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Noisy Neighbors: Acoustic Interference and Vocal Interactions between Two Syntopic Species of Ranid Frogs, *Rana clamitans* and *Rana catesbeiana*

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Abstract.—**American Bullfrogs (*Rana catesbeiana*) and Green Frogs (*Rana clamitans*) share ranges and breeding seasons, are ecologically similar, and often occupy the same breeding ponds throughout the summer. Males of both species use vocalizations to defend territories and attract females; however, Bullfrogs have longer calls and call much more frequently than Green Frogs. The calls of the two species overlap in frequency; thus, Bullfrog calls are a likely source of acoustic interference for Green Frogs that could affect their ability to attract females. Nevertheless, in natural settings where these species co-occur, Green Frogs reproduce successfully. This suggests that Green Frogs respond to the calling patterns of Bullfrogs in ways that maximize Green Frog signal-to-noise ratio. We used long-term pond environment recordings and bioacoustics analyzing software to explore the influence of Bullfrog calling patterns on the vocal activity of syntopic Green Frogs. We found both species call most actively within the same seasonal and diel periods. Our results show that Green Frogs avoid overlapping their calls with Bullfrogs more often than expected by chance. Therefore, to avoid Bullfrog call overlap, Green Frogs use the fine-scale behavioral response of placing their calls in silent gaps between the calls of Bullfrogs. This pattern was even more pronounced in interactions between nearest neighbors in which there was no overlap observed between Bullfrogs and their nearest neighbor Green Frog.**

Interspecific reproductive interference occurs when the reproductive behavior of one species disrupts the reproductive behavior of another (Gröning and Hochkirch, 2008). In some cases, such as mismatings between males and females of different species, the result can be hybridization or even failed reproduction. In other cases, such as signal jamming, interspecific reproductive interference may reduce the fitness of individuals of one species or the other. For animals that use acoustic signals to communicate with conspecifics, the calls of other species can be a major source of acoustic interference (Latimer, 1981; Greenfield, 1988; Amézquita et al., 2006; Brumm, 2006; Wells and Schwartz, 2006; Luther, 2009; Hartbauer et al., 2012; Schwartz and Bee, 2013; Wiley, 2015). Auditory masking of a male's signals by the calls of another species can reduce the ability of males to attract conspecific females, thereby reducing the reproductive success of the males (Schwartz and Wells, 1983; Wollerman, 1999; Wollerman and Wiley, 2002; Marshall et al., 2006). There are several strategies for avoiding acoustic interference from heterospecifics: 1) call from different habitats; 2) use different frequency bands; or 3) partition calls on various timescales (Littlejohn, 1977; Samways, 1977; Greenfield, 1988; Gerhardt and Schwartz, 1995; Sueur, 2002).

Among anuran amphibians, different species calling in the same habitat often use different perches or microhabitats as calling stations (Duellman, 1967; Hödl, 1977; Bowker and Bowker, 1979; Garcia-Routledge and Narins, 2001), but there is little evidence that such differences in microhabitat choice are sufficient to reduce or eliminate acoustic interference from nearby heterospecifics (Wells, 2007). Many multispecies assemblages of frogs exhibit some degree of call frequency partitioning (Hödl, 1977; Drewry and Rand, 1983; Duellman and Pyles, 1983; Garcia-Routledge and Narins, 2001) and some flexibility in spectral properties of calls (Both and Grant, 2012). The significance of this partitioning is unclear because the amount of acoustic frequency separation between species is typically no more than expected by chance (Chek et al., 2003). Therefore, the importance of the avoidance strategies detailed above has not been determined for any interacting anuran species.

Acoustic interactions are likely between two North American ranid frogs, the Bullfrog (*Rana catesbeiana*) and the Green Frog (*Rana clamitans*) (nomenclature following Yuan et al., 2016; AmphibiaWeb, 2018). Both species breed primarily in permanent ponds during the summer (Wells, 2007). Males of both species are territorial and defend oviposition sites that are attractive to females (Emlen, 1968, 1976; Wells, 1977, 1978; Howard, 1978; Bee and Perrill, 1996). Surveys of breeding ponds have shown a positive association between Bullfrog presence and Green Frog presence (Collins and Wilbur, 1979; Hecnar and M'Closkey, 1996, 1997a), although Bullfrogs are more abundant in ponds containing fish, and Green Frogs are more abundant in ponds without fish (Hecnar and M'Closkey, 1997b). Neither species clusters preferentially with conspecifics, and male Green Frogs often have Bullfrogs as their nearest neighbors (Herrick, 2013). Hence, these species are not using microhabitat differences to avoid call interference. Additionally, the calls of the two species broadly overlap in frequency (Wells, 1978; Bee, 2004); hence, they cannot avoid acoustic interference via minor differences in call frequency.

In this study, we investigated temporal partitioning of calls of the two species on three time scales: 1) seasonal partitioning of calling activity; 2) diel partitioning of calling activity; and 3) fine-scale behavioral responses of males to calls of the other species. We used automated 24-h recordings of the whole pond as well as focal-animal recordings of heterospecific nearest-neighbor pairs to investigate acoustic interactions between the two species. Because Bullfrogs have longer, more frequent calls, often produce calls in multicall bouts and will commonly exchange calls (note-for-note or call-for-call) with neighbor Bullfrogs (Simmons et al., 2008), we predicted that Bullfrog calls are a major source of acoustic interference for Green Frogs, but the reverse is not necessarily true, because Green Frogs have shorter calls and are much less likely to give multinote calls. Therefore, we analyzed interactions to test the hypothesis that Green Frogs respond to Bullfrog chorusing on a fine temporal scale by placing their calls between the notes of Bullfrog calls.

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Materials and Methods

Fieldwork.—All fieldwork was conducted on Caleb's Pond, an open-canopy, human-made pond located in a hayfield in Lebanon, New London County, Connecticut (41°41′17″N, 72°12′30″W). The pond was dug in the 1950s and is 50 m long, 25 m wide, and ~4 m deep at the pond center. Calling males of both species were found mostly in shallow parts of the pond, within 1–2 m of shore. Males of both species defend territories along the shoreline and exhibit some microhabitat partitioning in terms of water depth and distance from shore (Herrick, 2013). The pond is spring-fed and a constant water level is maintained throughout the year. The open-pipe drain flows into a swamp located 30 m from the pond.

Hourly air and water temperatures were monitored by six DS1921K iButton recorders (Thermocron, Inc., Holland, MI; www.maxim-ic.com), accurate to within 1°C from −30°C to +70°C. We attached temperature recorders to stakes placed in the pond about 2 m from shore and spaced about every 25 m along the pond perimeter. Each stake held two iButton recorders in fine-scale plastic netting. The netted recorders were individually stapled to the stakes such that one recorder was 5 cm above and one was 5 cm below the water surface.

A census of active frogs on the pond was performed at least every other evening. During these censuses, all calling males, satellite males, females, and egg masses were recorded. We recorded the pond's acoustic environment over two breeding seasons (mid-May through early August in 2006 and 2007) using an automated digital recording system that operated nearly continuously throughout the two breeding seasons. The recording system consisted of a PMD660 digital recorder (Marantz Corp., Yokohama, Japan) powered by a model 74522 6-volt rechargeable battery (Mattel/Fisher-Price, Inc., East Aurora, NY) and a microphone assembly. The K6/ME66 shotgun microphone (Sennheiser Electronics, Wedemark, Germany), with its foam windscreen, was wired through the neck and attached to the inside of a 2-L plastic soda bottle with the bottom cut off, that protected the microphone from rain. The bottle was clamped to the top of a 2-m PVC pole. To keep the recorder and battery dry, the microphone wire was fed to the recorder through a gap in the drawers of a plastic three-drawer cart (Sterilite Corp., Townsend, MA). To reduce bias attributable to the behavior of a few dominant individuals, a numbered reference stake was placed every 3 m along the pond edge, and the recording apparatus was placed at a randomly selected stake every 24 to 36 h. The microphone was set 2 m above the pond surface and directed toward the center of the pond. We recorded a total 2,398 h of recordings in MP3 format, which later were converted to WAV. This maximized the length of time between memory card changes; the level of detail recorded in WAV format was unnecessary for this study. Converting from MP3 to WAV format required the bioacoustics software Acez MP3-WAV Converter (www.micocosoft.com), then mining for individual frog calls and the temporal data that accompanied each call.

Data Extraction.—To extract call data from the recordings, we used Song Scope 2.4® bioacoustic analyzer program (Wildlife Acoustics, Inc., Maynard, MA). To create a training set by which unknown calls could be automatically identified, we selected several hundred calls of each species, free of background noise and other anomalies. Song Scope® applies classification algorithms to the training data to produce a call recognizer (Ingranat, 2007, 2009) that represents an idealized exemplar call for that species. The user specifies permissible variance from the recognizer in multiple sound characteristics such as duration, gain, delay, and range. User specification of permissible limits is subject to judgment about the relative importance of accuracy (minimizing misidentifications) and sensitivity (minimizing nondetections). For this study, we chose to emphasize accuracy over sensitivity. Further details can be found in Supplemental Information.

Once the recognizers, one for each species, were optimized and validated, each sound found in the recordings was compared to the recognizers and classified as a call if it fell within permissible limits, and assigned a quality score according to the degree of deviation from the recognizer. Each noise extracted by the software included the date and time the noise occurred as well as the date and time it ended. The start and end date and time for each noise allowed us to calculate call duration as well as to know when the noise occurred relative to other recorded noises. All recordings were analyzed using both recognizers concurrently. The program recognized 808,572 calls, 332,904 labeled as Bullfrogs and 475,668 as Green Frogs. The distribution of Bullfrog call durations clearly included some spurious data consisting of a small mode indicating anomalously short duration times for Bullfrogs (0.3–0.6 sec per single note call, see Capranica, 1965). A broad sample of these very short sounds were listened to and determined to be a variety of environmental noises such as gunshots, bird calls, and deer vocalizations. All events marked as Bullfrog calls that were shorter than 0.25 sec (34,070) were culled from the data set, leaving 298,834 Bullfrog calls. There were no indications of spurious data in the Green Frog data set; thus, no Green Frog calls were culled.

Seasonal Call Patterns.—The question of whether the seasonal calling pattern differed between species was addressed using the entire post-processing data set, with one exception. To avoid bias attributable to uneven hourly representation, we eliminated the 14 recorded days with <20 continuous hours of recording. The remaining 27 recorded days were aggregated into weeks, and the average number of calls per hour was calculated. We tested for differences between species in the distribution of weekly averages via a *t*-test for data with unequal variances.

Diel Variation in Calling.—The question of whether calling activity varies with time of day between species was addressed using the entire post-processing data set. We aggregated calls into clock hours and calculated the average number of calls, normalized by the number of nights. We tested for nonrandom distribution of calling activity via Rayleigh's Test (Batschelet, 1981), and species differences in the temporal distribution of calling via *t*-test.

Fine-Scale Behavioral Interactions.—To explore the question of whether there were fine-scale vocal interactions between these species, the timing of the two species' calls were examined using 30-min samples between 2100 and 0300 h, taken from the 24-h pond recordings. The very high numbers of calls made analysis of the entire data set nearly impossible. Therefore, a stratified subsample of five 30-min samples for each of the two years (four from late May, two from middle June, three from late June, and one from early July, a total of 10 samples) was chosen to represent the span of the entire breeding season. Each 30-min sample was broken into 100-msec intervals. Each interval was scored according to whether it contained one, both, or neither of the species' calls, yielding a percentage of intervals in which the calls overlapped in time. We tested whether the call overlap was less than expected if overlap was random via a randomization test.

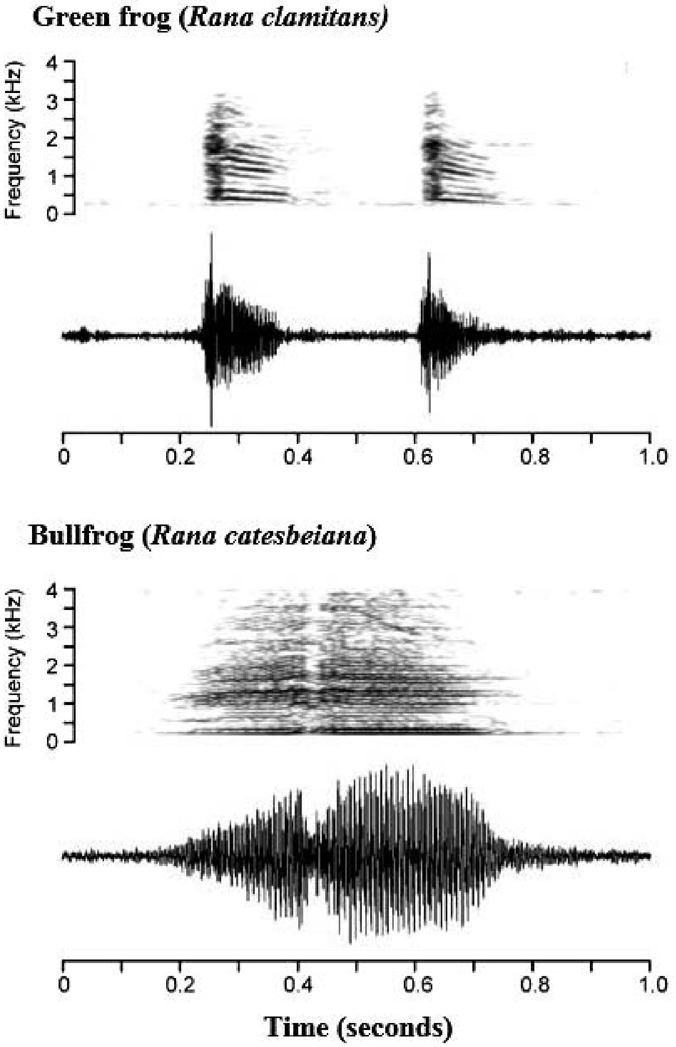


FIG. 1. Waveforms of single-note *Rana clamitans* and *Rana catesbeiana* advertisement calls. Each call was recorded from a single male at Caleb's Pond in Lebanon, Connecticut. Recordings made in May 2006. Each typical advertisement note for *Rana clamitans* is ~0.07 to 0.43 sec long with a frequency range of about 250–3,200 Hz. *Rana catesbeiana* advertisement notes are ~0.3 to 0.6 sec long with frequencies ranging between 200 and 4,000 Hz.

For 2,500 iterations (R Core Team, 2015), we randomized the start times of Green Frog calls, keeping the duration of these calls intact, while holding the start time and duration of Bullfrog calls fixed. The observed overlap percentage was tested against the null hypothesis of random overlaps of calls represented by the distribution of randomized values.

Focal Pair Interactions.—We conducted an additional test of fine-scale temporal partitioning by focusing on heterospecific nearest-neighbor pairs (average distance = 3.0 m, range 0.6–6.1 m). Using a PMD430 Marantz stereo cassette recorder and two SME-V6502 Mineroff directional microphones (Saul Minneroff Electronics, Inc., Elmont, NY) for 30 min, we recorded 14 focal pairs in 2005, 3 in 2006, and 7 in 2007. All recordings were made between 2100 and 0100h on dates between 26 May and 18 June in all years. Call characteristics (dates, time, and timing of calls) were extracted using Audacity® 2.0.3 (2015). Similar to the analysis of whole-pond acoustic data, we tested for overlap of calls by heterospecific nearest-neighbor pairs by randomizing Green Frog call onset (10,000 randomizations) and evaluating the percentage of Green Frog calls that overlapped a Bullfrog call.

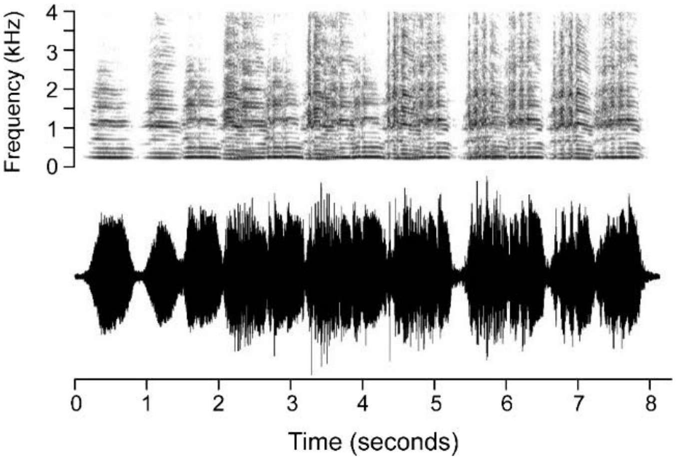


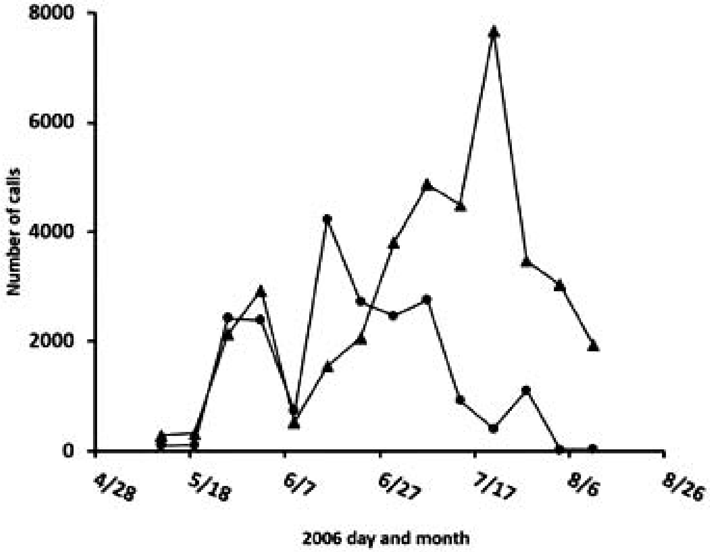
FIG. 2. Example of a typical Bullfrog/Green Frog chorusing event over an 8-sec period with few gaps in noise. Two Bullfrogs and one Green Frog participated in this example chorus. Chorus recorded in June 2006 on Caleb's Pond, Lebanon, Connecticut.

Unlike the whole-pond data, wherein calls were recorded for many frogs, there was a low rate of calling activity in some pairs that would inflate the type II error rate. We recorded a total of 103 and 544 calls in the 30-min periods; hence, the likelihood of randomizations including substantial incidence of zero interruptions was accordingly high. To address this problem, we used a power analysis to exclude recordings with low calling activity; we used bootstrapping to create randomized data sets at each of 56 evenly spaced calling activity levels between 50 and 600 total calls, each with 10,000 randomizations. The empirical data were sampled with replacement to determine the ratio of Bullfrog to Green Frog calls, and Bullfrog and Green Frog call durations. Using linear interpolation between activity levels, this analysis indicated that calling activity yielding <237 calls in a 30-min period would be too low to statistically evaluate the significance of observing zero Green Frog call interruptions (at $\alpha = 0.05$). Therefore, ultimate analysis of the nearest-neighbor pairs was performed by creating a single empirical density function using randomization data from all 16 data sets with >237 total calls (7 sets in 2005 recorded on 05, 06, and 9 of June; 3 sets in 2006 recorded on 14 and 18 of June; 6 sets in 2007 recorded on 26, 29, and 30 of May), resulting in the exclusion of 8 low-activity data sets.

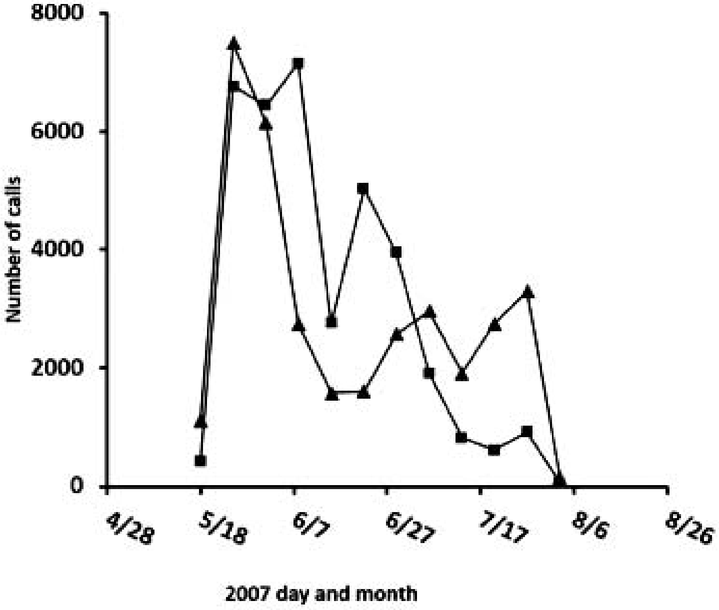
RESULTS

Call Structure.—Bullfrogs and Green Frogs overlap broadly in call frequency (Fig. 1). Bullfrogs produce much longer calls than Green Frogs and are more likely to produce calls in multinote bouts or engage in precise alternation of calls with other Bullfrogs (Fig. 2).

Seasonal Patterns.—Seasonal differences in both calling and egg laying activity varied little between the species. They called in the same weeks in the 2006 breeding season, with Bullfrogs very active somewhat earlier (22 June) than Green Frogs (8 July) ($t_{164} = 1.012 \times 10^{-12}$, $P = 0.999$) and Green Frogs persisting with higher levels of calling effort about one week later than Bullfrogs (Fig. 3). In both years, few Green Frog eggs were deposited late in the season after Bullfrog calling began declining. The early part of June 2006 was cooler than 2007 and most eggs were laid in the



Week of	18 May	25 May	01 June	08 June	15 June	22 June	29 June	06 July	13 July	20 July	27 July	03 Aug	10 Aug
Bullfrog	0	9	0	0	2	0	1	2	0	0	0	0	0
Green frog	0	0	0	0	1	1	2	3	3	2	0	0	0
Ave temp °C	12.8	15.8	19.3	15.9	20.2	22.4	23.0	22.5	23.8	24.3	23.8	25.9	20.4



Week of	18 May	25 May	01 June	08 June	15 June	22 June	29 June	06 July	13 July	20 July	27 July	03 Aug	10 Aug
Bullfrog	0	3	0	1	1	3	0	1	0	0	0	0	0
Green frog	0	3	0	0	2	1	0	0	0	0	1	0	0
Ave temp °C	14.2	19.0	19.4	17.9	18.4	19.0	21.7	21.2	22.9	21.4	22.8	25.0	21.5

FIG. 3. *Rana catesbeiana* and *Rana clamitans* call activity each week of the 2006 and 2007 breeding seasons. Activity is defined as the average daily number of calls for each species per week normalized to the number of hours recorded each day. Only days with at least 20 h of continuous recordings (54 days in 2006; 23 days in 2007) were used for this plot. Bullfrogs indicated with circles; Green Frogs indicated with triangles. Average daily water temperatures and egg masses per week are below each year's call activity.

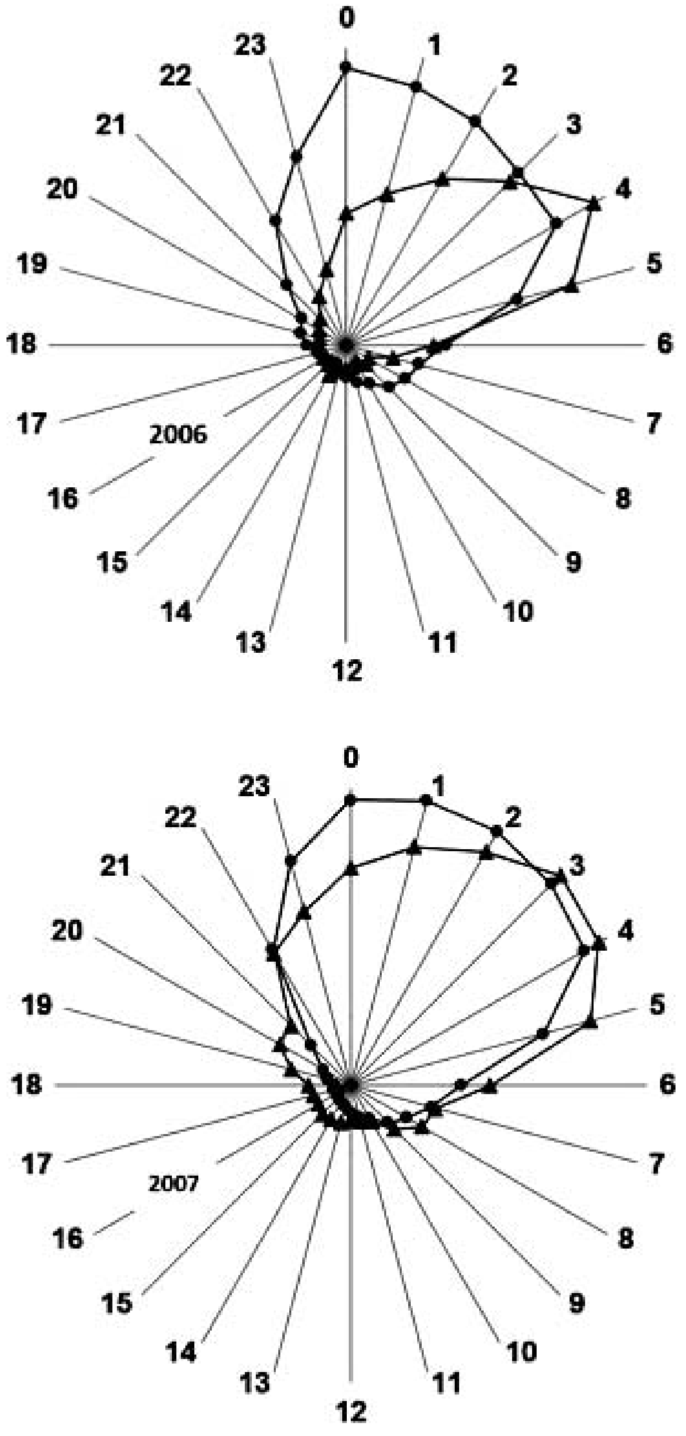


FIG. 4. Hourly calling rate for the 2006 and 2007 breeding seasons, scaled per species. Each arm is marked for a 24-h clock with the center of clock indicating zero calls and the outer edges of the distributions representing relative number of calls per hour. Only days with at least 20 h of continuous recordings (54 days in 2006; 23 days in 2007) were used for this plot. Bullfrogs indicated with circles; Green Frogs indicated with triangles.

middle of the season. In 2007 both species began calling in mid- to late May with Bullfrogs declining in late June and Green Frogs declining in mid-July. The majority of eggs were laid earlier in 2007 than 2006. Mean date of peak calling in 2007 was not different between the species ($t_{87} = 0.0878$, $P = 0.93$) with Bullfrogs calling most actively on 11 June and Green Frogs on 16 June. As in 2006, both species ceased calling in early August of 2007. The main result of interest is that Green Frogs had few opportunities to call when Bullfrogs were completely inactive; thus, seasonal partitioning of calling activity was not an effective mechanism for avoiding acoustic interference.

Diel Patterns.—Another strategy that could be employed to avoid acoustic overlap is for the two species to call at different times of day. In this case, the data supported the null hypothesis: there was no difference in the time of day during which each species was calling (Rayleigh's test of random temporal distribution $P > 0.05$ for both species; Fig. 4). This indicates the species share a preferred time of day during which to call. The diel timing of calling activity in 2006 was not different between the species ($t_{164} = 0.025$, $P = 0.98$) with Bullfrogs most active at 0222 h and Green Frogs at 0317 h. They were also not different in 2007 ($t_{87} = 0.839$, $P = 0.40$), with Bullfrogs most active at 0237 h and Green Frogs at 0348 h. In both years, there were no periods of the evening in which Bullfrogs were completely quiet while Green Frogs were calling.

Fine-Scale Behavioral Interaction.—There was strong evidence that call partitioning does occur on a finer time scale (Fig. 5A,B). For example, in a 30-sec sample of calling activity from late May 2007, both species were active, but Green Frogs avoided calling at the same time as Bullfrogs (Fig. 5B). In fact, Green Frogs overlapped Bullfrog calls only once. All other Green Frog calls fell within gaps between Bullfrog calls. In late May, when males were first gathering on the pond and establishing territories, call rates were very high and call overlap was expected to be fairly high as well. For this particular evening, Green Frog calls overlapped Bullfrog calls about 1% of the time. The randomizations for this same period of activity revealed that call overlap, if it occurred at random, should have happened between 6% and 8% of the time (Fig. 6).

Randomization tests indicate that temporal overlaps occur less frequently than expected. When individual calls and call patterns for each sampling night were compared, avoidance of call overlap on the event scale was obvious (Fig. 7). Observed rates of call overlap did not fall within our predictions based on 2,500 random simulations of 180,010 calls (i.e., $P = 0$) for 9 of 10 test periods (Fig. 6). In one testing period (12 June 2006), the observed rate of call overlap (0%) did fall within the predictions of our simulations; however, this particular test period fell during a week in which temperatures were unusually cool and calling rates were very low, such that the simulations predicted low rates of overlap. Overall the data do not support the null hypothesis. Instead, the data tell us that Green Frogs actively avoided call overlap with Bullfrogs, and this avoidance is on the fine time scale of call-by-call.

Focal Pair Interactions.—At an even finer scale, that of two heterospecific nearest neighbors interacting, we found avoidance of call overlap to be even more precise. Individual Green Frog males never overlapped calls with their nearest Bullfrog neighbor. For the 16 high-activity data sets, the observed percentage of call interruption (0%) was significantly less than the 5% that was expected by chance and 95% of the randomizations resulted in over 3% of overlap ($P = 0.004$) (Fig. 7).

DISCUSSION

Our results showed little evidence of temporal partitioning of calls between Bullfrogs and Green Frogs on either a seasonal or diel timescale. Both species began calling at approximately the same time each season (late May to early June). Both stopped

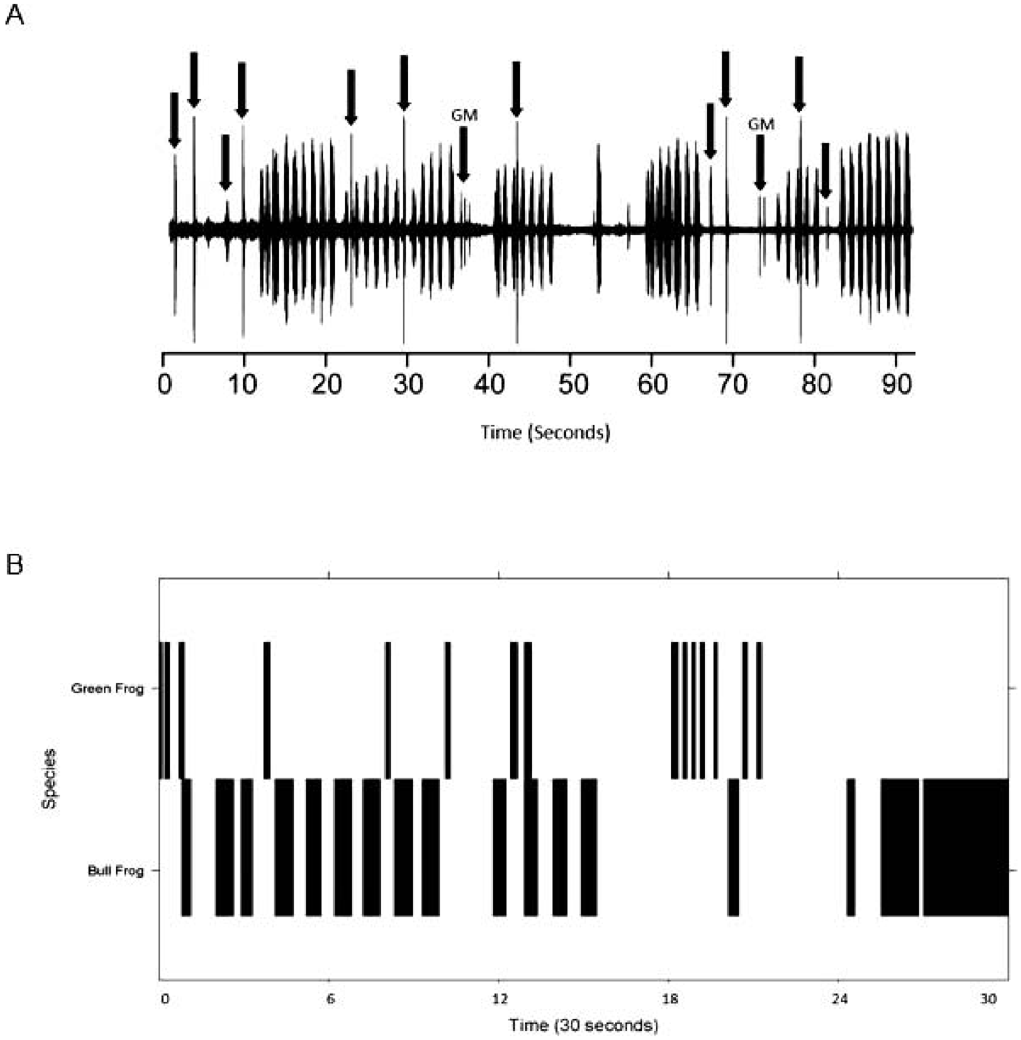


FIG. 5. (A) Ninety-second example of Bullfrog chorusing event showing Green Frog calls inserted without overlapping Bullfrogs. Arrows not labeled indicate single-note Green Frog calls. Arrows labeled GM indicate multinote Green Frog calls. (B) Sample 30-sec period of *Rana clamitans* avoiding overlapping calls with *Rana catesbeiana* (on 27 May 2007). Call onset time and duration for each species over the period were separated by species. Each 100-msec interval was scored as "true" if a call was heard during that interval or "false" if none was calling. When the scores were then compared, call overlap avoidance on the event scale becomes clear. In this figure, Green Frogs overlap a Bullfrog call only once, and it appears the masked call was emitted at the same time as the Bullfrog call. All other Green Frog calls fall within gaps of Bullfrog noise.

calling by early August. The beginning of calling activity probably is constrained by temperature, as both species are warm- weather breeders. We found that males seldom called at water temperatures below 20°C. There is no obvious temperature limitation on calling at the end of the breeding season; however, males may gradually deplete energy reserves until they can no longer call—summer-breeding male ranid frogs, including these two species, have been reported to deplete energy reserves or lose body mass throughout the season (Jenssen, 1972; Byrne and White, 1975; Wells, 1978, 2007; Given, 1988, Loumbourdis and Kyriakopoulou-Sklavounou, 1991). Additionally, conditions for larval development could potentially deteriorate late in the season. Tadpoles of both species overwinter in Connecticut, and tadpoles without sufficient growth time in warm weather may be at a disadvantage. In any case, these species appear to be precluded from partitioning the breeding season to avoid acoustic interference.

Another constraint on seasonal partitioning of calling activity is the potential to limit the reproductive opportunities of females. Females of both Green Frogs and Bullfrogs return to breeding ponds several weeks after depositing a first clutch of eggs and produce a second clutch (Wells, 1976; Emlen, 1977). Consequently, any attempt by males to separate their calling seasons, such that one species calls earlier in the season than the other, could limit reproductive success. In fact, reduced acoustic interference from Bullfrogs late in the season, especially in 2006, did not obviously increase reproductive success of male Green Frogs, because females had largely stopped producing eggs at that point in the season.

Diel partitioning of calling times probably is limited by the nocturnal habits of these species. Both Bullfrogs and Green Frogs call sporadically during daylight hours, but our 24-h recordings showed that high rates of calling always occurred at night, often ≥4 h after sunset. This pattern was clear in the combined data for the whole season (Fig. 4) and for each week of the season analyzed separately (unpubl. data). Previous work with Green Frogs has shown that calling rates by males early in the evening are negatively correlated with light levels (measured with a light meter); thus, the onset of darkness appears to trigger active calling (Wells, 1978). Active calling gradually

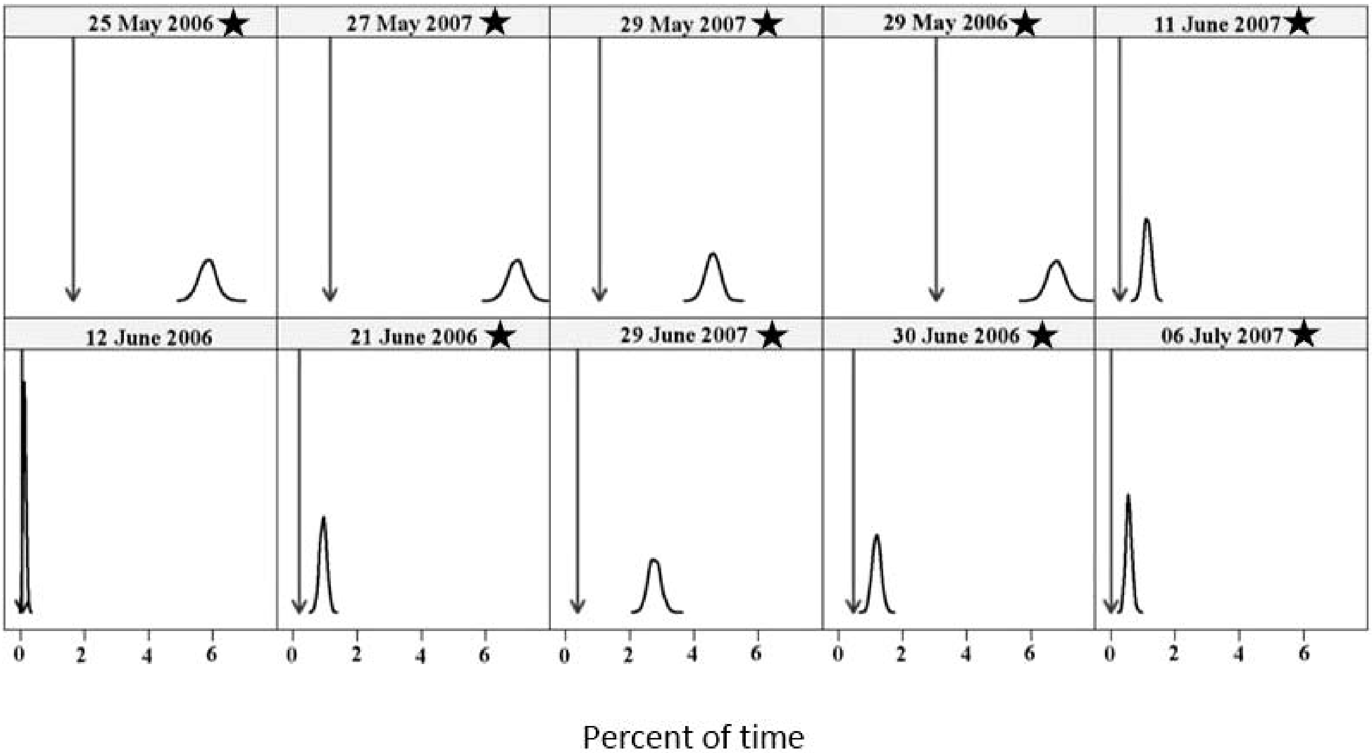


FIG. 6. Results of 2,500 randomizations of Green Frog versus Bullfrog calling activity. Each distribution curve represents the percent of time that Green Frogs would be expected to overlap Bullfrog calls if overlaps occur randomly. The arrows represent the observed percent of time Green Frogs overlapped Bullfrogs in 30-min periods over 10 different days (180,010 calls). Stars indicate statistical significance via randomization test.

diminishes with the approach of dawn. Although peak calling times were slightly different between the two species in 2006, this pattern was not observed in 2007. In both years, most calling by the two species occurred during the same time window, and Green Frogs never experienced a time window entirely free of Bullfrog calls.

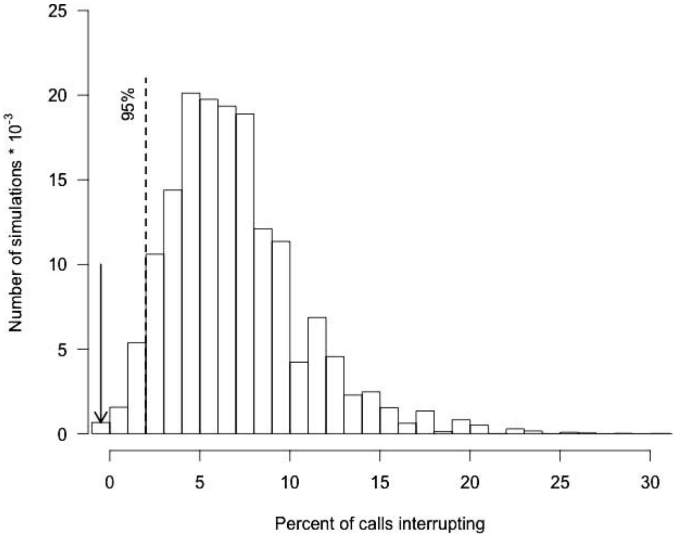


FIG. 7. Histogram showing results of 10,000 randomizations of Green Frog versus Bullfrog focal pair (N = 16 pairs) calling activity. Distribution represents the percent of Green Frog calls that overlap its near neighbor Bullfrog calls if overlaps occur randomly. The empirical observation for each of the 16 pairs is 0% overlap. Dashed line indicates one-tailed 95% confidence level (= 2.0%).

The absence of seasonal and diel partitioning of call times leaves only behavioral avoidance of heterospecific calls as a viable mechanism to reduce acoustic interference. This appears to be the most common mechanism to reduce heterospecific acoustic interference across a wide range of taxa, including frogs (Wells and Schwartz, 2006; Schwartz and Bee, 2013), birds (Brumm, 2006; Planqué and Slabbekoorn, 2007; Luther, 2009), and insects (Latimer, 1981; Latimer and Broughton, 1984; Schatral and Yeoh, 1990; Greenfield, 2002; Hartbauer et al., 2012). Such behavioral interactions can even cross taxonomic lines. For example, the calls of cicadas in a tropical forest can completely inhibit calling by Strawberry Poison Frogs (*Oophaga pumilio*), which use overlapping call frequencies (Páez et al., 1993; Wong et al., 2009).

The fact that Green Frogs avoid calling when Bullfrogs are calling is particularly interesting in light of the fact that these species have much lower calling rates than do many species that were previously investigated. For example, Schwartz and Wells (1984) found that males of a Panamanian treefrog, *Dendropsophus ebraccatus*, insert their calls between bouts of calling by a closely related species, *Dendropsophus microcephalus*. The latter species produces calls with up to 16 notes in succession, and an individual can produce up to 6,000 call notes per hour. Groups of conspecific males call in bouts in which calls of individuals follow each other in close succession, thereby monopolizing a considerable amount of the available acoustic space. Bullfrogs, however, produce only a few hundred call notes per hour. Even though they also call in bouts with several males interacting (Simmons et al., 2008), much of the acoustic space in the pond is left unoccupied. Consequently, predicted overlap of Green Frog calls with Bullfrog calls is only on the order of 2–6%. Nevertheless, Green Frogs timed their calls more precisely than this expectation. This means that even without trying to avoid overlap, they would be relatively successful doing so simply by calling at random. Full pond recordings produced observed overlaps consistently lower than expected by chance, and 30-min recordings of 16 heterospecific nearest-neighbor pairs produced no instances of call overlap.

In examples of interspecific acoustic interference, the interactions of two species often are asymmetrical, with one species often suffering a higher fitness cost than the other (Gröning and Hochkirch, 2008). Asymmetry of interactions is particularly clear in examples of signal jamming, where species with longer or more continuous calls typically mask the signals of species with shorter, or less continuous, calls. This pattern has been documented in frogs (Littlejohn and Martin, 1969; Littlejohn et al., 1985; Wells and Schwartz, 2006; Schwartz and Bee, 2013), birds (Ficken et al., 1974; Bremond, 1978; Popp et al., 1985; Popp and Ficken, 1987), and insects (Latimer, 1981; Latimer and Broughton, 1984; Greenfield, 1988; Gerhardt and Huber, 2002). The asymmetry between Bullfrogs and Green Frogs is obvious in Figure 5A—calls of Bullfrogs are longer than those of Green Frogs and often clustered into multimale bouts. Green Frogs insert their shorter calls into spaces between Bullfrog calls.

In summary, this is one of the first studies to test acoustic interference between co-occurring frogs of different species on three time scales. Additionally, this is one of the first times automated recording equipment and acoustic analysis software has been used to explore natural behavior in the field. We show that most avoidance occurs via behavioral avoidance of individual calls rather than through partitioning of the season or hours of the day. Most of the studies of interspecific acoustic interference in frogs done to date focused on species with very dense choruses and very high calling rates. Our results suggest that, even in frog species with relatively low expected call overlap, males enjoy some fitness advantage from further decreasing acoustic interference through fine-scale behavioral adjustments.

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Supplementary Data

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