Male Calling Behavior, Female Discrimination and Acoustic Interference in the Neotropical Treefrog Hyla microcephala under Realistic Acoustic Conditions
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Male calling behavior, female discrimination and acoustic interference in the Neotropical treefrog *Hyla microcephala* under realistic acoustic conditions

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Summary. Anuran choruses are acoustically complex assemblages of calling males. Little is known about the behavior of males or females in such natural sound environments. I studied calling behavior of males of *Hyla microcephala* in nature by using an interactive computer-based system that allowed me to simulate call interruptions by a number of males. I also monitored the calling behavior of groups of four to six males. When a male is interrupted by the call of another frog, he increases the spacing between the notes of his call. Responses of this kind are strongest to the loudest neighbor, and some males may ignore interruptions by all but a single close male. Interruptions using synthetic calls with silent gaps indicated that males respond vocally to reductions in sound intensity as brief as 20 ms. This ability helps to explain how males can rapidly alternate notes during pairwise interactions. Amounts of acoustic overlap between pairs of males in the choruses were usually below 10% of an individual's total calling time during bouts. The time a male spent calling that was free of acoustic interference by any other male ranged from 34–92% of his total calling time. When group size was decreased, this unobstructed calling time increased. Previous research showed that females of *H. microcephala* discriminate against calls that overlap so that the call pulse-train structure is degraded. Here I show that a 6 dB difference in intensity between the overlapped calls is sufficient to reduce the degradative effect of call interference. Females were also given a choice between interfering calls broadcast from two adjacent and two widely separated speakers. An angular separation between speakers of 120° was insufficient to elicit a preference for the separated sources. Together, data on behavior of males and females indicated that males actively reduce acoustic interference with those loud individuals most likely to degrade seriously the temporal structure of their calls.

Introduction

If one listens to the sounds coming from a typical frog chorus, one is confronted with what appears to be a disorganized cacophony. In the tropics, the impact on a listener can be quite profound since choruses often consist of large multi-species assemblages of very vocal male frogs (Aichinger 1987; Duellman 1978; Hödl 1977). In the midst of this acoustic farrago, females must be able to discriminate the calls of conspecific males from heterospecific males, choose among conspecifics, and then orient toward and localize a particular male (Gerhardt 1982; Narins and Zelick 1988). To facilitate mate attraction, male frogs may make adjustments in the timing of their calls or the calls' constituent notes (Littlejohn 1977; Schwartz 1991). They also use intensity cues, aggressive calls, and even fighting to regulate spacing in the chorus (Wells 1988).

Most data on male vocal or female phonotactic behavior have come from studies in which much of the complexity of the natural chorus was excluded (Klump and Gerhardt 1992). For example, playbacks to individual males or two-channel recordings of pairwise male-male interactions have provided most of the evidence that males shift the timing of calls or notes in response to one another (e.g., Schneider et al. 1988). These adjustments have been explained as mechanisms to reduce acoustic interference (Narins and Zelick 1988). However, it is not clear whether acoustic interference is reduced only among close neighbors in the chorus or whether more widely separated males act in ways to limit call overlap. In choice tests, most experimental designs have used only two speakers to explore discrimination among different calls by females (Gerhardt 1988, 1992). When increased acoustic complexity is incorporated, discrimination by females is reduced (Gerhardt 1982). Using a four-speaker design, I determined that call alternation by males can function to preserve signal integrity (Schwartz 1987a). However, even in this experiment, the acoustic conditions were somewhat unnatural and represented only one of many possible arrangements of interfering and alternating sound sources.

In this study, I examined the vocal behavior of frogs under acoustic conditions representative of those that the animals commonly encounter in the field. The subject of this paper, *Hyla microcephala,* has been studied for many years (Schwartz 1986, 1987b, 1991; Schwartz and Wells 1985; Wells and Taigen 1989). Males call, often in dense aggregations, in freshwater wetlands in Panama during the rainy season (Duellman 1970; Fouquette 1960). Advertisement and aggressive calls are complex (Schwartz and Wells 1985), consisting of a primary note and 0–17 (usually fewer than 7) biphasic secondary notes. The call notes are amplitude modulated, and the pulse rate is a species-specific feature that is critical to species discrimination by females in multi-species choruses (Schwartz 1987b). Interacting males typically give multi-note calls in which individual notes are alternated with those of the other male, thereby reducing acoustic interference. In part, this precise note-by-note alternation is possible because each male delays production of its secondary notes when another male's call notes fall within the inter-note intervals of its own calls (Schwartz 1991; Schwartz and Wells 1985).

Previous studies used two-channel recordings of males engaged in pairwise vocal interactions or computer interruptions of single males (Schwartz 1986; Schwartz 1987a; Schwartz 1991; Schwartz and Wells 1985). These data cannot be used to determine how males of *H. microcephala* adjust the timing of their call notes in a dense chorus. Males might, for example, attempt to avoid acoustic interference with all of the males they hear or, alternatively, they might adjust note-timing only in response to the calls of their nearest neighbors. If two males are calling simultaneously, will a third male interfere with one or both males, or will he avoid calling altogether? Brush and Narins (1989) recently addressed similar questions in an elegant study of the chorus dynamics of *Eleutherodactylus coqui.* They used a custom-built frog-call encoder (which allowed them to record the calls of up to eight males) to show that males actively avoid interference with just two of their neighbors, a result predicted by their computer model. Here, I used a conceptually similar device to elucidate patterns of calling in the chorus environment. In addition, I employed an interactive, computer-based system of stimulus presentation to simulate the simultaneous calls of pairs of males. Experiments using these stimuli, which interrupted test males, were designed to learn how males respond to some of the acoustic complexity in a real chorus.

Although alternation of calls or notes among neighboring male frogs helps to minimize acoustic interference, there often are so many vocalizing frogs in a densely packed chorus that effective temporal partitioning of calling periods of males is impossible. Acoustic interference can degrade fine-scale temporal information critical for mate attraction and species discrimination in those species with amplitude modulated advertisement calls. For example, I demonstrated that females of *H. microcephala* will select two call-sources with alternating notes over two call-sources from which multi-note calls are timed to interfere degradatively (i.e., the two calls overlap so as to disrupt the fine temporal structure of each note). In these experiments, both interfering and alternating sound sources were separated by 180° (Schwartz 1987a). When a gravid female enters a chorus, calling males are located at a variety of angular separations and distances from her. Moreover, as she moves, her position shifts relative to the males. Although my 1987 study demonstrated that there was some degradation in the fine temporal structure of overlapped calls as perceived by females, the work did not address the effect of relative call intensity on degradation. Also, my experiments did not address the question of whether females could use directional information (i.e., cues used to localize a sound source) to help 'extract' the pulse rate in interfering calls, as occurs in some orthopterans (Pollack 1986; but see von Helverson 1984). Directional information has been shown to enhance call detection of unpulsed signals in the presence of masking broadband background noise in the green treefrog, *H. cinerea* (Schwartz and Gerhardt 1989).

In the choice experiments described here, I incorporated different spatial arrangements and intensities of sound sources. The data suggest how noise generated by different males may impair the ability of a female's auditory system to encode the species-specific pulse-rate of the advertisement calls of a male close to her. Moreover, the susceptability of interfering pulsed calls of different males to signal degradation may be important in determining patterns of vocal interaction within the chorus. Therefore, the results of the female-choice experiments could help explain data obtained from observations of natural interactions and from playback tests to males.

Methods

Study area

Experiments were conducted in June and July 1991 in Gamboa, Panama. The field site was a meadow with scattered pools of water and ditches containing dense stands of aquatic grasses (see Schwartz and Wells 1984 for further details). Temperatures during field work, which was conducted between 1930 and 2330 h, ranged from 24 to 27° C.

Natural group interactions

The calling dynamics of groups of males were monitored by using a Commodore Amiga 500 computer and an eight-channel interface board designed and built by the author (with the assistance of Robert Moore, Brown University; Fig. 1; see Appendix A.). In the field, an Azden unidirectional microphone (ECZ-660) mounted on a tripod was positioned directly in front of each frog and then connected to the interface board. The temporal resolution of the circuit was adjusted so that each note of a male's calls triggered an individual output pulse on that male's channel. The gain controls were adjusted so that the calling of each frog triggered only one channel. The computer was programmed to store the data automatically on a floppy disk every 5 min, at which time acquisition of data ceased for approximately 25 s. Before these recording

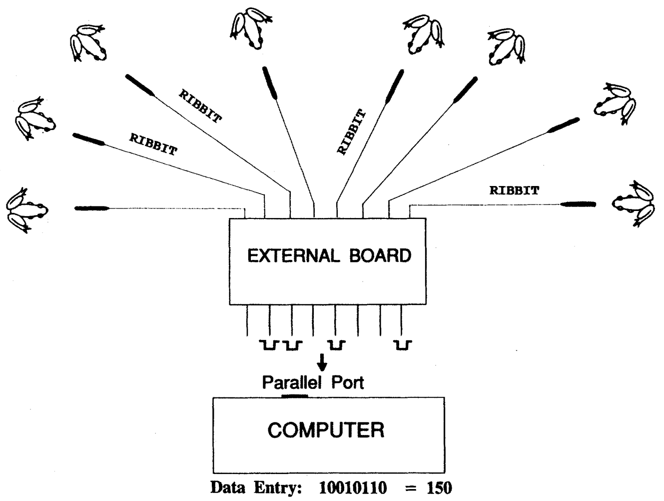


Fig. 1. Diagram of equipment used to moniter groups of calling male frogs in the field. Calls detected by directional microphones triggered a high-to-low voltage pulse on each of up to eight data lines. These pulses were sampled via the *parallel port* of an Amiga 500 *computer*. The resulting bit pattern and decimal data-byte entry for one time-sample with four calling males, each indicated with the onomatopoietic word '*ribbit*', is shown

sessions, as well as the playback tests described below, I made an attempt to remove any additional males near my experimental subjects. If a nearby male began to call during a test, he was immediately removed. For two of the four chorus groups that I worked with, I also removed some of the subjects after monitoring the intact group. This was done to assess the effect of group size on call interference.

After a test, I marked the position of each male in the group with a numbered stake and recorded his angular orientation in the group. The following day, the distances between the stakes were measured and their relative positions recorded. I also estimated the sound intensity of each male's calls at the position of every other male in the previous night's group by broadcasting recorded calls of *H. microcephala* from a speaker (University 4401 driven by a Marantz PMD 360 tape recorder) and measuring sound intensities (peak dB SPL; dB re 20 µPa) with a calibrated (Gen Rad 1562A) Gen Rad 1982 precision sound-level meter (flat weighting). Call intensity from the speaker was adjusted to 106 dB sound pressure level (SPL) at 50 cm, the modal SPL of the advertisement calls of *H. microcephala* (range: 101–109 dB SPL; Schwartz and Wells 1984). The measurements of sound pressure level (dB SPL) for each male dyad were converted to absolute sound pressure in µPa for averaging; these means were then converted back to dB to give an estimated SPL. It was unnecessary to adjust my estimates of SPL according to the orientation of males in the groups. Sound level measurements at 0°, 90°, and 180° at 50 cm from additional calling males indicated that directionality was slight.

To test whether males adjusted timing of their notes and calls, I analyzed the data in two ways. First, I compared the note spacing of males during times when they were interrupted by another male in the chorus with their note spacing during times when they were not interrupted. Second, I compared the observed amount of overlap between a male's calls and those of his neighbors with that expected if males did not alter their calling to avoid overlap. To calculate the expected distribution of overlap, I randomized the time of occurrence of the calls of each male, as well as his inter-call intervals, and then recalculated acoustic overlap among males. I operationally defined overlap as occurring when a male's call both interfered with, and followed the call of, another male. This method of calculating an expected level of overlap has recently been advocated by Popp (1989) and also was used by Brush and Narins (1989). My specific randomization procedure was conducted so as to keep each multi-note call intact so that unrealistic patterns of note timing would not be created. I also restricted the analysis to calling bouts because males of *H. microcephala* call in bouts often separated by long quiet periods (Schwartz 1991; Schwartz and Wells 1983). In any subscripted notation that follows, the 'interfering' male is [*i*] and the 'leading' male is [*j*]. To test for differences between observed and expected overlaps, I repeated the randomization procedure 100 times. For any pair of males, I considered that significantly less overlap than expected had occurred if observed overlap was less than that in at least 95 of the 100 randomized data sets.

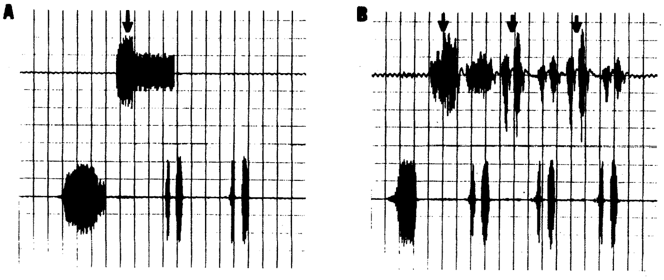


Fig. 2. **A** Oscillograms of overlapping 60- and 200-ms stimuli (*top trace*) interrupting a male *Hyla microcephala* giving a three-note call (*bottom trace*). The intensity of the 200-ms stimulus is −6 dB relative to that of the 60-ms stimulus (*arrow*). **B** Oscillograms of the two three-note stimulus calls (*top trace*) interrupting a male giving a four-note call (*bottom trace*). The second stimulus call is −6 dB relative to the first (*arrows*). The biphasic secondary notes each consist of two elements. Each *time division* equals 50 ms

Interruption experiments

I conducted three field playback experiments with males using a computerized presentation system (see Fig. 1 in Schwartz 1991; Appendix B). The system was interactive (*sensu* Dabelsteen 1992) and could be programmed to respond to the calls of males in different ways. Prior to experimental broadcasts, calls of frogs were recorded for an initial 2-min (no-stimulus) control period. During an experiment, the computer simultaneously monitored the male's vocal responses and recorded note timing along with the time and type of each stimulus. These data were stored on a floppy disk after each test.

To learn how the adjustments that males make in note timing may be influenced by the simultaneous calls of other frogs at different distances from them, I conducted two playback experiments. In these tests, calls simulating those of different males were used to interrupt subjects at different relative intensities.

Experiment M1. In this experiment, the computer was programmed to interrupt a calling male with a stimulus consisting of two overlapped synthetic call notes of 60 and 200 ms (Fig. 2A). Stimulus notes were designed to resemble primary notes of *H. microcephala* in spectral and fine temporal features and were created by using software written by the author (see Schwartz 1991 for details). Two different note durations were used so that it would be possible to differentiate the responses to one note from those to the other note. The shorter note, similar in duration to that of a natural secondary note (Schwartz and Wells 1985), was presented at a constant intensity. The relative intensity of the longer note was varied randomly from 0 to −15 dB SPL in minimum increments of 3 dB (using software control of the sound output from the Amiga computer). Therefore, the 60-ms note simulated the call of a male at a constant distance from the subject while the 200-ms note mimicked other males calling at six distances. The stimulus note of constant intensity was presented to 15 males at an intensity of 85 dB SPL. Eight of these males also were exposed to interruptions at an intensity of 90 dB SPL. Based on data from previous studies (Schwartz 1991; Schwartz and Wells 1985), it was known that interruptions at these intensities would elicit increases in inter-note spacing by males. Higher stimulus intensities were not used because these often elicited bouts of aggressive calling. The intensities of the stimulus calls of 90–75 dB correspond to those of a male calling at the modal sound intensity (Schwartz and Wells 1984) approximately 3.2–17.7 m from the subject (assuming no excess atenuation). Intensities of stimulus calls of 85–70 dB correspond to distances of 5.6–31.5 m.

The stimulus was broadcast approximately 35 ms after the end of the subject's primary note and so interrupted males during the first inter-note interval of their multi-note calls. When the two stimulus notes were at equal relative intensities, I expected males to often time their notes to accommodate the 200-ms interruption (Schwartz 1991). As the relative intensity of this long note declined, I expected that subjects eventually would respond only to the 60 ms note. To ensure a reasonable sample size of interrupted calls, individual tests lasted for 5–25 min, depending on the call rate of the subject.

Experiment M2. In this experiment, interrupting test stimuli were two three-note calls simulating those of two interacting males. The notes of these two overlapping calls alternated (Fig. 2B), as frequently occurs in calls of interacting males in a natural chorus. As in experiment M1, one call was presented at constant intensity and one varying intensity (0 to −15 dB down). When the relative-intensity difference was large (e.g., >6 dB), I predicted that subjects would place the second note of their interrupted calls in the first inter-note interval of the constant-intensity stimulus call. When the intensity difference was small (e.g., <9 dB), I predicted that the frogs would wait longer before giving their second note, perhaps even terminating their call and starting a new one after the entire stimulus ended. In these tests, the constant-intensity call was presented at 85 dB SPL (9 males) and 90 dB SPL (11 males).

Experiment M3. A third experiment using interrupting stimuli was designed and conducted while experiment M2 was in progress (see explanation in Results). In experiment M3, males were interrupted by a 200-ms synthetic call that incorporated centrally placed silent gaps of 10, 20, 30, or 40 ms. Thus, the total durations of all stimuli were identical. The computer selected these 200-ms 'gap' stimulu randomly, and they were broadcast at an intensity of 85 dB SPL (7 males) or, if the background noise levels produced by the chorus seemed high, they were presented at 90 dB SPL (5 males).

The durations of inter-note intervals from the field experiments were calculated by using programs written by author and statistically analysed with SAS (SAS Institute 1988; version 6.07). Oscillograms were prepared with a Kay Model 5500 DSP Sona-Graph.

Tests with females

Gravid females of *H. microcephala* were captured while they were in amplexus and transported to a nearby apartment. They were tested indivudually in an indoor arena measuring 2.0 × 2.0 m. Two mattresses and large couch cushions formed the walls of the arena and served to minimize reflection of sound. A 25-W red incandescent light bulb suspended from the ceiling provided illumination for the testing arena. For all tests, centrally facing speakers (Realistic Minimus 0.3; amplitude-frequency response: ±3 dB, 1.0–12.0 kHz) were located at the perimeter of a circle 150 cm in diameter within the arena. Before each test, I placed individual females under a small plastic funnel located at the center of this circle. After 30 s exposure to the test stimuli, I raised the funnel by using a cord and pulley. I scored a positive response if the subject came within 10 cm of a sound source within 10 min. The temperature during these experiments was 26° ± 1 C.

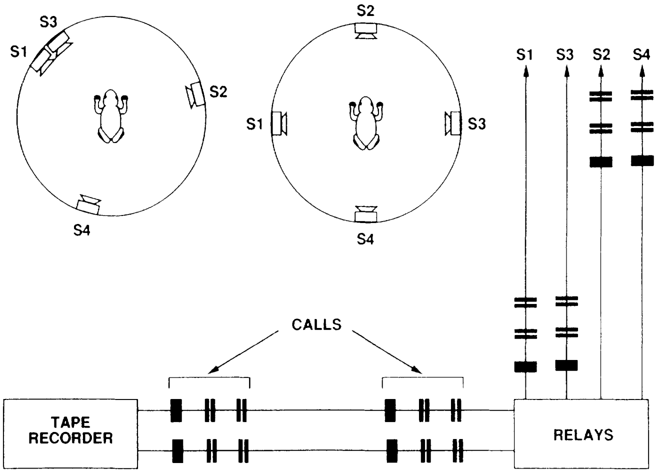


Fig. 3. Diagram of the equipment, female-choice arena and the speaker arrangements used in experiment F1 (*arena on left*) and experiment F2. For experiment F1, the *angular separations of speakers* of 5° vs. 120° are shown. Only degradatively interfering stimulus calls are illustrated

For all tests, the stimulus from each speaker was a three-note conspecific advertisement call broadcast at a rate of 10 calls/min. The stimuli were prepared by digitizing a call recorded at the field site at 26° C (Marantz PMD 360 stereo cassette tape recorder, Realistic 33-1062 unidirectional microphone) with an Amiga 2000 computer equipped with an Applied Visions FutureSound (TM) audio digitizer. The call was low-pass filtered (Krohn-Hite model 3550) at 8 kHz and digitized at 20 kHz. Stimulus tapes were prepared by playing this digitized call (low pass filtered at 8 kHz, World Precision Instruments LPF-30) from two channels using the Amiga 2000 and software written by the author.

Experiment F1. This experiment, consisting of four tests, was designed to assess the effect of angular separation of degradatively interfering sound sources on female phonotaxis. Degradatively interfering calls, broadcast by a pair of speakers, were timed relative to one another so that pulses were 180° out of phase (i.e., time-shifted by 50% of the pulse period). This had the effect of degrading the fine temporal structure within a signal produced by the addition of the two calls (Schwartz 1987a), and, to a human listener, the pulse rate of the calls appeared to have doubled. One pair of speakers had a large angular separation (120°) while the other pair of speakers had a smaller angular separation (either 5° in test A or 15° in test B; Fig. 3). The interfering calls from one pair of speakers (for example, speakers S1 and S3 in Fig. 3) were alternated with those broadcast from the other pair (S2 and S4 in Fig. 3). Playback intensities of calls at the release point of the females were 80 dB ± 1 dB (peak SPL; dB re 20 μPa). Two types of control test also were conducted. In the first control test (test C), to verify that degradation of the interfering calls could be detected by females, females were exposed to non-overlapped calls broadcast from a single speaker alternating with interfering calls broadcast from a pair of speakers separated by 5° (essentially adjacent). The single speaker was located 180° from the line bisecting the adjacent speakers. If, in test A or test B, discrimination by females occurred, then it could be due to a preference for the angular separation of the sound sources itself, rather than due to improved recognition of pulse structure in interfering calls. A preference for separated call sources has been demonstrated for *Hyperolius marmoratus* (Telford 1985). To test for this possibility in *H. microcephala*, females were exposed to calls from two pairs of speakers separated by 5 and 120°. However, in this second control test (test D), calls from each pair of speakers were timed so that their notes alternated (i.e., interdigitated) rather than interfered degradatively. Therefore, call overlap was 'nondegradative'.

Experiment F2. Experiment F2 was conducted to determine the effect of relative intensity on temporal degradation of interfering calls. Two sets of female-choice experiments were conducted using a design with four speakers equally spaced (90° separation) at the perimeter of the circular arena (arena on right in Fig. 3). In one set of tests (A and B), females were presented with three-note advertisement calls interfering degradatively with those broadcast from the speaker on the opposite side of the arena for one speaker-pair (for example, speakers S1 and S3 in Fig. 3). From the remaining speaker-pair (for example, speakers S2 and S4), calls were timed so that their notes alternated (not shown in Fig. 3) with those broadcast from the opposite side of the arena. The timing of the interfering and interdigitating calls was identical to the timing used in the main tests (A and B) and the second control test (D) of experiment F1. However, the intensity of broadcasts from one of the speakers giving interfering calls was to be lowered (in 3-dB steps in separate tests) until a level was reached at which discrimination in favor of the interdigitating calls failed to occur. Stimulus intensities of the interdigitating calls were equalized at 85 dB SPL (the intensity used in the related experiment of Schwartz 1987a). Intensities of calls timed to interfere degradatively were either 85 and 82 dB SPL (test A) or 85 and 79 dB SPL (test B).

The second set of tests of experiment F2 (C and D) were similar to the first set, except that all of the speakers broadcast calls that interfered with those from their opposite speaker (for example, calls from speaker S1 interfered with calls from speaker S3, and calls from speaker S2 interfered with calls from speaker S4 in Fig. 3). Broadcast intensity from one source was lowered until discrimination against the constant-intensity sources occurred. Therefore, the first and second sets of tests served as two approaches to testing the intensity difference at which out-of-phase overlap fails to degrade the pulse structure of an advertisement call. The stimulus intensities from three speakers were adjusted to 85 dB, and, in separate tests, the attenuated stimulus speaker was adjusted to broadcast at either 82 (test C) or 79 dB SPL (test D).

Test stimuli were played back during choice tests from a Marantz PMD 360 tape recorder. Four-speaker sound output was achieved by using a custom-built circuit containing call-triggered relays to switch the two-channel signal and ground lines from the Marantz tape recorder back and forth between the two pairs of speakers. Playback intensities for each speaker were regulated by separate 75-W Realistic L-pads (Radio Shack 1992 catalog number: 40–977) and were adjusted with a calibrated (Gen Rad 1562A) Gen Rad 1982 precision sound-level meter. During successive tests, I alternated either the relative positions of the widely separated and narrowly separated speakers (experiment F1) or the speaker intensity assignments (experiment F2).

Results

Natural group interactions

Four natural interactions of groups of males were monitored. Group 2 contained six males, group 3 five males, and groups 4 and 5 four males each. These groups were monitored for 10, 15, 20, and 45 min, respectively. The spatial distributions of males are shown in Fig. 4. Since adjustments of note timing are probably an adaptation of males to reduce interference, I examined the inter-note intervals of males when interrupted by other individual males in their chorus group. This is one way of revealing to which other males each individual attends, and with which he attempts to reduce interference, and so actively interacts. Data from group 2 and group 5 are summarized graphically in Figs. 5, 6. Group 2 was the largest assemblage with which I worked, and group 5 was monitored for the longest period of time. Except as described below for group 3, these data are qualitatively similar to those obtained during the other interactions. Each plot in these figures shows the durations of inter-note intervals for each frog when interrupted by only one other male in his group. The estimated sound intensities of interrupting calls at the position of the subject male are also shown.

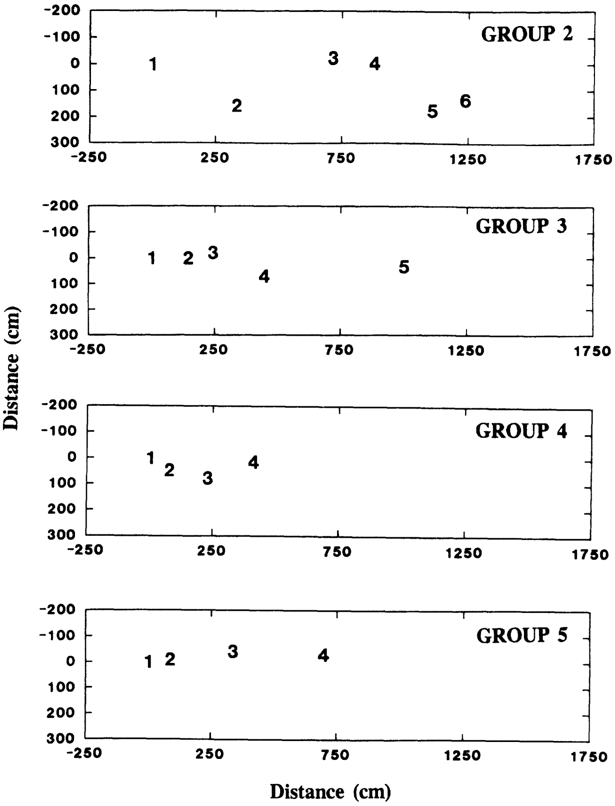


Fig. 4. The locations of males of *H. microcephala* in the four groups for which calling was monitored. The position of each frog, as seen from above the chorus, is plotted in cm relative to that of *male 1* (plotted at distance 0, 0) for each group

In general, males were most responsive to interruptions by males whose calls were loudest; these were usually, but not always, their closest neighbors in the chorus. For 12 of 14 males in three of the four groups, there was a significant effect of interrupting-call intensity on duration of inter-note intervals (Kruskal-Wallis test, $P < 0.05$). Notable exceptions to this pattern were the five males in group 3. In this group, there was no significant intensity effect. This result was not too surprising because in group 3 most instances of interruption were by males less than 500 cm from the responding male. Therefore, the range of sound intensity for vocal interruptions experienced by males in this group was smaller than that experienced by most other males in Groups 2, 4 and 5.

Another way to test for male responsiveness to interruptions is to compare the durations of inter-note intervals when males were interrupted to those when they were not interrupted. These latter, baseline durations are indicated by the dashed lines in Figs. 5, 6. Of the

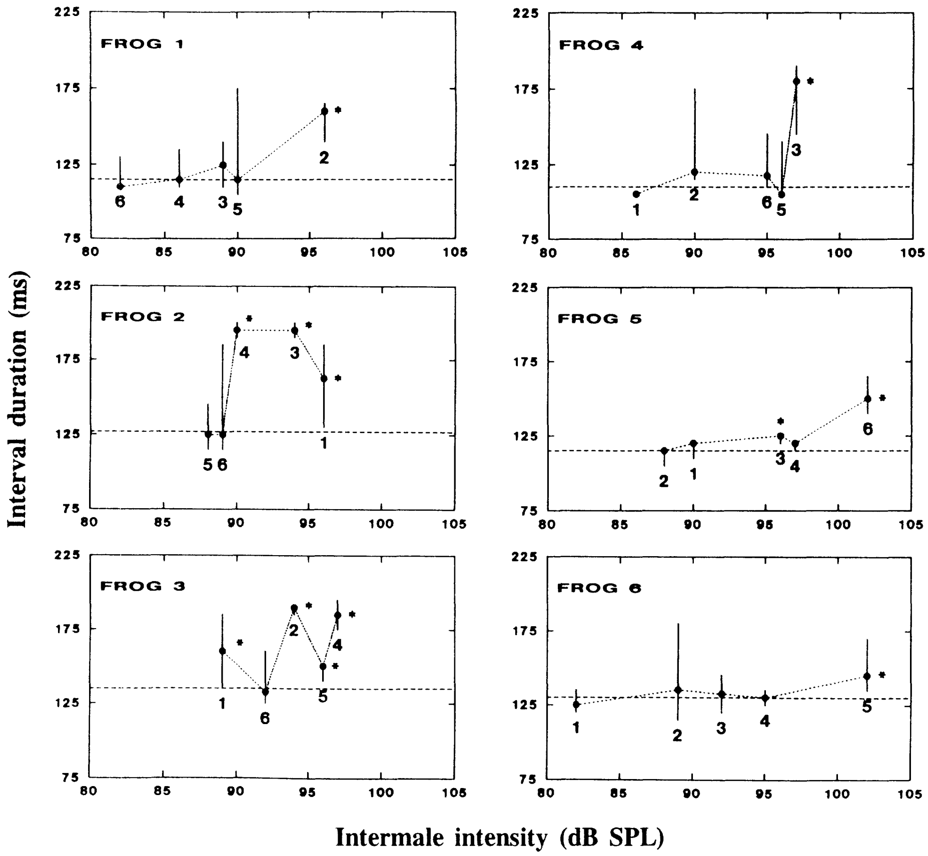


Fig. 5. Data from group 2. Durations of the interrupted inter-note intervals of each of six frogs when interrupted by one other frog at a time in his group. The interrupted 'subject' frog is indicated in the *upper left corner* of each box. The estimated sound intensity (peak, dB SPL) of the notes for each interrupting male at the position of the subject is shown along the *abscissa*. The interrupting male is indicated by the *number* below each median value and its approximate 95% confidence interval. An asterisk indicates that the durations of interrupted intervals were significantly greater ($P<0.05$, Wilcoxon 2-sample test) than the subject's uninterrupted intervals (median duration indicated by the *dashed line*). The 95% confidence interval around the median duration of uninterrupted intervals (not shown) was 5 ms or less for all frogs except male 1 (10 ms)

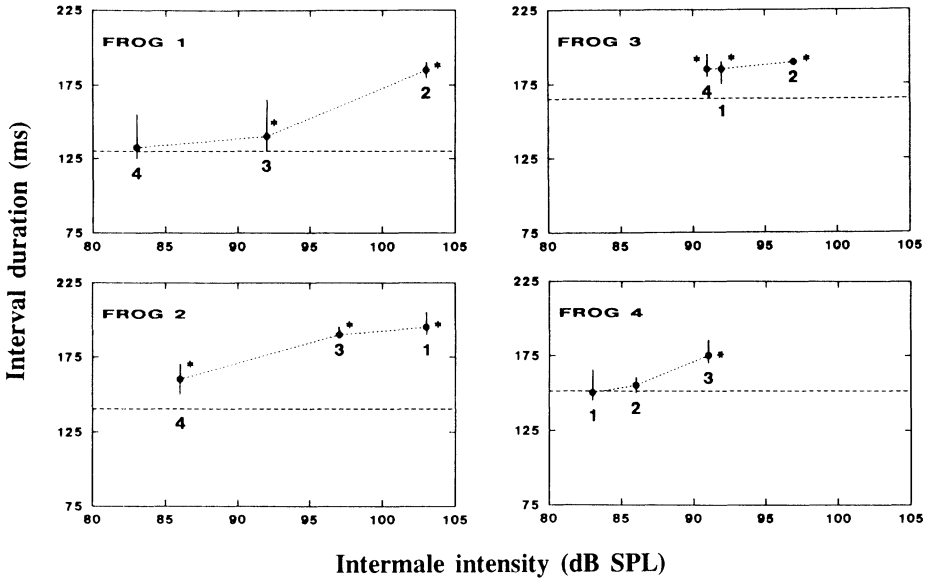


Fig. 6. Data from group 5. Durations of the interrupted inter-note intervals of each of four frogs when interrupted by one other frog at a time in his group. The frogs in this group are not the same individuals as those shown for group 2. See legend of Fig. 5 for details. The 95% confidence interval around the median duration of uninterrupted intervals (not shown) was 5 ms or less for all frogs

19 males 17 increased intervals in response to interruptions of their loudest neighbor, while only 4 of 19 responded significantly to those of their quietest neighbor (Wilcoxon 2-sample test, $P<0.05$). Because multiple comparisons were made, I also retested for significance ($\alpha=0.05$) using the sequential Bonferroni test advocated by Rice (1989). Using this procedure, both of these significance totals stayed the same.

In many instances, males failed to respond to interruptions that were certainly above their auditory thresholds, even given the presence of background noise in the study area. For example, in group 2, frog 4 did not respond to interruptions by male 5, although these were estimated to be only 1 dB below those of male 3. Frog 4 responded strongly to male 3, its closest neighbor (dB SPL=97). In only a small number of instances, males (1) responded to a more distant or less loud male while failing to respond significantly to a closer or louder individual (5/68 dyads), or (2) responded to the louder male that was not closer to him (1/68 dyads). Finally, males

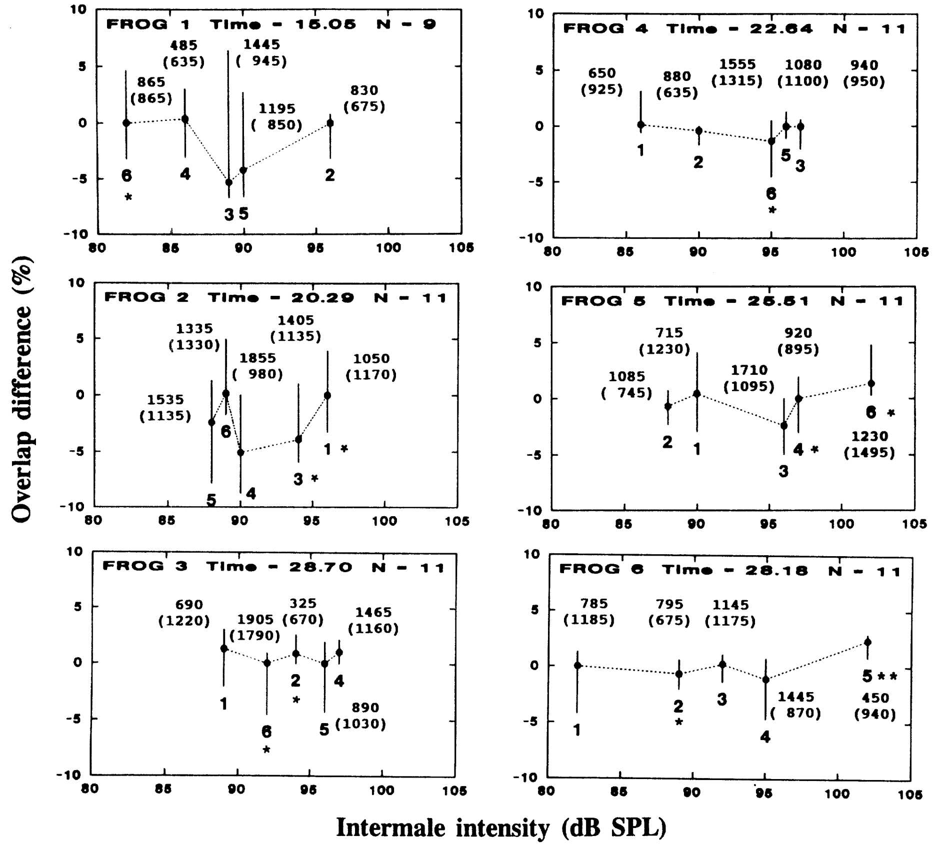


Fig. 7. Data from group 2. Differences in the expected and observed overlap between each of six frogs [*i*] and the other five frogs [*j*] in his group. The difference in overlap is shown as a percent of the calling time (per bout) of each male [*i*] (see text). This male is identified in the *upper left corner* of each box. The estimated sound intensity of the notes for each male [*j*] at the position of male [*i*] is shown along the *abscissa*. Males [*j*] are indicated *below each median value* and its approximate 95% CI. These medians are based on data from the number of calling bouts in which both male [*i*] and male [*j*] called. The number of *asterisks* near each number identifying a male [*j*] indicates the number of bouts in which the observed overlap was significantly less than expected. *Smaller numbers* printed near each median give the total observed and expected (in parentheses) overlap (ms) for each male [*i*] and male [*j*]. Also shown at the top of each box is the total calling time (s) of male [*i*], and the number bouts in which he called (*N*)

located at or near the edge of a group responded strongly to fewer males than did males more centrally located (in Group 2, compare responses of frogs 2 and 3 with frogs 1 and 6).

Actual levels of acoustic overlap between pairs of males within bouts for the four groups ranged from 0 to 100% of a male's calling time (time actually emitting sound); however, in most cases overlap was below 10% (group 2: median = 3.2%, range = 0–100%, $n = 320$; group 3: median = 4.7%, range = 0–85%, $n = 208$; group 4: median = 2.2%, range = 0 – 100%, $n = 312$; group 5: median = 2.1%, range = 0 – 63%, $n = 888$).

The total observed and expected overlaps between males summed for all the bouts monitored are printed on Fig. 7 for group 2 and Fig. 8 for group 5. Also shown is a measure of the difference between the observed and expected overlap. This 'overlap difference %' was calculated as follows:

$$\frac{100 \times (\text{Expected overlap } [\mathrm{i}]\ [\mathrm{j}] - \text{Observed overlap } [i]\ [j])}{(\text{calling time } [i])}$$

The measure was computed for each bout and plotted as a median within approximate 95% confidence intervals. It is clear from the figure that observed and expected overlaps usually differed by little relative to the total amount of time each frog called. In fact, significantly less overlap than expected occurred only 23 times out of 1728 pairwise comparisons (male pairs × bouts called per male × chorus groups).

Another way of assessing the level of acoustic interference is to consider the percentage of time that a male called when no other frog in his chorus group called. This unobstructed calling time ranged from 33.5% to 91.6% when calculated over the entire monitoring period (Fig. 9). With only one exception (group 3, frog 3, two males removed), interference was reduced when group size was decreased. When two frogs were removed from group 4, unobstructed calling time increased from 71% to 97% and from 79% to 98% for the two remaining males. When two frogs were removed from group 3, the changes were 34% to 63%, 54% to 74%, and 67% to 97%. Observed relative to expected levels of overlap for pairs of males decreased in response to these group-size manipulations. In group 3, this decrease was significant for three of six pairwise interactions of the three remaining males; in group 4 this decrease was sig-

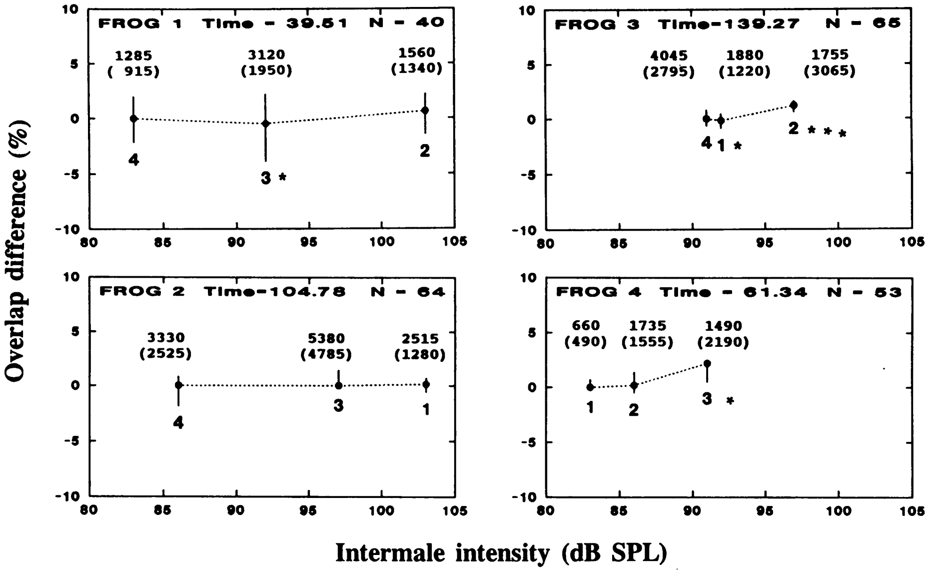


Fig. 8. Data from group 5. Differences in the expected and observed overlap between each of four frogs [*i*] and the other three frogs [*j*] in his group. See legend of Fig. 7 for details

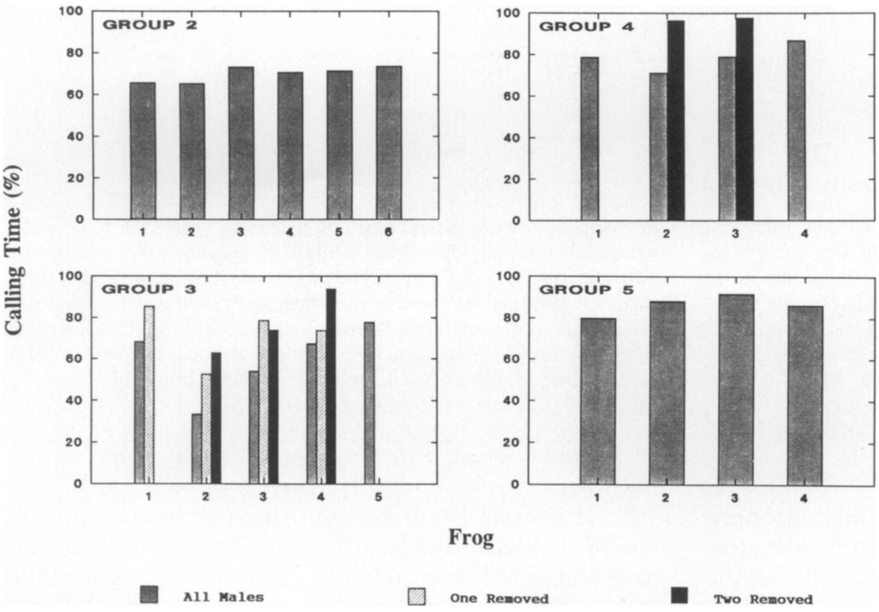


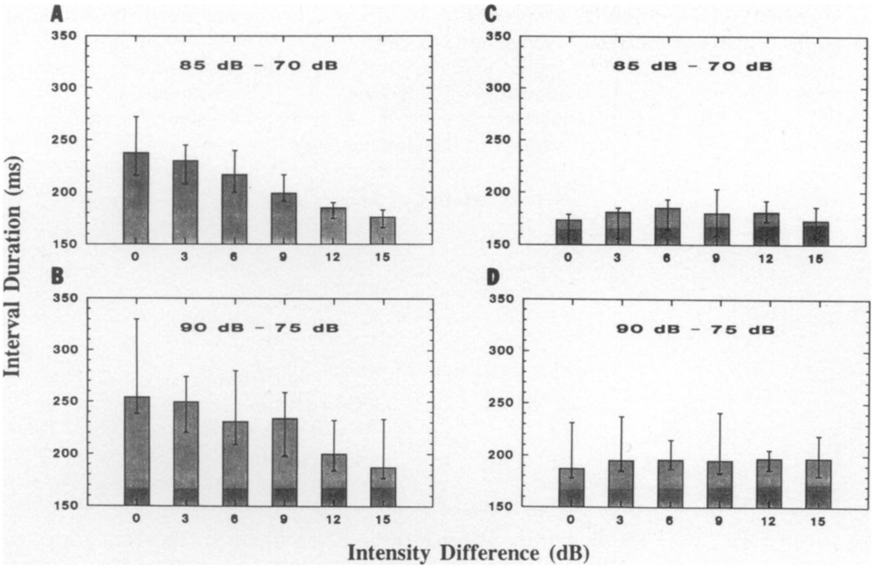
Fig. 9. The percent of each male's total calling time that was unobstructed by any other frog in his group. For group 3 and group 4, histogram *columns* with different fills indicate this percent for the males remaining following size reductions of each group (see text). In group 3, male 5 was first removed and subsequently male 4 was removed. In group 4, males 1 and 4 were removed

nificant for one of two interactions of the two remaining males ($P < 0.05$; *G*-test).

Playback tests

Experiment M1: 60/200 ms interruptions. The average of the inter-note intervals during stimulus broadcasts and the percentage of times that the stimulus overlapped the following note of each subject were calculated for each frog and treatment. The results supported the prediction that males would reduce their responsiveness to the longer note as its intensity decreased and eventually time their response notes so as to avoid interference with only the shorter 60-ms interruption. At both high (60-ms note at 90 dB) and low (60-ms note at 85 dB SPL) stimulus intensities, the intensity difference between the 60-ms note and the 200-ms note had a significant effect on male inter-note interval durations. Inter-note intervals were longer (Kruskal-Wallis test, $P < 0.01$), and acoustic interference with the 200 ms component of the interruption was reduced (Kruskal-Wallis test, $P < 0.03$), as this intensity difference became less pronounced (Fig. 10A, B). As the intensity difference increased, the change from longer to shorter intervals was fairly smooth rather than abrupt. Median interval durations were greater when the 60-ms stimulus was presented at 90 dB SPL than at 85 dB SPL at all intensity differences, and significantly so at differences of 9, 12, and 15 dB SPL (Wilcoxon 2-sample test, $P < 0.05$).

Experiment M2: interrupting three-note calls. In contrast to their behavior during the previous experiment, males did not change inter-note intervals in response to



Figs. 10. A, B Durations of inter-note intervals, within calls of males, given in response to overlapping interruptions of 60 and 200 ms. The range in broadcast intensity (peak dB SPL) of the 200 ms stimulus is given within each *bar graph*. The 60-ms stimulus was broadcast at the greatest intensity (85 or 90 dB). Data are presented as medians (+/− approximate 95% CI). The difference in relative intensity between the 60- and 200-ms stimulus is shown along the abscissa. *A*, $n=15$ males; *B*, $n=8$ males. **C, D** Durations of inter-note intervals, within calls of males, given in response to interruptions by the two three-note stimulus calls. The intensity difference between the first and second stimulus call is shown along the *abscissa*. *C*, $n=9$ males; *D*, $n=11$ males

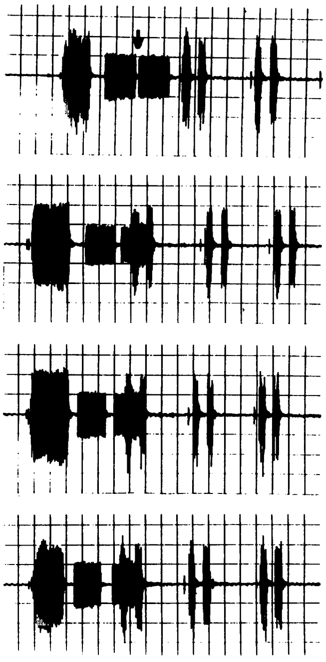


Fig. 11. Oscillograms showing responses of a male of *H. microcephala* to the presentation of interrupting 200-ms stimuli with gaps of 10, 20, 30, and 40 ms (*top to bottom*). Note that for all interruptions except that with the 10-ms gap (*arrow*), the male overlapped the stimulus with the second note of his call. Each *time division* equals 50 ms

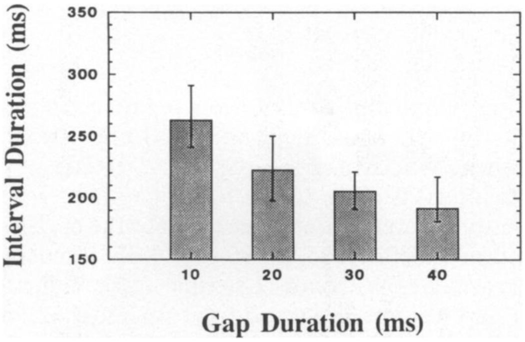


Fig. 12. Durations of inter-note interval of males ($n=12$) in response to an interrupting 200-ms stimulus with gaps of 10, 20, 30 and 40 ms. Stimuli were broadcast at 85 or 90 dB (peak SPL). Data are presented as medians (+/− approximate 95% CI)

changes in the relative intensities of the two stimulus calls. Males responded as if interrupted by a single note, rather than a much longer stimulus, and they usually overlapped the first note of the second three-note stimulus call (Fig. 2B). Responses were similar at both high (first call at 90 dB SPL) and low (first call at 85 dB SPL) intensities (Fig. 10C, D). One important difference between the stimuli used in this and the previous experiment was the presence of brief quiet gaps (30 ms) between the alternating notes of the former. To investigate whether these gaps might account for the different response to the three-note interruptions, I performed the experiment using gap stimuli.

Experiment M3: gap stimuli. When males were interrupted by 200-ms synthetic calls incorporating gaps of 10–40 ms (Fig. 11), stimulus intensity (85 or 90 dB SPL) had no significant effect on interval duration (Wilcoxon 2-sample test, $P>0.4$). Therefore, data for broadcasts at these intensities were pooled. Gap duration had a significant effect on male inter-note interval duration (Kruskal-Wallis test, $P<0.001$). Males had shorter inter-note intervals when interrupted by notes with longer gaps than when interrupted by notes with shorter gaps (Figs. 11 and 12). Moreover, at 85 and 90 dB SPL, the durations of intervals in response to the 40-ms gap note were similar to those given to the three-note interrup-

Table 1. Responses of females to three-note advertisement calls broadcast from speakers with different angular separations (experiment F1)

Test	Angle of separation of speakers Number of females choosing:		Number tested	*P*
	Degradative interference			
A	5°	120°		
	7	13	27	NS
B	15°	120°		
	5	4	9	NS
C	Single speaker	5°		
	10	1	15	0.012
	Nondegradative overlap			
D	5°	120°		
	9	9	22	NS

NS = not significant at 0.05 level; P = probability (two-tailed binomial)

Table 2. Responses of females to advertisement calls broadcast at different intensities (experiment F2)

Test	Intensities of broadcasts Number of females choosing:		Number tested	*P*
	Nondegradative	Degradative		
A	85–85 dB	85–82 dB		
	24	3 2	38	a: 0.036
B	85–85 dB	85–79 dB		
	15	8 0	28	a: NS
	Degradative interference – all speakers			
C	85–85 dB	85–82 dB		
	10	7 3	22	b: NS
D	85–85 dB	85–79 dB		
	0	9 0	10	c: <0.001

The intensities of broadcasts for each pair of speakers are given in dB SPL (peak). NS = not significant; P = probability (a: two-tailed binomial test using 50% of the number approaching both 85 dB nondegradative speakers, and the total number approaching the single 85 dB degradative speaker, b: χ^2 test assuming equal probabilities of approach to the speakers, c: χ^2 test under the conservative assumption that no females would approach the speaker broadcasting at 79 dB)

tions, differing significantly only for one relative intensity treatment (first three-note call at 85 dB and second call 15 dB down; Wilcoxon 2-sample test, $P < 0.05$).

Inter-note intervals given to the 10-ms gap note were not significantly different from those given to the 60/200-ms interruption at either 85 or 90 dB (0 dB intensity difference treatment; Wilcoxon 2-sample test), indicating that the gap was probably too brief for most males to respond to. However, inter-note intervals in response to stimuli with gaps greater than 10 ms long were significantly shorter than those given to the 60/200-ms interruptions at 90 dB (0 dB intensity difference treatment). At 85 dB, intervals were significantly shorter only in response to notes with gaps of 30 or 40 ms.

Tests with females

Experiment F1. If directional information on calling males can enhance substantially the ability of females of *H. microcephala* to extract pulse rate information from interfering calls, then large angular separations between speakers broadcasting such calls should have resulted in significant discrimination in Experiment F1. However, although there was a bias in the results for the 120° separation, females failed to demonstrate discrimination between the interfering sound sources of large and small angular separation (two-tailed binomial test; Table 1 A, B). The first control test (Table 1 C) demonstrated significant degradation of the pulse pattern in the overlapped calls. The second control test (Table 1 D) indicated that there was no inherent preference by females for widely spaced relative to narrowly spaced sound sources, in the absence of degradative call interference.

Experiment F2. In this experiment, it was necessary to use just two relative intensities for call broadcasts. A reduction in the relative sound intensity of an interfering sound source by 6 dB was sufficient to eliminate female phonotaxis in favor of calls timed to overlap in a nondegradative fashion (Table 2B). However, a reduction of only 3 dB SPL was insufficient to do so (Table 2A). The second set of tests also demonstrated that degradative interference is ameliorated when one sound source is attenuated by 6 dB SPL (Table 2D). Females discriminated against the overlapped calls of equal intensity in favor of the 85–79 dB SPL overlapped calls. However, discrimination was not demonstrated when the difference in intensity of interfering calls was only 3 dB SPL (Table 2C).

Discussion

Unlike previous research on males of *H. microcephala* (Schwartz 1991; Schwartz and Wells 1985), this study indicates the true magnitude of acoustic interference in choruses and the role of acoustic complexity in eliciting adjustments in the timing of notes by males. Therefore, the study demonstrates the utility of using a recording system capable of simultaneously monitoring the vocal activity of more than two members of an anuran assemblage. The behavior of females observed during the phonotaxis experiments indicates that details of chorusing behavior should enhance a male's ability to attract a mate.

Average levels of acoustic overlap among pairs of male *H. microcephala* in choruses of six or fewer individuals are low. This pattern of low interference is probably not a result of the adjustments of call timing that males make with respect to calls of another male. The randomized data sets indicated that three were few instances in which observed overlap was significantly less than expected. Rather, overlap levels may be low because the amount of time when a male is emitting sound (the calling time) is small relative to the time when he is not, even during a calling bout (Schwartz and Wells 1985). For example, the duty cycle of a three-note call is approximately 50%; i.e., nearly half of the call is devoted to intervals between the notes. Inter-call intervals also are large relative to call durations. Even if a male is calling at a rate of 6000 notes/h, giving an average of three notes per call, approximately 75% of the total advertisement time (calling time + inter-note intervals + inter-call intervals) will consist of inter-call intervals. Assuming that there are no constraints on call timing, the expected overlap between two males giving three-note calls will be less than 2% of each male's calling time.

Because calls do not occur randomly in time, and males have short latency responses to one another (Schwartz and Wells 1985), interference levels between pairs of individuals are often higher than the estimate of 2%. Moreover, in assemblages of more than two males, individuals may simultaneously respond to the call of another male and so acoustically interfere. While it is impossible to determine whether such responses are the true cause of particular instances of call overlap, I observed potential cases when scanning the bit patterns in the primary data files. Cases of overlap that may be explained by simultaneous responses of males have been reported for other species of frogs (Arak 1983; Foster 1967; Schneider et al. 1988). Schneider et al. (1988) also found that overlap levels rose dramatically in aggregations of three and four males of the leptodactylid *Adenomera hyladactyla* compared with those observed during duets. Clearly, avoiding acoustic interference is more difficult for males in large choruses than males in small choruses. An enhanced interference problem was reflected in the changes in unobstructed calling time in the two groups of *H. microcephala* in which I manipulated numbers of males (Fig. 9). The results of this experiment suggest that males could enhance their signalling effectiveness by spacing out in large aggregations. Intermale spacing could be particularly important in areas like those along the Chagres River in Gamboa where hundreds of *H. microcephala* call from floating and emergent vegetation (personal observations).

If call overlap occurs, then males can adjust the timing of notes to reduce or avoid interference. Note timing may account for the similarity in shapes of the plots of interval durations (Fig. 5, 6) and overlap difference (Fig. 7, 8) for some males (group 2: males 5 and 6; group 5: males 3 and 4). My data indicate that males respond most strongly to interruptions by their loudest, and usually nearest, neighbors. This response behavior was observed when subjects were interrupted by the 60-ms and 200-ms stimulus calls simulating overlapping males at different distances (Fig. 10). There were gradual decreases in the durations of the subjects' inter-note intervals as the relative intensity of the 200-ms stimulus was reduced. For intensity differences of 15 dB SPL, most adjustments in timing of notes accommodated only the 60-ms interruption. Masking of the 200-ms interruption by the background noise of the chorus may have contributed to the lower responsiveness when the difference in intensity was large. However, the intensity of interruption, per se, may also partially account for the observed pattern. Median durations of inter-note intervals, for all intensity differences (0–15 dB SPL), were slightly longer when the peak stimulus intensity was 90 dB than when it was 85 dB (Fig. 10). Because I worked with subjects that were well separated from other calling frogs, it is unlikely that masking can explain this result when the intensity difference was small. Nevertheless, my interpretation can be conclusively supported only by testing males in an environment acoustically isolated from background noise.

During separate instances of interruption, a number of individuals adjusted their inter-note intervals in response to more than one male in their group (Fig. 5, 6). These males were typically those with others on both sides of them, and they responded well to louder calls. It is noteworthy, however, that many individuals exhibited significant shifts in note timing only in response to their loudest neighbor. This pattern of calling was most often the case for males at the edge of an aggregation. These data also are inconsistent with an explanation entirely based on masking of less intense interruptions. Whether the restricted responses of some males to only their loudest neighbor are related to the well-known phenomenon of temporary hearing threshold shift (Moore 1982; Zelick and Narins 1985a) is unknown. Interestingly, Rose and Brenowitz (1991) have reported that the lowest amplitude of advertisement calls that would elicit aggressive calls from male Pacific treefrogs, *Hyla regilla*, (the 'aggressive threshold') increased with the maximum amplitude of the calls of their nearest neighbors in the chorus.

Competition among males for females is intense in *H. microcephala* choruses; operational sex ratios on most nights are biased heavily towards males (personal observations). One manifestation of this competition is that males add secondary notes to their calls in response to the calls of other males (Schwartz and Wells 1985). Based on results of female-choice experiments (Schwartz 1986), this behavior should enhance the relative attractiveness of any given male. If the calls of two males overlap in time, the males may alternate their notes, and so avoid or reduce acoustic interference. Any reduction in signal degradation improves a male's chances of attracting a female who may be listening nearby (Schwartz 1987a). In addition, note alternation should enhance the ability of each male to detect the other's notes (Narins 1992a; Schwartz 1987a; Schwartz and Rand 1991) and so may result in the production of longer multi-note calls. However, for two frogs to alternate notes effectively, each male must be able to respond very rapidly to the brief reductions in background sound intensity which occur after the end of each note of the other male. This requirement is evidently why males failed to increase their inter-note intervals in response to the broadcasts of interrupting interdigitating three-note calls. The reductions in sound level accompanying the brief gap between the first two notes of the stimulus elicited a more rapid vocal response from the subject; i.e., the subject's second note was delivered sooner than it otherwise would have been. The playback experiment using gap stimuli supports this explanation and indicates that males can detect gaps at least as brief as 20 ms.

The degree of sensitivity of males of *H. microcephala* to gaps in synthetic notes falls within the range of gap detection thresholds determined in other vertebrates (Fay 1985; Klump 1991) and is not surprising based on levels of temporal resolution measured in another anuran species, *Eleutherodactylus coqui* (Narins 1992b). Dunia and Narins (1989) obtained minimum integration times for fibers in the peripheral auditory system ranging from 0.17 to 2.9 ms. These data indicate that some neurons can encode the presence of discrete sounds separated in time by less than 1 ms. However, the neurophysiological study (Dunia and Narins 1989) employed a different experimental paradigm than that used in my study and may be most relevant to discussions of auditory system encoding of pulse or amplitude modulation rate. Therefore, a more appropriate comparison to make is between my data and those obtained by Zelick and Narins (1985b) in a playback experiment. Zelick and Narins showed that males of *E. coqui* were able to place their calls in pseudorandomly timed 750-ms quiet gaps between tone bursts. To accomplish this, males would need to detect gaps as brief as a few tens of milliseconds. It would be particularly interesting to learn whether males of *E. coqui* are more responsive to gaps than are males of *H. microcephala* because the former use tonal rather than amplitude-modulated calls (Narins and Capranica 1978). The interpulse interval of the advertisement call of *H. microcephala* (approximately 2 ms) probably sets a lower bound on the gap duration that triggers a vocal response. Otherwise, gaps between pulses would elicit vocal responses. In light of the putative roles of refractory periods and phases of excitation and inhibition in call timing behavior of frogs (Klump and Gerhardt 1992; Moore et al. 1989; Narins 1982), it would be interersting also to investigate how shifting the position of a gap in an interrupting stimulus influences note delay of males of *H. microcephala*.

The results of the computer interruptions suggest that the ability of males of *H. microcephala* to adjust rapidly the timing of notes is an adaptation to facilitate note alternation with a single neighbor. As experiment M2 demonstrated, because males respond vocally to reductions in sound intensity following each interrupting note of another frog, males are not effective in reducing acoustic interference with any additional males that also may be alternating their notes with this neighbor. Essentially, in order to achieve precise note alternation, males must suffer some acoustic interference with other males calling at the same time. The data from this study also suggest why calling males of *H. microcephala* are stimulated to call, rather than inhibited from calling, by natural or simulated background noise of a chorus (Schwartz 1991). The rapid fluctuations and brief quiet gaps in background sound intensity could disrupt inhibition of note production that may be operating in the male's nervous system. Together, the data from the natural interactions and the playback tests demonstrate that males of *H. microcephala* change note timing in response to interruptions by a subset of males in the chorus. Therefore, males actively avoid acoustic interference with those individuals most able to seriously degrade the temporal structure of their calls. My data are consistent with those of Brush and Narins (1989), which showed that males of *E. coqui* only avoid overlap with, at most, a few individuals.

The results of the female-choice experiment F2 demonstrate that females of *H. microcephala* only show discrimination against out-of-phase overlapped calls (i.e., interference is degradative) if these calls are similar in intensities. If the difference in call intensities at her position is 3 dB or less, then a female approaches non-overlapping calls. If the difference in call intensities is 6 dB (or, presumably, greater), then females do not demonstrate discrimination against the louder overlapping calls. Obviously, the relative sound intensities of the calls of different males change as a female moves in or near the chorus (Forrest and Green 1991). Assuming that a female's responses to overlapped calls over a range of audible sound amplitudes are consistent with my empirical results at 85 dB, then males should delay the production of subsequent notes in response to interruptions by males less than twice as far from a female as they are themselves. This is a conservative prediction and assumes: (1) that interfering calls which differ by 3–6 dB in intensities at the female's position will also be discriminated against (relative to calls which do not interfere); and (2) there is a reduction of 6 dB in call intensity for each doubling of the distance between an emitting male and a receiving female, in accord with the inverse distance law for the spherical spread of sound. However, until a female moves very close to him, a male frog has no way of determining where she is sitting. Therefore the relative sound intensities of his and other males' calls at her position are also 'unknown' to him. Given this unavoidable ambiguity, based on the results of the female-choice tests, a male should shift his note timing so as to reduce overlap with the notes of his louder neighbors. As demonstrated by the data from the natural interactions, this is what a male *H. microcephala* does. In a large aggregation, avoiding interference with more than those males in his immediate vicinity may not significantly improve his ability to attract a mate.

The data from experiment F1 demonstrated that an angular separation of 120° for males equidistant from a female does not appreciably influence the selectivity of her response to degradatively overlapped calls. Therefore, the contribution of directional cues to discrimination (as indicated by phonotaxis), if they exist, must be small, and below the limit of resolution of my experimental paradigm. In fact, results of experiment F1 indicate the contribution is probably less than 6 dB. This result is not surprising given the magnitudes of estimates of directionality of the anuran peripheral auditory system as well as results of phonotaxis experiments using other species. There have been only two published reports on directionality using data obtained from awake frogs (Jorgensen et al. 1991; Michelsen et al. 1986). The data of Michelson et al. (1986) on monaural directional sensitivity in *Hyla cinerea* indicated an expected difference in tympanic vibration velocity for tones broadcast at positions separated by 120° of approximately 7–8 dB (see their Fig. 2). The interaural vibration amplitude difference (the vibration amplitude of the left eardrum minus that of the right eardrum) was approximately 16 dB in *E. coqui* (angle of sound incidence = 120°; at the frequency of maximum effect with the frog's glottis closed; Jorgensen et al. 1991). Females of both *H. cinerea* and *E. coqui* [approximate snout-vent length (SVL) = 50 mm] are considerably larger than female *H. microcephala* (SVL = 25 mm) and males use vocalizations of lower frequencies than *H. microcephala* (Gerhardt 1978; Narins and Capranica 1978; Schwartz and Wells 1985). In a behavioral study of *H. cinerea*, Schwartz and Gerhardt (1989) estimated the improvement in signal-to-noise ratio accompanying the separation by 90° of a call and a broadband noise source to be 3 dB or less. While this improvement was sufficient to improve the detectability of calls and so facilitate a release from auditory masking in females, it was insufficient for call discrimination of the unmodulated advertisement calls and the amplitude modulated aggressive calls. Gerhardt (1978) has shown that in *H. cinerea* females fail to demonstrate discrimination between synthetic aggressive calls which differ in depths of amplitude modulation by less than about 40%. This percentage is equivalent to a 4.4 dB difference in experiment F2.

In summary, directional cues are probably insufficient to provide females with the necessary improvement in signal-to-noise ratio to extract an undegraded pulse rate from interfering calls of males *equidistant* from her. However, if the directionality of the auditory system of *H. microcephala* is similar to that of *H. cinerea*, then the negative effects of overlap of calls among males at *different* distances from the female conceivably could be eliminated by large angular separation of males. In this regard, it would be particularly interesting to directly measure the directionality characteristics of the auditory periphery of *H. microcephala.*

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Appendix

A. The computer was powered in the field by a custom-built rechargeable battery pack, which provided 150 volts d.c. and supplied current to the switching regulator of the Amiga. A small liquid crystal display television (Realistic model 16–165) was used as a monitor. The interface board, in a small plastic case, accepts up to eight microphone inputs, and the output of the broad is sent to the computer via the parallel port. The board has eight parallel channels, each consisting of an amplifier section, a voltage comparator, and a retriggerable monostable multivibrator (SK4098B). The output for each channel of the board undergoes a votal transition, of preset duration, in response to above threshold input from a microphone. This threshold level is set manually by using separate gain controls for each channel and each of eight LEDs.

The outputs of the board's eight channels were sampled at a rate of 200 Hz from the eight data lines of the computer's parallel port. Thus, for the duration of a note of a calling frog, the output from the monostable multivibrator was low, and each sample taken by the computer recorded a zero for the data bit corresponding to that frog. The specific frogs that were calling, or not calling, at a particular time were recorded as the pattern of zeros and ones in a byte (eight bits) of data.

B. The core of the playback system was identical to that described above, except that an eight-bit sound digitizer (Applied Visions FutureSound) was attached to the parallel port of the Amiga 500 computer. The digitizer was used to monitor each subject while different programs were executed. Acoustic stimuli were delivered to frogs using the two audio outputs of the Amiga 500. Signals were introduced into one channel of a Marantz PMD 360 stereo cassette tape recorder, amplified, and then broadcast from a distance of 1 m to the subjects by using a University 4401 horn speaker mounted in a wooden baffle (dimensions: 14 × 24 cm) and supported by a tripod (elevation: 50–75 cm). The frogs' responses were recorded by using the second channel of the tape recorder and a Realistic 33–1062 directional microphone. The output of the microphone was divided by a Y-cord, and two signals were individually fed into the Marantz tape recorder and into the sound digitizer.

Before testing began, the gain on the digitizer was adjusted so that peak digitized voltage values of amplified calls were approximately the same for all subjects; in this way variations in the computer-based timing of both the subject's call notes and the call-triggered stimuli were minimized. Trigger thresholds were then entered in the computer program; these values were the same for all frogs. To prevent calls of other frogs, or the stimulus output, from triggering a response from the computer, the microphone was positioned as close as possible to each male and pointing away from the speaker. A software routine was used to check that the peak values of the digitized outputs of the speaker were below trigger thresholds. If not, the microphone was repositioned.

Stimulus intensities for the interruption experiments (peak sound pressure level; dB SPL re 20 μPa) were predetermined at 1 m with a Gen Rad 1982 precision sound-level meter set for flat weighting and a Realistic sound-level meter (Radio Shack 1992 catalog number: 33–2050) set for C-weighting and fast response. Only the second meter was available for field use. The voltage level of a 2 kHz calibration sine wave stored in the memory of the computer and measured at the 8-ohm speaker output of the Marantz recorder was also predetermined for each stimulus-intensity combination. In the field, a Micronta pocket digital multimeter (model: 22–171) was used to adjust the output voltage during playback of this tone for each desired stimulus intensity level. This proved to be a covenient and accurate method of setting the intensities of the acoustic stimuli. Following the tests, the stimulus intensity was directly measured at the frog's position by using the Realistic sound-level meter. No male was tested on more than one night.