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Responses of male cricket frogs (*Acris crepitans*) to attenuated and degraded advertisement calls

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Abstract

We examined the vocal and non-vocal responses of male cricket frogs (*Acris crepitans*) to conspecific advertisement calls that had been attenuated or degraded by reducing the depth of amplitude modulation (AM). Both are characteristic of changes to the call as it is transmitted through natural habitats. As stimulus calls became more intense or less degraded, male cricket frogs gradually decreased their call rate and increased the number of call groups and pulse groups in their calls, changes indicative of increased aggressive interactions. At the higher intensities and lower degradation levels, the probability that males would shift to one of two non-vocal behavioral responses, attacking the perceived intruder or ceasing calling and abandoning the call site, gradually increased. The results show that differences in signal attenuation and AM degradation levels are perceived by males and trigger both vocal and non-vocal behavioral responses consistent with their use in evaluating the distance to a challenging male. Furthermore, the results indicate that the male responses are graded, increasing as intensity rises and degradation falls, and hierarchical, with vocal responses preceding behavioral responses over the range of intensities and degradation levels presented.

KEYWORDS
acoustic communication, aggression, amphibians, cricket frogs

1 | INTRODUCTION

In many invertebrate and vertebrate communication systems, signal intensity and temporal properties are important acoustic features mediating signal-receiver interactions (acoustic communication reviews and examples studies: insects: Gerhardt & Huber, 2002; birds: Catchpole & Slater, 2008; Brumm & Naguib, 2009; anurans: Wells, 1977, 2007). Signal transmission through natural habitats, however, results in attenuation (a decrease in signal amplitude) and degradation (a decrease in signal fidelity) with propagation distance due to a variety of stationary and non-stationary heterogeneities (Morton, 1975; Penna & Moreno-Gómez, 2015; Ryan & Sullivan, 1989). Temporal signal structure is degraded during transmission due to reflection and diffraction in complex environments (Wiley & Richards, 1982). The suite of changes that occur to an acoustic signal can vary considerably due to the particular static features of the habitat (foliage, substrate characteristics, etc.) as well as variable features such as temperature, wind, humidity, and time of day.

A number of studies have shown that attenuation of spectral signal components might constrain long-range acoustic communication. Similarly, Ryan and Sullivan (1989) suggested that levels of AM degradation found in the natural habitats of *B. americanus* and *B. fowleri* might place limits on species recognition at far distances. Conversely, changes in signal structure may be used by a receiver as cues to the distance between sender and receiver, a process called "ranging" (Naguib & Wiley, 2001). Much of the previous work on assessing relative distance from sender to receiver has focused on bird communication (Radziwon & Dent, 2010; Radziwon, Welch, Cone, & Dent, 2011). These studies have suggested that birds may use components of degraded song (Holland, Dabelsteen, Pedersen, & Larsen, 1998; Naguib, 1998; Naguib & Wiley, 2001; Richards, 1981) and song amplitude (Naguib, 1995, 1997) to assess distance from a signaler.

Assessing distance based on signal parameters would be of use to other taxa as well. Call amplitude does seem to be used as a cue to regulate inter-male spacing in a frog chorus for example (Brenowitz, Wilczynski, & Zakon, 1984; Robertson, 1984; Rosen & Lemon, 1974; Telford, 1985). While not a perfect surrogate for distance, due to the variability induced by microhabitat characteristics and, for amplitude, source amplitude, a decrease in amplitude or a smearing of the temporal structure of the signal could serve as an indicator of the distance to a rival male, at least indicating that the rival is very close or very far. If receivers do use signal amplitude or degradation as indicators of a rival's distance, one would predict their behavior to change in a reliable manner as either signal feature changes. As signals become more intense or less degraded, a receiver should respond progressively with changes to its behavior or vocalizations indicative of perceiving a threat. We investigated receiver responses to attenuated and degraded versions of their advertisement call in male cricket frogs (*Acris crepitans*).

In anurans (frogs and toads), the male advertisement call mediates both female mate choice and male–male interactions. The advertisement call is involved in a number of male agonistic behaviors, such as the maintenance of chorus calling via antiphonal signaling, triggering aggressive interactions, and maintaining inter-male spacing (Brenowitz et al., 1984; Burmeister, Konieczka, & Wilczynski, 1999; Robertson, 1984; Rose & Brenowitz, 1991; Telford, 1985). Cricket frogs are typical of anuran amphibians in these features of their acoustic communication system. The advertisement call of male cricket frogs serves as a mate attraction signal to females (Nevo & Capranica, 1985; Ryan, Perrill, & Wilczynski, 1992; Ryan & Wilczynski, 1988, 1991). It also underlies male–male agonistic signaling (Burmeister, Ophir, Ryan, & Wilczynski, 2002; Burmeister, Wilczynski, & Ryan, 1999; Burmeister, Konieczka, et al., 1999; Perrill & Shepherd, 1989; Wagner, 1989a, 1989b). Unlike many anuran species, however, cricket frogs have a "graded communication" system (Bradbury & Vehrencamp, 1998; Greene & Marler., 1979) in which they change their single advertisement call in a graded fashion to challenging conspecific calls rather than switch at some threshold to a separate aggressive call (Burmeister, Wilczynski, et al., 1999; Wagner, 1989a, 1989b). Graded calls were first documented in the neotropical frog *Hyla ebraccata* (Wells & Schwartz, 1984) and subsequently described in several other hylids (Wells, 2007). This graded response allowed us to assess continuous variation in their vocal responses across a range of stimuli rather than only monitoring a dichotomous switch from one type of call to another.

The cricket frog advertisement call consists of a series of amplitude-modulated pulses repeated in rapid succession (Figure 1). Calls are produced in bouts, or call groups (Micancin & Wiley, 2014; Ryan & Wilczynski, 1991). Both call intensity and temporal structure appear to be important factors in the natural calling behavior of male cricket frogs. Natural agonistic interactions occur when a nearby silent satellite male initiates calling or a new male approaches an established calling male. During such agonistic interactions, both spectral and temporal call parameters of the receiver change in a graded fashion depending on how "aggressive" the challenger's call appears to be (Burmeister, Konieczka, et al., 1999; Burmeister, Wilczynski, et al.,
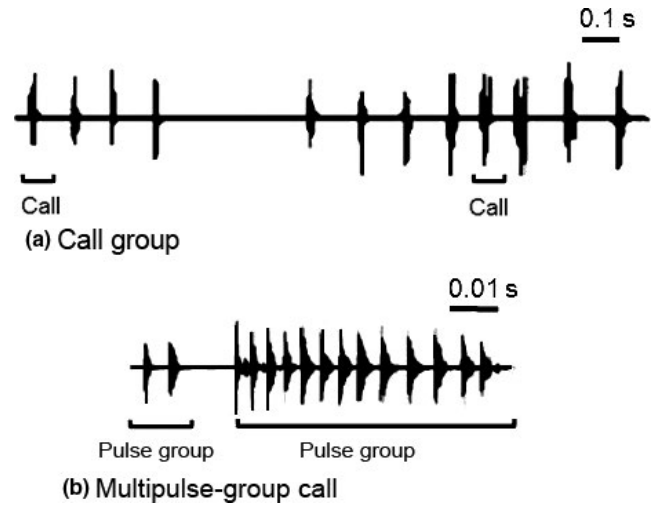

FIGURE 1 Diagram of cricket frog advertisement calls. (a) Calls are arranged in a call group which may be split into two or more sections. (b) Individual calls within a call group are composed of pulses which may be arranged in separate pulse groups within the call; call diagramed here is the same as the call marked on the right of the call group

1999; Burmeister et al., 2002; Wagner, 1989a, 1989b). Males involved in aggressive interactions produce longer call groups, with lower call group rates. Individual calls increase in duration, having more pulse groups and pulses. Perceived call amplitude also influences male calling behavior. In response to high call amplitudes, individuals increase call duration and the number of pulses within their own calls and alter their non-vocal behavior (Wagner, 1989a, 1989c). Behavioral changes also occur in response to calls with different temporal structure (Burmeister, Wilczynski, et al., 1999). Depending on the signal, they may stop calling and search for or attack the calling conspecific, or they may abandon their call site and move to another.

We examined whether male cricket frogs responded vocally to calls that were progressively attenuated or degraded in the same graded fashion in which they respond to calls with different degrees of aggressive characteristics. We simultaneously monitored whether the probability of switching to various non-calling behavioral responses changed with progressively attenuated or degraded calls.

2 | METHODS

We conducted experiments on male cricket frogs, *Acris crepitans blanchardi*, calling in their natural choruses between 2100 and 0230 hr at McKinney Falls State Park, Travis County, Texas, over two consecutive summers. Tests were run on nights from May to October with calm wind conditions and no rain. Temperature ranged from 21 to 28°C. We investigated the vocal and behavioral responses of male frogs in two separate playback studies, one examining attenuation and one examining amplitude modulation (AM) degradation, using variations of a synthetic advertisement call. Each study used five call stimuli. The attenuation stimuli varied only in broadcast call intensity. The

degradation stimuli varied only in the depth of amplitude modulations, that is, in the ratio of the amplitudes of the pulse and the interpulse interval of the call.

All stimulus calls had a dominant frequency of 3.65 kHz, falling within the natural population range of 3.1–4.1 kHz. The synthetic calls consisted of discrete amplitude modulations, comprised of pulse and interpulse intervals, as found in natural calls (Burmeister, Wilczynski, et al., 1999; Ryan & Wilczynski, 1991; Wagner, 1989b, 1989c). Each call was comprised of seven pulses in a single group at a pulse rate of 0.22 pulses per ms and a total call duration of 31.5 ms. Calls were grouped in a single call group of nine calls with an intercall interval of 146 ms, resulting in an intergroup call rate of 5.5 calls per s and a total call group duration of 1.6 sec. Call groups were presented at a rate of 18 groups per min. The stimulus structure mimicked the call of an undisturbed male without any shift in temporal structure indicative of an aggressive response. The call was synthesized by digitally adding sine waves (after Wagner, 1989a). Playback experiments consisted of two stages: (i) a two-min pre-stimulus period during which we recorded the natural calling of a focal male; (ii) a two-min playback period during which we recorded male vocal response and categorized male behavioral response to the stimulus presentation. Each male was tested with only one stimulus. Stimuli were broadcast from an active speaker system (Sony SRS A-11) at 0.5 m from a focal male. All stimuli were broadcast over limestone rock or algae mats. These substrates had been found to induce minimal attenuation and degradation of cricket frog calls at this distance (Venator, 1999). The calling intensity of the nearest neighbor for all tested males was less than 80 dB SPL (re: 2×10^{-5} N/m^2). Recordings were made onto Type IV metal audiotapes using a Sennheiser directional microphone (ME 80) and Marantz recorder (PMD 420). Males were observed with a six-volt headlamp. Following playback experiments, we toe clipped individuals to prevent repeated testing.

For the attenuation study, we broadcast the synthetic advertisement call to each male at one of five stimulus call intensities: 82, 88, 94, 100, and 106 dB SPL (re: 2×10^{-5} N/m^2, Peak) at the position of the test male. Intensity was determined using a Bruel & Kjaer sound level meter (model 2230). An amplitude of 106 dB SPL represents the presence of a calling intruder at a distance of approximately 0.5 m from a test male and elicits robust vocal responses from calling males (Wagner, 1989b; personal observation). The vocal responses of 15 males were recorded for each stimulus intensity except 94 dB, for which we recorded the response of 14 males. The behavioral responses of 15 males were recorded for each stimulus intensity.

AM degradation was measured as the ratio of the amplitudes of pulse and interpulse interval comprising the synthetic call, indicating the depth of amplitude modulation. The measure of this ratio was $\Delta V = 1 - (RMS\ IPI/RMS\ P)$, where RMS IPI is the root-mean-square amplitude of the interpulse interval, and RMS P is the root-mean-square amplitude of the pulse. We broadcast the synthetic advertisement call to each male at one of five ΔV values: 0, 0.25, 0.50, 0.75, and 1.0, with 0 representing the most degraded and 1.0 representing the least degraded stimulus. Stimuli were made by adding white noise (0.01–20 kHz) to the synthetic advertisement call in Soundedit

Pro®. All stimuli were broadcast at 106 dB SPL at the position of the test male. We recorded the vocal responses of 15 male frogs for each stimulus except 100% noise ($\Delta V = 0$), for which we recorded 14 males. The behavioral responses of 15 males were recorded for all stimuli.

Pre-stimulus and stimulus 2-min recordings of each subject male were digitized into Soundedit Pro®, and call rate and multi-pulse group rate were calculated. Call rate is the total number of calls per min. Multi-pulse group rate is the total number of pulse groups comprised of three or more pulses per min. The multi-pulse group rate measure reflects changes in both pulse number and pulse group number. We examined changes in vocal behavior by comparing these two call variables during the stimulus presentation with their pre-stimulus values. We calculated the relative change in call rate and multi-pulse group rate by subtracting the pre-stimulus values from stimulus response values. Thus, a score of zero would represent no difference in calling behavior between pre-stimulus and stimulus periods. Using difference scores in lieu of absolute values for each subject reduced the error variance attributable to factors such as ambient temperature.

We categorized the non-calling behavioral responses of males during the two-min stimulus presentation into one of three groups: attack, abandon, or call throughout (modified from Burmeister, Konieczka, et al., 1999; Wagner, 1989b). Male behavior was categorized as attack if the subject approached the speaker, coming within a radius of 10 cm, at least once. Male behavior was categorized as abandon if during stimulus presentation the animal stopped calling or vacated the calling site. Males that maintained calling behavior throughout stimulus presentation were categorized as call throughout.

Parametric statistics were computed using SuperANOVA®. *G*-tests were computed in Microsoft Excel®.

All procedures were approved by the University of Texas Institutional Animal Care and Use Committee.

3 | RESULTS

3.1 | Vocal responses to attenuated calls

3.1.1 | Call rate

Changes in call rate showed significant variation with stimulus intensity (ANOVA: $F_{(4,69)} = 6.38$, $p < .0001$). Stimulus intensities of 82, 88, and 94 dB resulted in an increase in call rate relative to pre-stimulus calling, while intensities of 100 and 106 dB resulted in a decrease in call rate (Figure 2). The change in call rate for 106 dB was significantly different from 82, 88, and 94 dB (Scheffe's S: $p < .05$).

3.1.2 | Changes in multi-pulse group rate

Changes in multi-pulse group rate varied significantly with stimulus intensity (ANOVA: $F_{(4,69)} = 3.14$, $p < .05$). As stimulus intensity increased, multi-pulse group rate increased (Figure 2) in a graded
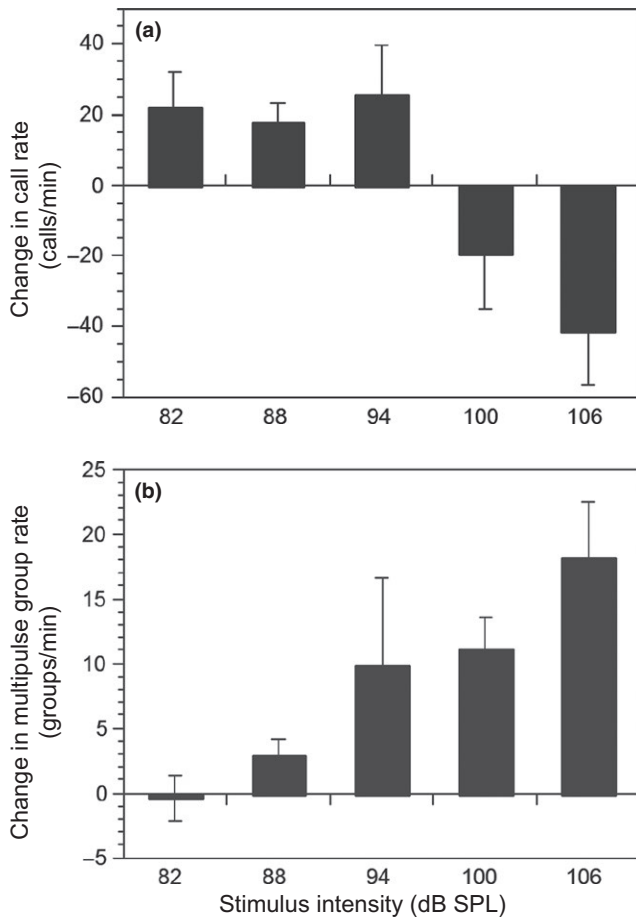
FIGURE 2 Influence of stimulus intensity on vocal responses of male cricket frogs. (a) Change in call rate compared to pre-stimulus levels. (b) Change in multi-pulse group rate compared to pre-stimulus levels. All values are mean ± *SE*

intensity increased, the probability of a male attacking or abandoning increased, while the probability of a male calling throughout decreased (Figure 3).

3.3 | Vocal responses to degraded calls

3.3.1 | Call rate

Changes in call rate were highly variable, with little mean change from pre-stimulus values over ΔV values between 0 and 0.5, while males appeared to decrease call rate as stimulus ΔV increased beyond 0.5 (Figure 4). However, over all stimulus conditions, the change was not significant.

3.4 | Multi-pulse group rate

Changes in multi-pulse group rate showed significant variation with stimulus ΔV (ANOVA: $F(4,69) = 3.76$, $p < .01$). As ΔV increased, multi-pulse group rate increased (Figure 4) in a graded manner. The change in multi-pulse group rate was significantly different between ΔV values of 0 and 1 (Scheffe's S: $p < .05$).

3.5 | Behavioral responses to degraded calls

Male responses varied with stimulus ΔV (Table 2). As for intensity variation, there was no significant difference between the number of males that attacked and abandoned in response to the degraded calls, while there were significant differences between the number of males that called throughout and either attacked ($G = 29.06$, $df = 4$, $p < .001$) or abandoned ($G = 26.74$, $df = 4$, $p < .001$). As

TABLE 1 Non-vocal behavioral responses of male cricket frogs to playbacks of mating calls with five different intensities

Call intensity (dB SPL)	Number of males attacking	Number of males abandoning	Number of males calling throughout
82	0	0	15
88	0	1	14
94	2	1	12
100	8	1	6
106	10	3	2

manner. The change in multi-pulse group rate was significantly different between 106 and 82 dB (Scheffe's S: $p = .05$).

3.2 | Behavioral responses to attenuated calls

Male responses to the five stimuli were significantly different (Table 1). While there was no significant difference between the number of males that attack and abandon in response to the five call intensities, there were significant differences between the number of males that called throughout and either attacked ($G = 41.70$, $df = 4$, $p < .001$) or abandoned ($G = 11.06$, $df = 4$, $p < .05$). As call

ΔV increased, the probability that a male would call throughout decreased, while the probability of a male attacking or abandoning increased (Figure 5).

4 | DISCUSSION

Aggressive calling behavior in cricket frogs consists of the production of calls containing more pulses and more pulse groups, resulting in calls with longer call groups and lower call rates (Wagner, 1989a). In response to calls with different degrees of aggressive components or different
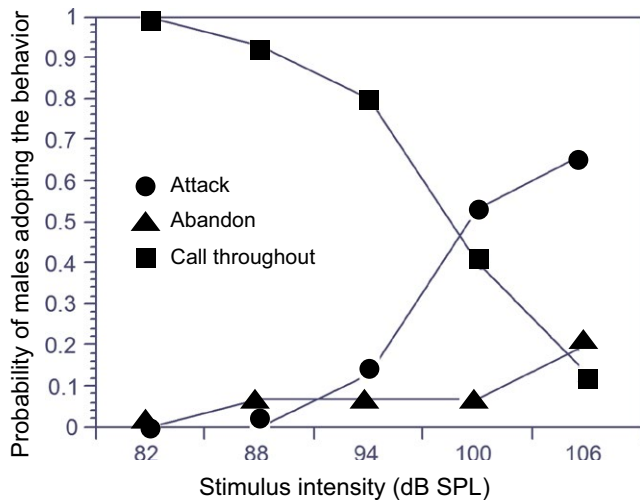
FIGURE 3 Influence of stimulus intensity on the probability of one of three non-vocal behavioral responses in male cricket frogs: Calling throughout the stimulus; attacking the perceived intruder; abandoning the call site
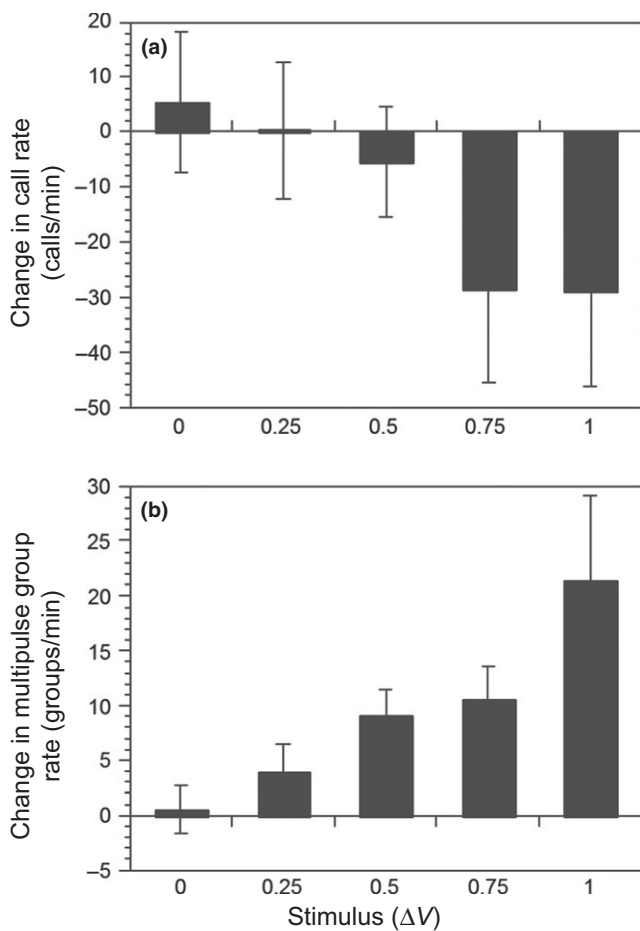

FIGURE 4 Influence of AM degradation on vocal responses of male cricket frogs. Degradation is defined as the ratio of amplitude of the pulses to the amplitude of the interpulse intervals of the call (ΔV). (a) Change in call rate compared to pre-stimulus levels. (b) Change in multipulse group rate compared to pre-stimulus levels. All values are mean $\pm$ *SE*

dominant frequencies, male cricket frogs change their overall call characteristics in a graded fashion (Burmeister, Wilczynski, et al., 1999; Wagner, 1989b). In this study, we found that cricket frogs also change their call characteristics and their probability of expressing a non-calling behavioral response in a graded fashion as call attenuation and degradation levels indicated decreasing distance. These changes are hierarchical in that changes in calling precede behavioral changes in both cases.

Two call variables, call rate and multi-pulse group rate, changed progressively toward values indicative of higher aggressive calling as stimulus calls increased in amplitude. Multi-pulse group rate, a measure that reflects changes in the number of pulses and pulse groups within the call, increased at all stimulus intensities from 82 to 106 dB. Changes in call rate were more complicated. Initially, males responded to even the lowest intensity stimulus calls with an increase in call rate. As stimulus calls reached the higher intensities used, 100 and 106 dB, males significantly decreased call rate. The large decrease in call rate between stimuli of 94 and 100 dB suggests that call intensities within this range may be particularly important in triggering an aggressive calling response. Wagner (1989a) previously demonstrated in this species a significant decrease in call rate in response to synthetic mating calls with dominant frequencies of 3.0 and 3.7 kHz between intensities of 100 and 105 dB. The present results indicate this to be part of a more general, graded suite of changes in call characteristics as a challenger's call increases in intensity.

Increased call intensity also increases the probability of switching among distinct non-calling behavioral responses. As mating call intensity increased, the probability that males would call throughout decreased while the probability of males attacking or abandoning increased. At intensities of 82 dB all males called throughout and at 88 dB 14 of 15 males called throughout. As call intensity increased above this, we observed marked and progressive changes in male behavioral responses to call intensities of 94, 100, and 106 dB. Males first attacked broadcast stimuli in response to calls at 94 dB, and the probability of attacking increased from 100 to 106 dB. When attacking, males initiated stereotypical aggressive behavior, consisting of leg extensions, calling directly next to the speaker, and increasing call complexity by increasing the number of pulse groups and call groups. As noted above, males increased call rate and multi-pulse group rate in response to calls at 94 dB, but decreased call rate in response to calls at intensities of 100 and 106 dB, when attacks were more frequent. The decrease in call rate at high call intensities may be attributed to the fact that males orient and move toward the broadcast stimulus, and in the process call less.

Calls with high ΔV levels, representing a high ratio of pulse amplitude to interpulse interval amplitude, also elicited graded changes in aggressive calling behavior in male cricket frogs. As with progressive increases in call amplitude, with progressive decreases in call temporal degradation (increasing ΔV), males decreased call rate and increased multi-pulse group rate. The most dramatic changes in call rate occurred at the two highest ΔV values: call rate decreased by 14.8 and 21.8 calls/min for ΔV values of 0.75 and 1, respectively, relative to 0.50 ΔV. Males also increased multi-pulse group rate in response to increases in stimulus ΔV.

Call ΔV	Number of males attacking	Number of males abandoning	Number of males calling throughout
0.00	0	0	15
0.25	0	1	14
0.50	1	2	12
0.75	5	2	8
1.00	8	3	4

TABLE 2 Non-vocal behavioral responses of male cricket frogs to playbacks of mating calls with five different degrees of AM degradation (ΔV)
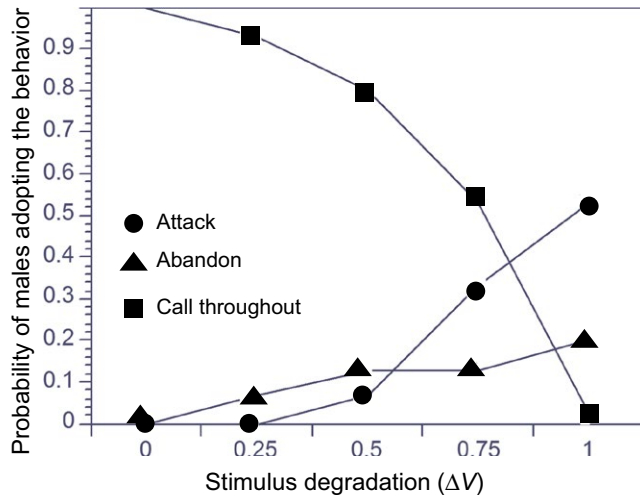

FIGURE 5 Influence of AM degradation (ΔV) on the probability of one of three non-vocal behavioral responses in male cricket frogs: Calling throughout the stimulus; attacking the perceived intruder; abandoning the call site

Similar to the results obtained with call amplitude changes, call changes preceded, then were accompanied by, progressive changes in the probability of non-calling behavioral responses. As ΔV increased, the probability that males would call decreased, while the probability that males would either attack or abandon increased. Our results indicate that although males did not give a behavioral response to calls with low ΔV values, they did change their vocal behavior in response to calls with low AM depths. At ΔV values of 0 and 0.25, all males called throughout. At a ΔV of 0 males increased call rate by 5.32 calls/min and at ΔV values of 0.25 males decreased call rate by 2.43, relative to pre-stimulus values. In contrast, we found distinct changes in male behavioral responses to calls with ΔV values of 0.50, 0.75, and 1.0. Males first attacked at 0.50 ΔV, and the probability of attacking increased from 0.75 to 1.0. These results suggest that although males change vocal behavior at low ΔV levels, initiation of aggressive behavior such as attacking is limited to ΔV values of 0.50 and greater.

Although males changed their behavior at the higher amplitudes and lower degradation values indicative of a close, calling intruder, in neither case did particular values predict whether males would abandon their calling site or defend the site by attacking the perceived intruder. Burmeister et al. (2002) reported a similar finding when presenting calls of different temporal characteristics to cricket frogs. There, temporal characters indicative of higher aggression increased

the probability that receiving males would either abandon their site or attack the speaker, but did not predict which of the two behaviors the male would adopt. Burmeister, Konieczka, et al., (1999) found that the most reliable predictors of that choice were factors extrinsic to the interacting dyad, namely local chorus density, nearest neighbor distance, and time in the breeding season. An additional factor complicating male responses is that the adoption of aggressive behavior may also be dependent upon previous experience. Burmeister, Wilczynski, et al., (1999) found that previous experience with calls from a particular location changed the propensity of cricket frog males to shift their calls in the aggressive direction. In *Hyla regilla* (= *Pseudacris regilla*), Rose and Brenowitz (1991, 1997) have shown that aggressive thresholds, the lowest playback intensity that elicits encounter calling, are plastic: Thresholds can be elevated by exposure to supra-threshold calls and lowered by acoustic isolation. Even more subtle distinctions are made by bullfrogs, which respond less aggressively to a familiar neighbor's call than to unfamiliar calls (Bee, 2003; Bee & Gerhardt, 2001a, 2001b; Boatright-Horowitz, Horowitz, & Simmons, 2000). We assume the same decision processes occurred here. Detecting a simulated intruder with a high amplitude or low degradation call triggers a decision to react behaviorally; what that reaction is may largely be the function of past experience and local conditions in the surrounding breeding chorus.

In our experiments, we varied signal amplitude and AM depth independently of one another to determine the relative importance of each cue on natural behavior. Attenuation stimuli possessed identical AM depths and all degradation stimuli were broadcast at an amplitude of 106 dB SPL. Under natural conditions, signals will undergo both attenuation and degradation with propagation distance. Therefore, presenting attenuation or degradation independently of one another would not represent completely reliable cues for assessing signaler distance because the pattern of attenuation and temporal degradation with distance may be highly variable among substrates (Venator, 1999). Furthermore, there is evidence that female treefrogs do vary phonotaxis responses to degraded calls depending on call amplitude (Kuczynski, Vélez, Schwartz, & Bee, 2010). Under natural conditions, frogs may assess concomitant changes in signal amplitude and temporal structure, and possibly changes in spectral composition, in order to determine signaler distance. Comparing multiple cues would likely increase accuracy of distance assessment (Naguib, 1995; Naguib & Wiley, 2001). In addition to amplitude and AM degradation, cues might also include comparing the relative intensities of low- and high-frequency signal components (Wiley & Richards, 1982) or other

changes in spectral composition, although no evidence exists indicating that male anurans might assess distance from a signaler using changes in spectral content. Other changes to temporal structure such as modification of the fine structure of the pulses making up the call might also serve as distance cues. Our stimuli therefore do not completely emulate natural call transmission, but males might be expected to respond at least to some degree to a change in either call character, as we have found here.

Although our results are consistent with male cricket frogs using attenuation and degradation as distance cues, we cannot completely rule out other explanations for the behavioral changes, particularly those related to differences in call degradation. High levels of call degradation may make the stimuli unrecognizable as conspecific advertisement calls, which would also cause the receivers' behavior to remain unchanged. Temporal changes of the type we employed might also result from high levels of masking due to environmental noise or exceptionally high chorus densities. It is not clear how cricket frogs normally respond vocally to such situations, but both Wagner (1989c) and Burmeister, Konieczka, et al., (1999) found that local cricket frog chorus dynamics do influence a male's vocal and non-vocal response to a challenge.

Our findings indicate that differences in signal attenuation and degradation levels are perceived by males and manifest themselves in both vocal and behavioral responses consistent with their use in evaluating the distance to a challenging male. Males gradually produced more aggressive calls, progressively decreasing call rate and increasing multi-pulse rate, in response to synthetic calls of increasingly high amplitude and high ΔV values. Furthermore, the probability that a male would attack or abandon increased progressively as signals increased in amplitude and ΔV level. These non-calling behavioral responses occurred at higher amplitudes and lower temporal degradation levels than did changes in calling. The results indicate progressive changes in two dimensions. As call characters change indicative of decreasing distance to the receiver, males change the aggressive indicators in their calls in a graded manner. In addition, they gradually shift from a vocal response to a non-calling behavioral response at the highest intensity levels and lowest degradation levels that would signal the very close presence of another male.

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