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THE FUNCTION OF CALL ALTERNATION IN ANURAN AMPHIBIANS: A TEST OF THREE HYPOTHESES[1]

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Abstract.—Males of many species of anurans alternate calls with those of their neighbors in a chorus. This pattern of calling reduces signal interference and may: 1) facilitate intermale spacing because males can better gauge the intensity of neighbors' calls if these calls do not overlap with their own; 2) help preserve species-specific temporal information in calls required to attract females; and/or 3) make it easier for females to localize males in the chorus. I tested these hypotheses with three species that exhibit call alternation, *Hyla crucifer, H. versicolor,* and *H. microcephala.* Males of all three species gave more aggressive calls to high-intensity synthetic stimuli that alternated with their calls than to those that overlapped their calls. These results support the first hypothesis. Results of four-speaker female choice experiments using alternating and overlapping calls indicate that preservation of signal integrity also is important in *H. versicolor* and *H. microcephala,* species that have fine-scale temporal information in their calls. However, the third hypothesis was not supported; females failed to discriminate among alternating and overlapping calls if the problem of signal disruption was eliminated or irrelevant.

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Males of many acoustically signaling species form dense assemblages in which they communicate with conspecifics. Advertisement calls (Wells, 1977*a*) contain information, encoded spectrally and/or temporally, important for species recognition (Gerhardt, 1982), and, often, attributes of the signaling males, such as body size, are transmitted as well (Arak, 1983*a*; Ramer et al., 1983; Ryan, 1985). This information may be relevant to both mate attraction and intermale spacing. In addition to inherent properties of the call, when the signal arrives at the receiver, sonic cues (such as intensity and phase) may provide information on both the distance and direction of a calling male (Rheinlaender et al., 1979).

Often, individuals within choruses change the timing of their calls in response to calls of other members of the assemblage in ways which preserve signal integrity or reduce acoustic interference (Wells, 1977*a*, 1977*b*; Awbrey, 1978; Cade and Otte, 1982; MacNally, 1982; Greenfield and Shaw, 1983; Zelick and Narins, 1982, 1983). Nonrandom patterns of call timing include synchronous patterns, in which calls of males or the repeating units within calls overlap fairly precisely (Walker, 1969) and alternating patterns, in which no overlap of call elements occurs (Shaw, 1968; Passmore, 1978; Schwartz and Wells, 1984*a*, 1984*b*). Alternation can occur if males are stimulated to call by the calls of others following a brief time delay (Schwartz and Wells, 1984*a*) or as a result of changes males may make in the rate and timing of their calls or call components when interacting vocally

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(Loftus-Hills, 1974; Latimer, 1981; Schwartz and Wells, 1985). Because call alternation is so widespread, students of both insect and anuran communication, in particular, have been interested in the factors responsible for this form of temporal organization (Littlejohn and Martin, 1969; Alexander, 1975; Greenfield and Shaw, 1983; Schwartz and Wells, 1983*a*, 1983*b*, 1984*a*, 1984*b*, 1985). Alternation of calls is a ubiquitous behavior in anuran amphibians (Wells, 1977*a*). Unfortunately, the functions of call alternation are currently poorly understood (Sullivan, 1985), and carefully designed experiments are needed to determine the selective advantage of this behavior. Three major hypotheses have been proposed, but none, until now, has been adequately tested:

1) Call alternation functions in territory maintenance by males. Acoustic overlap impairs a male's ability to assess the intensity of neighbors' calls and thus maintain adequate intermale spacing within the chorus (Jones, 1966; Lemon, 1971; Passmore and Telford, 1981).
2) Acoustic interference obliterates or disrupts temporal information that is critical for species discrimination. Therefore, males should either alternate or precisely synchronize calls to prevent signal degradation (Littlejohn, 1977; Greenfield and Shaw, 1983; Wells and Schwartz, 1984).
3) Males avoid overlapping calls because acoustic interference among neighboring males makes the task of localizing a sound source difficult for females (Jones, 1966; Passmore and Telford, 1981; Zelick and Narins, 1983; Wells and Schwartz, 1984).

A study by Passmore and Telford (1981) was designed to assess the significance of call alternation in *Hyperolius marmoratus.* In two-speaker experiments they found no significant difference in the time of approach of females to sources broadcasting overlapping or alternating calls. They concluded that females do not find overlapping calls more difficult to locate. However, their work only addressed hypothesis-3, because the overlapping calls were precisely synchronized (Wells and Schwartz, 1984), and the advertisement call of the species they used is a frequency-modulated tone without fine temporal structure (see sonagram in Telford [1985]). In addition, the timing of approach began after females left their central container or made a positive orientation movement. If females had difficulty initially orienting towards an overlapping source, this would not have been detected.

The purpose of my study was to test all three hypotheses using playback experiments with both males and females of three species of frogs, all of which alternate calls or call notes (Rosen and Lemon, 1974; Lemon and Struger, 1980; Fellers, 1979; Schwartz and Wells, 1985; Fig. 1). In two of these species, *Hyla versicolor* and *H. microcephala,* advertisement calls are composed of pulse trains (Gerhardt, 1978; Schwartz and Wells, 1985). In the third species, *H. crucifer,* advertisement calls consist of frequency-modulated tones of 80–200 msec duration (Doherty and Gerhardt, 1984). *Hyla versicolor* (Gerhardt, 1982) and *H. microcephala* females (Schwartz, 1987) are capable of fine levels of call discrimination based on pulse-repetition rate, implicating the importance of this parameter in species recognition and reproductive isolation. *Hyla crucifer* advertisement calls lack fine temporal structure which could be obscured by call overlap.

MATERIALS AND METHODS

Study Area.—Field playback experiments with male *H. crucifer* and *H. versicolor* were conducted in two ponds near Storrs, Connecticut from April through July 1985. Males establish calling sites on vegetation in or near water and may advertise for females from dusk until near midnight (Rosen and Lemon, 1974; Wells and Taigen, 1986). *Hyla microcephala* males were studied in July and August 1985 in a flooded meadow in Gamboa, Panama, a town bordering the Panama Canal. Field work was done between 7:30 P.M. and 11:30 P.M.; calling by males of this species usually ceases after midnight.

Experiments.—The experiments with males were designed to test hypothesis-1. In all three species, tests with males were facilitated by a tendency for calling individuals to maintain a degree of intermale spacing (Fellers, 1979; Brenowitz et al., 1984; Schwartz and Wells, 1985). However, because *H. microcephala* and *H. crucifer* choruses can be especially dense, it was sometimes necessary to remove nearby males that were interacting vocally with the subject. Calling males were exposed to calls generated by a portable frog-call synthesizer constructed by the author. Conceptually, this device is similar to the "Coqui-Synthesizer" used by Narins and Capranica (1978), although its design and capabilities are different. The synthesizer can generate both pulsed and tone-like calls, and relevant call features such as duration, pulse rate, pulse shape, and spectral structure can be independently varied. The unit can be set to trigger the onset of a frog call after a preset time delay. Digital integrated circuits are employed to produce temporal features of calls and to control call timing; spectral structure is adjusted using two voltage-controlled oscillators, the output of which may be phase-locked.

In the field, the output of the synthesizer was fed into one channel of a Marantz PMD 360 stereo cassette tape recorder, which amplified the signal, and then broadcast from 1 m to the frogs via either a University 4401 horn speaker (*H. crucifer* and *H. microcephala*) or a Heppner mid-range horn speaker (*H. versicolor*) mounted on wooden baffles. The amplitude-frequency responses of these speakers are essentially flat from 1.1 to 14.5 kHz. Recordings of males were made using the remaining channel of the Marantz and a Realistic 33-1062 directional microphone. The output from the microphone was split using a Y-cord and simultaneously fed into an operational amplifier in the synthesizer. The signal was then low-pass filtered and used to trigger a time delay circuit which in turn triggered the output of a synthetic call. Prior to field work, the settings on the synthesizer were adjusted using both a Tektronix 5111 storage oscilloscope and a Uniscan Model 4500 real-time spectrum analyzer. During the course of the study, periodic checks were made on the output of the synthesizer to determine whether retuning was necessary.

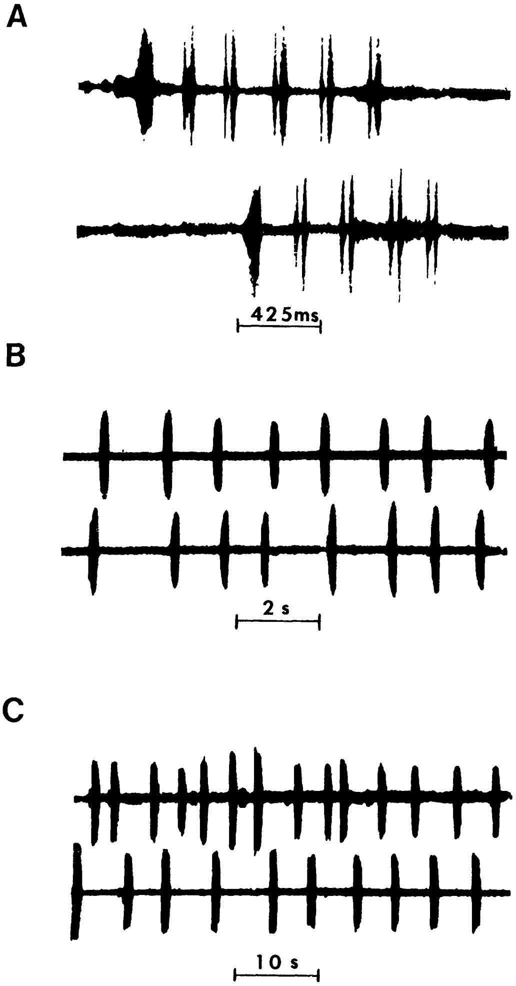

FIG. 1. Oscillograms of calls of interacting male *H. microcephala* (A), *H. crucifer* (B), and *H. versicolor* (C) showing alternation of calls or notes.

The artificial calls were designed to correspond closely to the natural advertisement calls of the species being tested (Fig. 2). For *H. crucifer* the call was a 2,880 Hz tone of 104 to 144 msec duration. For *H. versicolor* it was a pulsed 1,520 Hz signal (20 pulses/sec) of 488 to 648 msec duration. The chosen frequency was intermediate between the energy peaks at 1 and 2 kHz in the natural *H. versicolor* call. Call duration in these two species is a linear function of body temperature (Gerhardt, 1978; Lemon and Struger, 1980) so, prior to tests, air temperature was determined and call duration on the synthesizer adjusted according to a precalculated regression equation. Although the pulse rate in *H. versicolor* calls also shifts with temperature, this parameter was not changed because it was difficult to

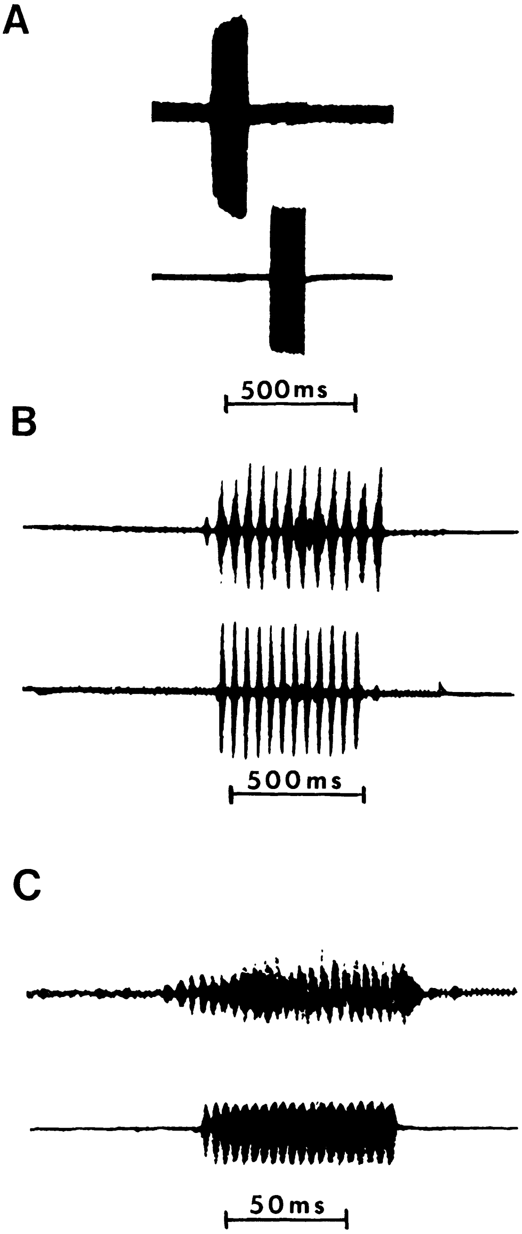

FIG. 2. Oscillograms of natural advertisement calls (above) and synthetic calls (below) used in tests with males. A) *H. crucifer*; B) *H. versicolor*; C) *H. microcephala.*

make such adjustments accurately in the field. However, the chosen value was close to predicted values of pulse rate reported by Gerhardt (1978) for the range of temperatures I measured during my work with this species (18°–24°C). For *H. microcephala,* the synthetic call was a pulsed signal (245 pulses/sec) of 85 msec duration. Spectrally, the signal consisted of two phase-locked sinusoids of 2,900 and 5,800 Hz. Synthetic call duration was not a problem in work with *H. microcephala* because temperature variation in the Gamboa study area varies little during the hours when males call (Schwartz and Wells, 1985).

Stimulus intensities were predetermined with a Gen Rad 1982 precision sound-level meter set for flat weighting and calibrated with a Gen Rad 1562A sound-level calibrator. I measured peak SPL (sound pressure level; db SPL re 20 μPa) at 1 m with a random-incidence microphone.

The experimental protocol was similar for all three species. A male was first recorded for a 2-min no-stimulus period to determine the baseline level of aggressive calling. Calls were then broadcast for 2 min at the lowest of a series of successively greater intensities (5-db SPL increments) with the trigger set so these either interrupted or alternated with calls of the subject. Initial stimulus intensity was 85 or 90 db SPL for *H. crucifer,* 90 db SPL for *H. microcephala,* and 105 db SPL for *H. versicolor.* After both interrupting and alternating calls were presented, the process was repeated at the next highest intensity. Stimulus intensity was increased until a level was reached which elicited an unambiguous increase in aggressive calling (for some males it was not possible to elicit such a response). After an equal number of alternating and interrupting 2-min presentations, the test was terminated. Order of presentation of the two stimulus types was alternated among males. In all, 12 *H. crucifer,* 12 *H. versicolor,* and 11 *H. microcephala* were tested in this fashion.

The recordings were analyzed by counting the number of advertisement and aggressive calls given by each subject during stimulus presentations. These call types are easily distinguished. In *H. crucifer,* advertisement calls are tone-like, and aggressive calls are pulsed. In *H. versicolor,* advertisement calls are pulsed, and aggressive calls are frequency-modulated tones (Fig. 3). In *H. microcephala,* aggressive calls have higher pulse-repetition rates than advertisement calls (Schwartz and Wells, 1985). As in many other anuran species (Littlejohn, 1977; Wells, 1977*a*), intermale spacing in

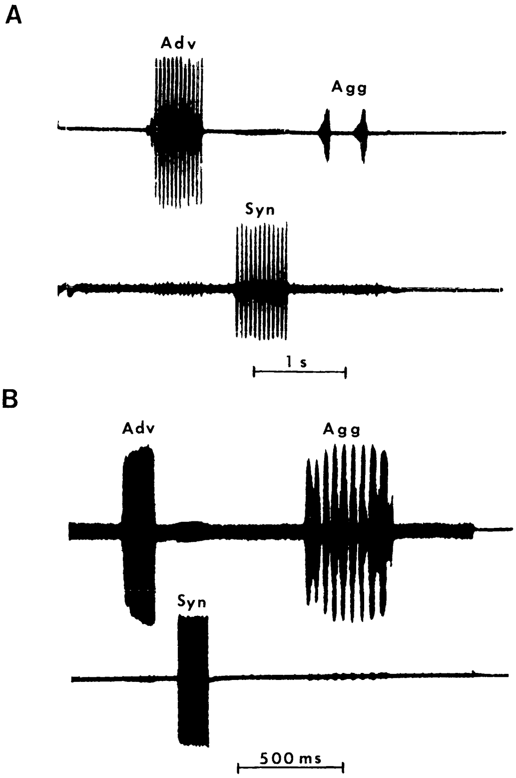

FIG. 3. Oscillograms of aggressive call responses by *H. versicolor* (A) and *H. crucifer* (B) to the broadcast of an alternating synthetic advertisement call (lower trace).

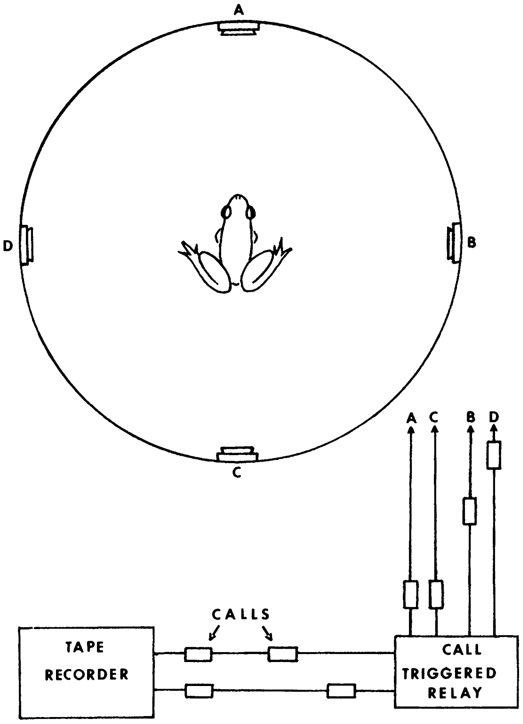

FIG. 4. Schematic diagram of the arena and equipment used in four-speaker female choice tests. The frog is not drawn to scale.

H. crucifer, H. versicolor, and *H. microcephala* is frequently mediated by aggressive acoustic interactions; if calls are perceived above a certain intensity, a male will give aggressive calls until the neighbor withdraws. Occasionally, physical combat occurs (Fellers, 1979; Schwartz and Wells, 1985). Hypothesis-1 suggests that males can more easily perceive the intensity of neighbors' calls when calls are alternated. If this is true, then test males would be more likely to give aggressive calls to alternating stimuli than to overlapping stimuli. If the ability of males to gauge call intensity is not impaired by overlap, then levels of aggressive calling should be equivalent or possibly biased in the other direction during both types of presentations.

Hypothesis-2 and hypothesis-3 were tested with four-speaker female-choice experiments. For *H. crucifer* and *H. versicolor,* these experiments were performed in a circular arena in a darkened apartment within three miles of the collection sites between 10:00 P.M. and 3:00 A.M. The arena, constructed from garden fencing and burlap, was 2 m in diameter and 1 m high. It was illuminated by a 25-w red bulb suspended from the ceiling. Four Realistic Minimus 0.3 speakers (amplitude-frequency response: ±3 db, 1.0–12.0 kHz) were spaced equidistant and facing the center of the arena (Fig. 4). Temperature was maintained at 17°–19°C during work with *H. crucifer* and 19°–23°C during work with *H. versicolor.* For *H. microcephala,* a square arena (1.6 m × 1.6 m) delimited by uniformly colored blankets was used in an apartment in Gamboa. The four speakers were placed at its corners facing the center along the arena diagonals. Temperature during the experiments was approximately 26°C.

Gravid females were captured in amplexus and placed in individual petri dishes. After 35–60 min, testing began. Each female was placed in the center of the arena in its dish covered by a piece of cardboard, which could be removed with a string from outside the arena. The top was removed from the petri dish 1 min after stimulus playbacks began. A positive response was scored if a female approached to within 10 cm of a speaker within 15 min. Most females responded within 5 min. Those that did not respond within the allowed time period or that exhibited extensive undirected wandering were removed and retested later.

Hyla crucifer, H. versicolor, and *H. microcephala* females were presented with stimulus calls which had the following temporal arrangement: 1) in-phase (i.e., precisely synchronized) overlapping calls vs. alternating calls; 2) overlapping (but out-of-phase) calls vs. alternating calls. For *H. microcephala,* a three-note call was used and the alternating stimuli timed so that notes in the two calls interdigitated in a noninterfering way (Fig. 1). The characteristics and timing relationships of the stimuli are given in Table 1.

If the temporal information hypothesis-2 is correct (and the ability to locate sound sources is not impaired by call interference), then *H. versicolor* and *H. microcephala* females should not discriminate between alternating and in-phase overlapping calls in choice experiment-1 but should prefer alternating to out-of-phase overlapping calls in choice experiment-2. *H. crucifer* females should not discriminate in either experiment because their calls lack fine temporal structure. If the "locatability" hypothesis-3 is correct, then females of all three species should discriminate in favor of nonoverlapped calls in both experiments. If neither hypothesis-2 nor hypothesis-3 is correct, then no discrimination should occur. Of course, hypothesis-2 and hypothesis-3 are not mutually exclusive, and results which supported the locatability hypothesis would not necessarily refute the signal-disruption hypothesis. Therefore, a third choice experiment was planned with *H. versicolor* and *H. microcephala* females if hypothesis-3 were supported. Stimuli consisted of overlapping out-of-phase calls versus overlapping in-phase (i.e., precisely synchronized) calls. If signal disruption is important, discrimination against the out-of-phase calls should occur. This test was conducted with *H. versicolor* only. In all choice experiments, calls in the same temporal category were broadcast from speakers facing one another and the stimuli shifted between pairs of speakers on alternate nights.

Stimulus calls presented to *H. versicolor* and *H. microcephala* were natural conspecific advertisement calls originally recorded with a Uher 4200 Report Stereo IC tape recorder and a Sennheiser MKE 802 directional microphone. *H. crucifer* females were presented with recorded artificial advertisement calls produced by electronically gating a sinusoidal signal of 3,000 Hz. Each final two-track stimulus tape was prepared by creating a tape loop with four recordings of the same call and rerecording it on a cassette. The timing relationship between calls and relative amplitude were checked with a storage oscilloscope. Calls were spaced so that one was broadcast from each speaker every 6 sec. A quadraphonic presentation system was obtained by constructing a circuit using digital-integrated circuits and two electronic relays (Radio Shack Catalog #275-215) to switch the stereo signal and ground lines from a Marantz tape recorder back and forth between the two pairs of speakers (Fig. 4). The relays were automatically triggered, following a preset time delay, by the onset of a call on one channel. Playback intensities for each speaker were regulated by separate Realistic L-pads and were equalized at 85 dB ± 1 dB (peak SPL; db re 20 μPa) at the female release point using the Gen Rad precision sound-level meter.

RESULTS

Hypothesis-1 was strongly supported for all three species. Males gave proportionately more aggressive calls to the alternating stimulus than to the overlapping stimulus (Friedman Test; *H. crucifer*: $P = 0.034$, *H. versicolor*: $P < 0.01$, *H. microcephala*: $P < 0.001$; Fig. 5). For *H. crucifer* and *H. microcephala,* this response was especially pronounced at high intensities. In *H. versicolor,* males gave aggressive calls only to alternating calls. *Hyla microcephala* males increase the duration of aggressive-call primary notes in response to increases in stimulus-call intensity (Schwartz and Wells, 1985). Therefore, as another test of the ability of males to gauge call intensity, I compared the duration of these notes given un-

TABLE 1. Timing relationships and call parameters of stimuli used in four-speaker female choice tests. Intercall intervals are the times between onsets of either alternating (ALT) or out-of-phase overlapping (OP) calls. In phase overlapping, calls were presented at precisely the same time. Call rate from each speaker was approximately 10 per minute. Stimulus types were alternated such that the midpoint of the interval between alternating calls fell about 3 sec after the start of the overlapping calls.

Species	Call duration (msec)	Pulses/sec	Intercall interval (msec) ALT	OP
H. crucifer	215	—	660	100
H. versicolor	664	23	1,840	64
H. microcephala	92*	228	84	12

* Primary note duration of a three-note call.

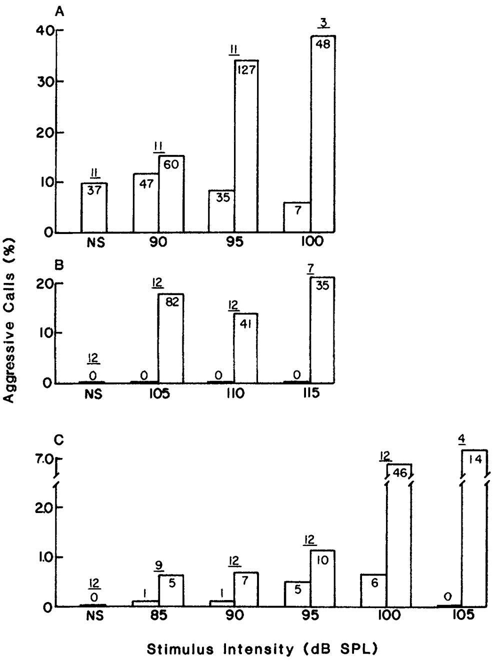

FIG. 5. Responses of males to interrupting (left bars) and alternating (right bars) synthetic stimulus calls at different broadcast intensities. Data are presented as the percentage of all vocalizations that were aggressive calls. Also shown is the percentage of aggressive calls during the no-stimulus (NS) periods. Data are pooled for all males. The number of males tested at each intensity is underlined above the bars. The number of aggressive calls is indicated within each bar. A) *H. microcephala*; B) *H. versicolor*; C) *H. crucifer.*

der the two presentation conditions. Again, data support the prediction of hypothesis-1; aggressive-call primary notes were longer in response to alternating stimulus calls at 95 and 100 db SPL (respective medians = 180 msec, 240 msec) than to overlapping calls at these intensities (respective medians = 144 msec, 96 msec) (Wilcoxon two-sample test, normal approximation, $Z = -2.84, -2.26$, $P = 0.004, 0.024$).

Females of all three species had no difficulty locating the overlapping calls provided these were in phase; there was no discrimination between these calls and alternating stimuli (Table 2). However, female *H. versicolor* and *H. microcephala* preferred alternating calls to overlapping out-of-phase calls; in *H. crucifer,* there was no discrimination between these stimuli (Table 2). Therefore, the data clearly support the temporal-information hypothesis (hypothesis-2), but fail to support the locatability hypothesis (hypothesis-3). As an additional test of these hypotheses, I gave 14 *H. versicolor* females a choice between in-phase and out-of-phase overlapping calls. Again, results (Table 2) are consistent with predictions of hypothesis-2: females discriminated against overlapping out-of-phase calls in which important temporal information (e.g., pulse-repetition rate) was obscured.

DISCUSSION

The results of this study support the view that male frogs avoid call or note overlap because it impairs both their ability to assess the intensity of neighbors' calls and their ability to transmit signals attractive to potential mates. During broadcast of synthetic calls, male *H. crucifer, H. versicolor,* and *H. microcephala* reacted in a way consistent with hypothesis-1; at high intensity, alternating calls elicited a stronger aggressive response than interrupting calls. While calling, a male's auditory system may be partially jammed or perhaps inhibited neurophysiologically (Counter, 1977) so he would be refractory to stimuli otherwise effective in eliciting aggressive calls. Experimental work with two Australian species, *Litoria ewingi* and *Uperoleia rugosa,* indicated that call-intensity assessment is important in maintaining intermale spacing within the chorus (Harrison, 1976; Robertson, 1984; also see Narins and Hurley [1982]). Information of this kind is also

TABLE 2. Results of four-speaker choice tests with *H. crucifer, H. microcephala,* and *H. versicolor* females.

	Number of females choosing:			Number of females choosing:			Number of females choosing:		
Species	Alternating calls	Overlapping in-phase calls	P^a	Alternating calls	Overlapping out-of-phase calls	P^a	Overlapping in-phase calls	Overlapping out-of-phase calls	P^b
H. crucifer	10	9	ns	9	9	ns	–	–	–
H. microcephala	8	10	ns	13	1	0.002	–	–	–
H. versicolor	8	9	ns	14	3	0.018	11	3	0.029

[a] Two-tailed binomial test.
[b] One-tailed binomial test.

available on two of the species studied here. Working with *H. crucifer,* Brenowitz et al. (1984) concluded that males distribute themselves in the chorus so that the amplitude of neighbors' calls is just above their detection threshold. However, Fellers (1979) noted that spacing in *H. crucifer* was influenced by chorus density and at extremely high densities might shift from even to random. Fellers's observations agree with my own observations in Connecticut and suggest that males of this species use call intensity in a facultative way to adjust their spacing. Fellers (1979) also found that *H. versicolor* males adjust their spacing in relation to the call intensity of nearby males and would move apart if such calls exceeded 93 db SPL. While quantitative data on spacing in *H. microcephala* are not available, males appear similar to *H. crucifer* in that they seem more tolerant of calling conspecifics in dense aggregations (pers. observ.). Because the maintenance of some degree of spatial separation among calling males in anuran choruses is a widespread phenomenon (Whitney and Krebs, 1975; Wells, 1977*a*; Arak, 1983*b*), it may be adaptive—perhaps because the behavior enhances male reproductive success (Telford, 1985). If so, it is not surprising that mechanisms to reduce call interference, and thus increase detectability of call intensity, have evolved.

My data indicate that in those species with calls incorporating fine-scale temporal structure, call overlap may disrupt information requisite for species recognition and phonotaxis by females. For *H. versicolor* and *H. microcephala,* the unambiguous behavior of females was not surprising. In both these species, two-stimulus tests using synthetic calls have demonstrated that females are sensitive to deviations from the pulse repetition rates of conspecific advertisement calls (Gerhardt, 1978; Schwartz, 1987). Because both *H. versicolor* and *H. microcephala* often breed in areas where heterospecifics use similar calls (Gerhardt, 1982; Schwartz and Wells, 1984*a*), this limited tolerance is probably critical in maintaining premating reproductive isolation.

On a fine temporal scale, three behavioral solutions to the problem of signal disruption are available: 1) males may shift the timing of individual calls so that these alternate with those of their neighbors; 2) males may adjust the spacing of individual notes (if calls are multinote) so that these do not interfere when calls overlap; or 3) males may precisely synchronize their calls so that the fine-scale temporal structure is not degraded by interference. The first solution is adopted by male *H. versicolor* (Fig. 1). *Hyla microcephala* males employ the second by alternating individual notes within calls (Fig. 1). This pattern of calling is rare in anurans (Schwartz and Wells, 1984*b*, 1985) but is more common in chorusing insects (Alexander, 1975; Latimer, 1981; Greenfield and Shaw, 1983). *Hyla microcephala* males further reduce the chances of note interference by rapidly lengthening internote intervals during call overlap (see oscillograms in Schwartz and Wells [1985]). Behavior consistent with the third solution has not been reported in frogs, but it is known in chorusing insects (Samways, 1976; Greenfield and Shaw, 1983). In anurans, pulses within calls or notes are often of such a fine scale (on the order of a few milliseconds) that it is unlikely the precision required to maintain signal integrity could be achieved. In synchronizing insects, song parameters (e.g., chirp period) important in mate attraction are usually longer than this (Walker, 1969; Alexander, 1975; Greenfield and Shaw, 1983). Therefore, the degree of synchrony necessary to preserve species-specific temporal patterns need not be as precise.

Perhaps the most surprising result of this study is the lack of support for the locatability hypothesis in any of the three species tested. Therefore, my results supplement those of Passmore and Telford (1981). I suspect that in our experiments any random movement of a subject away from the central release point of the choice arena resulted in differences in direction and sound intensities of the sources sufficient to permit localization (Wilczynski and Capranica, 1984). This capability suggests that the acuity of the localization system is considerable.

Because three species were examined in this study, I believe the results have wide applicability. However, while call alternation among males appears to be the norm in anuran choruses, some species seem to time their calls to increase call overlap. In *Smilisca sila,* for example, this pattern of calling may be related to the behavior of the frog-eating neotropical bat *Trachops cirrhosus.* Playback experiments demonstrated that bats are less responsive to synchronous than asynchronous *Smilisca* calls (Tuttle and Ryan, 1982). Sullivan (1985) reported that *Bufo punctatus* males frequently initiated their calls shortly after broadcast of a 7.0 sec conspecific stimulus call, so that considerable overlap occurred. Data on the precise timing of these responses was not obtained so it is unclear how much interference actually occurred during these long vocalizations. For both these species, female-choice experiments are needed to clarify costs, if any, of call overlap. Wells (1977*a*) suggested that among explosive breeders (e.g., *Bufo americanus*) in which males obtain mates through active searching rather than female choice, call overlap may not be disadvantageous. Finally, in *H. ebraccata,* males may exploit call interference to enhance their mating success. When a male responds to a multinote call, his longer primary note frequently overlaps, and thus obscures, the first, shorter secondary note of his competitor. Female-choice experiments indicated that this pattern of vocal interaction reduces the relative attractiveness of the first male's call (Wells and Schwartz, 1984). These examples underscore the value of continued research in the area of temporal organization of anuran choruses.

A satisfactory understanding of the phenomenon of call alternation would also benefit from neurophysiological research on species for which we have good behavioral data. While much progress has been made recently in work on the processing of spatial information in the anuran auditory system, the actual mechanism of sound localization is not known (Wilczynski and Capranica, 1984). Studies are needed to test the sensitivity of the system to intensity differences in simultaneous binaural stimuli. In addition, it would be valuable to know how the neuronal capacity for temporal pattern recognition (Rose et al., 1985) is influenced by call overlap. Are amplitude-modulated stimuli from each ear combined prior to analysis in the central nervous system, for example? Are anurans incapable of direction-specific pattern recognition? Questions such as these have recently been addressed in studies of orthopteran communication (Helverson, 1984; Pollack, 1986), and similar experimental work with anurans would enhance our understanding of the evolution of their vocal behavior.

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