

Effect of temporal and spectral noise features on gap detection behavior by calling green treefrogs



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ABSTRACT

Communication plays a central role in the behavioral ecology of many animals, yet the background noise generated by large breeding aggregations may impair effective communication. A common behavioral strategy to ameliorate noise interference is gap detection, where signalers display primarily during lulls in the background noise. When attempting gap detection, signalers have to deal with the fact that the spacing and duration of silent gaps is often unpredictable, and that noise varies in its spectral composition and may thus vary in the degree in which it impacts communication. I conducted playback experiments to examine how male treefrogs deal with the problem that refraining from calling while waiting for a gap to appear limits a male's ability to attract females, yet producing calls during noise also interferes with effective sexual communication. I found that the temporal structure of noise (i.e., duration of noise and silent gap segments) had a stronger effect on male calling behavior than the spectral composition. Males placed calls predominantly during silent gaps and avoided call production during short, but not long, noise segments. This suggests that male treefrogs use a calling strategy that maximizes the production of calls without interference, yet allows for calling to persist if lulls in the background noise are infrequent.

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1. Introduction

Whenever many individuals gather to display simultaneously, such as in leks and choruses, they create “noisy” social environments that may pose challenges to the very purpose of those gatherings – effective sexual communication (Narins and Zelick, 1988; Gerhardt and Huber, 2002; Brumm and Slabbekoorn, 2005; Vélez et al., 2013). Interference from the chorus background noise can constrain signal detection and recognition (Ehret and Gerhardt, 1980; Gerhardt and Klump, 1988; Wollerman, 1999; Bee, 2007; Bee and Swanson, 2007), and limit the ability of females to discriminate among conspecifics (Schwartz and Gerhardt, 1989; Wollerman and Wiley, 2002; Bee, 2008). Signalers have evolved a range of behavioral strategies to mitigate the problem of noise interference from different sources (natural, anthropogenic, etc.). Some increase calling activity (e.g., call rate, call duration) (Penna et al., 2005; Kaiser and Hammers, 2009), increase vocal amplitude (Brumm and Todt, 2002; Penna and Hamilton-West, 2007), shift their call frequency above the level of the masking noise (Slabbekoorn and Peet, 2003; Feng et al., 2006; Luther and Baptista, 2010), or use other signal

modalities that are not affected by the noise (Preininger et al., 2009). Another frequently observed adjustment strategy is gap detection. Here, males take advantage of the fact that noise is rarely of uniformly high amplitude and display primarily during lulls in the background noise (Zelick and Narins, 1982, 1983; Brumm, 2006).

When attempting gap detection, signalers have to deal with two problems: (i) unpredictable variation in the spacing and duration of silent gaps within noise, and (ii) different types of noise (i.e., conspecific, heterospecific, ambient), which may vary in the degree in which they impact communication. Gaps in background noise may appear at unpredictable intervals or be of short duration. In either case, the ability to quickly produce a signal once such an opportunity arises should be beneficial, and indeed has been reported for several acoustically communicating species (Zelick and Narins, 1982; Moore et al., 1989; Grafe, 1996; Brumm and Todt, 2004). How signalers deal with the noise surrounding silent gaps is less clear, however. Producing signals free of noise interference should be ideal, yet if noise is much more frequent than silent gaps, producing overlapped signals may still be better than refraining from signaling for too long. This predicts that the most effective signaling strategy may be to place signals mainly in silent gaps, refrain from signaling during short periods of noise, but eventually resume signaling during prolonged noise.

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Noise varies in origin and spectral composition. The effects of anthropogenic noise pollution have received increased attention lately (Sun and Narins, 2005; Bee and Swanson, 2007; Lengagne, 2008; Luther and Baptista, 2010), yet challenges created by natural noise interference (i.e., wind, rushing water) and biotic noise interference (both conspecific and heterospecific) are the ones that are most prevalent in nature and often have profound effects on signal production and perception (Littlejohn and Martin, 1969; Greenfield, 1993; Schwartz and Wells, 1983a,b; Páez et al., 1993; Wollerman and Wiley, 2002; Brumm and Todt, 2004; Feng et al., 2006; Penna et al., 2005; Wong et al., 2009). The degree to which communication is impaired should be a function of whether, and how much, the frequencies of interfering noise overlaps with the critical bands constituting the frequencies of the conspecific signal (Schwartz and Wells, 1983a,b; Klump, 1996). This predicts that heterospecific noise interference should be less problematic than conspecific one, yet whether this is indeed the case is surprisingly little studied (but see Zelick and Narins, 1982; Schwartz and Wells, 1983a).

Acoustic communication plays a central role in the reproduction of most anuran amphibians. Many species communicate in dense choruses, and the high noise levels associated with large breeding aggregations (e.g., Narins, 1982; Swanson et al., 2007) suggest that noise interference is a ubiquitous challenge for these animals. I conducted playback experiments with male green treefrogs (*Hyla cinerea*) to examine how the temporal and spectral composition of background noise affects calling behavior. In particular I was interested in how males deal with the problem that producing calls during noise may interfere with effective sexual communication, yet refraining from calling also limits a male's reproductive success. The hypothesis that there is a trade-off between the need to avoid call overlap and the need to maintain calling to attract females makes three predictions: males will (i) place most calls into silent gaps, (ii) avoid call overlap with short periods of noise, and (iii) produce overlapped calls when periods of noise are prolonged. I also tested three predictions of the hypothesis that broader overlap with the frequencies emphasized in the conspecific call constitutes a more severe problem for communication. If so, conspecific noise should elicit stronger overlap avoidance behavior than heterospecific noise, and males should (i) place a higher proportion of their calls in gaps in conspecific compared to heterospecific noise, (ii) refrain more from calling during conspecific compared to heterospecific noise, and (iii) maintain call inhibition longer when confronted with conspecific compared to heterospecific noise segments.

2. Material and methods

2.1. Study species and study sites

The green treefrog, *H. cinerea*, the focal species in this study, is a common inhabitant of ponds and lakes in the southeastern part of the USA. It shares breeding ponds with the barking treefrog, *Hyla gratiosa* in the eastern part, but is allopatric in the northwestern part of its range (Conant and Collins, 1998). Green treefrogs prefer to call from elevated perches (cattail, etc.), but will call from the ground along the pond margin or from floating mats of vegetation, while barking treefrogs call while floating on the water surface. Both species are closely related, and their vocal repertoires are structurally and functionally similar (Fig. 1A). Calls of both species are about 150 ms long and repeated 1–2 × per second; in both species calls are composed of a series of harmonics, two of which are emphasized in the call; in *H. cinerea* the 0.9 and 3.0 kHz harmonic is emphasized, in *H. gratiosa* it is the 0.5 and 2.0 kHz harmonics (Oldham and Gerhardt, 1975). Thus, calls differ mainly in

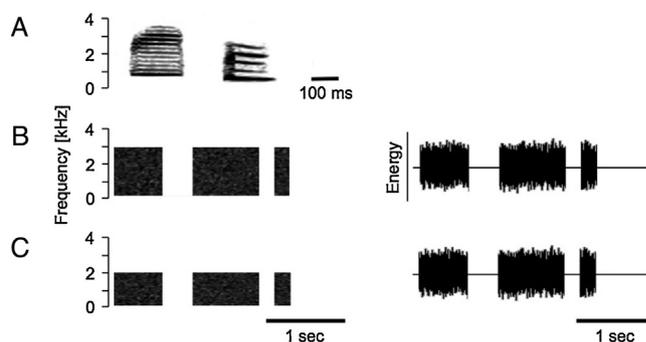


Fig. 1. Spectrograms of a call of *H. cinerea* (A, left) and *H. gratiosa* (A, right), as well as spectrograms (B and C left panels) and oscillograms (B and C right panels) of the noise stimuli used during playback trials. The frequency range of the conspecific noise stimulus (*H. cinerea*) was 0.1–3.0 kHz (B, left panel), that of the heterospecific noise stimulus (*H. gratiosa*) was 0.1–2.0 kHz (C, left panel). Chorus noise segments (200, 400, 600 and 800 ms) were grouped with periods of silence (“gaps”) into 1-s noise + gap sequences (e.g., 600 ms noise + 400 ms silence, etc.) (B and C right panels), which were then presented in random order.

frequency content with *H. gratiosa* calls covering the lower 2/3 of the frequency range of *H. cinerea* (Fig. 1B and C).

I conducted the study during the 2001 and 2003 breeding seasons (May–August) at Welder Wildlife Refuge, San Patricio Co., Texas (hereafter, TX), and Hobcaw Barony, Georgetown Co., South Carolina (hereafter, SC). The population at the SC site is sympatric with *H. gratiosa*, while the one at the TX site is allopatric (Höbel and Gerhardt, 2003). To ensure that motivation to call when confronted with a noise playback was comparable between males and sites, I conducted all playback experiments during the species' peak breeding season and during the first 2 h after sunset when calling activity was highest.

2.2. Experimental design

I presented focal males with playbacks of simulated chorus noise, and scored (i) whether noise suppressed calling, (ii) whether males were able to detect and call during short silent gaps embedded in the noise, and (iii) whether conspecific and heterospecific noise was equally effective in suppressing calling behavior.

2.2.1. Stimulus design

I used bandpass-filtered white noise as chorus stimuli, instead of recordings of actual chorus background noise. This allows for better control of stimulus parameters and prevents having to account for fluctuations in amplitude levels and spectral composition that are prevalent in natural chorus noise (Vélez and Bee, 2010). To generate conspecific and heterospecific chorus stimuli, I used noise-generation and filter functions provided by CoolEdit96 (Syntrilium Software Corp., Phoenix, Arizona, USA). Since *H. cinerea* calls have most energy between 0.9 and 3.0 kHz (Oldham and Gerhardt, 1975), I bandpass-filtered white noise between 0.1 and 3.0 kHz to generate conspecific noise (Fig. 1B). To create heterospecific noise (Fig. 1C), I filtered white noise between 0.1 and 2.0 kHz, since most of the energy in *H. gratiosa* calls is concentrated between 0.5 and 2.0 kHz (Oldham and Gerhardt, 1975). I then used editing functions in CoolEdit96 to create chorus noise segments of four durations (200, 400, 600 and 800 ms), and combined them with periods of silence (“gaps”) to form 1-s noise + gap sequences (e.g., 400 ms noise + 600 ms silence) (Fig. 1 B and C). I generated mono files that repeated the four noise + gap sequences in random order (either conspecific or heterospecific chorus noise) and recorded them onto two cassette tapes, which I later used during field playback trials.

2.2.2. Experimental procedure

The playback setup consisted of a RadioShack Optimus XTS-40 speaker, driven by a Sony WM-D6C recorder and amplified by a RadioShack Optimus XL-50 Stereo Amplifier (RadioShack Corporation, Fort Worth, Texas, USA). The signal from the playback recorder was split so it could be recorded on one channel of a Sony TC-D5M stereo tape recorder via the line input (Sony Corporation, Tokyo, Japan), while the other channel recorded the focal male using an Audio-Technica U.S.ATR55 microphone (Audio-Technica U.S., Inc., Stow, Ohio, USA). I later digitized (at 22.5 kHz) the recordings with CoolEdit96.

I avoided adjusting playback levels *in situ* since this would have resulted in too much disturbance of the focal male. Rather, before starting trials each evening I used a RadioShack 33-2050 Realistic SPL meter (C weighting, fast response) to adjust the output gain setting of the playback recorder so that the *H. cinerea* noise stimulus broadcast at an amplitude of 80 dB SPL at 2 m distance from the speaker. This amplitude is below the call amplitude of individual males, but above the amplitude of natural choruses, and it is comparable to other studies investigating gap detection in frogs (i.e., Narins, 1982; Grafe, 1996). Because the *H. gratiiosa* noise stimulus had a different frequency bandwidth it would have been broadcast at a lower amplitude from this same speaker; I accounted for that when making the stimulus tapes, recording the *H. gratiiosa* stimulus at higher intensity than the *H. cinerea* stimulus, such that when broadcast the amplitudes were equal.

At the pond, I selected an isolated male (nearest neighbor >10 m) that was calling regularly, and placed the speaker and the microphone, each mounted on tripods, 2 m away from it. I started playbacks of the chorus noise stimuli once male resumed normal calling. I presented each male with 100 stimulus repetitions (i.e., 100 1-s noise + gap sequences composed of the four different noise durations) per noise type (conspecific or heterospecific). Trials with different noise types were presented in random order, with a rest period of 5 min. After completing trials with a given male, I measured the actual stimulus amplitude at the location of the focal frog, as well as the air temperature (to the nearest 0.1 °C). To verify that my experimental playbacks were louder than the local background noise, I measured the relative amplitudes of the playback noise and the natural background noise from each focal male's experimental recordings (measured from the microphone-recorded track).

I presented chorus noise playbacks to 12 males in TX and 18 males in SC. Average SPL \pm SD of the noise stimuli was 80 ± 2 dB, average difference \pm SD between stimulus noise and natural chorus background noise at the location of focal males was 36 ± 5 dB, and the average temperature \pm SD at the calling site was 24 ± 1 °C. There was no significant difference in stimulus amplitude ($t = 0.27$, $DF = 10.56$, $P = 0.79$), stimulus to natural noise difference ($t = 0.40$, $DF = 11.12$, $P = 0.70$), nor temperature ($t = 0.36$, $DF = 11.94$, $P = 0.72$) between sites.

2.3. Data analysis

To describe the effectiveness of call suppression by conspecific and heterospecific background noise, I first counted the number of calls given during periods of noise as well as those given during silent gaps. To further describe call suppression behavior, I focused on calls that overlapped with the noise segments. From every overlapped call given by a male, I determined the overlap latency by measuring the time from the beginning of the noise segment to the beginning of the call. When obtaining overlap latency data, I also noted the duration (200, 400, 600, 800 ms) of the noise segment with which each call overlapped. Based on these overlap latency values I determined (i) the suppression latency and (ii) the suppression release (see Fig. 2 for definitions of terms). I consider suppression latency and suppression release to be different traits,

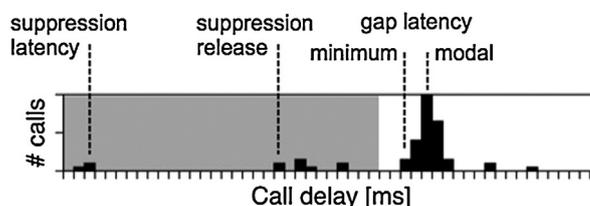


Fig. 2. Analysis of calling behavior in response to noise + gap sequences (example shows the 600 ms noise + 400 ms gap sequence). First, I measured all calls the male gave either overlapping with the noise segment, or during the silent gap (shown as histogram data). Calls that overlapped with the noise segments (indicated by gray shading) generally showed a bimodal distribution; I used the first peak to estimate suppression latency (i.e., how quickly noise suppresses calling), and the second peak to estimate suppression release (i.e., how long call suppression lasts during persisting noise). I defined suppression latency as the time from the onset of noise to the onset of the last call associated with the first histogram peak. I defined suppression release as the time from the onset of noise to the onset of the first call associated with the second histogram peak. Calls that were placed into silent gaps (indicated by white background) generally showed a single histogram peak; I used this peak to estimate minimum and modal gap latency. I defined minimum gap latency as the time from the onset of the gap to the onset of the first call that was placed in the gap. I defined modal gap latency as the time from the onset of the gap to the time where the male placed most of his calls (i.e., histogram peak). Thus, although I measured many calls per male, each focal male provided a single value for suppression latency, min. gap latency, and modal gap latency, separately for each level of two predictor factors (duration of noise segments, $n = 4$; and noise type, $n = 2$), except for suppression release for which I only obtained data for duration of 800 ms noise segment, $n = 1$; and noise type, $n = 2$) (see Section 2).

because the suppression latency may indicate a physiological limit of how quickly noise suppression can take effect, while suppression release may reflect the amount of time a call-motivated male is willing to refrain from calling when confronted with acoustic interference. Suppression latency was quite short (see Figs. 2 and 5A), which allowed me to obtain suppression latency values for each of the four noise duration segments per noise type per focal male. By contrast, I only obtained one suppression release value per noise type per focal male. The reason for this is that since suppression release is measured within noise segments, calls overlapping short noise segments cannot show suppression release values above the length of the stimulus (i.e., for the 200 ms noise segment only suppression release values below 200 ms are possible, and values below 400 ms in the 400 ms noise segment, etc.). Although some suppression release values were short (starting around 200 ms, data not shown), I conservatively only compare suppression release data from calls that overlapped with the longest (800 ms) noise segments.

To describe gap detection behavior, I focused on the subset of calls that occurred in the silent gaps. For every call given during a silent gap I determined the gap latency by measuring the time from the beginning of the gap to the beginning of the call, and I also noted the duration of the gap in which each call was placed. Based on these call latency values I determined (iii) the minimum gap latency and (iv) the modal gap latency (see Fig. 2 for definitions of terms). Thus, each focal male contributed eight minimum and modal gap latency values [one value per gap duration segment ($n = 4$) for each stimulus noise type ($n = 2$), for a total of $4 \times 2 = 8$]. I consider minimum and modal gap latencies to be different traits, because the minimum latency may be related to a physiological response to the occurrence of a silent gap, whereas the modal gap latency may reflect a male's individual call timing preferences when presented with a silent gap in noise. (Nota Bene: My experimental design used 1-s noise + gap sequences, such that short gaps were always preceded by long noise segments, and long gaps by short noise segments. When calling during a silent gap the test male has experienced the pre-gap noise segment and it's duration, but is unaware how long the gap is going to last. It is therefore probably a more biologically relevant measure

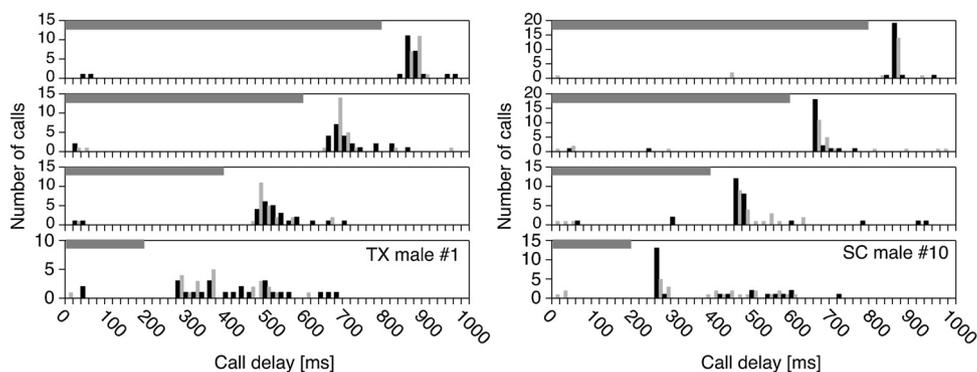


Fig. 3. Call responses to silent gaps inserted into conspecific (black) or heterospecific (gray) background noise. Representative examples of call responses of two males (left from TX, right from SC) to the four presented noise/gap combinations (stimuli were presented in random order, but aligned here to facilitate comparison). Shown is the frequency of calls that began within each of 50 consecutive 20 ms bins, bin one starting at the onset of the noise stimuli (indicated by dark gray horizontal bar). Males were inhibited from calling during noise stimulus presentation, and placed most of their calls shortly after the onset of the silent gap. Note how calls of the male from South Carolina (right column) are grouped closely together shortly after the end of the noise stimuli, while those of a male from Texas (left column) start later and are produced over a longer time period after the end of the noise stimuli.

to relate pre-gap noise duration (not gap duration) to gap latency, and this is what I will compare below).

2.4. Statistical analysis

To test whether males place more calls in silent gaps than expected by chance, I compared the observed proportion of calls given during silent gaps (arcsine transformed) with an expected proportion of 0.5 as the value for random calling (although the duration of the noise and gap segments varied from 200 to 800 ms, the average time of noise to silent gap presented to the frogs was 50%). I used the non-parametric Wilcoxon rank sum test for this comparison because arcsine transformation did not achieve conditions of normality (Shapiro–Wilk test) and equal variance (Levene's test). To test whether call suppression was stronger with conspecific than heterospecific noise, I used a mixed model implementing REML, which provides *P*-values for fixed factors, and confidence intervals for random factors; confidence intervals overlapping zero indicate non-significant effects. I entered the proportion of calls in gaps (arcsine transformed) as test variables, noise treatment, study site and their interactions, as fixed predictor variables, and male ID as random factor.

To test what noise features affected call suppression behavior I also used a mixed model implementing REML. I entered suppression latency or suppression release, as test variables, and noise treatment, noise duration, study site and their interactions, as predictor variables, and male ID as a random factor. To test what gap or noise features affected gap detection behavior I also used a mixed model implementing REML, and entered minimal or modal gap latencies, as test variables, and noise treatment, gap size, study site and their interactions, as predictor variables, and male ID as a random factor. All statistical tests were performed using JMP 8.0 (SAS Institute, Cary, NC, USA).

3. Results

3.1. Gap detection behavior

Noise did suppress calling in *H. cinerea*, and the duration of the gap and noise segments was more important than the type of noise presented to the males. Simulated chorus noise suppressed calling behavior (Fig. 3), and males positioned more calls in silent gaps than expected by chance (Wilcoxon rank sum test: $Z=9.66$, $P<0.0001$). The proportion of calls initiated in silent gaps was not significantly different in conspecific or heterospecific background noise

Table 1

Results of a mixed model (REML) comparing the effect of study site, noise stimulus type (con/het), and their interaction on call suppression.

	<i>F</i>	<i>df</i>	<i>P</i>
Study site	0.07	1,27.52	0.80
Treatment (con/het)	0.42	1,23.85	0.52
Site × Treatment	0.27	1,23.85	0.61
Male (Random)	Not overlap 0		

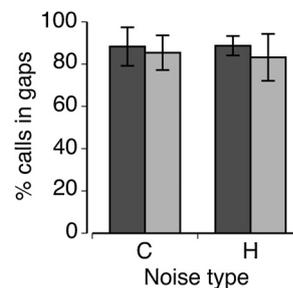


Fig. 4. Males in both populations placed the majority of calls within silent gaps, irrespective of the type of noise presented (con/het). Dark gray bars represent TX, light gray bars represent SC.

treatments (Table 1, Fig. 4), indicating that heterospecific noise was as effective in suppressing calling as conspecific noise. Suppression latency was a little shorter in heterospecific compared to conspecific noise (Table 2, Fig. 5A), while suppression release did not differ for calls that overlapped with either noise type (Table 2, Fig. 5B). Thus, while males may respond to conspecific and heterospecific noise in subtly different ways, at the intensity levels used in the present tests they do not differentiate between both noise types in a biologically relevant way. Gap detection was only affected by the temporal composition of the noise and gap segments (Table 3). Minimum and modal gap latencies of calls placed in gaps appearing within conspecific or heterospecific noise were similar (Fig. 6A and B), but both minimum and modal gap latencies decreased as the pre-gap noise segments increased in duration (Table 3, Fig. 6C and D).

3.2. Geographic variation

Males from both populations were equally good at placing calls into silent gaps (Table 1, Fig. 4). The significant site × pre-gap noise duration interaction term shows that the slope of the decrease in gap latency associated with increased pre-gap noise duration

Table 2

Results of a mixed model (REML) comparing the effect of study site, noise stimulus type (con/het), noise duration, and their interactions, on suppression latency and suppression release. For suppression release only the data from 800 ms noise segments was included in the analysis. Significant effects are set in bold.

	Suppression latency			Suppression release		
	F	df	P	F	df	P
Study site	0.23	1,109.5	0.63	0.90	1,15.82	0.36
Treatment (con/het)	10.88	1,102.6	0.001	0.75	1,11.2	0.41
Noise duration	1.17	1,100.7	0.28	n.a.		
Site × Treatment	0.63	1,102.3	0.43	0.09	1,11.2	0.77
Site × Noise duration	1.22	1,99.2	0.27	n.a.		
Treat. × Noise duration	0.62	1,97.6	0.43	n.a.		
Site × Treat. × Noise dur.	1.70	1,98.4	0.20	n.a.		
Male (Random)	Overlap 0			Not overlap 0		

Table 3

Results of a mixed model (REML) showing the effect of study site, noise stimulus type (con/het), pre-gap noise duration, and their interactions, on minimum gap latency and modal gap latency. Significant effects are set in bold.

	Minimum gap latency			Modal Gap Latency		
	F	df	P	F	df	P
Study site	6.80	1,25.3	0.015	10.99	123.7	0.003
Treatment (con/het)	1.23	1,178.4	0.27	0.49	1,183.7	0.49
Pre-gap noise duration	157.2	1,169.2	<0.0001	81.42	1,68.1	<0.0001
Site × Treatment	0.002	1,178.4	0.97	1.33	1,183.7	0.25
Site × Pre-gap noise duration	21.6	1,169.2	<0.0001	19.55	1,168.1	<0.0001
Treatment × Pre-gap noise duration	2.40	1,169.2	0.13	2.01	1,168.1	0.16
Site × Treat. × Pre-gap noise duration	0.25	1,169.2	0.61	1.16	1,168.1	0.28
Male (Random)	Not overlap 0			Overlap 0		

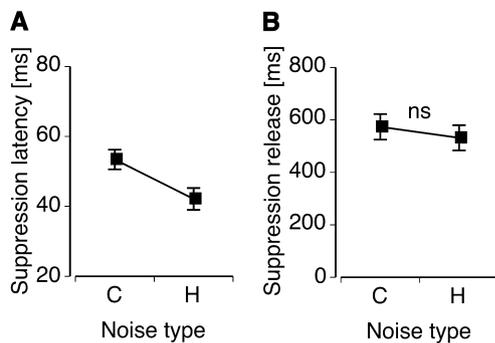


Fig. 5. Effects of noise type on call suppression. (A) Suppression latency was affected by noise type treatment, with heterospecific noise eliciting shorter suppression latencies than conspecific noise. (B) Suppression release (conservatively calculated for only the 800 ms noise segment) was not affected by noise type treatment. Shown are least square mean (LSM) and standard error (SE).

differed between sites: frogs from TX showed a stronger decrease in gap latency than males from SC (Fig. 6C and D). Interestingly, gap latencies from both populations were only different for short pre-gap noise durations, but converged for longer ones (Table 3, Fig. 6C and D). Finally, comparisons never involved a significant site × treatment interaction, which would have been indicative of reproductive character displacement (RCD) in male responses to conspecific and heterospecific chorus noise.

4. Discussion

Anuran amphibians are highly vocal and often communicate in dense choruses where noise interference presents a ubiquitous problem. Since calling in anurans is one of the most energetically taxing behaviors in any vertebrate (Wells, 2007), producing calls that cannot be effectively evaluated by females because they are masked by background noise should carry a fitness cost. Yet, males need to vocalize in order to attract females because the anuran mating system relies on females approaching the caller after having evaluated his call features and localized him in the chorus

(Gerhardt and Huber, 2002). It appears that male green treefrogs, and other anurans (i.e., Narins, 1982; Grafe, 1996), solve this problem by using a calling strategy that maximizes the production of calls without noise interference (i.e., gap detection), yet allows for calling to persist if silent gaps occur too infrequently.

4.1. Effect of spectral and temporal noise features on gap detection

The level of variation in background noise spectral composition used in this study had little effect on calling behavior in *H. cinerea*, which is consistent with observation from other species where calling can be suppressed by noise or tone bursts of different frequencies (Littlejohn and Martin, 1969; Zelick and Narins, 1982; Schwartz and Wells, 1983a; Wong et al., 2009). Nevertheless, variation in spectral structure can affect call suppression, and in not always straightforward ways: stimuli of similar deviation above or below the conspecific frequency range can have very different effects on call suppression (Schwartz and Wells, 1983a), and sometimes stimuli with frequencies well below the conspecific range can result in the strongest call suppression (Zelick and Narins, 1982).

Variation in temporal noise structure affected male calling behavior more strongly than variation in spectral composition. This may ultimately result from the way many rhythmically signaling animals such as frogs, katydids and fireflies produce their signals when calling alone, and adjust their signals relative to those of other signalers when calling in groups. Here, signaling appears to be driven by an internal pacemaker that rises from baseline to trigger level, at which point a signal is produced and the pacemaker returns to basal level, and so on (Greenfield, 1994). Exogenous stimuli can modify the output of this endogenous rhythm, which allows signalers to adjust to changes in their acoustic environment. As an interference is perceived, the pacemaker is reset to the basal level, and it remains inhibited for the duration of the interference. Upon the offset of the interference the pacemaker ascends again, and another signal is produced. This inhibitory-resetting mechanism was proposed to explain call-timing interactions between neighboring males, but it can also account for the ability of many

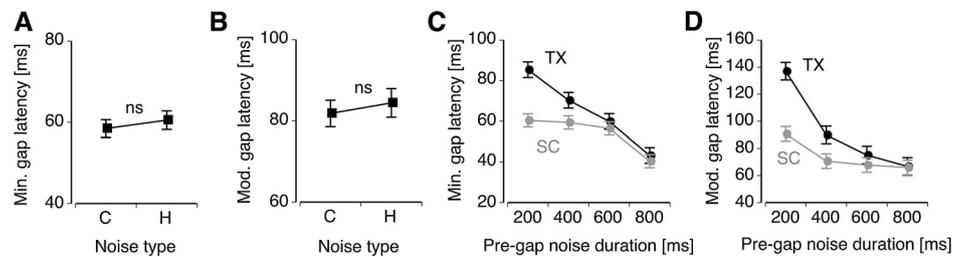


Fig. 6. Effects of noise type, and noise and gap duration, on gap latency. (A, B) Neither minimum nor modal gap latency was affected by noise type treatment. (C) Minimum gap latency and (D) modal gap latency were shorter when the pre-gap noise segment was longer, and there was geographic variation in how frogs responded to variation in the duration of noise segments before silent gaps. Noise-segment related variation in gap latency was overall smaller in SC than in TX, and frogs from both populations converged on similar gap latency values when the gaps appeared after longer noise segments. Shown are least square mean (LSM) and standard error (SE).

anurans to produce calls within short silent gaps if call production is inhibited during noise, and the offset of noise results in release from inhibition (Zelick and Narins, 1982, 1983; Moore et al., 1989; Grafe, 1996). Further, signal-timing adjustments are very fast – in the tenth of milliseconds range (i.e., Höbel and Gerhardt, 2007) – and the associated short integration times may limit the processing capability of males, allowing only for coarse “noise avoidance” adjustments without finer processing of the type of noise. This may explain why males were able to quickly respond to the presence of a silent gap, but did not differentiate between noise types varying in frequency composition (at least with the level of variation used in this study).

Background noise lasts much longer than individual calls, and inhibitory-resetting might thus result in prolonged noise-induced inhibition. Yet, if inhibition wears off over time, inhibitory-resetting could produce fast gap detection in short-duration noise, and eventual call production during long-duration noise. Two observations are in line with this hypothesis: first, calls were given more quickly (i.e., shorter gap latencies) after longer duration noise. Second, during noise segments male green treefrogs remained inhibited for about 600 ms, but started calling if the noise persisted beyond that. A similar pattern of shorter gap latencies after longer duration noise stimuli, and resumption of call production after longer-duration noise has also been documented in African Reed frogs (Grafe, 1996), suggesting that it may be a general phenomenon.

The playback stimuli used here had an average 50/50 noise to silence ratio, and no noise segments longer than 800 ms, which may have maintained call motivation in the focal males and kept them from falling silent permanently. Whether calling males would respond to prolonged, high-amplitude noise with permanent call suppression, or eventually ignore the noise and resume calling is largely unclear. Studies investigating behavioral responses to gaps in background noise use relatively short gap/noise combinations (≤ 30 s; Schwartz and Wells, 1983a; Zelick and Narins, 1983; Grafe, 1996), and most studies employing longer noise treatments (i.e., to study effect of anthropogenic noise) do so at much lower noise amplitudes (i.e., Cunnington and Fahrig, 2010; Kaiser et al., 2011). To my knowledge the only study that presented calling males with prolonged traffic noise at high amplitude (88 dB) did indeed find that noise reduced calling, but did not extinguish it. However, it was not clear from the study whether lower average call rate was the result of males calling continuously but at a slower pace, or from males falling silent at the beginning of the noise treatment, but then calling at regular pace once they started to call again (Lengagne, 2008).

4.2. Geographic variation

An earlier study on cross-species effects on *H. cinerea* communication behavior had documented a pattern of reproductive character displacement (RCD) in the strength of preference for the

conspecific call in females, as well as differences in the calls and the call perches of males (Höbel and Gerhardt, 2003). Here I extend this investigation in asking whether there is RCD in how males respond to conspecific and heterospecific noise interference, and did not find support for RCD in gap detection. To confidently reject the hypothesis it would be necessary to evaluate a larger number of populations, especially since there is often geographic variation within allopatry and sympatry (Gabor and Ryan, 2001; Höbel and Gerhardt, 2003). However, given the likely mechanism involved in gap detection (inhibitory-resetting), and the probably higher importance of temporal compared to spectral noise features (see above), increasing sample size will likely not change this result.

I did find geographic differences in how males respond to variation in pre-gap noise duration, with a small increase in gap latencies in SC, but a strong increase in TX. This, however, is probably not due to real differences in gap detection, but an artifact of other differences in calling behavior between TX and SC populations. As can be seen from the call delay histograms, call timing in response to noise, as well as to individual calls (see Höbel and Gerhardt, 2007) is more precise in SC than in TX. Höbel and Gerhardt (2007) suggested that this may be related to differences in the call repetition rate typical for each population. Call rate is higher in TX than SC, and males in the two populations may follow different strategies of how to be attractive to females. Due to the incredibly quick adjustments necessary for effective signal timing (in the 20 ms range), it may not be feasible to call at a high rate and at the same time perform precise call timing; TX males may opt to maximize attractiveness by increasing call repetition rate at the expense of precise call timing, while SC males may opt for call timing precision (Höbel and Gerhardt, 2007).

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