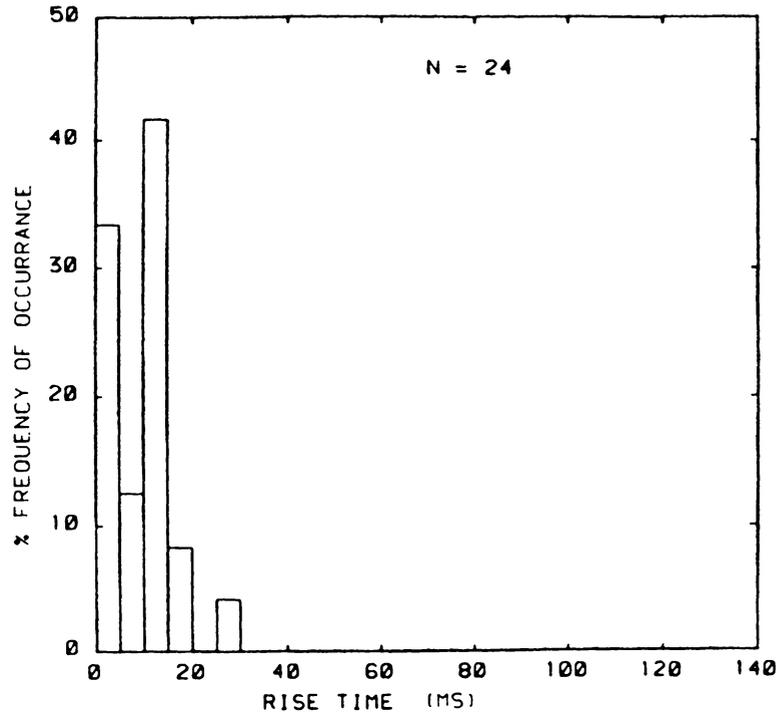


(a) tapered call

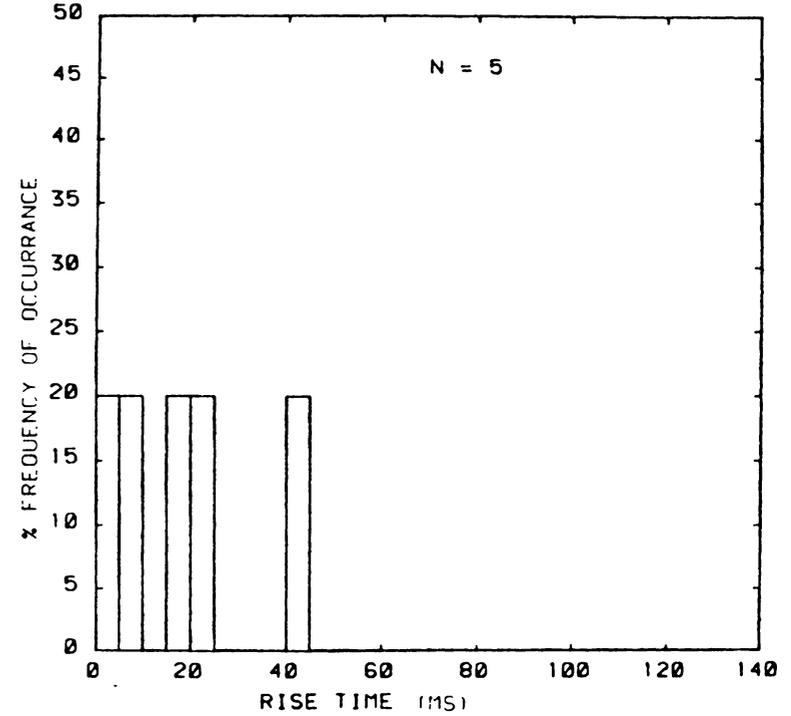


(b) peep

Fig. 16 a,b. Histograms comparing rise times of Hyla crucifer call types. The rise time of tapered calls is significantly different from that of other trills. Most peep rise times are similar to those of trills (next page).



(c) trill



(d) small-pulsed call

Fig. 16 c,d. Histograms comparing rise times of Hyla crucifer call types. The rise time pattern of trills is similar to that of peeps.

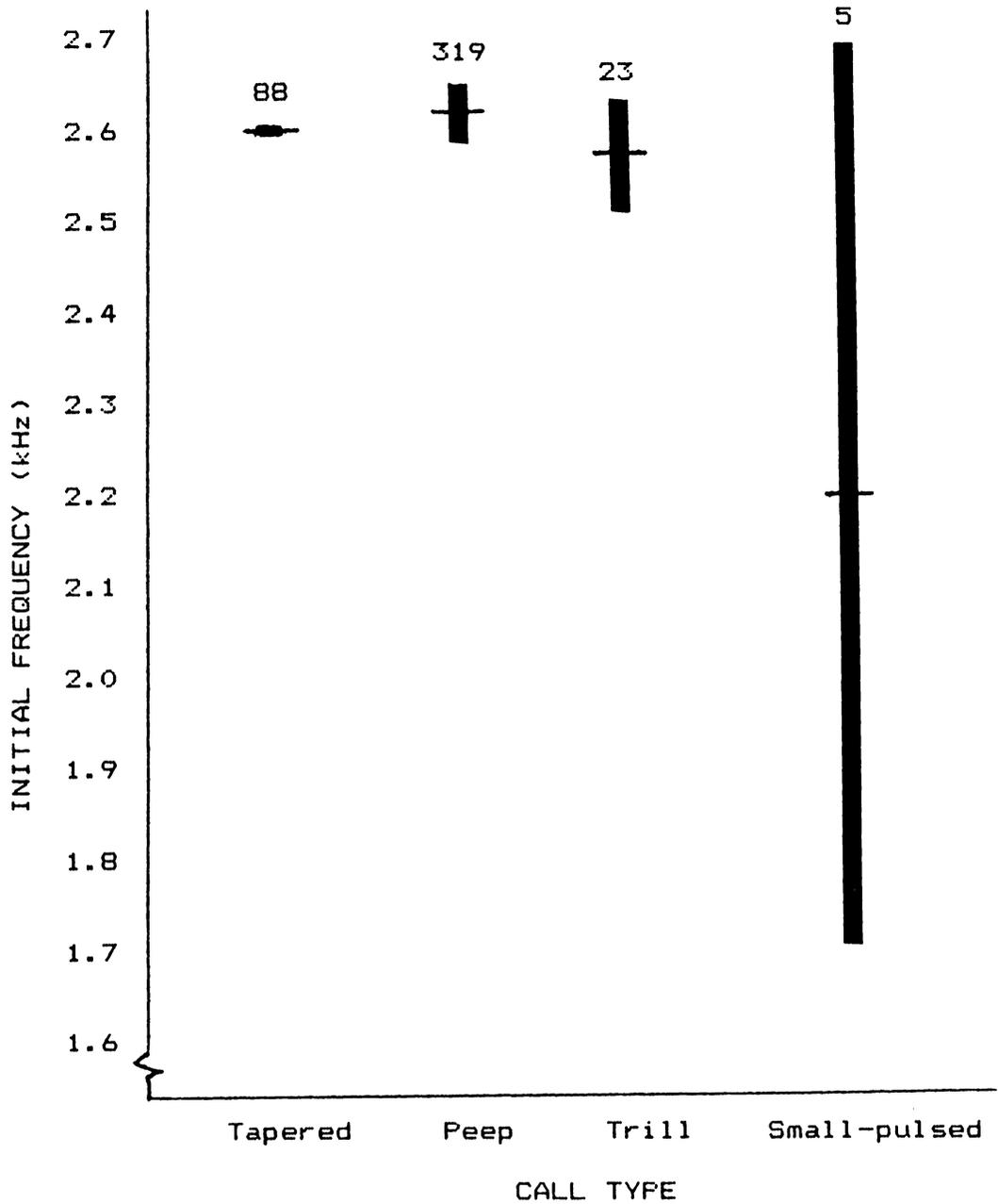


Fig. 17. Initial call frequencies of four types of *Hyla crucifer* calls. Means are indicated by horizontal lines; 95% confidence intervals by solid bars. Only the small-pulsed calls' initial frequency is significantly different ($p \leq 0.05$, SNK-test).

The lengths of the intervals before calls were significantly different (SNK-test) only in the case of trills (Fig. 18).

Attempts to Establish Context

The results of the experiments to establish call contexts were disappointing. The large encounter arena appeared to inhibit calling despite efforts to the contrary. Those frogs placed in the smaller aquarium did call and interact, but their behavior was far more agonistic than that of frogs in the field. This was probably due to the space restriction, and the inability of subordinate frogs to escape. Therefore, it is uncertain whether these data are true reflections of free ranging frog behavior.

I discovered that there was a great deal of distortion in the attack transients of calls recorded on video tape. The Sanyo tape deck's automatic level control completely eliminated the longer, gradual attacks of tapered calls, making them look like peeps. Early in the taping I had compared a portion of video recording with a Uher recording to check on this possibility. By chance, the portions contained nearly all peeps, so the problem was not detected until half-way through the analysis of all the video tapes.

The failure of the "floating islands" experiment was due to the presence of emergent vegetation. The noise of passage made by the "islands" through the weeds silenced

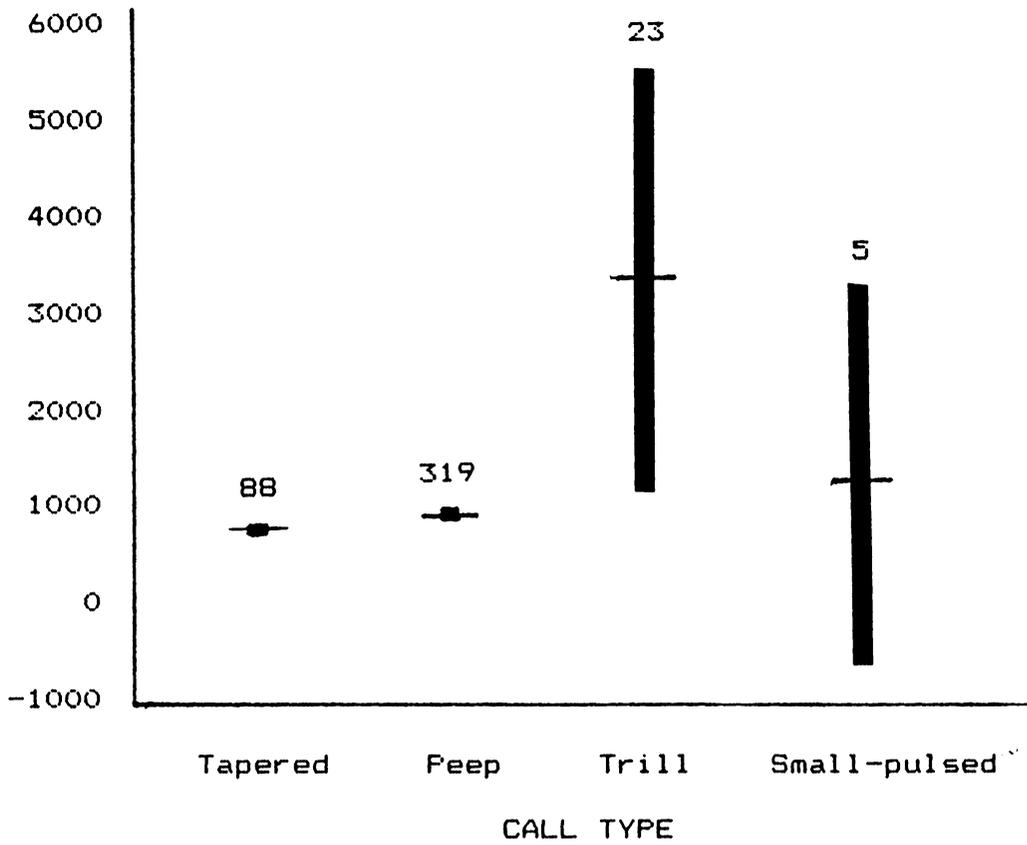


Fig. 18. Lengths of intervals prior to calls found in four types of *Hyla crucifer* calls. Means are indicated by horizontal lines; 95% confidence intervals by solid bars. Only trills have significantly different interval lengths ($p \leq 0.05$, SNK-test).

both the free and captive frogs.

The results of the playback experiments were not conclusive, although all switches from peep to trill occurred at less than 1 m. In all cases the caller matched his calling rate to that coming from the speaker.

Energy Considerations

As a basis for comparison, I calculated the total and mean energy expended during a call for a representative peep, tapered call, and trill. This was done by integrating the square of the call envelope (the outline of the amplitude vs. time plot) over the length of the call. I found that trills required the least energy output, while tapered calls required twice as much as trills, and peeps required nearly three times as much as tapered calls (Table 3).

The H. crucifer calling system seems to be an "all or none" arrangement. Once a frog begins calling, with the exception of the first few and last few calls in an undisturbed sequence, the amplitude stays fairly constant (Fig. 19) and call duration varies little (Table 4, Fig. 20). An intruder can cause a resident to change these call variables. Typically, when an intruder appears, a resident frog calls more loudly and rapidly and the call duration tends to decrease. If the intruder continues to approach, or does not withdraw, the resident changes his call to a

Table 3. Total energy and mean power during call required for three representative calls of Hyla crucifer

Type of Call	Total Energy, millijoules	Mean Power, milliwatts
Tapered call	1.90	11.1
Peep	5.37	35.0
Trill	0.961	4.43

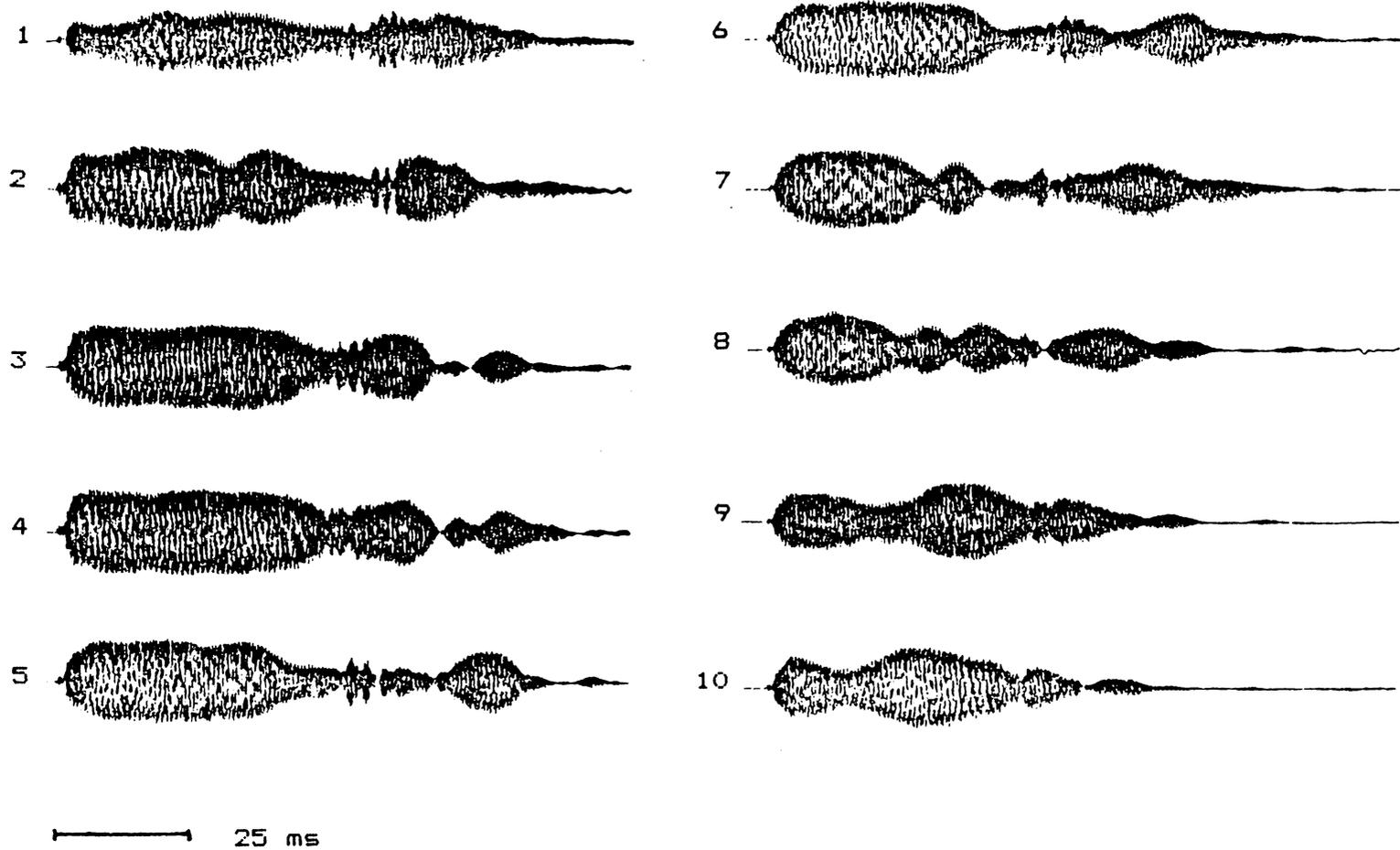


Fig. 19. A numbered sequence of Hyla crucifer peeps showing gradual changes of amplitude pattern.

Table 4. Call durations within ten sequences of Hyla crucifer calls

Sequence Number	Mean Duration (ms)	Range (ms)	Standard Error
1	112.25	106.85 - 119.00	1.81
2	160.47	150.95 - 173.15	3.58
3	131.69	114.85 - 149.10	2.58
4	138.88	109.20 - 154.55	4.35
5	121.20	110.70 - 131.05	2.74
6	106.84	100.70 - 112.60	1.34
7	159.56	150.00 - 170.70	2.44
8	166.71	152.50 - 184.80	1.52
9	92.44	85.80 - 104.40	2.40
10	110.71	81.90 - 132.20	2.99

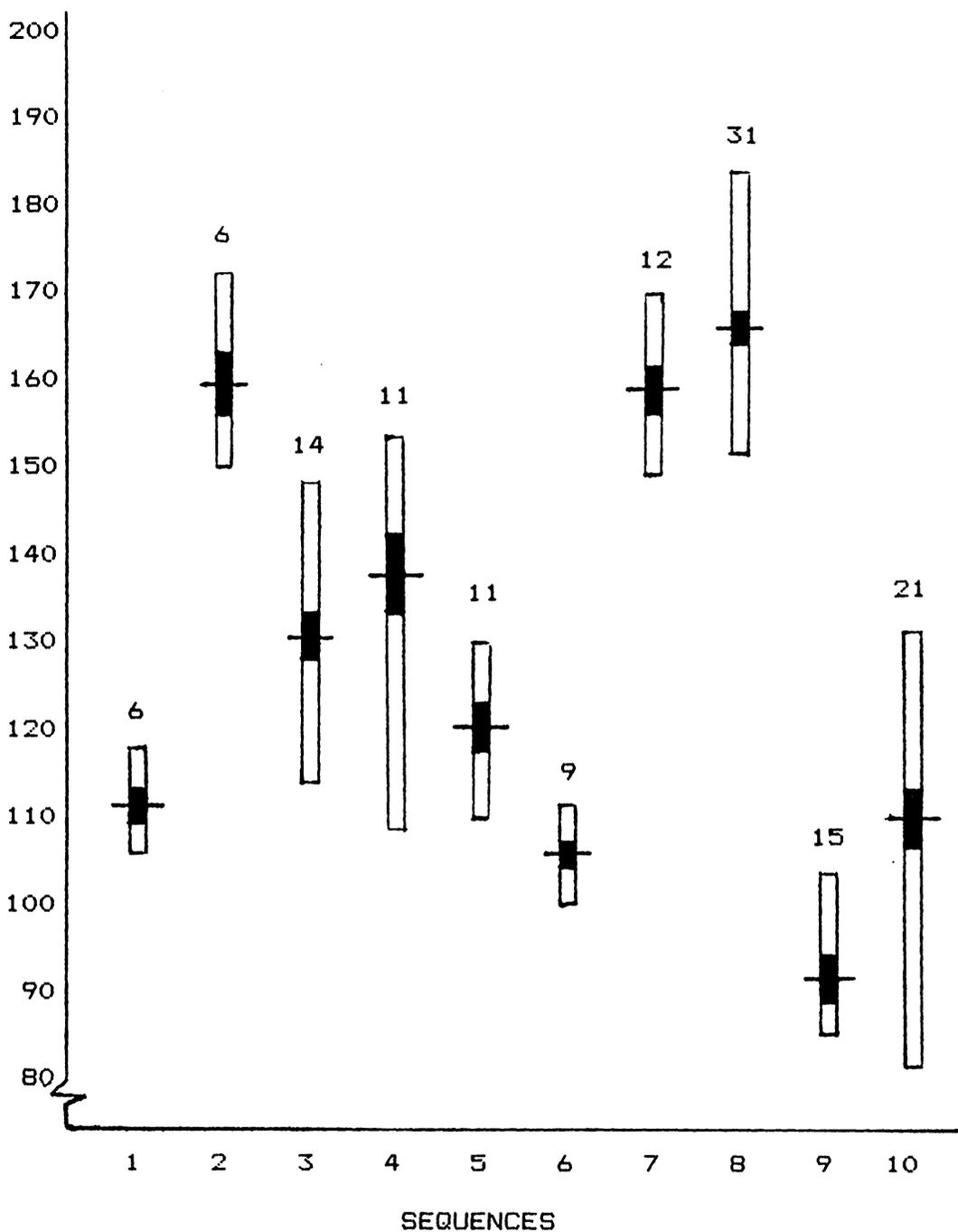


Fig. 20. Ranges of call durations in ten sequences of *Hyla crucifer* calls. Horizontal lines indicate means; open columns indicate ranges; solid portions show standard errors.

trill. A sudden movement by the intruder may cause the resident to switch mid-call from a peep or tapered call to a trill (Fig. 21).

The trill usually occurs after a longer interval than that required for a peep (Table 2). This is probably due to the trill's being of longer duration, and therefore requiring a longer refractory period (Lemon and Struger, 1980; Paillette, 1976).

Possibility of Another New Call

The existence of another, possibly separate, call should be mentioned, although none of the variables I measured would distinguish it from the other calls. This is the two-note call (Fig. 22). It is characterized by two distinct sections or notes which are contiguous. That it is a single call, and not two separate but overlapping calls, is indicated by its smooth frequency sweep and by the lack of a second frequency spike in its analysis. Peeps and tapered calls often are somewhat pulsed, but the amplitude modulations are not as dramatic as those in the two-note calls. In the two-note call the amplitude between the two notes approaches zero, while in other calls it merely dips. The call is readily distinguishable by the human ear, and the oscilloscope tracing reflects its two definite parts. I have found some to have attack transients of the two sections of peep-peep, peep-tapered and tapered-peep

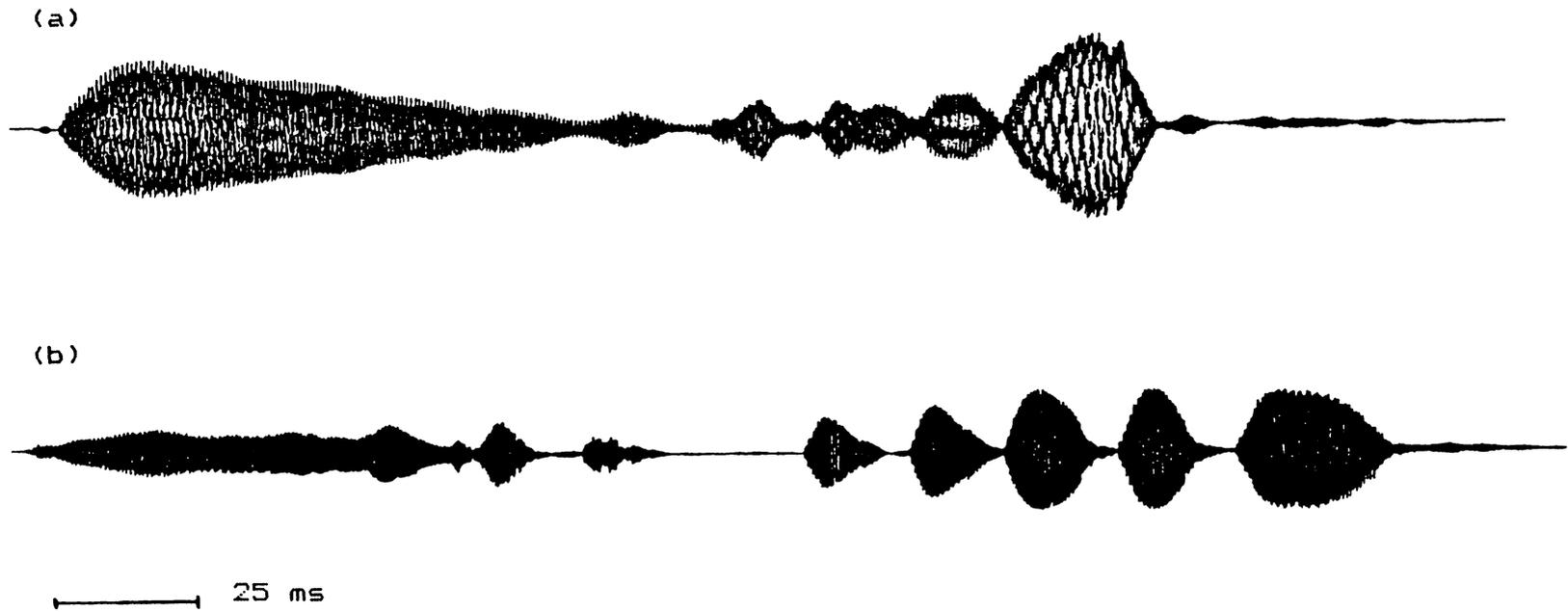


Fig. 21. *Hyla crucifer* peep (a) and tapered call (b) changing to trill within same call.

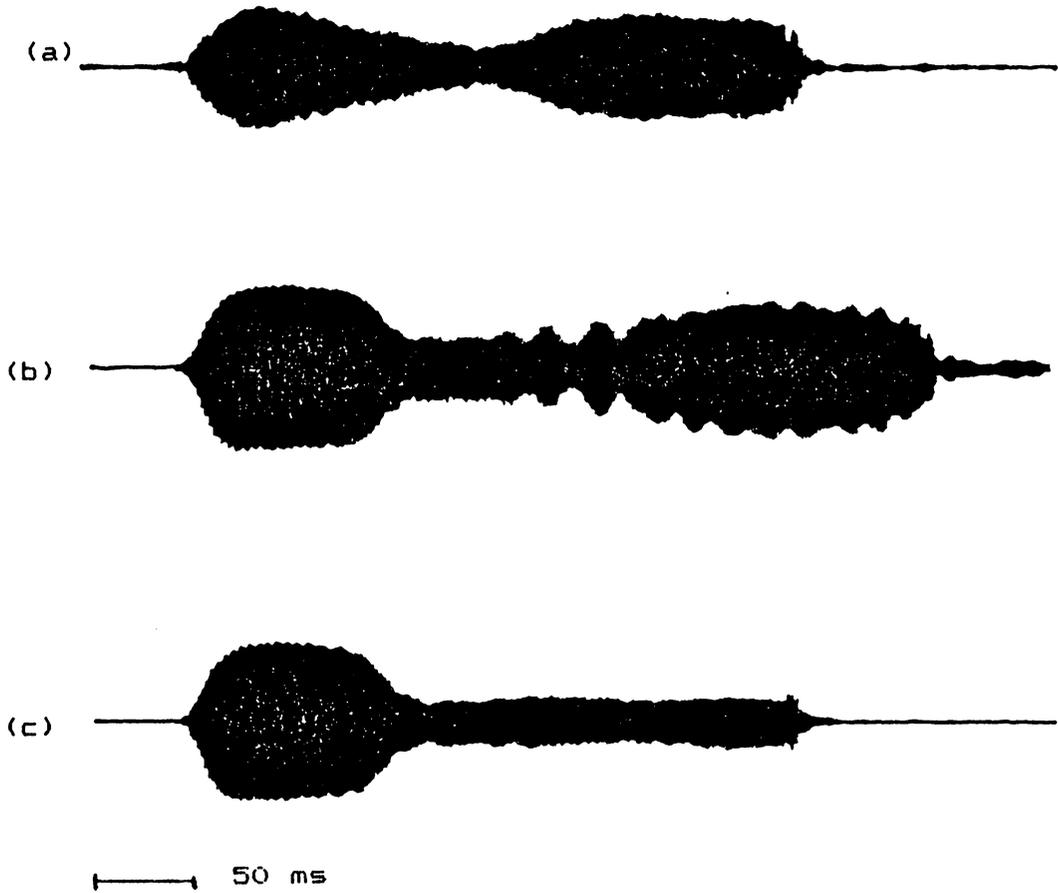


Fig. 22. Two-note *Hyla crucifer* calls of (a) peep-peep, (b) peep-tapered (with some interference), and (c) peep-? configurations.

configurations, but none of the tapered-tapered type.

V. DISCUSSION

The Hyla crucifer repertoire, while produced by a rather simple physical system, is more varied than previously reported. The tapered call has not been described previously. That there is sufficient evidence for separating the tapered call from the peep is demonstrated by the discriminant analysis. Separation by human judgement of the two calls was 72% correct in the case of tapered calls and 99% correct in the case of peeps according to the discriminant analysis program. There is some intergradation between the two calls which leads me to speculate that they may be produced by the caller and processed by the recipient frog as a graded signal.

The primary variable distinguishing between the tapered call from the peep is the attack transient (expressed as rise time). If the two calls are perceived by the frogs as a graded signal, the attack transient would be well suited as an indicator of relative aggression. It is at the beginning of each call (an advantage during ensemble calling) and is under the individual frog's control, like call duration and sweep (Blair 1964). In contrast, frequency and pulse rate have been shown to be species-specific for other species (Blair, 1964; Gerhardt, 1974; Nevo and Schneider, 1976; Sullivan, 1982) and not under an individual's control.

Frequency is correlated with body size, and pulse rate is genetically controlled.

There is no reason to suppose that the frogs are incapable of processing calls continuously. Gerhardt (1978) showed that H. cinerea was able to discriminate between single amplitude modulations in trials involving 0 to 7 pulses. Furthermore, the human ear (a non-adapted receptor) can distinguish reasonably well between peeps and tapered calls.

There would be some advantage, particularly to the lead caller in an ensemble, to encoding relative aggressive intent in the attack transient of each call. During ensembles (duets, trios, quartets) calls are carefully spaced, usually allowing each participant to complete his call (Fellers, 1976; Lemon and Struger, 1980). However, sometimes the calls in an ensemble overlap, in which case the lead caller would be better able to present his message of arousal since subsequent callers' attack transients would be lost in the tails of the preceding calls.

While frequency in the bullfrog (Capranica, 1968) and green tree frog (Gerhardt, 1974) and pulse rate in H. regilla and H. cadaverina (Straughan, 1975) and the Litoria ewingi complex (Littlejohn, 1977; Loftus-Hills and Littlejohn, 1971 b) have been identified as major species discriminatory factors, it seems reasonable to suggest that

attack transient in H. crucifer is worthy of measurement as a possible indicator of relative arousal.

The frequencies of all calls, except the small-pulsed call, were remarkably pure tones. I found no evidence of a second band of frequencies such as reported by Blair (1959) (see Figs. 6 - 9). Blair examined the calls of four individual H. crucifer from as widely separated populations as Ontario, Texas, and Michigan, and found large variability in the frequency pattern and in the amplitude of the low frequency component. The absence of the low frequency component in my frogs may be a population difference.

Although the evidence is anecdotal, the function of the tapered call is probably purely advertisement as suggested by Wells (1977). It appears to be less aggressive than a peep. Its long attack transient with its low amplitude for so much of its length could be perceived as coming from a distance and therefore not seem particularly threatening to a recipient. It could serve the purpose of indicating the general position of the caller to an oncoming female, while not inciting nearby males. The tapered call's lower energy requirements fit in with the supposition that it may have less agonistic connotations than the peep.

The peep, on the other hand, seems to serve a dual function: that of an "encounter" call as suggested by McDiarmid and Adler (1974), and also an advertisement call

since many frogs call in peeps during solo calling. In three video-taped encounters which were simultaneously recorded by the Uher, when one male was chasing another, the beginning slope of the call envelope was nearly vertical and the recipient was exposed to a sudden wall of sound. In such instances the calls were spaced very closely together, and often the caller broke into a trill eventually.

My field observations support the idea that the peep is more aggressive than the tapered call. During one observation, when a territorial resident was pursuing an intruder, the intruder escaped to beyond the territory of the resident; the resident's vigorous peeps switched to tapered calls. The withdrawal of the intruder removed the need for calls of a higher aggressive level, and the resident switched to a less aggressive call type having lower energy expenditure. Tapered calls are frequently heard from single frogs early and late in the evening before and after territorial disputes and ensemble calling becomes common.

The reclassification of 25 of the tapered calls as peeps and 4 of the peeps as tapered calls by the discriminant analysis program also supports the hypothesis that tapered calls and peeps are graded signals. The ranges of rise time of peeps and tapered calls overlap considerably. Tapered calls with rise times of less than

49.20 ms were reclassified as peeps, and peeps having rise times greater than 53.65 ms were reclassified as tapered calls. This fairly large overlap in rise times precludes the idea that these may be two typical intensities (such as discussed by Morris, 1957) along a signal continuum. Typical intensities reduce the ambiguity of signals, and tend to have discrete ranges of variation. In this case there are no such discrete ranges, but tapered calls and peeps do overlap and the possibility of misinterpretation exists.

It would seem more important that a peep, being the more aggressive call, not be mistaken in meaning than that a tapered call be mistaken. The relatively smaller percentage of peeps which were reclassified (7.4% versus 28.4% for tapered calls) bears this out. Probably the frogs are less likely to confuse the two calls.

The trill has been thought to be the only encounter call. Fellers (1976) described an encounter call among H. crucifer differing in its temporal aspects from the mating call. Presumably this is the trill. Wells (1977) also treated the trill in this fashion. Oplinger (1963) listed the trill as part of the H. crucifer repertoire without assigning it a function. Occasionally I heard a highly excited male who was peeping rapidly and at full amplitude break mid-call into a trill (see Fig. 21). The male had an

alert stance, inflated throat sac and body, and often shifted his body slightly in a restless fashion. The trill seems to be the last warning prior to physical combat. It is similar in function to the many-pulsed call described in H. cinerea by Gerhardt (1978). The trill probably should be considered the most aggressive call; the peep also conveys some agonistic meaning, but to a lesser degree than the trill.

It should be noted that the trill has a very sharp attack transient. If this parameter does, indeed, indicate relative arousal, a series of short attack transients within a short interval of time would present the receiver with multiple messages of arousal. The trill could be considered to be just such a series, barraging the receiver with 10 to 18 aggressive messages in the period of time necessary to produce one or two peeps which also have sharp attacks. This would be a far more efficient way of delivering the message, and the energy saved could be held in readiness for physical combat. This would be particularly suitable for an animal whose periods of calling and fighting probably involve anaerobic metabolism (Wells, 1977). Activity would result in an oxygen debt, followed by a necessary recovery period. If the next step following a trill could possibly be physical combat it would be better to use a warning call of low energy outlay prior to activity involving large energy

expenditure.

Small-pulsed calls are given by a male when he is mounted by another male. They are the release calls described by other authors (Bogert, 1960; Capranica, 1968; Schmidt, 1972 a,b). The carrier frequency of the small-pulsed call is lower than that of other calls, as is its amplitude. The low amplitude probably renders it not threatening to the mounting frog. Its effect may depend as much on tactile as auditory perception. The mounting male can feel with his hind legs the characteristic short sharp contractions of the musculature of the lower male's sides when he gives the call. These rapid side movements are described by Schmidt (1972 b) and seem to be present in release calls of all the species he studied.

Still another type of call which has been described by other authors (Bogert, 1960; Capranica, 1968; Oplinger, 1963) is the distress call. I only heard it once when a frog was accidentally squeezed too tightly about the thorax, but never in natural conditions. This parallels Capranica's (1968) experience. The call was produced with the mouth open, unlike other calls. There is some question whether this is a legitimate call, or could merely be a physical result of the frog's being compressed, forcing air from its lungs past its vocal cords and out its mouth which would be forced open by the passing air.

VI. CONCLUSIONS

The attack transient of Hyla crucifer calls emerges as an additional parameter in the investigation of frog calls. It acts as a discriminating character between types of calls, and it may indicate the relative aggression of the caller.

The tapered call merits consideration as a separate call. Its beginning low amplitude which gradually increases over a long rise time may be perceived by the receiver as being less aggressive than the peep. It probably serves as an advertisement call. The frogs are probably processing the calls as graded signals mainly based on attack transient. The tapered call with its long attack transient would occupy a node at one end of the scale, and the peep with its short attack transient would occupy a second node at the other end. Between the two there is some overlap which probably represents a transitional phase.

In a study of the energy required for the tapered call, peep, and trill, the tapered call was found to require 65% less energy output than the peep. The trill requires only 18% of the energy found in a peep, a notable energetic savings over the expenditure that would be necessary for production of many rapid aggressive peeps.

LITERATURE CITED

- Allan, D. M. 1973. Some relationships of vocalizations to behavior in the Pacific tree frog, Hyla regilla. Herpetologica 29: 366-371.
- Blair, A. P. 1941. Isolating mechanisms in tree frogs. Proc. Nat. Acad. Sci. US 27: 14-17.
- Blair, W. F. 1958 a. Call structure and species groups in U. S. tree frogs (Hyla). Southwest. Natur. 3: 77-89.
- Blair, W. F. 1958 b. Mating call in the speciation of anuran amphibian. Am. Nat. 92: 27-51.
- Blair, W. F. 1960. Mating call as evidence of relations in the Hyla eximia group. Southwest. Natur. 5: 129-135.
- Blair, W. F. 1962. Non-morphological data in anuran classification. Syst. Zool. 11: 72-84.
- Blair, W. F. 1964. Isolating mechanisms and interspecies interaction in anuran amphibians. Quart. Rev. Biol. 39: 334-344.
- Bogert, C. M. 1960. The influence of sound on the behavior of amphibians and reptiles. IN: W. E. Lanyon and W. N. Tavolga (eds.), Animal Sounds and Communication, pp. 137-320. Am. Inst. Biol. Sci. Publ 7, Washington, D.C.
- Brattstrom, B. H. 1962. Call order and social behavior in the foam-building frog, Engystomops pustulosus. Amer. Zool. 2: 394.
- Brattstrom, B. H. and J. W. Warren. 1955. Observations on the ecology and behavior of the Pacific treefrog, Hyla regilla. Copeia 1955: 181-191.
- Bunnell, P. 1973. Vocalizations in the territorial behavior of the frog Dendrobates pumilio. Copeia 1973: 277-284.
- Capranica, R. R. 1966. Vocal response of the bullfrog to natural and synthetic mating calls. J. Acoust. Soc. Am. 40: 1131-1139.
- Capranica, R. R. 1968. The vocal repertoire of the bullfrog (Rana catesbiana). Behavior 31: 302-325.

- Capranica, R. R., L. S. Frishkopf, and E. Nevo. 1973. Encoding of geographic dialects in the auditory system of the cricket frog. *Science* 182: 1272-1275.
- Conant, R. 1958. A field guide to the reptiles and amphibians. The Riverside Press, Cambridge. 366 pp.
- Dixon, W. J., and M. B. Brown. (eds.) 1979. Biomedical Computer Programs P-Series. Univ. Cal. Press, Berkely. 880 pp. Program revision data (output) developed at Health Sciences Computing Facility UCLA. HSCF-UCLA sponsored by NIH Special Research Resources Grant RR-3.
- Duellman, W. E. 1966. Aggressive behavior in dendrobatid frogs. *Herpetologica* 22: 217-221.
- Duellman, W. E. 1967. Social organization in the mating calls of some neotropical anurans. *Amer. Midl. Natur.* 77: 156-163.
- Fellers, G. M. 1976. Social interactions in North American treefrogs (*Hyla*). Ph.D. Diss. University of Maryland.
- Gannett, E. K., E. C. Day, H. J. Carter, S. Greer (eds.) 1972. IEEE standard dictionary of electrical and electronics terms. Wiley-Interscience, New York. 716 pp.
- Goin, C. J. 1949. The peep order in peepers; a swamp water serenade. *Quart. J. Florida Acad. Sci.* 11: 59-61.
- Gerhardt, H. C. 1973. Reproductive interactions between *Hyla crucifer* and *Pseudacris ornata* (Anura: Hylidae). *Amer. Midl. Nat.* 89: 81-88.
- Gerhardt, H. C. 1974. The significance of some spectral features in mating call recognition in the green tree frog (*Hyla cinerea*). *J. Exp. Biol.* 61: 229-241.
- Gerhardt, H. C. 1975. Sound pressure levels and radiation patterns of the vocalizations of some North American frogs and toads. *J. Comp. Physiol.* 102: 1-12.
- Gerhardt, H. C. 1978. Discrimination of Intermediate sounds in a synthetic call continuum by female green treefrogs. *Science* 199: 1089-1091.
- Gerhardt, H. C. 1981 a. Mating call recognition in the green treefrog (*Hyla cinerea*): importance of two frequency bands as a function of sound pressure level. *J. Comp Physiol.* 144: 9-16.

- Gerhardt, H. C. 1981 b. Mating call recognition in the barking treefrog (Hyla gratiosa): responses to synthetic calls and comparisons with the green treefrog (Hyla cinerea). J. Comp. Physiol. 144: 17-25.
- Gerhardt, H. C., and K. M. Mudry. 1980. Temperature effects on frequency preferences and mating call frequencies in the green treefrog Hyla cinerea (Anura: Hylidae). J. Comp. Physiol. 137: 1-6.
- Jenssen, T. A., and W. B. Preston. 1968. Behavioral responses of the male green frog, Rana clamitans, to its recorded call. Herpetologica 24: 181-182.
- Lemon, R. E. and J. Struger. 1980. Acoustic entrainment to randomly generated calls by the frog, Hyla crucifer. J. Acoust. Soc. Am. 67: 2090-2095.
- Littlejohn, M. J. 1972. Long-range acoustic communication in anurans: an integrated and evolutionary approach. in Reproductive biology of the amphibia, D. H. Taylor and S. I. Guttman, (eds.) Plenum Press, New York 263-294.
- Loftus-Hills, J. J. 1974. Analysis of an acoustic pacemaker in Strecker's chorus frog, Pseudacris streckeri (Anura: Hylidae). J. Comp. Physiol. 90: 75-87.
- Loftus-Hills, J. J., and B. M. Johnstone. 1970. Auditory function, communication, and the brain-evoked response in anuran amphibians. J. Acoust. Soc. Am. 47: 1131-1138.
- Loftus-Hills, J. J., and M. J. Littlejohn. 1971 a. Mating-call sound intensities of anuran amphibians. J. Acoust. Soc. Am. 49: 1327-1329.
- Loftus-Hills, J. J., and M. J. Littlejohn. 1971 b. Pulse repetition rate as the basis for mating call discrimination by two sympatric species of Hyla. Copeia 1971: 154-156.
- Lutz, B. 1960. Fighting and an incipient notion of territoriality in male tree frogs. Copeia 1960: 61-63.
- Martof, B. S. 1953. Territoriality in the green frog, Rana clamitans. Ecology 34: 165-174.

- Martof, B. S. 1961. Vocalization as an isolating mechanism in frogs. *Amer. Midl. Nat.* 65: 118-126.
- McDiarmid, R. W. and K. Adler. 1974. Notes on territorial and vocal behavior of neotropical frogs of the genus Centrolenella. *Herpetologica* 30: 75-78
- Morris, D. 1957. "Typical intensity" and its relation to the problem of ritualization. IN Patterns of Reproductive Behavior. 1970. Jonathan Cape, London. 528 pp.
- Narins, P. M., and R. R. Capranica. 1977. An automated technique for analysis of temporal features in animal vocalizations. *Anim. Behav.* 25: 615-621.
- Narins, P. M., and D. D. Hurley. 1982. The relationship between call intensity and function in the Puerto Rican coqui: (Anura: Leptodactylidae). *Herpetologica* 38: 287-295.
- Nelson, C. E. 1973. Mating calls of the Microhylidae: descriptions and phylogenetic and ecological considerations. *Herpetologica* 29: 163-176.
- Nevo, E. and H. Schneider. 1976. Mating call pattern of Green toads in Israel and its ecological correlate. *J. Zool.* 178: 133-145.
- Noble, G. K. 1955. The biology of the amphibia. Dover Publications, New York. 577 pp.
- Oplinger, C. S. 1963. The life history of the Northern Spring Peeper, Hyla crucifer, Wied at Ithaca, New York. Ph.D. Diss. Cornell University.
- Paillette, M. 1976. Etude experimentale des interactions sonores dan les choeurs de rainettes Hyla meridionalis (Amphibien Anoure) par stimulation avec des signaux sonores periodiques de synthese. *Terre et Vie* 30: 89-120.
- Pierce, J. R., and D. B. Ralin. 1972. Vocalizations and behavior of the males of three species in the Hyla versicolor complex. *Herpetologica* 28: 329-337.
- Perrill, S. A., H. C. Gerhardt and R. Daniel. 1978. Sexual parasitism in the green tree frog (Hyla cinerea). *Science* 200: 1179-1180.

- Rosen, M., and R. E. Lemon. 1974. The vocal behavior of spring peepers, Hyla crucifer. Copeia 1974: 940-950.
- Ryan, M. J. 1980. Female mate choice in a neotropical frog. Science 209: 523-525.
- Schmidt, R. S. 1972 a. Action of intrinsic laryngeal muscles during release calling in Leopard frog. J. Exp. Zool. 181: 233-244.
- Schmidt, R. S. 1972 b. Release calling and inflating movements in anurans. Copeia 1972: 240-245.
- Straughan, I. R. 1975. An analysis of the mechanisms of mating call discrimination in the frogs Hyla regilla and H. cadaverina. Copeia 1975: 415-424.
- Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco. 776 pp.
- Sullivan, B. K. 1982. Significance of size, temperature and call attributes to sexual selection in Bufo woodhousei australis. Jour. of Herpetology 16: 103-106.
- Wells, K. D. 1977. The social behaviour of anuran amphibians. Anim. Behav. 25: 666-693.
- Wells, K. D. 1978. Territoriality in the green frog (Rana clamitans): vocalizations and agonistic behaviour. Anim. Behav. 26: 1051-1063.
- Wells, K. D. and B. J. Greer. 1981. Vocal responses to conspecific calls in a neotropical hylid frog, Hyla ebraccata. Copeia, 1981: 615-624.
- Whitford, W. G. 1967. Observations on territoriality and aggressive behavior in the western spadefoot toad, Scaphiopus hammondi. Herpetologica 23: 318.
- Wright, A. H., and A. A. Wright. 1949. Handbook of frogs and toads. Cornell Univ., Ithaca. 640 pp.

APPENDIX

Table A-1. Eigenvalues, Canonical Correlations and Canonical Variables Evaluated at Group Means Used in the Discriminant Analysis

Eigenvalues	4.26789	1.74645	0.90246
Canonical Correlations	0.90009	0.79743	0.68874
Canonical Variables Evaluated at Group Means:			
Tapered Calls	0.30513	2.58932	0.20403
Peeps	0.60209	-0.68680	-0.06895
Trills	-7.64124	-0.58484	1.86922
Small-pulsed Calls	-8.63355	0.93590	-7.79000

Table A-2. Summary Table - Stepwise Discriminant Analysis

Step No.	Variable Entered	F Value to Enter	No. of vbls.	U-stat.	Approx. F-Stat.	Deg. of Freedom
1	No. pulses	359.79	1	0.2905	250.8	3 431
2	Duration	252.90	2	0.1051	298.9	6 860
3	Rise Time	232.96	3	0.0400	319.5	9 1044
4	Max Ampl.	9.16	4	0.0376	231.9	12 1133
5	Init.Freq.	4.82	5	0.0363	182.6	15 1179

All steps were highly significant ($p \leq 0.001$)

**The vita has been removed from
the scanned document**

THE VOCAL REPERTOIRE OF Hyla crucifer

by

Nancy Case Hurst

(ABSTRACT)

A new, tapered call was discovered in the Hyla crucifer repertoire with the aid of a digital processing oscilloscope. The attack transient was found to be a distinguishing characteristic between the newly discovered tapered call and other calls. Energy requirements for production of the tapered call, peep and trill were calculated and the trill was found to have a much lower energy outlay than the other calls. The implications of the lower energy expenditure in a trill are considered, and the possibility of two calls in the H. crucifer repertoire being nodes in a graded signal is discussed.