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Call matching in the quacking frog (*Crinia georgiana*)

Abstract Males of the quacking frog *Crinia georgiana* produce calls consisting of 1–11 notes. Playback experiments using synthetic calls showed that males tend to match the number of notes in 2-note and 4-note stimuli; however, males tended to produce more than 1 note in response to a 1-note stimulus and fewer than 8 notes in response to an 8-note stimulus. Successive playbacks of two, 4-note calls from separate speakers indicate that males are likely to match the combined number of notes in the calls of two neighbors, even if they are not equidistant from the focal male. The results are compared with the few other studies of matching in anurans, and interpreted in terms of hypotheses developed to explain matching in songbirds. One attractive and testable hypothesis for call matching in *C. georgiana* is that males are attempting to produce calls that are at least as attractive to females as those of rivals, without wasting energy.

Key words Call matching · Male competition · Frogs · *Crinia georgiana*

Introduction

Competition among males for mates takes many forms (Andersson 1994). Males may fight over receptive females or for territories containing resources needed by females or serving to improve detection of a male's signals. Endurance rivalry is another important form of competition, where males attempt to out-signal one an-

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other or to maximize their participation in signaling aggregations that form in places where females arrive for mating. In numerous species, mating success is positively correlated with the rate or duration of signaling and with attendance at display areas (Andersson 1994).

Displays are often energetically demanding, and in species with long breeding seasons, signaling males often lose a significant proportion of their body mass. Signaling males may also incur increased risks of detection by predators, parasites, or both (e.g., Given 1988; Grafe 1996a; Murphy 1994; Zuk et al. 1998). Because of these costs, we might expect to find mechanisms that allow males to adjust their signaling effort according to that of their nearby rivals rather than always signaling at the maximum sustainable rate.

Most studies of male-male interactions between vocalizing frogs have focused on the signaling used to acquire and defend territories (Wells 1988) or on the timing of the signals of neighbors, which is usually some form of call alternation (Grafe 1996b; Klump and Gerhardt 1992; Schwartz 1993). As in some acoustic insects, pairs of males rapidly alternate calls, and their signals rarely overlap; however, because of female preferences, males may compete to produce leading rather than lagging signals (Greenfield 1994). Call matching, another form of vocal interaction which is probably competitive, has been described in a few species of frogs. In these species, the number and complexity of calls that are produced by a male are approximately matched by its neighbor. In the Neotropical treefrog, *Hyla microcephala*, males match secondary, click-like notes that are produced after long introductory notes (Schwartz 1986). In a Sri Lankan species, *Philautus leucorhinus*, neighboring males match the number of notes in calls during exchanges of multi-note aggressive calls (Arak 1983). Call matching by number and song type also has been well described in birds (e.g., Catchpole and Slater 1995; Krebs et al. 1981; see Discussion).

In this paper, we discuss experimental studies of call matching in an Australian frog, *Crinia georgiana* (Myobatrachidae), a species with a complex mating system
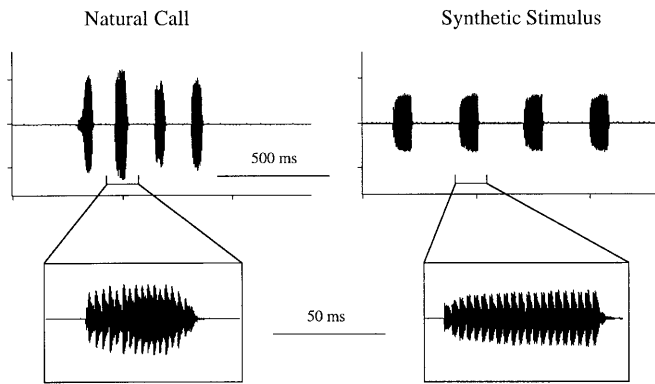
Fig. 1 Oscillograms of a 4-note advertisement call and a representative 4-note synthetic call
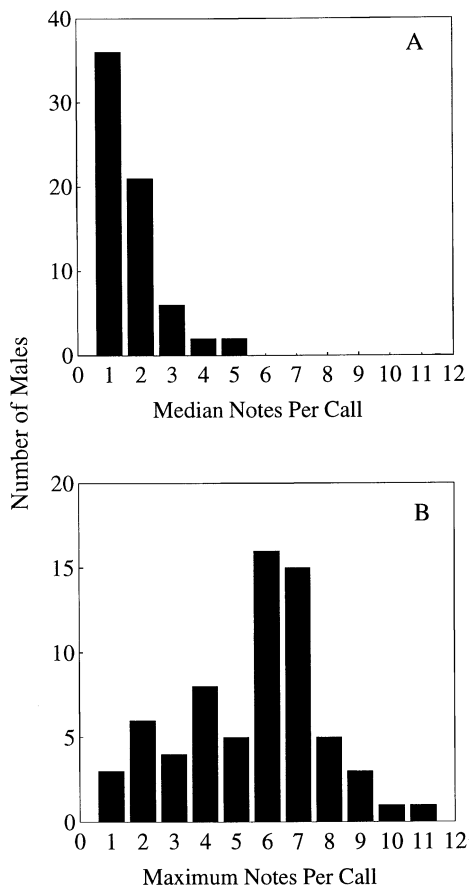

Fig. 2 Histograms showing frequency of occurrence of calls with different note numbers. Values are median note numbers (**A**) and maximum note numbers (**B**) recorded from individual males (*n*=67) during 10-min recording sessions

that includes frequent polyandrous matings resulting from other males joining conventionally amplexed pairs (Byrne and Roberts 1999; Roberts et al. 1999). Males of this species produce advertisement calls that consist of 1 to 11 pulsed notes (Figs. 1, 2). A previous laboratory study showed that males tended to alternate calls with an artificial acoustic stimulus and increased then reduced

the number of notes in their calls as the rate of stimulus presentation increased (Ayre et al. 1984). These authors interpreted these results as a tactic to reduce the likelihood of call overlap. The acoustic stimuli they used did not, however, simulate the natural calls of this species, nor were the responses of males interpreted as call matching. In this paper, using more realistic stimuli and field playbacks, we show that call matching is well developed in *C. georgiana* and that males might match the combined number of notes produced by two neighbors. We argue that call matching functions to adjust a male's energetic output to equal that of his rivals in order to conserve energetic reserves while still effectively competing for females.

Methods

Field assessments of advertisement calls, male attributes, and calling behavior

We recorded the advertisement calls of 116 males on magnetic tape using Sony WMD6C (Walkman), TCD5PRO, or TCD5ProII cassette tape recorders and Beyer M88, M100, or Sennheiser ME88 microphones. This total included many of the males that we tested in playback experiments. We measured the air and water temperature at the calling site, body mass, and snout-vent length (SVL). We also measured the call amplitude [sound pressure level (SPL) in decibels re 20 µPa; C-weighted and peak or fast root mean square settings (RMS)] at distances of 30 cm in front of a subset (*n*=30) of males using a Brüel and Kjœr type 2231 sound level meter with a type 4155 microphone. These data were used to assess correlations between body size, call amplitude, and attributes of the calls such as dominant frequency and median and maximum numbers of notes per call and to set intensity levels during call playbacks. The number of males used in these correlations is sometimes less than the sample sizes stated here because we failed to measure all attributes for all males.

We used a computer-based system to record the number of notes per call produced by groups of up to eight males (*n*=67; see Schwartz 1993 for details). Up to eight directional microphones (Audio-technica ATR-55) were connected to a battery-powered interface board that sent its output to an IBM 733 Thinkpad via the parallel port. The output for each of eight parallel channels of the board underwent a retriggerable voltage transition, of preset duration, in response to above-threshold input from a microphone. The duration of the output pulse from the board (7.5 ms) and the sampling rate of the computer (100 Hz) were set so the temporal resolution of the system was more than sufficient to discern individual notes in the calls of *C. georgiana*. Data were filed to disk every 10 min. We used custom software (J.J. Schwartz, unpublished) to convert the raw binary data files into ASCII files listing the start and end times of the calls of each male as well as a note count within each call. These files were subsequently analyzed using SAS (Cary, N.C., version 6.12). The distances between males (*n*=66), their mass and SVL (*n*=61), and temperature at each calling site were measured after the recordings were completed.

Acoustic stimuli

Acoustic stimuli consisted of synthetic signals that were created by a custom-designed program written by J. Schwartz. The digital files consisted of 8-bit data with an output sampling rate of 20 kHz. The acoustic properties of these signals were chosen to match estimated mean values of the following properties of samples of natural calls recorded at two temperatures (11 and 14°C): pulse rate, note duration, note rise-fall times and shapes, and carri-

er frequency. The synthetic calls did not incorporate the relatively small changes in pulse rate that occur within notes, nor the slight, within-note frequency modulation. The oscillograms of Fig. 1 compare a recorded 4-note advertisement call with a 4-note synthetic call. Calls were played back from an IBM 733 Thinkpad (interfacing hardware and software from Siliconsoft) through an Aiwa Mini Compo Stereo Integrated Amplifier 16 and Sonics Mini 7 speakers. In 1997, we also used a Hewlett-Packard 350D Attenuator Set to vary relative output levels from two speakers. In standard playbacks, amplifier and attenuator settings were adjusted to achieve SPLs of approximately 80–85 dB at a distance of 50 cm in front of the speaker. The intensity of the advertisement calls of six males at 50 cm ranged from 82 to 88 dB SPL (fast RMS).

General playback procedures

Persistently calling males were located, and any other calling males within about 2 m of the target male were removed. We measured air and water temperatures near the male and chose the set of synthetic calls that best matched field temperatures (±1.5°C). One or two speakers were positioned about 50 cm from the male. Speaker orientation in single-speaker tests was in a frontal zone from between about 90° left to 90° right of the frog; the angle varied depending on vegetation and frog movements. The speakers in two-speaker tests were positioned, to the extent possible, at 90° left and 90° right relative to the frog. Playbacks commenced after the frog had produced several spontaneous calls, and its responses as well as our acoustic stimuli were recorded. After completion of a playback, we captured the frog, weighed and measured it as described above. The microphone of the sound level meter was then placed at the frog's original position, and the actual SPL of the synthetic signal was measured at that point. The SPL of the stimulus varied between 80–85 dB.

Experiment 1:
call matching in response to playbacks from a single speaker

In September 1996, we tested 19 males using a repeated-measures experimental design. A stimulus call contained 1, 2, 4, or 8 notes. A complete test consisted of broadcasts of two repetitions of each of these stimuli in each of five consecutive random sequences for a total of 40 stimulus presentations. The order of the sequences was determined randomly for each new subject. Calls within sequences were separated by call periods of 8–10 s, and consecutive sequences were separated by 15–30 s. The two intervals between playbacks of calls used here and in experiment 2 (see below) were both within the range of variation for call period: about 8 to >60 s (mean=27.7 s). Due to technical difficulties with the playback system during one test, one male included in our dataset heard 12 1-note, 11 2-note, 9 4-note, and 8 8-note stimuli.

From the recordings of each test, we determined the proportion of times a male responded to each of the four stimuli, and we determined the number of notes in the first call produced during the interval between two consecutive stimuli. Using the oscilloscope mode of a Kay DSP Sona-Graph Model 5500, we measured (to the nearest millisecond) the latency of the first note produced by a male in response to a synthetic call from (1) the beginning of the first note of each stimulus (latency A) and (2) the end of the last note in each stimulus (latency B). One subject did not respond to any of the 1-note stimuli and was excluded from the analyses of response latency and note number.

Experiment 2:
call matching in response to playbacks from two separate speakers

In August 1997, we tested eight males in a second within-subjects experiment to determine whether males match only the notes in the calls of their closest neighbor or whether they might produce multi-note calls that matched the sum of the call notes of two neighbors. We also varied the relative SPL of the playbacks from the two speakers to simulate two neighbors at different distances from the target male. This procedure was designed to determine if the number of notes produced by a male was influenced only by the calls of very close neighbors or whether males might be influenced by the calls of a nearby neighbor and a relatively distant one. We presented males with a 4-note call from a single speaker as a control stimulus. As test stimuli, we presented four 8-note calls in which the first 4 notes and the last 4 notes were broadcast from different speakers separated by 180°. To simulate neighbors at variable distances, we attenuated the second 4 notes by 0, 6, 12, or 20 dB. During a test, we broadcast each of the five stimuli (the four 8-note calls and the control) between 2 and 28 times in a randomly determined order. Seven of eight males heard each stimulus at least six times. We counted the number of notes in each response call.

Statistical analysis

We calculated the mean number of notes in responses to each stimulus for each subject in experiments 1 and 2, and the mean latencies to respond (A and B, defined above) in experiment 1. The data on the number of notes in each response in experiment 1 met the assumptions of parametric statistics so we used repeated-measures analysis of variance (ANOVA). Relationships between response variables and both body size and temperature were examined with Pearson's product-moment correlations, and we applied a sequential Bonferroni correction to adjust the experimentwide α-level (Rice 1989). We used the modification of the Freeman and Tukey (1950) arcsine square root transformation suggested by Zar (1984) to transform the proportion of times males responded to each stimulus in experiment 1. The transformed proportions for responses to the 8-note stimulus still departed from normality because most males responded to every presentation of this stimulus. These data were also analyzed using repeated-measures ANOVA, however, because parametric statistics are widely regarded as robust to violations of the assumption of normality (e.g., Lindman 1974). Because omnibus repeated-measures tests can violate the additional assumptions of compound symmetry and sphericity, we applied the Greenhouse and Geiser (1959) method to adjust the degrees of freedom for each test. We report P-values for these adjusted degrees of freedom, but report the unadjusted degrees of freedom for each F-test. We also computed linear contrasts and used Scheffé's multiple-comparisons test to compare responses to each stimulus.

We analyzed response latency using Friedman's two-way ANOVA by ranks instead of the parametric repeated-measures test for two reasons. First, variances were not homogeneous: responses to the 1-note stimulus were considerably more variable than other responses. Second, the variance in latency B was positively correlated with mean values across treatment groups. We compared responses to each stimulus using the all-pairs multiple comparison suggested by Hollander and Wolfe (1973).

Because our sample size for the two-speaker playbacks was small (n=8), we were not confident in our tests of the assumptions of parametric statistics. Therefore, we used Friedman's ANOVA and the simultaneous inference test comparing treatments to a control described by Hollander and Wolfe (1973), which we used to compare responses to each of the 8-note stimuli to the 4-note control.

In all analyses, we adopt the conventional significance level of P=0.05 for rejecting null hypotheses. Because of the small sample size, failure to reject the null hypothesis in some tests (noted below) is probably attributable to low statistical power rather than to the lack of an effect.

Table 1 Pearson product-moment correlations between body size (snout-vent length, *SVL*), body mass, temperature, the dominant frequency of the first call note (averaged over 1–16 calls), and sound pressure level (*SPL*; measured as peak SPL at 30 cm in front of the calling male). Sample sizes and *P*-values are provided for each correlation

	Temperature	SVL	Mass	Dominat frequency
SVL	$r=0.05$ $n=116$ $P=0.59$			
Mass	$r=0.04$ $n=116$ $P=0.64$	$r=0.93$ $n=116$ $P<0.001$		
Dominant frequency	$r=0.11$ $n=113$ $P=0.24$	$r=-0.77$ $n=103$ $P<0.001$	$r=-0.74$ $n=103$ $P<0.001$	
SPL	$r=0.65$ $n=30$ $P<0.001$	$r=0.59$ $n=28$ $P<0.001$	$r=0.61$ $n=28$ $P<0.001$	$r=-0.18$ $n=15$ $P=0.53$

Results

Analysis of call structure in natural choruses

Figure 2 shows the median and maximum numbers of notes per call produced by 67 males over 10-min periods in natural choruses. A comparison of the two measures reflects our impression of calling behavior in this species. When males were not interacting with a nearby neighbor, they tended to produce mostly 1- and 2-note calls; however, during relatively brief interactions with neighbors, multi-note calls were commonly produced. There were weak trends for larger males to produce fewer notes per call. From our dataset of 10-min recording sessions, we computed correlations between body mass and median and maximum note number ($r=-0.12$, $P=0.38$, $n=61$ and $r=-0.28$, $P=0.027$, $n=61$, respectively; the latter correlation is not significant after a sequential Bonferroni correction). The distance to the nearest neighbor did not appear to influence either median or maximum note number ($r=0.04$, $P=0.75$, $n=66$ and $r=0.10$, $P=0.41$, $n=66$, respectively).

A summary of correlations between temperature, body mass, body size, dominant frequency of the first note of the advertisement call, and SPL is shown in Table 1. Dominant frequency was strongly and negatively correlated with body mass and SVL, whereas SPL was positively correlated with body mass and size.

Experiment 1

Repeated-measures ANOVA revealed significant differences in the proportion of times males responded to each stimulus ($F_{3,54}=39.04$, $P<0.0001$). Males responded to proportionally more presentations of a stimulus as the
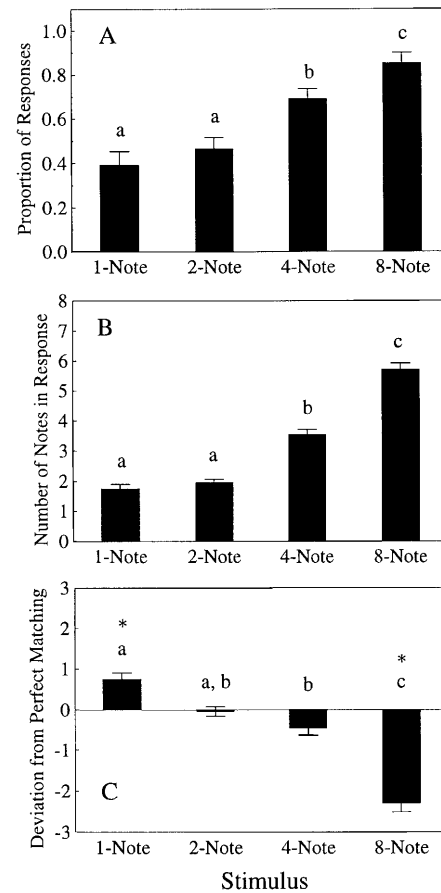

Fig. 3A–B Responses to the 1-, 2-, 4-, and 8-note stimuli in experiment 1. Different letters indicate significant differences using Scheffé's all-pairs multiple comparisons following a significant repeated-measures ANOVA (*$P<0.05$ for test of departure from perfect matching). **A** Mean (±SE) proportion of times males responded to each stimulus. **B** Mean (±SE) number of notes in response to each stimulus. **C** Mean (±SE) deviations from perfect matching calculated as the difference between the number of notes in a male's response and the number of notes in the stimulus

number of notes in the stimulus increased (Fig. 3A). This trend is reflected by a significant linear contrast across stimuli (linear contrast: $F_{1,18}=68.67$, $P<0.0001$). Pairwise multiple comparisons revealed that males responded equally as often to the 1- and 2-note stimuli (Scheffé: $P=0.56$). Males responded more often to the 4-note stimulus than to the 1-note stimulus (Scheffé: $P<0.0001$) and the 2-note stimulus (Scheffé: $P<0.0001$). Responses occurred more often to the 8-note stimulus than to the 4-note stimulus (Scheffé: $P<0.01$), the 2-note stimulus (Scheffé: $P<0.0001$), and the 1-note stimulus (Scheffé: $P<0.0001$). There was also a strong negative correlation between body size and the proportion of times a male responded for the 13 males for which SVL measurements were available: 1-note stimulus ($r=-0.66$, $P=0.015$, $n=13$); 2-note stimulus ($r=-0.64$, $P=0.019$, $n=13$); 4-note stimulus ($r=-0.49$, $P=0.087$, $n=13$); 8-note stimulus ($r=-0.62$, $P=0.024$, $n=13$). None of these correlations was significant after a sequential Bonferroni correction, probably reflecting low statistical power due to small
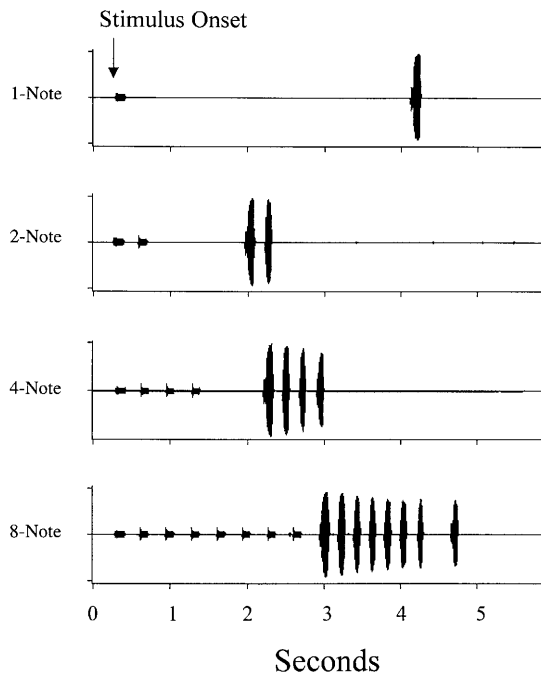
Fig. 4 Oscillograms showing an example of male responses to the synthetic 1-, 2-, 4-, and 8-note stimuli in experiment 1

Fig. 5A–B Box plots representing the median (*line*), interquartile range (*box*), and range (*whiskers*) of latencies to the 1-, 2-, 4-, and 8-note stimuli in experiment 1. Different letters indicate significant differences using Dunn's all-pairs multiple comparisons following a significant Friedman's test. **A** Latency A measured from the beginning of the first note of the stimulus. **B** Latency B measured from the end of the last note of the stimulus

sample sizes. Temperature was not correlated with the proportion of times a male responded to any stimulus.

As the number of notes in the stimulus increased, males increased the number of notes in their responses (Fig. 3B). There were significant differences in the mean number of call notes among responses to the four stimuli (ANOVA: $F_{3,51}=71.54$, $P<0.0001$). The number of notes in response calls increased linearly as the number of stimulus notes increased (linear contrast: $F_{1,17}=122.21$, $P<0.0001$). Responses to the 1- and 2-note stimuli did not differ significantly (Scheffé: $P<0.93$). However, responses to both the 4- and 8-note stimuli consisted of significantly more notes than responses to the 1- and 2-note stimuli (Scheffé: $Ps<0.0001$), and males produced significantly more call notes in responses to the 8-note stimulus than to the 4-note stimulus (Scheffé: $P<0.0001$). There were no significant relationships between either SVL or temperature and the number of notes in responses to each stimulus.

Some males were quite good at precisely matching the number of notes in each stimulus (Fig. 4). In general, however, males did not match the number of notes in each stimulus perfectly. To examine the departure from perfect matching, we calculated deviation scores by subtracting the expected number of notes in response to each stimulus (1, 2, 4, or 8) from the mean number of notes in each male's responses to that stimulus (Fig. 3C). There were significant differences among deviation scores in response to the four stimuli (ANOVA: $F_{3,51}=36.02$, $P<0.0001$). Contrast analysis revealed a decreasing linear trend in deviation scores as the number of stimulus notes increased (linear contrast: $F_{1,17}=62.31$,
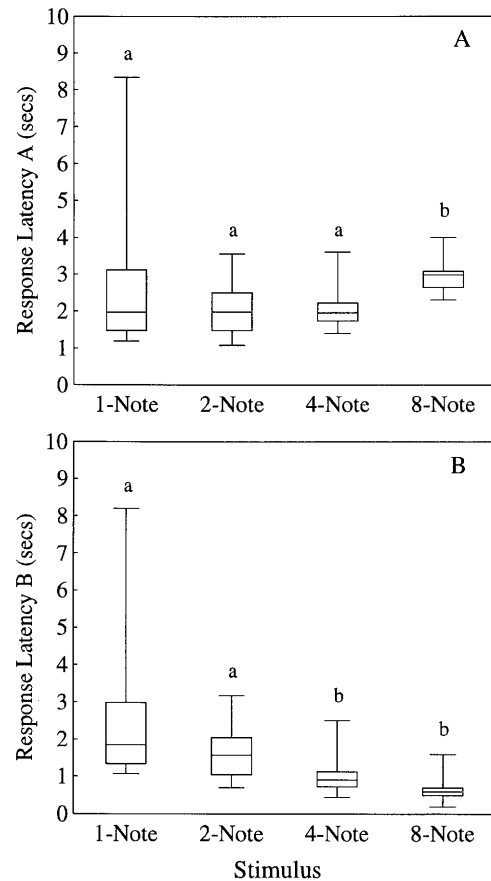
$P<0.0001$). In their responses to the 2- and 4-note stimuli, males tended to produce 2- and 4-note calls, respectively. The number of notes in responses to these two stimuli did not significantly depart from what would be expected if males were perfectly matching the number of notes in the stimulus (independent t-test: 2-note stimulus, $t_{34}=-0.20$, $P=0.85$; 4-note stimulus, $t_{34}=-1.34$, $P=0.19$). In response to the 1-note stimulus, however, deviation scores were positive and males produced calls with significantly more notes than expected for perfect matching (independent t-test: $t_{34}=2.47$, $P=0.02$). In contrast, deviation scores for responses to the 8-note stimulus were negative and males produced calls with significantly fewer than 8 notes (independent t-test: $t_{34}=-5.56$, $P<0.0001$).

Latencies to respond to a particular stimulus were in part determined by the number of notes in the stimulus (Fig. 5). There were significant differences among the median latencies to respond to the four stimuli for latency A, measured from the beginning of the stimulus (Friedman's test: $\chi^2=42.47$, $df=3$, $P<0.0001$), and
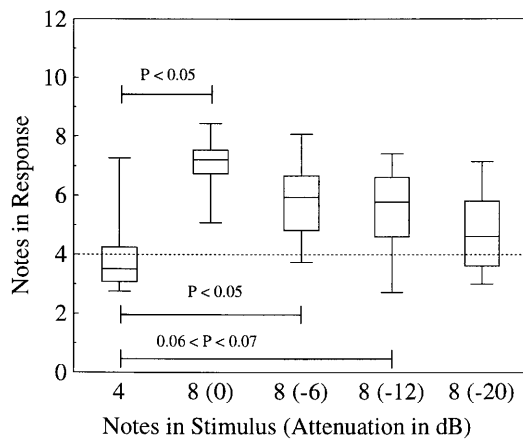
Fig. 6 Box plots as in Fig. 5 representing the number of call notes in responses to a 4-note stimulus and four 8-note stimuli in which the second 4 notes were attenuated by 0, 6, 12, or 20 dB. *P*-values are for a post hoc comparison of each 8-note stimulus to the 4-note control following a significant Friedman's test

for latency B, measured from the end of the stimulus (Friedman's test: $\chi^2=11.53$, *df*=3, *P*<0.0092). For latency A, the median latency to respond to the 8-note stimulus was significantly longer than latencies to the 1-note (*P*<0.05), 2-note (*P*<0.05), and 4-note (*P*<0.05) stimuli, which did not significantly differ (Fig. 5A). In contrast, for latency B, latencies tended to become shorter as the number of notes in the stimulus increased (Fig. 5B). Pairwise multiple comparisons revealed that latencies to the 1- and 2-note stimuli were not significantly different, and latencies to the 4- and 8-note stimuli also did not differ. All remaining pairwise comparisons were significant (*P*s<0.05). There were correlations between SVL and response latency to the 4-note stimulus (latency A: *r*=0.62, *P*=0.024, *n*=13; latency B: *r*=0.60, *P*=0.029, *n*=13), but these relationships were not significant after a sequential Bonferroni correction. Response latencies were not related to temperature.

Experiment 2

In this experiment, we predicted that if males attempt to sum the call notes of more than one neighbor, then the number of notes in responses to the 8-note stimuli, 4 notes of which were emitted by two separate speakers, should be significantly greater than the number produced in responses to the 4-note control stimulus broadcast from a single speaker. There were significant differences in the number of notes in responses to the 4-note call and the 8-note calls with different degrees of attenuation (Friedman's test: $\chi^2=24.35$, *df*=4, *P*<0.0001; Fig. 6). Compared to the 4-note control, males produced calls with significantly more notes when the second 4 notes of the 8-note stimulus were not attenuated (i.e., 0 dB; *P*<0.05) and when they were attenuated by –6 dB (*P*<0.05). Males also gave calls with more notes in response to the 8-note stimulus in which the second 4

notes were attenuated by –12 dB, but the differences were marginally non-significant (0.06<*P*<0.07). Males did not produce significantly more notes in response to a 20-dB attenuation (0.25<*P*<0.29). Although males produced calls with significantly more notes in responses to some 8-note stimuli compared to responses to the 4-note stimulus, they tended to produce fewer notes in responses to attenuated 8-note stimuli compared to the unattenuated 8-note stimulus (see Fig. 6).

Discussion

Our playback experiments demonstrate that *C. georgiana* males frequently match the number of notes in synthetic advertisement calls but matching is imperfect. Although males tended to match stimuli that had 2 or 4 notes, they regularly produced more than 1 note in response to a 1-note stimulus but produced less than 8 notes in response to an 8-note stimulus (Fig. 3).

Latency to respond was also related to the number of notes in the stimulus. Latency A (from the beginning of the stimulus) was constant for 1-, 2- and 4-note stimuli but was significantly longer for 8-note stimuli. Latency B declined with increasing note number in the stimulus (Fig. 5B). These data are consistent with a simple model of calling behavior. Frogs have a fixed latency to call measured from the start of a stimulus call. However, if the stimulus call is longer than average (e.g., longer than the modal maximum note numbers of 6 and 7; Fig. 2B), then calling is inhibited. If frogs called at a fixed delay after the end of a stimulus, e.g., as seen in call alternation patterns in *Pseudacris* (=*Hyla*) *crucifer* (Rosen and Lemon 1974), then latency B would be constant, and latency A, an increasing function of stimulus duration.

Males usually called in small groups and tended to cluster their calls in the time period immediately after the first male's calls, an impression that was enhanced by the fact that inter-call intervals were long relative to the call duration of multi-note calls. Experiment 2 was designed to explore response patterns to calls of neighboring frogs. As long as the amplitude of the second stimulus was not more than about 10–12 dB less than that of the first stimulus, males tended to produce more notes in their responses than they did to a 4-note control call (Fig. 6).

Experiment 2 was potentially unrealistic in three ways: (1) the target male always heard the louder calls simulating the closer neighbor first in those tests in which calls from one speaker were attenuated; (2) the notes from both sound sources had the same carrier frequency and temporal properties, and (3) the delay between the last note of the first stimulus and the first note of the second stimulus was the same as that between the notes in all multi-note stimuli (at a given temperature) and therefore shorter than expected (cf. delay periods; Fig. 5). These three aspects of the design need to be addressed in future studies. Perhaps males are less likely to match the total number of notes if the less intense

calls of a distant neighbor are heard first. Pilot experiments indicate that males still matched the total number of notes, even if the stimuli produced by the two speakers had different carrier frequencies (H. Gerhardt, D. Roberts, M. Bee, unpublished data), but more data are clearly needed. Additionally, preliminary experiments indicate that if the time interval between two consecutive 2- or 4-note stimuli is increased by a factor of four or more (>1.5 s), then males often begin to respond to the first stimulus before the second stimulus occurs. Males seemingly ignore the second stimulus and usually match the number of notes in the first stimulus; thus, the second stimulus neither inhibits them nor elicits additional notes (H.C. Gerhardt, J.D. Roberts, M.A. Bee, unpublished data). Additional analyses of the calls of neighbors monitored in the field, and more realistic playback designs may further unravel the complexity of male-male interactions.

Comparisons with call matching in other species

Timing relationships

C. georgiana males almost always wait until the end of a neighbor's calls before calling. Similar calling interactions, in which one male's signals follow the completion of a neighboring male's calls, have also been described for *Hyperolius tuberilinguis* (Pallett and Passmore 1988) and *Rana nicobariensis* (Jehle and Arak 1998). The relatively long intervals between relatively short advertisement calls in *C. georgiana* give the impression of distinct leader-follower relationships. We are currently analyzing multi-channel recordings of *C. georgiana* choruses to determine whether consistent leader-follower relationships between interacting neighbors occur in this species.

In contrast to the species just discussed, *P. leucorhinus* males show a distinctive alternation of multi-note calls which, although they seldom overlap, are repeated at intervals comparable to, or just slightly longer than the call duration. Inspection of an oscillogram of the calls of a pair of interacting frogs indicates that leader and follower roles change during the exchange of calls (see Fig. 3 in Arak 1983). *H. microcephala* and *Hyla phlebodes* males differ from those of *P. leucorhinus* by the precise interdigitation of secondary click notes when their multi-note advertisement calls overlap those of neighboring males (Schwartz 1993; Schwartz and Wells 1984, 1985). *H. phlebobes* males may interdigitate 15 or more secondary notes during their interactions between males, which seem to add notes on a one-by-one basis depending on the addition of notes by rivals. However, no formal analysis of matching is available for this species.

Precision of matching

In comparison to *C. georgiana*, *P. leucorhinus*, and *Hyla microcephala*, call matching is very crude in *H. tuberilinguis*. Males increased the production of 2-note and (less often) 3-note calls when confronted with 2-, 3-, or 4-note stimuli, but did not regularly match the number of notes in the stimulus. Males are capable of producing as many as 6 notes but rarely do so except in peak periods of breeding activity (Pallett and Passmore 1988). *R. nicobariensis* males appear to be more precise than *Hyperolius*, but nearly always produced the same or fewer notes per call than the number in the playback stimulus (Jehle and Arak 1998). Poor matching at high note numbers might result from an energetic or size constraint. In *C. georgiana*, the energy required for repeated muscle contractions, or the volume of gas in the lungs needed to generate 8-note or longer calls might not be generally available, as reflected in modal maximum note numbers of 6–7 notes in natural choruses (Fig. 2B).

Presumed call type of matched signals

C. georgiana and *H. tuberilinguis* males are almost certainly matching advertisement calls. We have never heard *C. georgiana* produce distinct aggressive calls (D. Roberts, personal observation), but *H. tuberilinguis* males have an aggressive signal in their repertoire (Pallett and Passmore 1988). The situation in *R. nicrobariensis* is more complex. The longer, multi-note calls that are produced during interactions between neighboring males or in response to playbacks at close range contain elements that Jehle and Arak (1998) interpret as aggressive in function. The distinctive signals that are matched in *P. leucorhinus* have only been heard during vocal interactions between males. *P. leucorhinus* males also produce a distinct advertisement call, which was heard when females approached. In *H. microcephala*, click notes normally follow the introductory note, which is necessary and sufficient to attract females (Schwartz 1986). The number of these click notes, which may be matched by neighbors, tend to increase during interactions between males (Wells and Taigen 1989).

Adaptive significance

Drawing on the literature on song matching in birds, Arak (1983) considered three hypotheses for call matching in *P. leucorhinus*. First, asymmetrical matching by a pair of interacting males could indicate dominance, as in marsh wrens (Kroodsma 1979). Arak rejected this hypothesis for *P. leucorhinus* because each male matched its rival. An analysis of natural interactions within groups of males is needed to test this hypothesis in *C. georgiana*. Large males were somewhat less likely to respond to playbacks than small males, but we found no pattern of size-dependent matching. Further research

should examine the possibility that a male's size relative to the perceived size of a rival, as indicated by its dominant frequency, could have an influence. Second, matching might be a mechanism to direct aggressive signals to particular males, perhaps even grading the response by the precision of matching (Bremond, in Armstrong 1973; Krebs et al. 1981). Arak (1983) considered this hypothesis to be the most likely explanation for call matching in *P. leucorhinus*. For *C. georgiana*, the results of our two-speaker playbacks cast doubt on this hypothesis because males tended to match the combined number of notes played back from separate speakers even when the playback level of the notes from one speaker was substantially less intense than that from the other speaker. This model could be tested further by playing back notes with different dominant frequencies from two speakers. If males detect the differences in frequency, intensity, or location, then they would be expected to match only one of the simulated rivals if call matching is used to direct an aggressive message to a particular rival. This also might be shown by different patterns of matching in natural choruses where adjacent males differ radically in size. Smallest and largest males in choruses can vary between <1 g and >6 g (M. Smith, unpublished data).

A third, non-mutually exclusive explanation for call matching is that females can better detect or prefer calls with multiple notes (Arak 1983): matching is then a mechanism for producing calls that are at least as attractive as those of neighbor(s) without wasting energy. This is an attractive hypothesis for call matching in *C. georgiana* that can be tested by determining how note number affects the relative attractiveness of signals to females and by estimating the energetic costs of producing many multi-note calls. This hypothesis is not, however, supported by the results of preliminary experiments with female choice tests in the laboratory. Given a choice of 2- and 4-note synthetic calls, females showed no preference for 4-note calls (eight preferred 2 notes, six preferred 4 notes; M. Smith and D. Roberts, unpublished data), but patterns of preference might differ in tests where the difference between alternative note numbers is greater.

Females might also simply not prefer higher numbers of notes beyond some minimum number, as in *H. tuberilinguis* (Pallett and Passmore 1988). Females of *Hyla versicolor* also show a decline in preference strength based on differences in call duration once the absolute durations of alternatives equal and exceed mean values (Gerhardt et al., in press). Clearly, playback experiments with females will be essential to understand the adaptive bases for call matching in *C. georgiana* and other species.

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