Neighbor Call Amplitude Influences Aggressive Behavior and Intermale Spacing in Choruses of the Pacific Treefrog...

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Neighbor Call Amplitude Influences Aggressive Behavior and Intermale Spacing in Choruses of the Pacific Treefrog (*Hyla regilla*)

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Abstract

Male Pacific treefrogs (*Hyla regilla*) aggregate in choruses during the breeding season. Within these choruses frogs distribute themselves nonrandomly. This study tested the hypothesis that the amplitude of neighbors' calls serves as a proximate cue in regulating the spacing of males in choruses, and that this is mediated by the incidence of aggressive-encounter calls by resident males. The amplitude of neighbors' calls showed little interindividual variation. Advertisement calls were played to males at three amplitudes that spanned the range of neighbor-call amplitudes measured between pairs of frogs. At playback amplitudes corresponding to the minimum neighbor-call amplitudes observed in choruses, frogs gave predominantly advertisement calls and few aggressive-encounter calls in response. As the playback amplitude was increased, subjects progressively decreased the number of advertisement calls and increased the number of encounter calls that they produced in response. The total number of calls (advertisement + encounter) given in response did not vary with playback amplitude. Intruders were likely to move away when a resident male gave encounter calls. In this way neighbor-call amplitude regulates intermale spacing in choruses.

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Introduction

In many species of anuran amphibians that adopt a 'prolonged breeder' strategy (Wells 1977), males form stable aggregations each night and produce species-specific advertisement calls. Conspecific females are attracted to these choruses and mates are chosen from within the aggregation (Wells 1977; Gerhardt 1982, 1983; Gerhardt et al. 1987). On any given night there is intense

competition among chorusing males to attract females. Within a chorus, a male's immediate neighbors pose the greatest threat to his ability to attract a female; they may mask his calls with their own, or physically intercept approaching females. The spatial distribution of males within choruses is influenced by these potential costs and has an important influence on mating success.

Studies of two frog species (*Hyla regilla*, WHITNEY & KREBS 1975a; AWBREY 1978; *Eleutherodactylus diastema*, WILCZYNSKI & BRENOWITZ 1988) demonstrated that males space nonrandomly in choruses. For a spacing strategy to be effective, males must be able to judge reliably the distance to neighboring frogs. Previous studies suggested that the amplitude of neighboring frogs' calls serves as a cue for spacing within choruses of different species. In the spring peeper (*Hyla crucifer*) males position themselves so that the amplitude of their immediate neighbors' calls falls at a level that coincides with their peripheral neural auditory thresholds for sound frequencies in the call (BRENOWITZ et al. 1984; WILCZYNSKI et al. 1984). In a neotropical frog, *E. diastema*, there is great consistency in the amplitude of neighboring frog calls at a focal male's position, despite extreme variation in intermale distance (WILCZYNSKI & BRENOWITZ 1988). These studies did not directly demonstrate, however, the behavioral mechanism by which neighbor-call amplitude mediates intermale spacing. The present study addressed this question in choruses of the Pacific treefrog (*Hyla regilla*).

Hyla regilla occurs abundantly throughout the western region of North America. Males form stable choruses in ponds over two months or more during the spring (SCHAUB & LARSEN 1978). Within choruses males generally call at or near water level, using emergent vegetation or floating debris as perches. Suitable perches do not appear to be a limited resource. Unlike other hylids, *H. regilla* males do not commonly call from elevated perches. Typical intermale distances observed are on the order of 75 cm (WHITNEY & KREBS 1975a; AWBREY 1978).

Male Pacific treefrogs have two general classes of calls. These are advertisement calls and encounter calls (see Fig. 1). Advertisement calls are those most commonly heard from males in stable choruses. Advertisement calls are of two distinct types; diphasic and monophasic (ALLAN 1973). Both calls are pulsatile (ca. 100—150 pulses/s) and contain dominant energy at about 2.0 kHz, with a fundamental at about 1.0 kHz. They differ in gross temporal structure. The advertisement calls attract females to choruses (WHITNEY & KREBS 1975b; pers. obs.). Furthermore, WHITNEY & KREBS (1975a) found that placing male frogs into enclosures in which advertisement calls were played over loudspeakers inhibited calling by these frogs.

The encounter call (equivalent to "trill" of ALLAN 1973) has the same dominant spectral structure as the advertisement calls, but a much slower pulse repetition rate (ca. 50 pulses/s; see Fig. 1). This call seems to be limited to use in agonistic contexts. It is most commonly heard in early evening when males first enter the chorus and are spacing apart from each other (ALLAN 1973; pers. obs.). Males switch from producing the advertisement call to the encounter call when another frog approaches closer than about 20—50 cm (AWBREY 1978; WHITNEY 1980). ALLAN (1973) observed that intruders are likely to move away when a resident male gives an encounter call. WHITNEY (1980) also found that frogs were
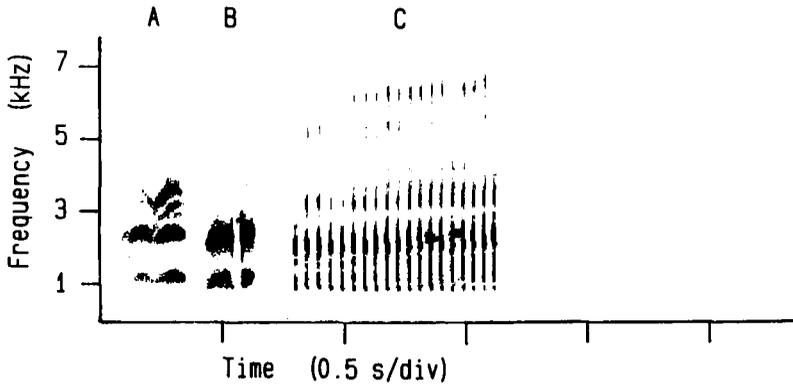
Fig. 1: Wide-band sound spectrograms (temporal resolution = 3.3 ms) of monophasic advertisement call (A), diphasic advertisement call (B), and aggressive-encounter call (C) produced by male *Hyla regilla*. These calls were recorded at an air temperature of 10 °C and a water temperature of 11 °C

more likely to respond with attack or "submission" to playback of encounter calls than they were to playback of advertisement calls. These results suggest that the encounter call communicates aggressive motivation of a resident male to intruding frogs.

The above studies of calling behavior in *H. regilla* suggested that vocalizations play a role in establishing and maintaining intermale spacing in choruses. These results did not indicate, however, what signal characteristics are important in the context of spacing. The present study tested the hypothesis that neighbor-call amplitude is important for intermale spacing in choruses of *H. regilla* (AWBREY 1978). To test this hypothesis I measured the incidence of encounter calling by individual resident frogs as an assay of aggressive motivation in response to playbacks of advertisement calls at different amplitudes. Comparison of effective playback amplitudes to neighbor-call amplitudes observed in choruses supports the conclusion that intermale call amplitude plays a fundamental role in the behavioral mediation of interfrog spacing.

Methods

The present studies were conducted from April 6 to May 14, 1988. Populations of male *Hyla regilla* in two ponds located in Discovery Park in Seattle, Washington were observed. The ponds were separated by about 50 m. At least 50 males called from each pond on any given night. Males in both ponds called from water level on emergent vegetation or floating debris.

Call Amplitudes

The maximum root-mean-square call amplitudes of 20 frogs were measured with a Bruel & Kjaer 2230 digital precision sound-level meter (fast setting). Amplitudes were measured using the "A" weighting scale to reduce the masking effects of low-frequency wind noise. This weighting does not interfere with the measurement of call amplitude because energy in the call only occurs at or above 1000 Hz. Measurements were made 50 cm from the frog with the microphone held level with its head

and pointing toward it. The meter was calibrated before and after each measuring session with a Bruel & Kjaer 4230 sound calibrator. 10 to 25 calls were measured for each frog. Readings were taken only after the vocal sac was fully inflated.

Neighbor-call Amplitudes

Pairs of calling frogs were located visually in the two ponds. When one calling male was observed, his neighbors who were calling were also identified. Individuals could have more than one calling neighbor. Only pairs in which each frog remained stationary for at least 15 min were studied. The maximum root-mean-square amplitudes of 9—16 calls from each neighbor were measured at the position of each focal male. To do this, the microphone of the sound-level meter was placed just above the focal male's head and pointed toward the calling neighbor. Amplitude measurements of 25 neighbors were obtained. Distances between 10 pairs of frogs chosen at random were also measured.

Playback Experiments

A series of playback experiments was conducted to quantify the response of individual frogs to presentation of advertisement calls at three different amplitudes. The stimulus used in all playbacks consisted of a 1-min sequence of 38 diphasic advertisement calls recorded from a male at one of the study ponds using a Sennheiser MKH-104 microphone and Sony TCD-5M cassette recorder. Call amplitude, as measured with the Bruel and Kjaer 2203 meter, varied by ± 1 dB during the 1-min period. In setting playback level, the tape recorder output was adjusted so that the modal call amplitude coincided with the desired playback amplitude.

Observations indicated that the mean amplitude of neighbors' calls at focal males' positions ranged from 86.7 dB SPL (re: 2×10^{-5} Pa) to 98.7 dB SPL. Playbacks of advertisement calls were therefore made at modal amplitudes of 87 dB SPL, 93 dB SPL, and 99 dB SPL 25 cm from the speaker; this encompassed the range of intermale call amplitudes measured. 16 frogs were presented with all three call amplitudes. Two additional males deserted their calling sites after completion of the 87 and 93 dB playbacks, and so were not presented with the 99 dB signal. Consequently, I played just the 93 dB and 99 dB signals to two other males. In summary, the 87 dB signal was played to a total of 18 frogs, the 93 dB signal to 20 frogs, and the 99 dB signal to 18 frogs.

To conduct playbacks, I visually located a calling frog in one of the ponds and held an Aiwa SC-A2 speaker 25 cm from his head; this was the maximum distance from the frog at which the highest signal amplitude could be played without speaker distortion. I waited at least 15 min, until the focal male resumed normal calling behavior. The number of calls given by the frog during a 1-min preliminary baseline period was counted. Advertisement calls and encounter calls were scored separately. These calls differ unambiguously in temporal structure (Fig. 1). I also attempted to distinguish between diphasic and monophasic advertisement calls, though this distinction was somewhat arbitrary because there was an acoustic gradient between these calls (pers. obs.).

Following the 1-min baseline period, playback of the test stimulus was initiated, but only when the focal male was calling. The number of advertisement and encounter calls given by the focal male during the 1-min playback period was counted, and any movements by the focal frog or other frogs were noted. Following cessation of the playback, the number of calls produced by the focal male was recorded for an additional 1-min post-playback period. There were, then, three 1-min sample periods for each playback amplitude.

In successive playbacks, the call amplitude was increased by 6 dB, which corresponds to a doubling of amplitude. The calls were played in order of increasing amplitude to mimic the situation of an intruding male progressively approaching the focal male's position. Also, the playback sequence minimized the probability of observing an increased response to a low amplitude signal due to sensitization resulting from previous exposure to a higher amplitude signal (e.g. BRENOWITZ 1981). Playbacks were separated by at least 5 min, and started when the focal male began his next bout of calling.

The playback experiments described above contain a potential confounding factor. Any changes in behavior observed over successive playbacks could possibly be due to repeated exposure to the test stimulus alone, and be unrelated to successive changes in signal amplitude. To test for this possibility, I did a set of control playbacks with 5 frogs. The protocol was the same as described above, except that signal amplitude remained at 87 dB SPL for each of the three successive playbacks.

Fig. 2: Mean amplitudes of neighbors' calls measured at a focal male's position (n = 25 neighbors)
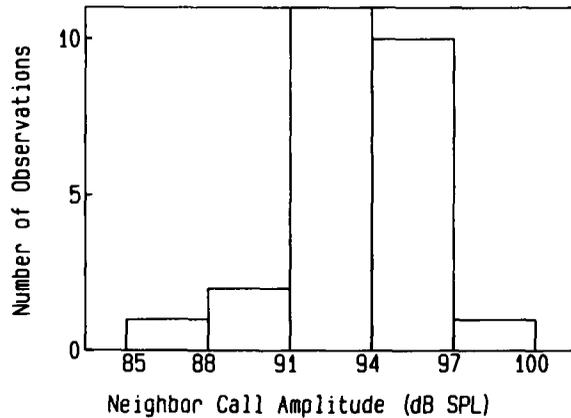
H. regilla males are relatively sedentary while at ponds (SCHAUB & LARSEN 1978). On a given night I sampled males only in one restricted section of a pond. Subsequent samples from the same pond were made at regions separated from the previous site by at least 20 m. No region of either pond was sampled more than once. This protocol minimized the chance of repeatedly testing the same individuals.

Statistical Analysis

The dB scale represents a logarithmic measure of relative sound pressure rather than true sound pressure; it is therefore not appropriate to perform statistics upon dB readings. Consequently, the measured call amplitudes and neighbor amplitudes in dB SPL were converted to absolute pressure in μPa (0 dB SPL = 2×10^{-5} Pa), and the means, SD, and F-statistics were computed from the converted values. Reconverting the values from the linear measure of absolute pressure to the logarithmic dB scale resulted in SD that are asymmetrical about the mean. The coefficients of variation (CV = SD/$\overline{X}$ × 100) of the call amplitudes and of neighbor amplitudes were calculated by dividing the larger of the asymmetric SD by the mean in dB. Variations in dB level are more meaningful than absolute-pressure measurements when related to animal audition because the vertebrate ear encodes sound pressure in a logarithmic rather than a linear manner (WILCZYNSKI & BRENOWITZ 1988).

Results

Call Amplitudes

Mean call amplitude at 50 cm ranged from 92.5 dB SPL to 100.7 dB SPL (n = 20 frogs). The mean ± SD call amplitude was 96.0 + 1.8, − 2.3 dB SPL. Call amplitude varied relatively little: CV = 2.4 %.

Neighbor-call Amplitudes

The mean ± SD neighbor amplitude was 93.9 + 2.13, − 2.92 dB SPL (Fig. 2). The range of mean intermale amplitudes was 86.7—98.7 dB SPL. The CV was 3.1 %. The intermale variance in neighbor-call amplitude did not differ from the intermale variance in call amplitude at the source (F = 1.56, df = 24,19, p > .05).

For 10 pairs of neighbors, intermale distance ranged from 50—110 cm ($\overline{X}$ ± SD = 77.5 ± 17.2 cm).

Advertisement Calls
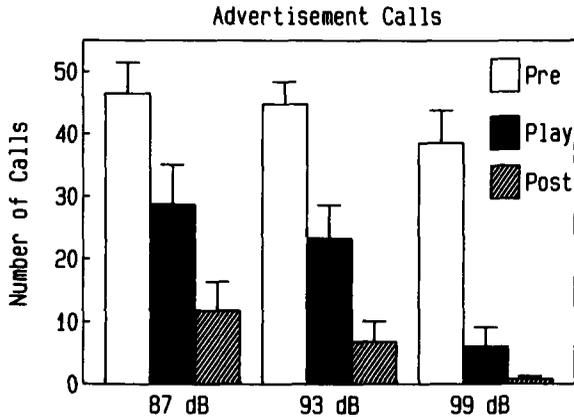
Fig. 3: Number of advertisement calls (X̄ + 1 SD) given during preliminary (pre), playback (play), and post-playback (post) sample periods. The duration of each period was 1 min. A 1-min sequence of recorded advertisement calls was played at 3 different amplitudes as measured at the focal male's position

Playback Experiments

The number of diphasic advertisement calls given did not differ significantly during the 3 preliminary periods (ANOVA, F = 0.79, df = 2,52, p > .05) (Fig. 3). The number of calls given during the playback period, however, did decrease significantly as signal amplitude increased (ANOVA, F = 5.17, df = 2,53, p < .01) (Fig. 3). For all playback amplitudes, frogs gave few if any calls during the post-playback period (Fig. 3). Rather, they usually became silent immediately following cessation of the playback.

There was no consistent change with signal amplitude in the production of advertisement calls classified as monophasic. An ANOVA of monophasic call number during the playback periods of the three amplitude sequences showed no significant change with amplitude (F = 2.44, df = 2,53, p > .05).

Encounter calls were generally given only during the playback period (Fig. 4). The number of encounter calls given during the preliminary periods of the three amplitude series did not differ significantly (ANOVA, F = 0.61, df = 2,52, p > .05) (Fig. 4). There was, however, a pronounced and significant
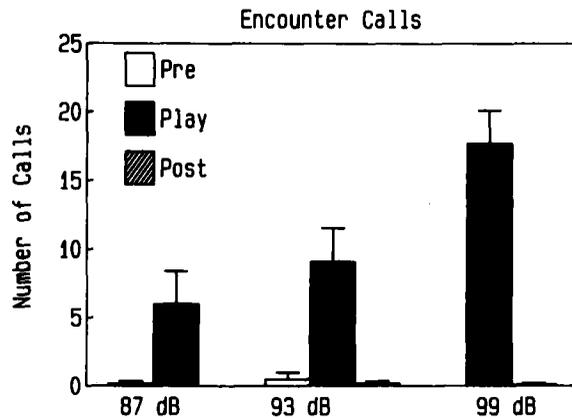
Encounter Calls

Fig. 4: Number of encounter calls (X̄ + 1 SD) given during preliminary (pre), playback (play), and post-playback (post) sample periods. The duration of each period was 1 min. A 1-min sequence of recorded advertisement calls was played at 3 different amplitudes

Fig. 5: Number of advertisement calls ($\overline{X}$ + 1 SD) given during preliminary (pre), playback (play), and post-playback (post) sample periods. The duration of each period was 1 min. In this control study, a 1-min sequence of recorded advertisement calls was played at the same amplitude of 87 dB SPL 3 times in succession

Advertisement Calls (Control)
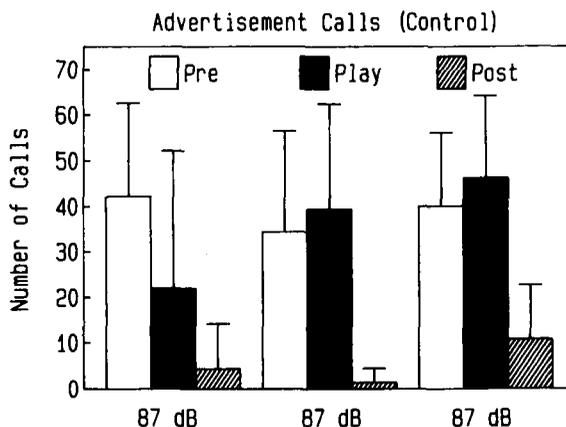
increase in the number of encounter calls given during the playback period as signal amplitude increased (F = 6.12, df = 2,53, p < .01).

The total number of calls (advertisement + encounter) given during the playback period did not vary significantly with signal amplitude (F = 0.89, df = 2,53, p > .05). Thus, while the number of encounter calls produced increased with amplitude, the number of advertisement calls decreased proportionately.

At the highest playback amplitudes the focal frogs commonly approached to within 10 cm of the loudspeaker while delivering encounter calls. Such close approaches to a resident frog by a calling intruder frequently led to physical encounters. These encounters usually resulted in the retreat of one frog, generally the intruder.

In the control study, signal SPL remained at 87 dB in the three successive playbacks. The number of advertisement calls given during the playback periods of the three signal presentations did not differ significantly (ANOVA, F = 1.32, df = 2,12, p > .05) (Fig. 5). One frog gave 9 encounter calls during the first control playback period, and another frog gave two encounter calls during the second control playback period. Encounter calls were not produced by frogs at any other times during the control sequence. Thus, repeated presentation of the stimulus at the same amplitude elicited neither a decrease in the number of advertisement calls nor an increase in the number of encounter calls as was observed with successive changes in signal amplitude.

Discussion

Hyla regilla males call at amplitude levels typical of hylid frogs of that general body size. Thus, the main SPL at 50 cm (96.0 dB) and the range (92.5—100.7 dB) for this species coincide closely with those reported by GERHARDT (1975) for the similarly sized *H. versicolor.* A F-test showed that the variance in call amplitude among *H. regilla* males (CV = 2.4 %) did not differ significantly from that observed among *E. diastema* males (CV = 2.9 %; WIL-

CZYNSKI & BRENOWITZ 1988) (F = 1.01, df = 19,5, p > .05). However, *H. re-gilla* showed significantly less variance in call amplitude than did *H. crucifer* (CV = 5.0 %; BRENOWITZ et al. 1984) (F = 3.42, df = 9,19, p < .05). Variability in call amplitude between frogs may reflect differences in body size or aspects of male condition (GERHARDT 1975; NARINS & HURLEY 1982; KLUMP & GERHARDT 1987). Other factors being equivalent, higher amplitude calls communicate a male's presence over a greater range.

The mean neighbor-call amplitude (93.9 dB SPL) observed at the positions of focal *H. regilla* males was relatively high, especially when compared with *E. diastema* ($\overline{X}$ = 64.4 dB SPL) and *H. crucifer* (X = 81.2 dB SPL) (BRENOWITZ et al. 1984; WILCZYNSKI & BRENOWITZ 1988). This high level is largely a function of the short intermale distances observed in choruses of *H. regilla* ($\overline{X}$ = 0.775 m), relative to those seen in choruses of *E. diastema* ($\overline{X}$ = 14.65 m) and *H. crucifer* ($\overline{X}$ = 2.11 m) (BRENOWITZ et al. 1984; WILCZYNSKI & BRENOWITZ 1988).

In *H. regilla* the variance in neighbor-call amplitude was significantly less than that for neighbor amplitude in either *E. diastema* (F = 4.51, df = 19,24, p < .01) or *H. crucifer* (F = 31.92, df = 35,24, p < .01) (BRENOWITZ et al. 1984; WILCZYNSKI & BRENOWITZ 1988). Thus, while call amplitude at the source was no less variable for *H. regilla* than it was for *E. diastema*, the amplitude of neighbors' calls at a focal male's position varied less in *H. regilla*.

The intermale distances that I observed are very similar to those reported for *H. regilla* by AWBREY (1978). Intermale distance is considerably less variable for *H. regilla* (CV = 22.2 %) than it is for either *E. diastema* (CV = 85.0 %) or *H. crucifer* (CV = 57.3 %) (BRENOWITZ et al. 1984; WILCZYNSKI & BRENOWITZ 1988). This may reflect the manner in which *H. regilla* females sample the calls of males. In phonotactic studies females preferentially approached the calls of males that initiated bouts of group calling (WHITNEY & KREBS 1975b). This strategy will only be effective if a female is able to hear the calls of several males simultaneously from her position in the chorus. Such a manner of sampling may force males to space at the relatively short distances observed in their choruses. It is not known if females of *H. crucifer* and *E. diastema* sample calls of local male groups in a similar manner.

In the present playback studies there was no significant difference in the number of either advertisement or encounter calls given during the preliminary periods of the three amplitude series. This suggests that frogs did not remain aroused from previous exposure to lower amplitude signals. Rather, calling behavior returned to its baseline level between successive playbacks.

The number of advertisement calls given during the playback period declined significantly with an increase in signal amplitude. Concurrently, the number of encounter calls produced during playbacks increased sharply as playback amplitude was raised. Successive presentations of the signal at the same amplitude produced no change in either the number of advertisement calls or encounter calls given by subjects. Calling behavior in *H. regilla* thus clearly was influenced by the amplitude of detected conspecific signals. A similar effect of playback amplitude on calling behavior was observed in the congeneric frogs *Hyla ebrac-*

cata (WELLS & SCHWARTZ 1984) and *Hyla arborea savignyi* (BRZOSKA et al. 1982), as well as in *Leptodactylus albilabris* (LOPEZ et al. 1988) and *Uperoleia rugosa* (ROBERTSON 1984). These authors did not, however, compare effective playback amplitudes with neighbor-call amplitudes.

The most novel observation of this study emerged from comparison of neighbor-call amplitudes in *H. regilla* choruses with the responses to playbacks of advertisement calls at different amplitudes. During playbacks at the highest mean neighbor amplitude measured (99 dB SPL), frogs gave fewer than 1/3 as many advertisement calls as they did in response to playbacks at the lowest neighbor amplitude (87 dB SPL), and emitted about three times as many encounter calls as observed during the 87 dB playback.

Previous studies (ALLAN 1973; WHITNEY 1980) indicated that the encounter call is used exclusively in aggressive contexts. The present results suggest therefore that aggressive motivation, as reflected by the incidence of encounter calling, increases in a graded manner as the perceived amplitude of neighbors' calls rises above the minimum levels normally observed in choruses. Neighbors are tolerated by a resident frog when the amplitude of their calls at his position falls below about 87 dB SPL. When a neighbor's calls arrive at the resident's position at levels about 87 dB SPL, he switches from delivering predominantly advertisement calls to producing increasing numbers of encounter calls.

If the received call amplitude rises progressively, as it did in the present study, the resident male can communicate a progressive increase in aggressive motivation to an apparently approaching intruder. This information may be conveyed both by altering the ratio of advertisement calls to encounter calls that he gives, and by the absolute number of encounter calls that he produces. Note that the total number of calls (advertisement + encounter) given by frogs during playbacks did not vary with signal amplitude. This suggests that males replace advertisement calls with encounter calls as aggressive motivation increases. At perceived call amplitudes matching the highest neighbor amplitudes observed in the choruses, frogs almost exclusively deliver encounter calls.

The results of this study support the hypothesis that intermale spacing in choruses of *H. regilla* is mediated by the amplitude of neighbors' calls, and is maintained through aggressive calling behavior. Several observations support this conclusion. In stable choruses neighbor-call amplitudes vary relatively little. Under such stable conditions, encounter calls are only rarely produced spontaneously by resident males. As the amplitude of the calls of apparent neighbors at a resident male's position rises above the minimum levels typically observed in choruses, the rate of encounter calling by resident males rises dramatically. As ALLAN (1973) demonstrated, intruders are likely to move away when a resident male gives encounter calls. In this way, call amplitude regulates intermale spacing within choruses.

Like *E. diastema* and *H. crucifer*, neighbor-call amplitude in *H. regilla* shows far less relative variability than does intermale distance (see WILCZYNSKI & BRENOWITZ 1988). It is clear that in each species males actively space apart in such a manner as to maintain the amplitude of their immediate neighbors' calls at a relatively constant level. The amplitude of acoustic signals attenuates with

distance through a given habitat in a predictable manner and so serves as a reliable cue for spacing (BRENOWITZ 1986).

This investigation reinforces the conclusion that male frogs of several species use the amplitude of neighbors' calls as a proximate mechanism for spacing within breeding choruses. Similar studies could be conducted profitably with a wide diversity of other chorusing animals. Such comparative studies will greatly contribute to our understanding of this topic.

Acknowledgements

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