RESPONSES TO CONSPECIFIC ADVERTISEMENT CALLS IN THE GREEN FROG (RANA CLAMITANS) AND THEIR ROLE IN MALE-MALE COMMUNICATION

by

MARK A. BEE¹ and STEPHEN A. PERRILL²)
(Butler University, Indianapolis, Indiana, 46208, USA)

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Summary

We investigated vocal communication between males in a central Indiana population of the green frog, Rana clamitans. Three playback experiments were conducted. In the first test, we broadcasted a single-note and a multiple-note conspecific advertisement call and a control call (Acris crepitans) to calling males. In response to the conspecific stimuli, males increased the number of calls made per minute, increased note duration, lowered the dominant frequency in the call, and often approached the speaker platform. In a second playback test, designed to examine changes in the sound pressure levels of response calls, we broadcasted a conspecific single-note advertisement call and the control call to calling males. Males in this test lowered the intensity of their responses to the conspecific stimulus. We take these altered response calls to be encounter calls used in the vocal defense of a territory during agonistic male-male interactions. We examine the function of these calls and discuss their possible role in communication between males. In the third test, we broadcasted a second type of conspecific multiple-note call and the control call. In their responses, males increased the number of the second multiple-note calls. The multiple-note stimulus used in this test failed to elicit the agonistic responses of the first two conspecific calls. The role of this second type of multiple-note call in male-male communication remains unclear.

¹) Current address: Division of Biological Sciences, University of Missouri, Columbia, Missouri, 65211, USA.
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Introduction

Male anurans use vocalizations to advertise their species identity, sex, and location to females for the purpose of breeding (Wells, 1977a). These vocalizations are generally termed ‘advertisement calls’ because males use them to announce themselves to females as prospective mates and to nearby males competing for the same females (Wells, 1977b). More recently, the importance of aggressive vocalizations in communication between conspecific males has been examined. These vocalizations are calls directed toward other males during agonistic encounters. The significance of such male-male communication is not as well established as the role vocalizations play in mate attraction.

There are two main contexts in which communication between conspecific males occurs. First, male-male communication plays a role in maintaining inter-male spacing in breeding choruses. This has been demonstrated in a number of species including *Acris crepitans* (Perrill & Shepherd, 1989; Wagner, 1989a, b), *Pseudacris crucifer* (Brenowitz et al., 1984; Gerhardt et al., 1989), *Uperoleia rugosa* (Robertson, 1986) and *Eleutherodactylus coqui* (Stewart & Bishop, 1994).

Second, communication between conspecific males allows opponents to assess one another during agonistic encounters. In some species, males use the dominant frequency (the frequency of maximum relative amplitude) of an opponent’s call to evaluate the size of the opponent (e.g. *Bufo bufo*: Davies & Halliday, 1978; *Bufo calamita*: Arak, 1983; *Rana clamitans*: Ramer et al., 1983; and *Uperoleia rugosa*: Robertson, 1986). Dominant frequency is negatively correlated with male size in a large number of species, and, in several studies, larger males won more aggressive physical encounters than smaller males (e.g. *Bufo bufo*: Davies & Halliday, 1978; *Rana clamitans*: Wells, 1978; *Bufo calamita*: Arak, 1983). A male frog may use the dominant frequency of an opponent’s call to assess his opponent’s relative size and, therefore, estimate his probability of winning an escalated encounter.

Anurans of the family Ranidae often have complex vocal repertoire in which several distinct call types are used in various contexts (Capranica, 1968; Wiewandt, 1969; Wells, 1978; Given, 1987). We examined male-male communication in the green frog, *Rana clamitans*. Wells (1978) described five call types in the vocal repertoire of the male green frog.
Males used the type I ‘advertisement call’ to announce their location in the pond both to neighboring males as reproductive rivals, and to females as prospective mates. The type I call was usually delivered as a single note, but could consist of several notes in rapid succession. The purpose of these additional notes is not clear, but Wells (1978) suggested they may serve as additional locational cues given in dense green frog choruses. Wells (1978) described the type II call as a ‘high intensity advertisement call’, which occurred much less frequently than the type I call in a green frog chorus. This multiple-note call differed structurally from the type I advertisement call in that the amplitude of each note is initially lower and rapidly increases with an abrupt termination. The type III call, which was termed the ‘encounter call’ by Wells (1978), functioned in aggressive interactions between males. This call was given as the resident male approached an intruding male and often preceded physical encounters. Fighting commonly occurred if an approaching intruder did not retreat after being challenged by one or two type III calls. Wells (1978) consistently evoked aggressive vocal responses, presumably the type III encounter call, from territorial males by the playback of the type I advertisement call. The two other calls described by Wells (1978), the type IV ‘growl’ and the type V ‘release call’, were not heard during our study.

Wells (1978) does not provide detailed analyses of the spectral qualities of these five call types. Ramer et al. (1983) provide spectral data for the type I advertisement call. In this study, we provide a description of the temporal and spectral properties of the type I, II, and III calls. We investigated the role of the type I and type II calls in male-male communication through a series of three field playback experiments. We report the results of these experiments in which we examined the responses of territorial males to the playback of a single-note and a multiple-note type I advertisement call, and a type II high intensity advertisement call. The contexts in which various calls most commonly occur are described, and the possible functions they serve in communication between males are discussed.

Materials and methods

We studied the vocalizations of male green frogs from 31 May to 19 July, 1994. Individual males were toe-clipped and fitted with uniquely colored waistbands of embroidery floss, which permitted identification from distances greater than 2 m without any unnecessary
disturbance of the animal. Late in the season the use of wastebands was abandoned due to physical injury incurred by some males. Subsequently, males were identified by individual dorsal color patterns. Upon initial capture, we measured the snout-to-vent lengths (SVL) of all males. Seven males were weighed during the last week of the study.

We recorded vocalizations using a Marantz PMD430 cassette recorder with an Audio-technica AT815a condenser microphone held 30-50 cm from a calling male. Recording levels were maintained at the same level for all recordings despite variations in the distance between subjects and the microphone. Measurements of sound pressure levels (SPL) were made with a Brüel and Kjær Precision Integrating Sound Level Meter Type 2230 mounted on a tripod that could be positioned in the water so that the microphone was 50 cm from a calling male. Playback broadcasts were made using a Marantz PMD420 or PMD221 cassette recorder with a Sony APM-090 Amplifier Powered Monitor mounted on a styrofoam platform floated to 1 m of the test subject. Stimuli were broadcast between 83 and 87 dB (re 20 μN/m RMS) at a distance of 1 m. These sound pressure levels closely approximate the intensity of natural calls at a distance of 50 cm. Recorded calls were analyzed using the SoundEdit program for Macintosh computers.

Three series of playback experiments were performed. The conspecific stimuli used for each of the three experiments were recordings of males in the population made during the first week of the study. They included: 1) a single-note type I advertisement call (dominant frequency = 339 Hz; duration = 0.21 s; 15-s tape loop; Fig. 1a); 2) a multiple-note type I advertisement call (3 notes; dominant frequencies of the first, second, and third notes = 382, 364, and 339 Hz, respectively; duration = 0.95 s; 20-s tape loop; Fig. 1b); and 3) a type II call (4 notes; duration = 6.28 s; 20-s tape loop; Fig. 1c). A synthetic *Acris crepitans* call was used as a control call in each experiment (10 notes per call group; 6 pulses per call; dominant frequency = 3500 Hz; duration of call group = 1.89 s; 7.20-s tape loop).

To conduct a test, we first located and identified a steadily calling male, quietly approached the male and floated the speaker platform to 1 m from the subject. This usually caused the test male to stop calling, and sometimes the animal dove, but usually resurfaced in or near the same area within one or two minutes. We began each test when the male resumed steady calling.

The first series of playback experiments (N = 12 males) consisted of four 6-min test periods. The first was always a period during which no stimulus was broadcast. The calls recorded during this period were considered unsolicited calls and they served as a control. During the subsequent three 6-min periods, three stimuli were broadcast sequentially: 1) single-note type I, 2) multiple-note type I, or 3) control call. The order of stimulus presentation was rotated for each test to reduce potential effects due to presentation order. We analyzed the dominant frequency and note duration of all calls given during each test to obtain means for all four test periods for each of 12 males.

In a second series of playback experiments (N = 10 males) we recorded changes in the sound pressure levels of calls made in response to a conspecific stimulus. Each test began with a no-stimulus period during which we recorded unsolicited calls. Each male was then presented with the single-note type I stimulus and the control call in sequence, with the order of presentation switched for each test. Sound pressure level readings were taken for six calls during the no-stimulus period and each of the two stimulus periods for each male. Four of these were root-mean square (RMS) values and two were peak values.
Fig. 1. Sonograms displaying relative intensities at various frequencies: A) single-note type I advertisement call; B) three-note type I advertisement call; C) the second, third, and fourth notes of a type II high intensity advertisement call; D) type III encounter call.

The final series of playback experiments (N = 16) had a design similar to the first series of tests. Each test began with a 6-min no-stimulus period during which unsolicited calls were recorded. This period was followed by two 6-min periods during which the type II stimulus and the control stimulus were broadcast in sequence, with the order of presentation of these two stimuli reversed for each test.

Correlations between dominant frequency and SVL were determined using calls recorded on nights when the water temperature varied between 26.8 and 31.9°C. A small temperature range was necessary to minimize the effect of temperature differences on dominant frequency. All correlation coefficients and descriptive statistics were determined using the Data Analysis tool of Microsoft Excel 5.0 for IBM computers. Non-parametric statistics and analysis of variance were performed using the statistical package Statview Student for Macintosh computers.

Results

During the eight week study, we captured and marked 61 adult green frogs. The mean SVL of adult males was 76.5 mm (SD = 4.6 mm, N = 53) and
of adult females, 81.2 mm (SD = 8.6 mm, N = 8). The mean mass for seven males was 35.7 g (SD = 5.9 g). We examined four types of male vocalizations: 1) single-note type I calls, 2) multiple-note type I calls, 3) type II calls, and 4) type III calls.

_Vocalizations of Rana clamitans_

Type I calls

The type I advertisement call is by far the most commonly heard call in a green frog chorus. The call consists of 1 to 6 notes, but the single-note call accounted for 99% of the unsolicited calls recorded in this study. Call duration for single-note type I calls ranged from 0.07 to 0.28 s (mean = 0.16 s, SD = 0.03, N = 182 calls). A steadily calling male typically produced one call about every 40 to 90 s, with a mean call interval of 50.9 s (198 calls in 168 min). RMS intensity values for single-note type I calls recorded at 50 cm ranged from 77.0 to 89.7 dB (mean = 83.2 dB, SD = 3.0 dB, N = 48 calls). Peak intensity values ranged from 96.3 to 106.8 dB (mean = 99.7 dB, SD = 2.5 dB, N = 18 calls).

The type I advertisement call has a broad band signal with substantial energy between 100 and 5000 Hz (Fig. 1a). Maximum energy is concentrated in two bands. The first high energy band occurs between 300 and 500 Hz. The second occurs between 1300 and 2100 Hz. The lower band contains the dominant frequency of the call. For the single-note type I calls and the first note of the multiple-note type I calls, dominant frequencies ranged from 353.6 to 484.5 Hz (mean = 400.6 Hz, SD = 34.0 Hz, N = 139 calls). There was a highly significant, negative correlation between a male's SVL and the dominant frequency of his advertisement call ($r = -0.79, p < 0.01, N = 19$; Fig. 2).

The multiple-note type I advertisement call consists of 2 to 6 notes (mode = 2 notes, N = 11 calls). In a multiple-note type I call the notes progressively decreased in amplitude (Fig. 1b), but because these notes are produced in rapid succession, we could not obtain SPL readings for each of the individual notes. The notes in the multiple-note type I call had a mean dominant frequency of 372.0 Hz (SD = 40.3 Hz, N = 23 calls). The mean note duration was 0.19 s (SD = 0.05 s, N = 23 notes) and the mean interval between successive notes in a multiple-note call was 0.47 s (SD = 0.27, N = 13 intervals).
Type II calls

The type II high intensity advertisement call is produced very rarely in comparison with the type I call. The call consists of between 2 and 13 notes (mode = 4 notes, N = 7 calls). These notes begin with relatively low amplitude and progressively increase in amplitude as the note proceeds, culminating in a sharp burst of sound (Fig. 1c). Typically, the first note is very similar to a single-note type I call. The mean dominant frequency for the first notes of type II calls was 373.4 Hz (SD = 0.69 Hz, N = 7), and the mean duration was 0.23 s (SD = 0.04 s, N = 7). The subsequent notes in the type II call were longer and lower in frequency, having a mean duration of 0.45 s (SD = 0.08 s, N = 23 notes) and a mean dominant frequency of 354.7 Hz (SD = 19.7 Hz, N = 23 notes).

Playback experiments

Experiment 1

In the first playback experiment, we examined four parameters of a male’s response to the broadcast of a conspecific call: 1) the behavioral response
of the animal, 2) the number of calls made, 3) the dominant frequency of the calls, and 4) the note duration of response calls.

As soon as the first conspecific stimulus was broadcast, all 12 males immediately oriented toward the speaker. All 12 males also made at least one move from their original position, and for 10 of 12 cases, at least one move was in the direction of the speaker. The number of moves made by the 12 males ranged from 1 to 11. When males moved to a new position, they often splashed a great deal by repeatedly spinning around after arriving in the new location. Six males mounted the speaker platform, and 4 of these males approached to within 5 cm of the face of the speaker. No males physically contacted the speaker.

Three parameters of vocal behavior were examined in the first playback experiment. The first was the number of calls each male made during each of the four 6-min test periods. There were significant differences in the number of calls given by males among the four test periods (ANOVA, $F_{3,33} = 15.0, p < 0.01$). Compared to the unsolicited period, males significantly increased the number of calls they made in response to the single-note and the multiple-note type I stimuli (single-note: Dunnett’s $t = 3.21, p < 0.01$; multiple-note: Dunnett’s $t = 4.75, p < 0.01$; Fig. 3a). There were no significant differences between the number of calls given in the unsolicited and control call periods (Scheffe’s $F_{1,33} = 0.431, p > 0.05$), or between the number of responses given to the single-note and multiple-note stimuli (Scheffe’s $F_{1,33} = 0.795, p > 0.05$).

Nine of the 12 males increased the number of calls they made in response to both conspecific stimuli. Two males gave an increased number of calls to only one of the two conspecific stimuli, one to the single-note stimulus and one to the multiple-note stimulus. One male reduced his calling during both stimulus test periods, and one individual gave no response to the single-note stimulus. In some cases, the increase in calling activity was dramatic. For example, one male gave 4 calls during the unsolicited portion of the test, and 32 calls in response to the multiple-note stimulus, representing an eight-fold increase in the rate of calling. In these extreme cases, the test animal sometimes gave more than one response each time a single stimulus call was broadcast. The effect was somewhat like a back-and-forth vocal contest, in which the test male would respond almost immediately to each call from the speaker with a vocalization of his own.
Fig. 3. A) Mean plus one standard deviation of the number of calls produced during the four test periods of playback experiment 1 (N = 12); B) Mean dominant frequencies of calls produced during the four test periods of playback experiment 1; C) Mean note duration of calls produced during the four test periods of playback experiment 1; D) Mean amplitude of calls produced during the three test periods of playback experiment 2 (N = 10). None = no-stimulus period, SN = single-note stimulus period, MN = multiple-note stimulus period, Control = Acris crepitans stimulus. Asterisks above error bars indicate significant differences from the unsolicited calling period. *p < 0.05, **p < 0.01.

In our examination of the dominant frequency of calls from the first playback experiment, only single-note calls and the first note of multiple-note calls were included in the analysis. The mean dominant frequency of unsolicited calls was 398.7 Hz (SD = 26.6 Hz, N = 78). In response to the broadcast of the single-note stimulus, the mean dominant frequency of the males’ response calls was 363.8 Hz (SD = 33.9 Hz, N = 157), a mean decrease of 8.8% (range = 4.5 to 15.9%; mean decrease = 34.9 Hz, SD = 17.9 Hz; Fig. 4). The mean dominant frequency for the response calls of males responding to the multiple-note stimulus was 362.2 Hz (SD = 31.6 Hz, N = 195), a mean decrease of 9.1% (range = 1.2 to 16.8%; mean decrease = 36.2 Hz, SD = 18.6 Hz). In both cases, the decrease
in dominant frequency represents a highly significant difference compared to dominant frequencies of unsolicited calls (ANOVA, $F_{3,30} = 14.4$, $p < 0.01$; single-note stimulus: Dunnett's $t = 5.25$, $p < 0.01$; multiple-note stimulus: Dunnett's $t = 5.43$, $p < 0.01$; Fig. 3b). There were no significant differences between the responses to the two conspecific stimuli in the extent to which males lowered the dominant frequency (Scheffe’s $F_{1,30} = 0.011$, $p > 0.05$), or between the dominant frequencies of calls made during the unsolicited and control periods (Scheffe’s $F_{1,30} = 0.984$, $p > 0.05$).

We further compared the dominant frequencies of the calls given in the unsolicited and stimulus test periods to see how well dominant frequency predicts male body size in calls given in response to a conspecific stimulus. Dominant frequency was significantly correlated with male SVL during the unsolicited and multiple-note stimulus periods, but not during the single-note stimulus period ($r = -0.78$, $p < 0.01$; $r = -0.73$, $p < 0.05$; and $r = -0.57$, $p > 0.05$, respectively; $N = 11$ for all correlations). We
examined and found no significant correlation between a male’s size and the extent to which he lowered the dominant frequency in his responses to either stimulus (single-note: $r = 0.08$, $p > 0.10$, $N = 11$; multiple-note: $r = -0.14$, $p > 0.10$, $N = 11$). We also examined and found no significant correlation between the extent to which a male lowered his dominant frequency and the probability he would attack the speaker (single-note: $r = 0.17$, $p > 0.05$; multiple-note: $r = -0.01$, $p > 0.05$). An attack was defined as mounting the speaker platform and approaching to within 5 cm of the face of the speaker during any broadcast of a conspecific stimulus. There was also no significant correlation between the extent of dominant frequency decrease in response to either conspecific stimulus and the number of moves a male made in his behavioral response (single-note: $r = 0.27$, $p > 0.05$; multiple-note: $r = 0.40$, $p > 0.05$).

A second vocal parameter we examined was the duration of single-note calls and of the first note of multiple-note calls made during the test. There were significant differences in note duration among the four test periods (ANOVA, $F_{3,30} = 5.56$, $p < 0.01$; Fig. 3c). The mean note duration for unsolicited calls was 0.18 s (SD = 0.03 s, $N = 78$). In response to the single-note stimulus, males lengthened the notes in their calls by an average of 14% (range = $-8.7$ to $37.5\%$, mean duration = 0.20 s, SD = 0.03 s, $N = 157$, Dunnett’s $t = 3.37$, $p < 0.01$). Eight of 11 males lengthened the notes in their response calls; two males did not change the duration of the notes of their calls; one male produced shorter notes in his response calls; and one male did not respond to the single-note stimulus. Males also produced significantly longer notes in response to the multiple-note stimulus, with an average increase in duration of 9.3% (range = $-9.5$ to $27.3\%$, mean duration = 0.20 s, SD = 0.03 s, $N = 195$, Dunnett’s $t = 2.70$, $p < 0.05$). Ten males produced longer notes; one male did not alter the length of his notes; and one male gave shorter notes in his response calls. There were no significant differences in note duration between the single-note and multiple-note stimulus periods (Scheffe’s $F_{1,30} = 0.152$, $p > 0.05$), or between the unsolicited and control periods (Scheffe’s $F_{1,30} = 0.055$, $p > 0.05$).

Note duration was not correlated with SVL for calls produced during any of the test periods. There was a strong negative, but non-significant, correlation between SVL and the extent of duration alteration in calls made
in response to the single-note stimulus \((r = -0.59, p > 0.05)\). We also examined the correlation between the extent of note duration alteration and the probability of attack and found a significant negative correlation for calls made in response to the single-note stimulus \((r = -0.67, p < 0.05, N = 11)\).

Experiment 2

Single-note unsolicited calls, measured at 50 cm, had a mean RMS intensity of 83.2 dB (SD = 3.0 dB, \(N = 40\) calls). Calls made in response to the single-note stimulus were significantly less intense with a mean value of 81.7 dB (SD = 2.7 dB, Wilcoxon matched pairs signed-ranks test, \(p < 0.01\); Fig. 3d), representing an average decrease in amplitude of 1.62 dB (SD = 1.15 dB, \(N = 10\) individuals). Nine of the 10 males tested decreased the sound pressure level of their responses. The intensity of calls made during the control periods did not differ significantly from unsolicited call intensities (Wilcoxon matched pairs signed-ranks test, \(p > 0.20\)). Amplitude was not significantly correlated with SVL in any of the test periods, and there were no significant correlations between the extent of amplitude decrease and the probability of attack.

Experiment 3

Playback of the type II call failed to elicit the same agonistic response as the single-note and the multiple-note type I calls. Four of 16 males in this test oriented to the speaker during the playback of the type II call, two moved away from the speaker and resumed normal calling, two approached the speaker, and none mounted the speaker platform. Most males remained in their original calling positions and continued normal calling.

We examined the type of calls given in each response: calls were scored as type I, II, or III. Type II calls were easily identified. Type I advertisement calls and type III encounter calls were distinguished primarily by differences in dominant frequency, based on the decrease in the dominant frequency of response calls observed in playback experiment 1. A male's response was designated as a type III call if its dominant frequency was 20 Hz or more below the mean dominant frequency of the unsolicited calls recorded for that particular male during the same test.
TABLE 1. Number of call types I, II, and III, given during the 28 no-stimulus, 12 single-note type I stimulus, 12 multiple-note type I stimulus, and 16 type II stimulus test periods

<table>
<thead>
<tr>
<th>Call type</th>
<th>None</th>
<th>Single-note</th>
<th>Multiple-note</th>
<th>Type II</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type I</td>
<td>196</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Type II</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Type III</td>
<td>0</td>
<td>157</td>
<td>97.5%</td>
<td>195</td>
</tr>
</tbody>
</table>

The broadcast of the type II high intensity advertisement call elicited more type II response calls than either the single-note or multiple-note type I stimuli (Table 1). About 13% (17 of 129) of the calls made in response to the type II stimulus were type II calls. Based on analysis of dominant frequency, 50% (65 of 129) of the response calls were single-note type I advertisement calls, and 23% (30 of 129) were multiple-note type I calls. Approximately 13% (17 of 129) of the calls made in response to the type II stimulus were type III encounter calls. However, most (13 of 17) of these type III calls were given by one male who aggressively approached the speaker. The other 4 type III calls were given by three other males in this test. Hence, with the exception of one individual, males rarely responded to type II calls with aggressive behavior and type III calls.

The broadcast of the type II call also had an effect on the chorus as a whole. When the type II call was broadcast, males on territories adjacent to that of the test animal often began giving type II calls. Then, sometimes, the males on the opposite side of the neighboring male began giving type II calls. The number of males producing type II calls might continue to increase until choruses of type II calls developed, similar to those described by Wells (1978).

Discussion

Type II high intensity advertisement calls

Wells (1978) and Ramer et al. (1983) describe the type II call as an intermediate and integral step in the escalation of an aggressive encounter. These calls are given when males respond to an initial disturbance in their
territories (Wells, 1978). This is consistent with the observations of Ramer et al. (1983) who were able to elicit the type II call when they broadcasted conspecific calls from a distance of 3 m.

If the type II call is intermediate in aggressive context, our inability to elicit the type II call using the type I stimuli can be explained as a function of perceived intruder distance. We played back the type I stimuli at a distance and SPL simulating an intruder calling from 50 cm. At this distance, an intruder likely represents an immediate threat to a calling male. Thus, males in our experiments would be expected to respond with their most aggressive call, the type III encounter call. However, this does not explain why males did not respond more aggressively to the playback of the type II call. Only four of sixteen males responded aggressively to the type II stimulus with encounter calls. Most males gave one or two type II calls during the initial portion of their response before resuming normal calling.

The specific context of the type II high intensity advertisement call, and the level of aggression contained in this call are unclear. It may be possible to demonstrate the context through further tests in which calling males are presented with playbacks of a type II stimulus which sequentially increases in SPL, simulating the approach of an intruding male. Such tests might clarify the inconsistencies reported in the literature (i.e. Jenssen & Preston, 1968; Wells, 1978; Ramer et al., 1983) concerning the sequence of aggressive escalation in green frogs, as well as the role of the type II call in this escalation.

Type III encounter calls

Wells (1978) consistently evoked aggressive responses with the playback of the type I advertisement call. Males in our playback experiments also responded aggressively to the type I call. This aggressive response included approaches to the speaker platform, and the alteration of various spectral and temporal characteristics in response calls. These altered response calls are the type III encounter calls (Fig. 1d) described by Wells (1978).

The type III encounter call differs from the type I advertisement call in three main respects: 1) the dominant frequency of the type III call is lower than the dominant frequency of the type I call; 2) the type III call has a longer note duration than the type I call; and 3) the type III call is less
intense than the type I call. In most cases, we could identify call types during a test based on their relative pitch, volume, and duration, with type III calls sounding lower in pitch, less intense, and slightly longer than type I advertisement calls.

**Male assessment and frequency alteration**

Most animal conflicts are considered to be asymmetric (Maynard Smith & Parker, 1976). When asymmetries in expected pay-off or fighting potential exist between combatants in a conflict, animals should assess their opponents before escalating the conflict (Dawkins & Krebs, 1978). Assessment can provide probabilistic predictions about the outcome of a fight between two individuals (Parker, 1974).

Because dominant frequency is negatively correlated with SVL in a number of anurans (Arak, 1983; Ramer et al., 1983; Ryan, 1985; Wagner, 1989a), and large males tend to win more fights than smaller males (Davies & Halliday, 1978; Wells, 1978; Wagner, 1989c), dominant frequency is probably a good cue for assessing the fighting ability of an opponent. Indeed, males use dominant frequency as a cue in assessing an opponent’s size in several anuran species (Davies & Halliday, 1978; Arak, 1983; Ramer et al., 1983; Robertson, 1986).

Wagner (1992) suggested that males of the cricket frog (*Acris crepitans*) use decreases in dominant frequency as an assessment cue during agonistic encounters. Frequency alteration during interactions between males has been rarely reported in anuran vocalizations. Lopez *et al.* (1988) observed frequency alteration in the white-lipped frog, *Leptodactylus albilabris*, in which males adjusted the pitch of their calls to match that of an opponent, either by raising or lowering the dominant frequency. The green frog is only the third anuran species shown to alter the dominant frequency of their calls during agonistic interactions between males.

Wagner (1992) proposed three hypotheses that potentially explain the function of decreases in dominant frequency during agonistic encounters. First, decreases in dominant frequency could provide dishonest information about the caller’s size if size and dominant frequency are negatively correlated. Second, males could provide a more accurate indication of their size through a decrease in dominant frequency. Third, males could provide
information about some parameter other than size, such as physiological condition, by a decrease in dominant frequency.

During agonistic contests, a male could send a deceitful signal about his size by lowering the dominant frequency in the call, making himself sound larger to his opponent than he actually is. Wagner (1992) found the extent to which male cricket frogs lowered their dominant frequencies to be positively correlated with the probability that they would attack an opponent. If a male were bluffing his size by altering the dominant frequency, he would not be expected to attack. Wagner (1992) concluded that male cricket frogs do not bluff their size by lowering the dominant frequency in their calls during agonistic encounters. We were unable to identify any significant correlation between the extent that male green frogs lowered their dominant frequency and the probability they would attack the perceived intruder. The results presented here on dominant frequency alteration in the green frog do not exclude the possibility of bluffing.

The second hypothesis proposed by Wagner (1992) to explain the decrease in dominant frequency in cricket frogs is the ‘signal of size’ hypothesis. This states that males provide better information to their opponent concerning their own size during conflicts. This information could be communicated in two ways. The production of lower frequency calls may predict size better than unaltered calls, or a male may more accurately indicate his size by the amount that he lowers the dominant frequency. Wagner (1992) was able to demonstrate that size became significantly less predictable in calls in which the dominant frequency had been lowered. He also found no significant correlation between SVL and the extent that males lowered the dominant frequency in their responses. Based on these findings, Wagner (1992) rejected the hypothesis that male cricket frogs are signaling their size by lowering the dominant frequency of calls given in agonistic encounters.

Our results do not support the hypothesis that male green frogs signal their size by lowering the dominant frequency in their calls. The dominant frequency of unsolicited calls was the best predictor of a male green frog’s SVL, and size became less predictable in calls made in response to both conspecific stimuli. We also found no correlation between SVL and the extent of dominant frequency alteration, indicating that male green frogs do not signal their size in the actual frequency decrease. These results
suggest that any signal contained in a decrease in dominant frequency is independent of a male's size.

The third hypothesis proposed by Wagner (1992) to explain decreases in dominant frequency is the 'signal of size-independent fighting ability', in which males provide a signal of some physical parameter indicative of their ability to win an escalated fight by decreasing their dominant frequency. Wagner (1992) accepted this hypothesis based on two observations in cricket frogs. First, the extent of dominant frequency decrease was significantly correlated with the probability that a male would attack (i.e. his fighting ability). Second, the decrease in dominant frequency was not correlated with size. Thus, any cue contained in the dominant frequency decrease was independent of size, and because the decrease was correlated with a male's potential to attack his opponent, Wagner (1992) concluded that male cricket frogs lower the dominant frequency of their calls to signal their size-independent fighting ability.

Our results on green frogs are insufficient to accept the hypothesis of 'signal of size-independent fighting ability'. We were unable to identify a significant correlation between the extent to which a male lowered his dominant frequency and the probability that he would attack. There were no relationships between the extent of dominant frequency change and the number of times males mounted the speaker platform or the number of moves they made in an effort to locate the sound source.

Finally, it is possible that the decrease in dominant frequency has no functional significance of its own in assessment between agonistic opponents. The type III encounter call, in addition to having a lower dominant frequency, also differed significantly from the type I advertisement call in note duration and call amplitude. The decrease in both dominant frequency and amplitude is potentially explained as a function of increased note duration.

Dudley & Rand (1991) suggested that frequency and amplitude modulation in the Túngara frog (*Physalaemus pustulosus*) were due to a decrease in the rate of air flow across the vocal cords. The situation may be similar in the green frog. The decrease in dominant frequency and amplitude associated with the type III call may be derived from the production of longer notes. If this is the case, the functional significance of a decrease in dominant frequency becomes less certain. It is, then, possible that males
communicate aggressively through the production of longer call notes, and decreases in dominant frequency and amplitude are artifacts of producing longer notes. However, this is unlikely given the observed negative correlation between duration increase and the probability of attack. Furthermore, males do not seem to be bluffing by an increase in note duration, since neither duration nor the extent of duration increase were correlated with male body size. It may be that the only way for males to decrease the dominant frequency in their calls is to decrease the flow rate of air across the vocal cords. In this case, the production of lower frequency calls would rely on pushing air across the vocal cords at a slower rate, thus longer notes would be produced. Further field manipulations, in which males are presented with multiple stimuli in which either dominant frequency or note duration are varied independently, could provide an answer to the question of whether males use dominant frequency or note duration as a cue for assessment purposes.

References


