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Call recognition in the bullfrog, *Rana catesbeiana*: Generalization along the duration continuum^{a)}

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Abstract

Male bullfrogs emit multicroak, quasiharmonic advertisement calls that function in mate attraction and neighbor recognition. The degree of variability of acoustic features in these calls can influence perceptual decisions by conspecific receivers. Analysis of duration of individual croaks in spontaneous advertisement calls of a sample of males shows considerable intraindividual variability in this feature, even within short chorusing bouts. The influence of this intraindividual variability on behavior was examined in a series of evoked calling experiments. When presented with synthetic calls whose croak durations varied over the range of the natural variability in this feature, males responded similarly to intermediate and long duration croaks, but significantly less to short duration croaks. When presented with playbacks of calls with croak durations outside the natural range of variability, males again responded significantly less to shorter durations. The response gradient for duration is thus asymmetrical, with stimuli at the shorter end of the continuum evoking fewer responses than stimuli at the longer end. This asymmetry may be related to the biological demands of rejecting perception of heterospecific advertisement calls, and of mediating appropriate responses to conspecific aggressive calls. The shape of the response gradient for duration may reflect a process of stimulus generalization.

I. INTRODUCTION

Male anurans of many species use a complex advertisement call to attract females for mating and to maintain territory boundaries against incursions from rival males. Spectral and temporal features of these calls can convey important biological information to receivers, including species identity, individual identity, size, physical condition, genetic fitness, and motivational state (Gerhardt and Huber, 2002). The analysis of physical acoustic features in advertisement calls and the “meaning” or salience of these features as derived from receiver response form the basis of much empirical and theoretical work in animal communication systems. Advertisement calls, in their role as conveying species identity, contain distinct, stereotyped species-specific attributes, with little variation between individuals within a species; conversely, other acoustic features in these calls may vary considerably between conspecifics. The variability, rather than stereotypy, of advertisement calls provides room for errors in species identification, leading to mismatings by females and subsequent declines in reproductive success (Wollerman and Wiley, 2002), as well as errors in individual identification, thus potentially disrupting stable male–male territorial interactions and the ability to discriminate neighbors from strangers (Davis, 1987; Bee and Gerhardt, 2001). Understanding the interplay of stereotyped and more variable features of advertisement calls in mediating both female choice and male/male interactions is of considerable interest in deciphering how animals make reproductive decisions in complex acoustic environments.

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Gerhardt (1991) examined the variability and repeatability of advertisement calls within males of three different species of North American treefrogs, and categorized specific acoustic parameters of these calls as being either static (stereotyped) or dynamic (more variable), based on the consistency of these parameters in the calls of individuals. Gerhardt and Huber (2002) extended this analysis to a group of 24 species. Their summary shows that carrier frequency, dominant frequency, and pulse rate can be classified as static properties, varying little within individuals, while call rate is a dynamic property, showing considerable intraindividual variability. Interestingly, call duration could not be easily classified, exhibiting different trends across species. Gerhardt and Huber (2002) suggested that short duration signals (<500 ms) are less dynamic and thus may be processed differently than long duration signals (>500 ms). Why call duration cannot be so easily classified as other acoustic features leads to questions about the importance of this particular parameter in mediating call recognition.

Variability in advertisement calls leads to plasticity in response behavior contingent on signaling, and thus can affect communication both ultimately (over evolutionary time) and proximately. In choice experiments, female anurans show different kinds of preference functions for static and dynamic properties of advertisement calls (reviewed in Gerhardt and Huber, 2002). For example, female *Hyla versicolor* prefer pulse rates (a static property) close to that of the mean of calls of males in the population, but prefer call durations (a dynamic property in that species) longer than those observed in the vocalizations of conspecifics (Gerhardt, 1991). These preferences may reflect different degrees of selection (stabilizing or directional) on call properties over evolutionary time (Gerhardt and Huber, 2002). The preference of some species of female anurans for stimuli with durations outside the range of natural variation in duration has been interpreted as a preference for “supernormal” or exaggerated stimuli (Ryan and Keddy-Hector, 1992) that ultimately contributes to the production of complex signals. Preference functions that are not tightly centered on the modal acoustic parameters in conspecific calls may also reflect a process of stimulus generalization in the perceptual representation of individuals (Malott and Malott, 1970), and this may also lead to permissiveness in call recognition (Ryan *et al.*, 2003).

Much of the literature on signal variation in call recognition is concerned with the role of variability of acoustic features in mediating or modifying female choice (reviewed in Gerhardt and Huber, 2002). There is relatively less known about how signal variability influences call recognition in male frogs (Capranica, 1965; Narins and Capranica, 1978; Penna *et al.*, 1997a; Ryan and Rand, 1998; Simmons and Bean, 2000; reviewed in Gerhardt and Huber, 2002). Because males and females derive different “meanings” from advertisement calls (for example, neighbor/stranger recognition and/or assessment of rivals by males as opposed to assessment of an appropriate mate by females), they may respond differently to variations in the same acoustic parameter (Searcy and Brenowitz, 1988). The distinction between static and dynamic properties of advertisement calls has typically been interpreted with regards to the influence of these different kinds of features on female perception and mate choice (reviewed in Gerhardt and Huber, 2002). Whether these distinctions also modulate patterns of male calling behavior is not as clear. Male frogs alter such dynamic properties as call rate and call duration in response to changes in playbacks of conspecific advertisement calls, but they can also alter static properties such as dominant frequency (reviewed in Gerhardt and Huber, 2002). It is also unclear whether or not males prefer, or respond more strongly to, so-called supernormal stimuli, in a manner paralleling female responses. The experiments described in this paper explore the range of natural variation in call duration, and male responses to variation in call duration in the bullfrog, *Rana catesbeiana*. The goal is to derive a response function (generalization gradient) for this particular acoustic property, and to test the hypothesis that males identify particular signal durations as species specific. In addition, the hypothesis that males respond preferentially to supernormal stimuli, as might be expected from responses of female frogs, is also addressed.

II. MATERIALS AND METHODS

The Brown University Institutional Animal Care and Use Committee approved the use of animals in this research. Male bullfrogs emit a multicroak (1–12), quasi-harmonic, long duration advertisement call, whose spectral and temporal properties have been described from both laboratory and field recordings (Capranica, 1965; Wiewandt, 1969; Megela-Simmons, 1984; Bee and Gerhardt, 2001). I first estimated the range of variability in individual croaks in spontaneous (not evoked by stimulus playback) advertisement calls of individual males, then conducted three playback experiments examining the strength (quantity) of evoked vocal responses to natural and synthetic advertisement calls with durations spanning or exceeding the natural range of variation in this acoustic parameter.

A. Field sites and target animals

Recordings of natural choruses and playback experiments were conducted at two natural ponds, located on private property, in Massachusetts and Rhode Island, in June and July, 2000–2002. Site 1 (Sterling, MA) is approximately 100 m long and 40 m wide, with a maximum depth of 8 m. Chorus density ranged from 7 to 15 vocalizing males over the course of the study. Individual males maintained territories of approximately 1 to 5 m in diameter, and intermale spacing ranged between approximately 5 and 20 m. Site 2 (Barrington, RI) is approximately 80 m long and 35 m wide with a maximum depth of approximately 1.25 m. Chorus density ranged from 6 to 13 males, spaced approximately 2 to 15 m apart. Both for recordings of chorus activity and for playbacks, a different male was chosen as the target, based on his location, subjective judgment of the “pitch” and “timbre” of his advertisement calls, and any identifying visual features. The fundamental frequency and dominant frequency of bullfrog advertisement calls show little variation within an individual male, and significant between-male variability (Bee and Gerhardt, 2001), suggesting that these features provide a reasonable metric for discriminating individuals. Subjective estimates of the relative fundamental and dominant frequencies of advertisement calls were later verified by digital analysis (see below). I have been conducting experiments at these two ponds yearly since 1989, and it is my experience that, once choruses are formed in late May, males, being territorial, maintain relatively fixed positions within the ponds. In neither pond did the entire chorus relocate during the calling season, as observed by Howard (1978) at a much larger site.

B. Stimuli

1. Recordings of natural choruses—The spontaneous advertisement calls of nine individual male bullfrogs at site 2 were recorded over 6 nights in one season. Each animal was monitored for 30 min. Vocalizations were recorded with a Sennheiser ME66 microphone with K6 power module (50–20 000 Hz, ± 2.5 dB) and SONY DAT Walkman TCD-D8 tape recorder (20–20,000 Hz, ± 1 dB). The microphone was placed on a floating styrofoam platform located 1 m away from and oriented towards the vocal sac of the target animal. Calls from individual frogs were converted to 44.1-kHz, 16-bit WAV format sound files using COOLEEDIT 2000 (Syntrillium) running on a Pentium computer. Acoustic analyses of the signals (fast Fourier transforms, stimulus autocorrelations) were computed using MATLAB v. 5.3 scripts (MathWorks, Natick, MA). Durations of individual croaks in multicroak calls and intercroak intervals were analyzed using COOLEEDIT software (1-ms resolution) by two assistants unaware of the hypotheses being tested.

2. Experiment 1—The purpose of experiment 1 (conducted in 2000) was to measure evoked vocal responses to a synthetic bullfrog advertisement call with croak duration within the typical range of variability of natural croaks. The synthetic croak stimulus consisted of 21 consecutive harmonics of 100 Hz, summed together with a starting phase of 0°. The dominant frequency (harmonic at a relative amplitude of 0 dB) was 200 Hz. The fundamental frequency of 100 Hz

was attenuated by 15 dB, and amplitudes of the other harmonics (300–2100 Hz) were attenuated by 3 to 20 dB relative to the dominant frequency. Stimuli with these parameters have been used previously in evoked calling studies (Simmons and Bean, 2000), and reliably elicit responses from males. Durations of the synthetic croaks used for playbacks were chosen based on the distribution of croak durations in spontaneous advertisement calls, recorded as described above. These were 420 ms (stimulus 1); 560 ms (stimulus 2); 700 ms (stimulus 3), and 840 ms (stimulus 4). All croaks had rise–fall times of 50 ms. Stimuli were recorded into DAT tapes as a series of six croaks of identical duration. Intercroak intervals equaled stimulus duration, so that duty cycle remained constant for all stimuli. Intercall intervals (intervals between each successive group of six croaks) were 30 s, within the range of typical intercall intervals recorded in the field.

3. Experiment 2—In experiment 2 (conducted in 2001), I examined evoked vocal responses to natural advertisement calls, some of which were manipulated to be outside the normal range of variability for the species. In order to avoid pseudoreplication problems (Kroodsma, 1989), stimuli for playbacks were derived from recordings of the spontaneous advertisement calls of three individual male frogs (called A, B, and C), made in 1994 at site 2. The natural, multicroak advertisement calls of these three males varied in spectrum and fundamental frequency; the calls were easily discriminated by human listeners. To derive the stimuli used for playbacks, I chose from each male's advertisement call one exemplar croak with a duration at the mean value for that male's calls. Exemplar A had a duration of 626 ms (periodicity 106 Hz, low and high spectral peaks at 214 and 1328 Hz), exemplar B had a duration of 572 ms (periodicity 125 Hz; spectral peaks at 250 and 1500 Hz), and exemplar C had a duration of 518 ms (periodicity 135 Hz; spectral peaks at 405 and 1220 Hz). These exemplar croaks were converted to 44.1-kHz, 16-bit WAV format sound files using COOLEEDIT 2000, low-pass filtered below 4000 Hz, and subjected to digital noise reduction through Fourier analysis of intercroak noise samples and statistical reduction of noise frequencies (50% power level). The files were then time compressed or stretched to 50% or 200% based on single croak duration using resampling temporal compression algorithms in COOLEEDIT software. These algorithms alter the duration (ratio or absolute duration) of a signal while maintaining its frequency content constant. This is accomplished by splicing isofrequency samples with overlap and splicing frequency determined by the individual signal. For example, to increase the length of an individual croak sample about 0.18 s long to one 0.26 s long with no transposition of frequency content (ratio of 0.67), the algorithm splices isofrequency harmonics with a splicing frequency of 54 Hz with 32% overlap. Higher frequency splicing increases precision of duration change but can enhance artifacts; higher overlap ratios also add to precision but can substantially increase processing time. To produce stimuli for the experiment, the standard exemplar was stretched to 200% (long exemplar), compressed to 50% (short exemplar), and stretched to 200% then compressed back to 100% (medium exemplar), to control for any artifacts introduced by the stretching/compression process. The resulting sounds had durations of 313, 626, 1252 ms (exemplar A), 286, 572, 1144 ms (exemplar B), and 259, 518, 1036 ms (exemplar C). Figure 1 shows the power spectral density and waveform fine structure of the three durations of exemplar A, to illustrate how the time compression algorithm affects the signal.

Stimuli used for playbacks were composed of six croaks of identical duration, with intercroak intervals set at 500 ms. Duty cycles varied from 34% for the short duration exemplar C to 73% for the long duration exemplar A. Stimuli were resaved as 44.1-kHz 16-bit WAV files and recorded onto DAT tapes in groups of 20 six-croak calls of an identical duration, with intercall intervals (intervals between each group of six croaks) ranging randomly from 10 to 120 s to avoid habituation. Stimuli will be referred to subsequently as short duration (313, 286, or 259 ms), medium duration (626, 572, or 518 ms) or long duration (1252, 1144, or 1036 ms).

4. Experiment 3—In experiment 3 (conducted in 2002), the total duration (“on time,” croak duration plus intercroak intervals) for the short duration exemplars was set equal to that for the medium duration exemplars, by doubling the number of croaks in the short stimuli from 6 to 12. This manipulation was performed to ascertain whether total stimulus on time rather than croak duration *per se* affected the frogs’ responses (the 12 short croak sequence had a total on time equal to that of the six medium croak sequence). In addition, testing with additional exemplars helps rule out problems associated with pseudoreplication (Kroodsma, 1989). Stimuli for playbacks were derived from the spontaneous croaks of three individual male frogs (exemplars D, E, and F), recorded in 1999 at site 1. Sounds were recorded and digitized as described for experiment 2. Exemplar D had a duration of 485 ms (periodicity 113 Hz; spectral peaks at 224 and 1460 Hz); exemplar E had a duration of 596 ms (periodicity 105 Hz; spectral peaks at 206 and 1473 Hz); and exemplar F had a duration of 563 ms (periodicity 108 Hz; spectral peaks at 210 and 950 Hz). These sounds were time compressed and stretched as described above to yield final durations of 242, 485, and 970 ms (exemplar D); 298, 596, and 1192 ms (exemplar E); and 282, 563, and 1126 ms (exemplar F). For the medium and long duration exemplars, stimulus calls used for playbacks were composed of six croaks of identical duration, with intercroak intervals of 500 ms. For the short duration exemplar, stimulus calls used for playbacks were composed of 12 croaks of identical duration, with intercroak intervals of 500 ms. Although stimulus on time for the short duration and medium duration stimuli were similar, duty cycles varied. Signals were presented as described for experiment 2, with intercall intervals ranging randomly from 10 to 120 s to avoid habituation.

C. Procedure

Experiments were conducted between the hours of 2200 and 0100 hours. Air and water temperatures were measured to an accuracy of 1 °C before and after each playback session. Before beginning playbacks, I recorded spontaneous calling for 10–15 min, and identified the positions, relative calling rates, and probable acoustic identity of appropriate target frogs. The amplifier/speaker used for playbacks (Pignose Hog30 model 7–300) was positioned between 6–15 m from a target frog, depending on the geography of the calling site. The recording microphone (Sennheiser) was placed on a floating styrofoam platform, and positioned approximately 1 m away from the target male. Because frogs were not restrained and were free to move, the exact spatial arrangement of target individuals to both the speaker and the microphone could vary within a playback session. To avoid stressing the animals, I did not physically move any other males close to the target male; in any event, since males tend to call preferentially to farther, rather than closer, neighbors (Boatright-Horowitz *et al.*, 2000), such a manipulation would have little effect on the target’s calling behavior.

Stimuli were played to the frogs through a Sony DAT TCD-D8 tape recorder and the Pignose amplifier/speaker. The intensity level of each stimulus was calibrated to 80 dB SPL rms (*re*: 20 μ Pa) at 1 meter, using a Realistic sound-level meter (flat weighting). I measured stimulus levels close to the position of each target frog both before playbacks began and after they ended; these levels varied from about 55 dB SPL at 15 m to about 80 dB SPL at 1 m. The male bullfrog’s evoked calling response is relatively insensitive to variations in signal intensity above some threshold level (Boatright-Horowitz *et al.*, 2000; Simmons and Bean, 2000). Spontaneous calling levels were recorded for 5 min before playbacks began, and again for five minutes after the end of playbacks. The males’ vocal responses were recorded onto one channel of a Marantz PMD430 (35–14 000 Hz, ± 3 dB) stereo tape recorder. The line output of the DAT recorder was recorded onto the second channel of this tape recorder as a stimulus marker.

In experiment 1, each male was presented with ten repetitions of each stimulus call, at interstimulus intervals of 30 s. In experiments 2 and 3, each male was presented with playbacks of one exemplar, at its three different durations (short, medium, and long). Each duration was

presented as a series of 20 six-croak calls, with intercall intervals ranging from 10 to 120 s, with the constraint that stimuli were only played when the target male and his immediate neighbors were not spontaneously vocalizing. The three different durations were presented in a random order. Between one and three individual frogs were tested, with a different exemplar, on a given night.

D. Data analysis

Because the experiment was conducted during active choruses, and because frogs were not moved or displaced from their natural calling positions during playbacks, it is possible that animals may have been responding to each other instead of to the playbacks. I attempted to separate responses from a target male to playbacks from his responses to other frogs, by counting as a response only the vocalizations of that male when he was the first to respond in the silent interval after a particular stimulus. If a neighboring male (within 12 m of the target male) vocalized in response to the stimulus before the target, these trials were excluded from analysis. This is because subsequent responses from the target male could represent responses to his neighbor, rather than responses to the stimulus playback. Responses that occurred during stimulus playbacks (either overlapping or alternating with the stimulus croaks) were treated separately for statistical analyses. Data from the three experiments were analyzed separately.

Data tapes were digitally sampled onto a Gateway Pentium computer at a sampling rate of 22 050 Hz. For each session, total responses (individual croaks) and mean latency to the first response (1-ms accuracy; measured from stimulus offset to response onset) of one individual male over the multiple repetitions of each stimulus were measured. In addition, the duration and the fast Fourier transforms of each answering croak were computed using MATLAB V. 5.3 scripts.

Statistical analysis of results was performed using SPSS v. 11.5 statistical packages. Degrees of freedom for repeated measures analysis of variance (ANOVA) were adjusted, if necessary, using the Greenhouse–Geisser (Greenhouse and Geisser, 1959) corrections to account for any violations of compound symmetry and sphericity. Statistical significance of *post hoc* pairwise comparisons was adjusted using the Bonferroni correction for multiple tests.

III. RESULTS

A. Natural variability in croak durations

Spontaneous advertisement calls ($N = 297$) of nine individual frogs were analyzed for individual differences and normal range of variability in croak duration. Calls consisting of only one croak were omitted, as were croaks with a signal-to-noise ratio of less than 3:1. The number of croaks analyzed per individual frog varied from 15 to 58. For each male, the durations of each croak in each of his multicroak calls were measured and averaged, and then treated as a repeated measure in ANOVA. The differences in croak duration between individual males were statistically significant [$F_{8,288} = 82.8$, $P < 0.001$]. Over all nine males, individual croak durations ranged from 370 to 970 ms, and the average croak duration (from each of that male's calls) ranged from 441 to 712 ms (sample mean 551 ms). The frequency distribution of croak duration across all nine males is shown in Fig. 2. An individual could show variability in croak duration over a range as large as 100 ms. The coefficients of variation ($100\% \times \text{standard deviation/mean}$; Gerhardt and Huber, 2002) calculated from the data for each individual range from 5.54 to 14.7. These data show that the stimulus durations used in experiment 1 extend across the range of variability, and that the short and long duration stimuli used for playbacks in experiments 2 and 3 are outside or at the extremes of the range of variability of spontaneous croak duration for these animals. Intercroak intervals measured from these data ranged from 373 to 772 ms, with a mean across all males of 529 ms. The intercroak intervals used in

experiment 1 extend across the range of variability seen in spontaneous advertisement calls, while the standard intercroak interval of 500 ms used in experiments 2 and 3 is near the mean of spontaneous intervals recorded at the study sites.

The croaks of one active caller were analyzed and compared across the three recording sessions (chorus nights) during which this male reliably vocalized. Durations of individual croaks for this male varied from 439 to 918 ms ($N = 58$ croaks analyzed per session; coefficients of variation 7 to 10.3). The main effect of recording session was not statistically significant, consistent with the observation that chorus density was similar across the three nights. Air and water temperatures varied between 20–24 °C across recording nights. There was no significant correlation between temperature and croak duration for either individual or the entire sample of frogs.

B. Experiment 1

Data were collected from seven frogs (five at site 1 and two at site 2). Mean ($\pm$ standard error) number of croaks to the different stimulus durations is shown in Fig. 3. Results of repeated measures ANOVA showed that the within subjects effect of stimulus duration was statistically significant ($F_{3,18} = 4.9$, $P < 0.05$). Frogs responded more to the stimulus with duration 700 ms than to the other stimuli, but results of pairwise comparisons showed that these differences were significant only when comparing responses evoked by the short duration stimulus (420 ms) and the 700-ms stimulus. Fewer responses were evoked by the 840-ms duration stimulus than by the 700-ms duration stimulus, but this difference was not statistically significant. Five of the seven individual frogs gave the largest number of answering croaks to the 700-ms duration stimulus, while the remaining two gave the largest number of answering croaks to the 560-ms duration stimulus. One frog did not vocalize at all in response to the 420-ms duration stimulus, and another frog did not vocalize at all to the 840-ms duration stimulus.

Duration of responding croaks was analyzed across the different stimulus durations, to determine if frogs matched their response duration with stimulus duration. Across all frogs, there was no significant relationship between response duration and stimulus duration. Individual data were then examined to determine if the lack of a significant relationship in the entire sample was due to averaging across individuals. Data from two individual frogs are shown in Fig. 4. Both of these individuals responded to all four stimuli, and also vocalized spontaneously in baseline (base) trials recorded before playbacks began. Each individual shows a great deal of variability in the durations of his croaks, even to the same stimulus (see responses to the 700-ms duration stimulus by both frogs). Although frog 1 showed a trend of increasing response duration with increasing stimulus duration, this trend was absent in the data for frog 2. Both frogs showed somewhat shorter croak durations in baseline trials compared to playback trials, but this was not observed consistently across the entire sample.

C. Experiment 2

Data were collected from nine individual males (three at site 1 and six at site 2). Data from two additional experiments were eliminated from analysis because the target frog moved away from the speaker during the playback in one, and in another, *post hoc* acoustic analysis revealed that an individual frog had been tested twice. Responses were obtained to four playbacks of exemplar A, three of exemplar B, and two of exemplar C. The total number of answering croaks to the three exemplars, summed across all three durations, did not vary statistically [$X^2_2 = 2.4$, $P > 0.05$], suggesting that the identity of the particular exemplar did not significantly affect responses. The number of playbacks of each exemplar was too small to justify use of a nested ANOVA, and subsequent statistical analyses were thus based on pooling responses from the short, medium, and long duration stimuli across the three exemplars.

Frogs responded differently to playbacks of different croak durations [repeated measures ANOVA: $F_{2,16} = 7.7$, $P < 0.01$]. These analyses include only those croaks that followed the end of each stimulus presentation (that is, answering croaks which were interspersed between the stimulus croaks were eliminated). Animals vocalized more in response to the medium duration stimulus (mean 23.7 croaks) than to the short duration stimulus (mean 14.1 croaks), with intermediate responses to the long duration stimulus [mean 19.9 croaks; Fig. 5(A)]. Significant *post hoc* differences were obtained between medium and short duration stimuli ($P < 0.05$); none of the other comparisons was statistically significant. In terms of individual data, seven of the males showed the absolute greatest number of evoked responses to the medium duration stimulus, one showed the greatest number of responses to the long duration stimulus, and one frog showed equal numbers of responses to the medium and short duration stimulus. Latency of response did not differ significantly across the three durations. For these analyses, no response was given a latency of 30 s. Mean latencies ranged from 9.1 to 11.4 s.

Duration of answering croaks to the three different stimulus durations was analyzed to determine if frogs adjusted their response durations to match stimulus durations. For these analyses, data from four frogs that did not respond at all to the short duration stimulus were excluded. Mean response durations across the five remaining frogs were 538 ms (standard error 5.2) for the medium duration stimulus, 533 ms (standard error 5.8) for the long duration stimulus, and 512 ms (standard error 4.6) for the short duration stimulus. These differences were not statistically significant. Data from individual frogs showed no consistent relationship between stimulus duration and response duration.

D. Experiment 3

Data were collected from 12 individual males (five at site 1 and seven at site 2). Data from three additional experiments were eliminated, because *post hoc* acoustic analyses of vocalizations indicated that individual animals had been tested twice. Responses were obtained from four playbacks of each exemplar. There was no difference in the total number of answering croaks to these three exemplars [$X^2_2 = 0.7$, $P > 0.05$], so data were combined across exemplars for subsequent analyses. Again, sample size was too small to use exemplar as a nested factor in an ANOVA.

Results of repeated measures ANOVA indicated that frogs responded differently to playbacks of stimuli of different durations [$F_{1,3,22} = 9.4$, $P < 0.01$]. For these analyses, only those answering croaks that followed the end of each stimulus playback (without being interspersed within the series of six stimuli) were counted. Frogs responded more to the medium duration stimulus (mean croaks 12.6) than to the long (mean 5.9 croaks) or short (mean 4.1 croaks) duration stimuli; these differences were statistically significant [$P < 0.5$ for both comparisons; Fig. 5(B)]. Differences in response between long and short duration stimuli were not significant. Nine individual frogs gave the absolute greatest number of responses to the medium duration stimulus, two gave the greatest number of responses to the long duration stimulus, and one gave equal responses to the long and short duration stimuli. Latency of response also differed significantly [$F_{2,22} = 7.3$, $P < 0.01$]. Latencies were significantly shorter for the medium duration stimulus (mean 4.8 s) than for the short (mean 15.8 s) duration stimulus ($P < 0.01$). Differences in latency of response to the medium or short duration stimuli and to the long duration stimulus (mean 11 s) were not statistically significant.

A major difference between data from experiments 2 and 3 is the smaller number of total answering croaks occurring after the end of each stimulus presentation in experiment 3. Choruses were larger and more active in 2002, and more frogs seemed to vocalize during, rather than after, each stimulus presentation. Croaks occurring during each stimulus presentation were analyzed separately, and divided into two categories, those alternating [Fig. 6(A)] and those not alternating [Fig. 6(B)] with the individual stimulus croaks. In the first case,

answering croaks were consistently interspersed in the silent intervals between individual stimulus croaks; in the second case, there was no consistent timing relationship between stimulus and response (the responses sometimes occur coincident with the stimulus). The distribution of alternating and nonalternating croaks varied significantly across the three stimulus durations ($X^2 = 25.6$, $P < 0.001$). There were significantly more instances of nonalternation and significantly fewer instances of alternation in response to the short duration stimulus than to the other stimuli. This suggests that the animals did respond selectively less to the short duration stimulus.

There was no significant relationship between stimulus duration and response duration, either in group data or in the responses of individual frogs.

IV. DISCUSSION

Analysis of the durations of croaks in spontaneous advertisement calls suggests that croak duration is a dynamic property, as defined by Gerhardt (1991), in bullfrogs. Evoked calling data (experiment 1) show that males vocalize in response to synthetic advertisement calls with durations spanning the natural range of variability, but that calling is less robust to a stimulus duration at the low end of the range. Experiments 2 and 3 show that males vocalize significantly less in response to very short duration stimuli, outside the normal range of variability in croak duration. This was true even under different chorus conditions (experiment 3 was conducted in a larger chorus than experiment 2), suggesting that any differences in calling “motivation” arising from overall chorus size do not eliminate differences in response related to stimulus duration. Responses to stimuli longer than spontaneous croaks were inconsistent between experiments 2 and 3, with males showing a steeper drop-off in response in the larger chorus (experiment 3). In any event, neither experiment 2 nor 3 shows any evidence of greater responding to supernormal stimuli. The results of experiments 1–3 suggest that bullfrogs show perceptual generalization across stimulus duration, with a steeper slope of the response gradient on the shorter end compared to the longer end of the continuum. The use of multiple exemplars in these experiments helps control for effects of pseudoreplication (Kroodsma, 1989).

A. Variability in croak duration

Classification of parameters of communication signals as static or dynamic (Gerhardt, 1991; Gerhardt and Huber, 2002) is made on the basis of the degree of variability in that parameter in the calls of individuals. Across different species, call duration can be either, raising questions about the information content of this temporal parameter. From their review of the literature, Gerhardt and Huber (2002) suggested that short duration signals show low variability, while long duration signals show high variability, with the cutoff between these two categories arbitrarily defined as 500 ms (coefficients of variation around 0.5). Individual croaks in bullfrog advertisement calls measured in this study range between 370–970 ms in duration (mean 551 ms), with coefficient of variation ranging from 5.5–14.7. Thus, croak duration fits the definition of a dynamic property. This range of variability is similar to that estimated by Bee and Gerhardt (2001) in a separate, larger sample of bullfrogs (3.0–12.9). The mean croak duration in my sample is shorter than that measured in that study (679 ms); however, my measurements are based on all croaks in a multicroak call, while Bee and Gerhardt’s numbers are derived from durations of the first croak only. Capranica (1965) recorded individual croak durations between 600–1500 ms from a group of males housed in the laboratory, but did not provide quantitative data on the range of variability of this parameter either within or between males. In my sample, there were no instances of croak durations over 1000 ms, in either spontaneous or evoked calling. It is possible that the differences in croak duration recorded in these different studies are due to sample (population) differences, differences in chorus density, or to longer croak

durations in the field being masked by background noise. This latter is unlikely in the present study, because only croaks with signal-to-noise ratios higher than 3:1 were measured.

The high variability in signal duration within a species raises issues about the importance of this parameter for communication. Gerhardt and Huber (2002) suggested that acoustic features with high variability do not reflect some physiological or mechanistic limit on production, but rather reflect attributes such as physical condition, fitness, or motivation. For example, it is possible that, in bullfrogs, croak duration is related to body size or physical condition. Because I did not individually mark each male in my sample, I could not directly test this hypothesis; however, Bee and Gerhardt (2001) observed no statistically significant correlation between snout-vent length and croak duration in their sample of animals. Similarly, Howard and Young (1998) found no relationship between call duration and body size in a group of male *Bufo americanus*. In terms of fitness, duration might reflect energetics of vocalizations, such that males could produce longer duration stimuli early in the chorus, when they are less tired, for example. This is not supported by the data in Fig. 2, which shows that individual males could vary their croak duration by as much as 100 ms over a time interval as short as 30 min. Similarly, in *B. americanus*, no relationship was found between call duration and body condition, an indirect measure of energetics (Howard and Young, 1998). Wells and Taigen (1986) reported a trade-off between call duration and call rate in *H. versicolor* as a function of chorus density. They also noted a negative relationship between call duration and total calling time, over periods as long as 4 h. In contrast, in the bullfrog, croak duration varied considerably, over short time scales during which chorus size (number of active callers) did not vary. It is possible, however, that overall call duration (number of croaks per advertisement call) might vary over the entire duration of a chorus, but this was not studied here, as measurements were taken only during the first 2–3 h of chorusing on a particular night.

Given the considerable intraindividual variability in croak duration, it is unlikely that this parameter acts like an honest signal in male–male interactions. It is still possible, however, that croak duration is somehow influenced by acoustic interactions within a chorus. One way to test for this would be to measure, for a particular target male, the duration of croaks of other males preceding and following his own. From this hypothesis, one might expect that croak duration in response to playbacks of particular duration would vary consistently with the duration of the playback. In the three experiments here, however, there was no relationship between response duration and croak duration, even for stimulus durations within the normal range of variability in croak duration (experiment 1).

B. Response gradients for croak duration

Even though duration is a dynamic acoustic property, males do not respond equally likely to variations in this parameter. Results of experiment 1 show that males vocalize significantly less often in response to croaks with durations at the lower (shorter) end of the continuum of spontaneous croak durations, than to durations in the middle of the range. Males also responded less to croaks with durations at the upper extreme of the natural duration continuum, although these differences did not reach statistical significance. The results of experiments 2 and 3 again show that males respond more to exemplars with durations near the mean of the duration continuum, with significantly fewer responses to stimuli at the short end of the continuum. Fewer responses were evoked by stimuli with long durations; this was statistically significant only in experiment 3. The different pattern of response to the long duration stimulus in the two experiments might relate to the differences in chorus size during the two experiments, or to the different timing of responses in the two experiments (more responses occurred during the playbacks than in the interstimulus interval following playbacks in experiment 3).

The shape of bullfrog's response function for signal duration suggests a generalization gradient for this signal parameter, with a steeper falloff in response strength at the low end compared

to the high end of the continuum. Typical generalization gradients, as defined in theories of learning, are based on changes in conditioned responses to test stimuli at some physical distance from the original stimulus used in acquisition trials (Malott and Malott, 1970). Animals may interpret these test stimuli as similar to (perceptual similarity) or different from (failure of discrimination) the conditioned stimulus. The shape of the generalization function is influenced by factors such as the degree of original learning and prior discrimination training. In the ethological literature (Ghirlanda and Enquist, 1999), “generalization” is determined from changes in unconditioned responses to stimuli varying along some dimension from the original stimulus. The underlying assumption is that the modified stimulus has acquired its relevance, not through explicit laboratory training, but through evolutionary processes (Ghirlanda and Enquist, 1999). For example, in experiments 2 and 3, the medium duration stimulus might represent some “modal” value, reinforced through evolutionary time, for which the animal has evolved a particular internal representation. When presented with novel or modified stimuli, the perceptual system may act by estimating the degree of similarity of these stimuli with the internal representation, and a generalization gradient is the behavioral result. Similar assumptions have been made by Ryan *et al.* 2003, who further argue that these types of generalization gradient reflect evolutionary pressures on signal form.

The observation that an asymmetrical generalization gradient for duration exists in the bullfrog is consistent with data from other species of anurans. A steeper drop in response strength (number of evoked vocal responses) across changes in call duration has also been observed by Narins and Capranica (1978) in *Eleutherodactylus coqui*. These asymmetrical preference functions are similar to those observed in the phonotaxis responses of female *H. versicolor* (Gerhardt *et al.*, 2000). In that species, females prefer, in a choice test, calls of average duration over those of short duration, and this preference is stronger than that between calls of average duration and those of long duration. The preference function was thus steeper on the short duration compared to the long duration side. The less vigorous responses to short duration stimuli in both *R. catesbeiana* and *E. coqui* may also reflect a mechanism for discriminating between conspecific and heterospecific advertisement calls. At my study sites, the green frog, *R. clamitans*, is present; the individual notes in the advertisement calls of this species are considerably shorter in duration (105 to 205 ms; Bee *et al.*, 2001) than bullfrog croaks. The shortest signal durations presented to bullfrogs in experiments 2 and 3 (242 ms) are longer than those observed in green frog calls, but even so evoked very little calling. The steep cutoff at the low end of the duration response function for bullfrogs is thus consistent with a mechanism to discriminate against perception of heterospecific calls. The shape of the response gradient in *E. coqui* can also be explained as an adaptation to discriminate against perception of calls of sympatric species (Narins and Capranica, 1978). If this principle is widespread, then the generalization gradient for *R. clamitans* would also be asymmetrical, but with a steeper cutoff on the high, rather than the low, end. The data of Penna *et al.* 1997a, who observed an asymmetrical duration preference function in male *Batrachyla antartandica*, with a steeper slope on the high end, might also be explained by this hypothesis.

Male bullfrogs’ lowered responsiveness to short duration stimuli may further represent a mechanism to discriminate between conspecific advertisement and encounter calls. The male bullfrog’s encounter call (the “bonk” of Wiewandt, 1969) is an aggressive vocalization used in territorial defense. Its spectral composition is similar to that of the advertisement call, but it is considerably shorter in duration (<100 ms). A male’s typical response to an encounter call is to move or to attack, not to give advertisement calls (Wiewandt, 1969). Stimulus duration may be the parameter allowing the male to discriminate between these two conspecific vocalizations.

C. Lack of preference for supernormal stimuli

Studies in several different anuran species show that females prefer high, over low or intermediate, values of call duration (in those species where duration is a dynamic property; reviewed in Ryan and Keddy-Hector, 1992; Gerhardt and Huber, 2002). Moreover, females can show preferences for stimuli with durations longer than those typically observed in the calls of conspecific males. Ryan and Keddy-Hector (1992) argue that female preferences for these supernormal or exaggerated stimuli reflect a preference for greater sensory stimulation (greater signal-to-noise ratios), and motivate the evolution of complex mating signals.

Preference tests of female bullfrogs for conspecific advertisement croaks or calls varying in duration have not been reported; however, because croak duration is a dynamic acoustic property for this species, preferences for longer duration croaks might be expected. The results of the experiments reported here show that male bullfrogs do not respond more to supernormal croak durations. In experiment 2, there were no significant differences in number of responses evoked by long duration compared to medium duration stimuli; however, in the responses of most individuals, more croaks were evoked by the medium duration stimuli. Results of experiment 3 showed a significant decrease in the number of croaks evoked by long duration compared to medium duration stimuli. However, neither response latency nor the number of evoked responses alternating with individual stimulus croaks varied between long and medium duration stimuli. Experiments 2 and 3 are thus consistent in showing no preference for supernormal durations.

If longer duration signals are preferred by females because they provide more stimulation of the auditory system (Ryan and Keddy-Hector, 1992), why are such signals not preferred by males? Wells and Taigen (1986) suggested that call duration is energetically constrained, and Gerhardt *et al.* 2000 argued that, because of the shape of the female generalization function, for males to increase their call duration beyond a certain limit would not increase their reproductive success. Moreover, if bullfrog croaks are used in neighbor recognition or male–male assessment (Davis, 1987; Bee and Gerhardt, 2001), then males might be expected to be tolerant of variations in the acoustic properties of these signals, in order to provide the maximal individual recognition. Males may not need to increase croak duration beyond some limit because they gain sufficient information about the identity of neighbors from shorter duration signals. Finally, in line with the “interference risk” hypothesis presented by Schwartz *et al.* 2001 to explain female choice behavior, tolerance of variability in croak duration would enable males to recognize croaks of neighbors in the midst of fluctuating background noise.

D. Call matching

In experiments 1–3, there was no significant relationship between stimulus duration and response duration in the croaks of individual males. Moreover, males did not consistently add more croaks to their advertisement calls in response to the longer duration stimuli, nor did they decrease the number of croaks to the shortest duration stimuli. These data are not consistent with those of Bee and Perrill (1996), who reported that male *R. clamitans* increased note duration in response to playbacks of conspecific stimuli differing in the number of notes; however, in that study, responses to playbacks of signals differing in the duration of these individual notes were not measured. Wells and Taigen (1986) reported that male *H. versicolor* gave longer calls in response to playbacks of longer calls, but here there was not a precise match between call duration and stimulus duration. These comparisons suggest that the bullfrog call recognition system is more permissive of variability in this specific parameter than that of these other species. This may be related to the relatively longer duration of croaks in bullfrog advertisement calls than notes in the advertisement calls of these other species. It is also possible that bullfrogs may match the number of croaks (and thus overall duration of

the entire advertisement call) to the number of croaks in a playback. This possibility was not addressed in the present study.

E. Physiological correlates of duration sensitivity

Responses of neurons in the ascending auditory system to variations in signal duration depend in large part on the classification of neurons as tonic or phasic (fast adapting or slow adapting). The most common response pattern in the auditory nerve and auditory brainstem to stimuli varying in duration is an increase in spike count with increases in duration, described as long-pass functions (Potter, 1965; Narins and Capranica, 1980; reviewed in Gooler and Feng, 1992). In the torus semicircularis of the midbrain of several different frog species, a diversity of response patterns to duration is seen, with some neurons showing bandpass (maximal response to some intermediate duration), short-pass (maximal response to short duration), or all-pass (nonselective) responses (Gooler and Feng, 1992; Penna *et al.*, 1997b). Some of these neurons show selective responses to species-typical stimulus durations (Narins and Capranica, 1980). Potter (1965) reported that neural responses in the bullfrog's midbrain to tones up to 500 ms long reached a plateau at some intermediate duration. These results are consistent with the behavioral data presented here; that shorter stimuli evoke fewer behavioral responses, and fewer neural responses. In the central nucleus of the thalamus of *R. pipiens*, a large proportion of bandpass response functions, with neurons seemingly tuned to particular durations, has been observed (Hall and Feng, 1986). The physiological data do not appear to show, however, a neural mechanism for selective response to supernormal stimulus durations, again consistent with the behavioral data presented here. That is, long-pass response functions with peaks at supernormal durations for that species are not over-represented in midbrain or thalamic responses.

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FIG. 1.

Power spectral density (left) and segment of the time-domain waveform (right) of exemplar A (experiment 2) after being subjected to the time compression algorithm. Top: long duration stimulus; middle: medium duration stimulus; bottom: short duration stimulus. Power spectral density plots were made using `MATLAB` v. 5.3 scripts. Time domain waveforms were exported from `COOLEDT` 2000.

FIG. 2.

Frequency distribution of croak duration in the spontaneous advertisement calls of nine individual male bullfrogs. Duration is divided into 20-ms bins. The data for each individual are shown by a different patterned bar; data from some individuals overlap.

FIG. 3.

The relationship between number (mean $\pm$ standard error) of answering croaks to stimulus duration. Repeated measures ANOVA showed a significant effect of stimulus duration. Frogs responded most to the stimulus with duration 700 ms, and responded significantly less (*) to the stimulus with duration 420 ms.

FIG. 4.

The duration of answering croaks by two individual frogs in response to different stimulus durations (experiment 1). Base = response duration during baseline (no stimulus) trials. Both of these frogs are included in the data in Fig. 3. For each stimulus duration, the durations of individual responding croaks are shown as a scatter plot (some symbols overlap). The circle/line graph represents the mean response duration for each stimulus duration and baseline period.

FIG. 5.

(A) Number (mean $\pm$ standard error, s.e.) answering croaks to stimuli of different durations (S = short duration exemplars; M = medium duration exemplars; L = long duration exemplars) in experiment 2. Frogs responded significantly less (*) to the short duration exemplars. (B) Number (mean $\pm$ standard error) answering croaks to stimuli of different durations (DS = short duration exemplars, 12 croaks; M = medium duration exemplars; L = long duration exemplars) in experiment 3. Frogs responded significantly less (*) to the short and long duration exemplars than to the medium duration exemplars.

FIG. 6.

(A) (top). Time domain waveform of the stimulus (top trace) and the frog's evoked vocal response (bottom trace) to a medium duration exemplar in experiment 3. The onset of each individual croak and the time of peak energy in each croak in the frog's response consistently occur in the time intervals between successive stimulus croaks. This type of pattern was termed alternating. (B) (bottom). Time-domain waveform of the stimulus (top trace) and the frog's evoked vocal response (bottom trace) to a short duration exemplar in experiment 3. The onset of each croak and the time of peak energy in each croak of the frog's response do not consistently occur in the time intervals between successive stimulus croaks. In particular, the peak energy in the second answering croak occurs simultaneously with the third stimulus croak. This type of pattern was termed nonalternating.