

Selective phonotaxis by male wood frogs (*Rana sylvatica*) to the sound of a chorus

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Abstract Frogs and toads commonly form large choruses around suitable breeding habitat during the mating season. Although often regarded as a constraint on the acoustic behavior of signalers and receivers, the sounds of a chorus could also serve as an acoustic beacon that allows some frogs to locate the breeding aggregation. Attraction to chorus sounds might be particularly important for explosively breeding frogs. In these species, which often mate just one or a few days during the year, the timing and location of breeding aggregations can be unpredictable because their formation often depends on local climatic factors, such as rainfall or a change in temperature. I used laboratory playback experiments to test the hypothesis that male wood frogs (*Rana sylvatica*), an explosively breeding frog, exhibit positive phonotaxis toward the sound of a conspecific chorus. Males were released at the center of a rectangular arena with a speaker positioned in each corner facing toward the release point. In a single-stimulus experiment, more males approached a speaker broadcasting a conspecific chorus than the three silent speakers in the arena. In a two-stimulus experiment, more males approached a speaker broadcasting a conspecific chorus compared to the two silent speakers or a fourth speaker simultaneously broadcasting the spectrally overlapping sound of a heterospecific (*R. septentrionalis*) chorus. These results are consistent with the hypothesis that male wood frogs could use the sound of a chorus as a beacon to locate a short-lived breeding aggregation.

Keywords Animal communication · Explosive breeder · Frog chorus · *Rana sylvatica* · Phonotaxis · Wood frog

Introduction

Anuran amphibians (frogs and toads) continue to serve as model organisms for understanding the mechanisms and evolution of acoustic communication and its function in animal social behavior (Ryan 2001; Gerhardt and Huber 2002; Gerhardt and Bee 2006; Wells and Schwartz 2006). One reason for this is that acoustic communication plays a fundamental role in anuran reproductive behavior across a wide diversity of mating systems (Wells 1977a; Gerhardt and Huber 2002). In “explosive breeders” (Wells 1977a), reproduction occurs over a short period (e.g., < 24 h) and commonly takes place in bodies of water that are often ephemeral or otherwise spatially and temporally unpredictable. In such species, the mating system is typically scramble competition polygyny. Yet males often vocalize while actively searching for, and competing for direct access to, receptive females (Wells 1977a; Howard 1980; Berven 1981). In “prolonged breeders” (Wells 1977a), reproduction often takes place in more predictable environments and can occur over much longer periods compared to explosive breeders. Prolonged breeding frogs exhibit a greater diversity of mating systems, which include lek polygyny (Grafe 1997; Friedl and Klump 2002; Murphy and Gerhardt 2002), resource defense polygyny (Wells 1977b; Howard 1978; Wells 1978), and even long-term pair bonding with biparental care (Caldwell 1997).

Most of what we know about the role of acoustic communication in frog reproductive behavior comes from experiments with prolonged breeding species. For example, numerous laboratory tests of species recognition and female

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mate choice in lek-breeding species have shown that the advertisement calls of individual male frogs are necessary and sufficient to elicit positive phonotaxis from gravid females and that females exhibit selective phonotaxis toward preferred signals (Ryan 1985; Ryan and Rand 1993; Schwartz 1994; Gerhardt 2001; Schwartz et al. 2001). Field playback studies have shown that vocalizations also mediate species recognition among male frogs (Amézquita et al. 2005) and play an important role in sexual selection by male–male competition in species with mating systems characterized as lek polygyny or resource defense polygyny (Wells 1978; Brenowitz 1989; Marshall et al. 2003; Narins et al. 2003). For example, among male frogs, vocalizations mediate assessments of an opponent's resource holding potential (Davies and Halliday 1978; Robertson 1986; Wagner 1989; Bee et al. 1999; Bee et al. 2000), inter-male spacing (Brenowitz 1989; Marshall et al. 2003) and the recognition of territorial neighbors (Davis 1987; Bee and Gerhardt 2001a,b,c; Bourne et al. 2001; Bee and Gerhardt 2002). This bias toward studies of prolonged breeders is no doubt due, in part, to the contribution that such studies make toward understanding acoustic communication in the context of sexual selection. The greater opportunity to collect data over an extended breeding period probably also contributes toward a bias of studies of prolonged breeding species. But acoustic communication is also a potentially important component of the reproductive behavior of explosively breeding frogs, although this has received less attention (but see, e.g., Howard and Palmer 1995; Howard and Young 1998).

Among the most notable acoustic properties of frog vocalizations is their amplitude: frog advertisement calls are typically quite loud (Loftus-Hills and Littlejohn 1971; Gerhardt 1975; Penna and Solis 1998). For example, in the study by Gerhardt (1975), the sound pressure levels (SPL re 20 μ Pa) of the advertisement calls of several North American frogs and toads ranged between 80 and 94 dB (fast root mean square) at a distance of 1 m, with peak SPL values ranging between 90 and 104 dB at this distance. The background noise levels generated by an aggregation of calling males can exceed peak levels of 85 dB SPL (Narins 1982), and the sounds of a chorus can propagate over distances of several hundred meters (Gerhardt and Klump 1988b). Chorus noise can constrain acoustic communication between the signalers and receivers in a chorus, and hence, interfere with acoustically mediated reproductive behaviors (Narins 1982; Gerhardt and Klump 1988a; Wollerman 1999; Schwartz et al. 2001; Wollerman and Wiley 2002). However, the sounds of a chorus need not always represent a constraint on anuran communication and reproductive behavior.

The sounds of a chorus of calling males could potentially serve as an acoustic beacon that facilitates orientation

toward a breeding aggregation, especially in explosively breeding frogs (Bogert 1960; Oldham 1966, 1967; Wells 1977a; Gerhardt and Klump 1988b). Current conservation efforts that use calling surveys to monitor anuran populations, such as the North American Amphibian Monitoring Program (Weir and Mossman 2005), take advantage of the fact that human observers can acoustically detect frog choruses from long distances and identify the species present in a chorus. Even some salamanders may use frog vocalizations to locate suitable breeding ponds (Diego-Rasilla and Luengo 2004). Can frogs do this too? Surprisingly, there have been few experimental tests of the hypothesis that frogs themselves use the sounds of a chorus as a beacon to locate active breeding aggregations of conspecifics (Gerhardt and Huber 2002). A few early studies investigated whether or not frogs approach the sounds of a chorus (e.g., Bogert 1960; Oldham 1966, 1967), but as noted by Gerhardt and Huber (2002), many of these early tests were not conducted under controlled conditions.

Gerhardt and Klump (1988b) were the first to show in rigorously controlled laboratory experiments that females of at least one frog species exhibit selective phonotaxis to the sounds of a chorus of conspecific males. They demonstrated that females of the barking tree frog (*Hyla gratiosa*) exhibited phonotaxis to conspecific chorus sounds broadcast at low sound levels that simulated choruses at various distances (Gerhardt and Klump 1988b). Moreover, they demonstrated that female barking tree frogs preferentially approached a mixed-species chorus that included the calls of conspecific males and those of the closely related green tree frog (*H. cinerea*) over a pure chorus of heterospecific *H. cinerea*. These results clearly supported the hypothesis that at least some frog species might use the sounds of a chorus to locate breeding aggregations. A recent study by Murphy (2003), however, casts some doubt on the importance of chorus sounds in allowing female barking tree frogs to locate suitable breeding sites. Even on nights when the chorus was experimentally silenced by removing calling males, there was a positive correlation between the number of males and females arriving at the breeding pond (Murphy 2003). Clearly, more work is needed to fully assess the hypothesis that frogs may exploit the sounds of a chorus as a beacon for locating breeding aggregations.

In this study, I report the results from an experimental test of the chorus attraction hypothesis in wood frogs (*Rana sylvatica*). Wood frogs range throughout the eastern USA, north into Canada and west to Alaska, and they are common in Minnesota, where this study was conducted (Martof and Humphries 1959; Oldfield and Moriarty 1994). Wood frogs are considered explosive breeders (Wells 1977a) because the mating activity is limited to one or a few days each year (Howard 1980; Berven 1981; Waldman

1982; Howard and Kluge 1985). The aim of this study was to determine whether or not male wood frogs exhibit selective phonotaxis in response to conspecific sounds, as represented by the sound of chorus of conspecific males.

Materials and methods

Subjects

The subjects in this study were collected from two ponds located in the Tamarack Nature Center in Ramsey County, MN, between April 6–10, 2006 (Fig. 1). The two ponds contained emergent vegetation (e.g., cattails) along their banks and are surrounded by tallgrass prairie and mixed hardwood forest. Although wood frogs can be heard calling during the day, they are most active between sunset and sunrise (Oseen and Wassersug 2002), with a peak in calling activity after midnight (personal observation), which is also when most oviposition occurs (Woolbright et al. 1990). I opportunistically collected both single, unpaired males and amplexed pairs of males and females between 2130 and

0200 hours. The ice on local bodies of water had melted within the previous week after the first spring rains. Air temperatures monitored at a nearby weather station during the 5-day period, when collections were made, ranged from 11 to 28°C for daytime highs and from –3 to 9°C for nighttime lows. During one active chorus, when acoustic recordings were made (see below), the air and water temperatures measured at the field site were 11.4 and 9.0°C, respectively. Frogs were returned to the laboratory in St. Paul, MN, and maintained at 5°C in a refrigerator until the day they were tested. Males that were collected in amplexus were allowed to remain in amplexus until the first day they were tested. On the day of testing, frogs were placed in a refrigerated incubator where they were maintained at a temperature of 11°C for a minimum of 1 h before testing. Frogs were tested at temperatures ranging from 9–14°C. All behavioral testing was completed by 12 April when frogs were returned to their location of capture.

General testing procedures

I tested phonotaxis behavior in a temperature-controlled, walk-in sound chamber (inside dimensions: 245 cm L × 215 cm W × 250 cm H). The chamber had a black carpeted floor with a Quiet Floor NP™ sound control floor underlay. The walls and ceiling of the chamber were covered with dark gray melamine acoustic foam wedges (15.24 cm thick) to reduce acoustic reflections. The inside of the chamber was quiet over the frequency range of primary interest here, with sound pressure levels in the 500-Hz to 4-kHz octave bands ranging from 9 to 20 dB SPL (LCF). A Brüel and Kjær Type 2250 sound level meter was used to measure sound levels in the chamber and to calibrate the playback levels of acoustic stimuli.

I tested frogs under infrared (IR) illumination and recorded their behavioral responses using an overhead, IR-sensitive Panasonic WV-BP334 video camera, which was mounted from the center of the chamber ceiling. The video feed from inside the chamber was simultaneously monitored in real time and digitized using an MPEG-PRO MVR analogue-to-digital encoder (Canopus) installed in a Dell Optiplex GX620 PC computer located outside the chamber. Acoustic signals were broadcast through ADS L310 speakers using a second Dell Optiplex GX620 computer also located outside the chamber. The acoustic stimuli consisted of digital sound files (44.1 kHz sampling rate, 16-bit resolution) that were broadcast using Adobe Audition 1.5 interfaced with an M-Audio FireWire 410 multi-channel soundcard. Output from the soundcard was amplified using a Sonamp1230 multi-channel amplifier (Sonance). One speaker was located on the floor in each of the four corners of the chamber and positioned to face toward the center of the chamber (Fig. 2). During testing,

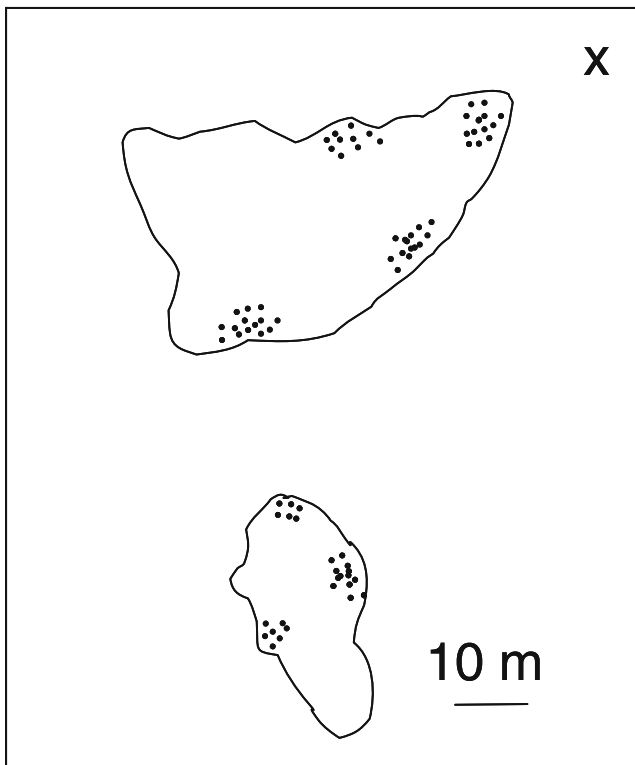


Fig. 1 Schematic outline of two wood frog breeding ponds at the Tamarack Nature Center field site. *Black dots* represent “snapshot” estimates of the approximate numbers of calling males on the night that the wood frog chorus stimulus was recorded from the position marked by the *X*. The *position of each black dot* is not intended to represent the precise positions of individual males, which are highly mobile and cruise through an area in search of females

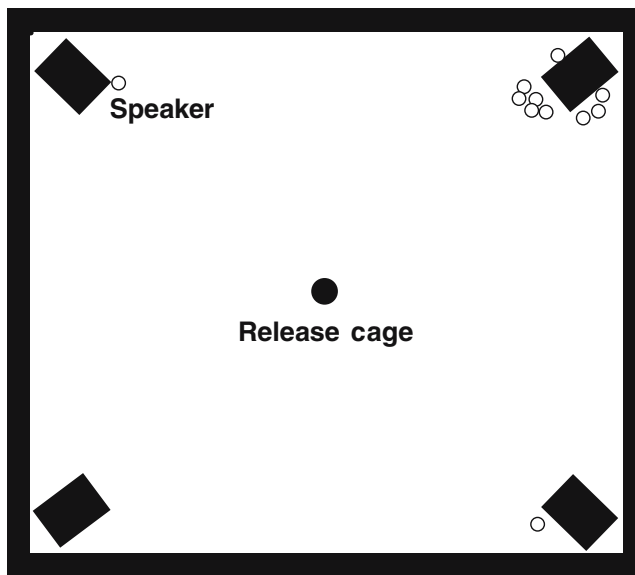


Fig. 2 Schematic diagram illustrating the rectangular testing arena in the sound chamber. The testing arena consisted of a central release cage (solid black circle) and a speaker in each corner of the sound chamber facing toward the center of the arena. The smaller, open circles depict the positions of the 11 frogs tested in Experiment 1 at the end of the test relative to the position of the speaker broadcasting the sounds of the conspecific chorus, which is represented here by the speaker in the upper right of the diagram. (Note that the actual positions of the speakers that were used to broadcast stimuli were systematically varied between tests of different subjects in both Experiment 1 and Experiment 2.)

frogs were remotely released from a small (9-cm diameter), acoustically transparent release cage located on the floor of the chamber at the focal point of the four speakers (Fig. 2). The face of each speaker was 125 cm from the center of the release cage. Because the chamber was rectangular, pairs of speakers in adjacent corners were either 160 or 190 cm from each other, measured from the center of each speaker face.

Experimental procedures

I tested males in two experiments. My testing procedures were the same for both experiments, and they generally followed well-established procedures used to test the phonotaxis behavior of female frogs (Gerhardt 1995). To begin an individual phonotaxis test, a male was removed from the incubator and placed in the release cage with an orientation that was random with respect to the four speakers. Males could freely move about and reorient inside the release cage. After a 1-min acclimation period, I started broadcasts of the acoustic stimuli, which were broadcast as a continuous loop during the entire duration of a test. After 2 min of playbacks, I remotely released the frog from the release cage using a rope and pulley system that could be activated from outside the chamber. All but

two males were given up to 10 min to meet a two-level response criterion. First, I required that all males exhibit characteristic phonotaxis behavior, such as episodes of short hops or walking punctuated by short periods of sitting in place and reorientation toward the speaker. Second, I only scored a response if a male approached to within 10 cm of one of the four speakers. Two males were given up to 12 min to respond because they exhibited characteristic phonotaxis movements toward a speaker but had not approached all the way to within 10 cm of the speaker at the 10-min mark.

I scored a response if the male approached to within 10 cm of any speaker regardless of whether or not that speaker was broadcasting a sound. This response criterion controls for the possibility that frogs approached a speaker broadcasting a target sound by chance. If a male first approached to within 10 cm of a silent speaker, this “response” was scored, and the test was allowed to continue until either the frog approached to within 10 cm of a speaker broadcasting a sound or a maximum of 10 min had elapsed. As is typical in many frog phonotaxis tests conducted under artificial conditions in the laboratory, some frogs never left the release cage, whereas others exhibited characteristic escape behavior that involved rapidly jumping to the wall of the sound chamber and seeking shelter in the acoustic foam wedges. Frogs exhibiting either of these two behaviors were considered unmotivated and data from these trials were not used. Males that exhibited one of these two behaviors in a particular experiment were retested in that experiment on a subsequent day. Of the 27 males tested in this study, 20 males (74%) responded in at least one of the two experiments.

Experiment 1: phonotaxis to a wood frog chorus

In an initial experiment, I tested the hypothesis that male wood frogs exhibit positive phonotaxis toward the sound of a wood frog chorus. The most common vocalizations made by male wood frogs consist of a series of short but variable chuck-like notes that are broadband and have their dominant spectral energy between 500 and 2 kHz. I made acoustic recordings of a wood frog chorus at the Tamarack Nature Center using a Marantz PMD 670 recorder and a Sennheiser ME66 microphone held 1 m above ground and pointed toward the chorus. For this experiment, I selected, as the single acoustic stimulus, a 4-min recording made from a position that was approximately 10 m from one of several aggregations of males that were calling in two adjacent ponds at the field site (Fig. 1). No attempts were made to precisely determine the number and exact locations of calling males in each pond. Based on field notes and focal observations made on the night of recording,

however, I estimate that there were approximately seven different aggregations of males spread around the perimeter of the two ponds (Fig. 1). I estimate that each aggregation consisted of between 5 and 25 calling males.

Figure 3a depicts the waveform and spectrum of a 12-s segment from the 4-min recording of the chorus that I used as a stimulus in this experiment. Note that this recording also included the calls from an aggregation of chorus frogs (*Pseudacris triseriata maculata*), which breed syntopically with wood frogs in Minnesota. These chorus frogs were a prominent component of the acoustic scene at the breeding site, and they are responsible for the spectral peak between 3 and 4 kHz in the wood frog chorus stimulus (Fig. 3a). Hence, what I refer to here for convenience as the “wood frog chorus” was actually a mixed-species chorus consist-

ing of wood frogs and chorus frogs. At present, the audibility of chorus frog calls to male wood frogs is not known. I chose not to filter out the calls of the chorus frogs to preserve the natural acoustic scene of a typical wood frog chorus in Minnesota. I return to this issue in the Discussion.

In each replicate of this experiment with a different subject, the stimulus was broadcast from only one target speaker; the other three speakers were silent. To control for any directional response biases in the sound chamber, I systematically varied which speaker was the designated target speaker by assigning the stimulus to different output channels of the sound card between replicates. The SPL of the chorus stimulus at the male release site (125 cm from the speaker) was 65 dB (LC_{eq} ; Table 1). This SPL was chosen subjectively to fall within the range of amplitudes of the wood frog chorus that I experienced while collecting frogs and making recordings. Table 1 provides additional information about the distribution of sound energy across the spectrum of the wood frog chorus stimulus. Over the duration of the 4-min stimulus, the SPL of the wood frog chorus recording varied over an 8-dB range of between 60 and 68 dB (LCF). The range of natural variation in the chorus SPL was somewhat higher (12–14 dB) in the 1- and 2-kHz octave bands (Table 1), in which most of the spectral energy of the wood frog chorus fell (Fig. 3a).

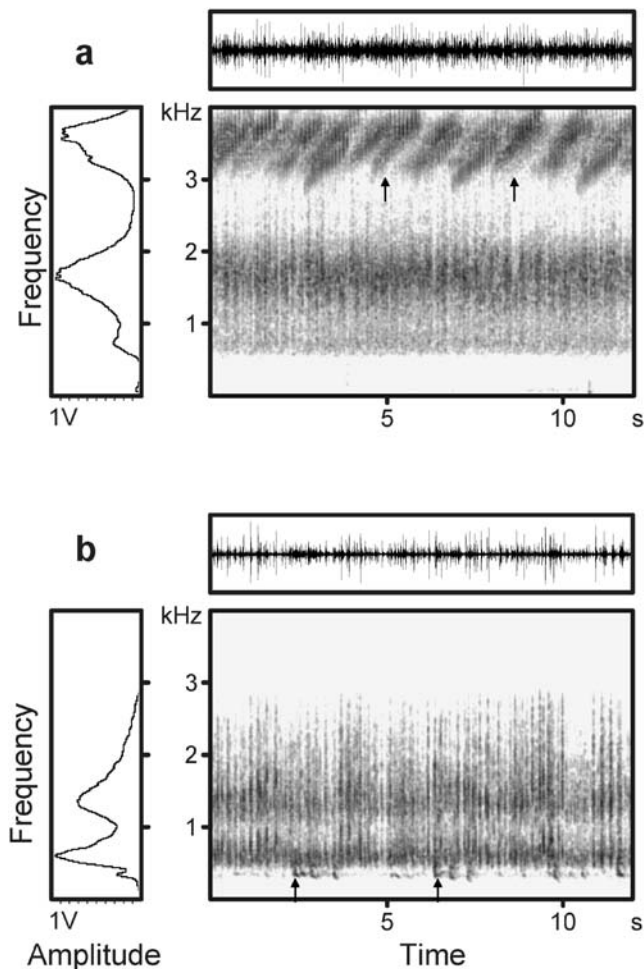


Fig. 3 Power spectra, oscillograms, and spectrograms of the 12-s recordings of a wood frog chorus (a) and a mink frog chorus (b) used as acoustic stimuli in Experiment 2. The excerpt shown in (a) is from the longer recording of a wood frog chorus used as a stimulus in Experiment 1. The arrows in (a) and (b) depict the calls of chorus frogs (*P. triseriata maculata*) and green frogs (*R. clamitans*), respectively

Table 1 SPL in dB (re 20 μ Pa, C-weighted) showing the equivalent noise level (LC_{eq}) and the minimum (LCF_{min}), and maximum (LCF_{max}) levels for the acoustic stimuli in Experiments 1 and 2

Sound level	Experiment 1		Experiment 2	
	Wood frog chorus ^a	Wood frog chorus ^b	Wood frog chorus ^b	Mink frog chorus ^b
Overall	LC_{eq}	65	67	68
	LCF_{min}	60	63	62
	LCF_{max}	68	69	73
500-Hz octave band (354–707 Hz)	LC_{eq}	51	54	64
	LCF_{min}	42	50	58
	LCF_{max}	55	57	69
1-kHz octave band (707–1,414 Hz)	LC_{eq}	60	62	63
	LCF_{min}	51	58	57
	LCF_{max}	63	65	70
2-kHz octave band (1,414–2,828 Hz)	LC_{eq}	61	64	57
	LCF_{min}	51	59	50
	LCF_{max}	65	67	63

Shown are values for the overall level and levels in the 500-Hz, 1-kHz, and 2-kHz octave bands (band limits are shown in parentheses). Measurements were made 125 cm from the speaker at the release point at the center of the test arena in the sound chamber.

^a Based on the 4-min loop used as an acoustic stimulus in Experiment 1

^b Based on the 12-s loops used as acoustic stimuli in Experiment 2

Experiment 2: selective phonotaxis to a wood frog chorus

In a second experiment, I tested the hypothesis that male wood frogs can acoustically discriminate between a conspecific chorus and a heterospecific chorus as demonstrated by selective phonotaxis to a conspecific chorus. From one speaker, I played back a 12-s loop from the same recording of a wood frog chorus that was used as the acoustic stimulus in Experiment 1 (Fig. 3a). I simultaneously broadcast a 12-s loop of a heterospecific frog chorus from the speaker in the opposite corner of the sound chamber (180° relative to the release cage). Both chorus sounds were started simultaneously at the end of the 1-min acclimation period, and they were broadcast concurrently until the end of the test. As the heterospecific chorus, I used a commercially available recording of a chorus of mink frogs (*R. septentrionalis*; Elliott 2004). In this recording, a few male green frogs (*R. clamitans*) could be heard calling in the background (Fig. 3b). I chose a mink frog chorus as the heterospecific chorus for two reasons. First, male wood frogs and mink frogs are similar in size (Oldfield and Moriarty 1994), and the frequency spectra of their calls broadly overlap between 0.5 and 2 kHz (Fig. 3). Because the peripheral tuning of the frog auditory system is most sensitive at the sound frequencies emphasized in conspecific calls (Capranica and Moffat 1983; Zakon and Wilczynski 1988), the overlap in the spectra of the two chorus sounds should make both sounds audible to wood frogs. Second, wood frogs and mink frogs can breed in the same ponds, but the two species have very different breeding phenologies (Oldfield and Moriarty 1994). In Minnesota, mink frogs breed from late May to early August, whereas wood frogs breed several weeks earlier (late March to early April). There is little or no overlap in the timing of chorusing behavior in these two species. Therefore, Experiment 2 presented male wood frogs with the perceptual task of discriminating between two simultaneously presented chorus sounds with frequency spectra that spanned similar ranges; only the sound of a wood frog chorus would be expected to elicit behavioral responses from male wood frogs if males of this species could perceptually discriminate between a conspecific chorus and a spectrally overlapping heterospecific frog chorus. Note that this approach differs from some other studies (e.g., Gerhardt and Klump 1988b) in that the heterospecific signal is not a signal that male wood frogs are likely to hear under natural conditions. Few other frog species breed as early in the year as wood frogs. The calls of other Minnesota species that do form choruses in the same ponds at the same time of year as wood frogs, such as chorus frogs (*P. t. maculata*) and spring peepers (*P. crucifer*), have higher spectral frequencies than wood frog calls (e.g., Fig. 3a). According to the matched-filter hypothesis of

anuran audition (e.g., Capranica and Moffat 1983), the wood frog auditory system would be expected to be less sensitive to the higher frequencies of these heterospecific signals. Hence, Experiment 2 does not test the hypothesis that male wood frogs discriminate between a chorus of conspecifics and a pure chorus of a potentially syntopically breeding heterospecific. Rather, a mink frog chorus was chosen as the heterospecific stimulus because this should create a more difficult perceptual discrimination task for a male wood frog compared to using a syntopically breeding species for the heterospecific chorus.

In this experiment, the two active speakers were always located in opposite corners of the sound chamber (250 cm apart). The designated pair of active speakers, and the stimulus assigned to each speaker, was varied between replicates of this experiment with different subjects to control for any possibility of a directional response bias. The sound level of each chorus sound was independently adjusted so that its amplitude was approximately 67 dB SPL ($L_{C_{eq}}$) at the male release site (125 cm from the speaker). As in Experiment 1, these SPL values were chosen subjectively so that the amplitude of the wood frog chorus stimulus fell within the range of amplitudes of the wood frog chorus experienced while collecting frogs. Table 1 shows the distribution of sound energy for each stimulus across relevant portions of the frequency spectrum. The range of variation in SPL over the duration of the stimuli was somewhat higher for the mink frog chorus (11–13 dB) compared to that of the wood frog chorus (6–8 dB; Table 1). Note also that the mink frog chorus had a relatively higher amplitude in the 500-Hz octave band, whereas the wood frog chorus had a higher amplitude in the 2-kHz octave band (see Fig. 3). Amplitudes in the 1-kHz octave band were similar.

Data analysis

In both experiments, the data of primary interest consisted of the number of subjects that approached each of the four speakers. The null hypothesis was that an approach to within 10 cm of any one of the four speakers in the sound chamber was independent of whether or not that speaker was broadcasting the sounds of a wood frog chorus. Thus, the null expectation was that 25% of the subjects meeting my response criterion in each experiment would approach each of the four speakers. I tested this null hypothesis against the alternative hypothesis that approaches to the four speakers were nonrandom, with the expectation that a greater proportion of males would approach the speaker broadcasting the sound of a wood frog chorus. I tested for statistical differences in the number of males approaching each speaker using a chi-square goodness-of-fit test ($\alpha=0.05$).

Results

Experiment 1: phonotaxis to a wood frog chorus

In Experiment 1, I tested a total of 11 males with the sound of a wood frog breeding chorus broadcast from one of four speakers while the other three speakers were silent. All 11 males met the response criterion of approaching to within 10 cm of a speaker. Nine males exhibited a response during their first test, whereas two males that exhibited an escape response during their first test were retested later and both approached one of the speakers during this second test. The number of males that responded to each speaker differed significantly from the null expectation that responses would be distributed evenly across the four speakers ($\chi^2=19.2$, $P<0.01$, $df=3$, $N=11$; Fig. 4a). Nine males (82%) approached the speaker broadcasting the wood frog chorus (Fig. 2). Two males (18%) approached a silent speaker. One of these males approached the speaker to the left of the target speaker, and one approached the speaker to the right of the target speaker (Fig. 2). Neither of these males approached the wood frog chorus before 10 min had elapsed. No males approached the speaker that was located directly opposite the active speaker. On average, males required 3.6 min (standard deviation=3.0 min) to approach to within 10 cm of a speaker.

Experiment 2: selective phonotaxis to a wood frog chorus

I tested a total of 27 males in Experiment 2, in which males were presented with a conspecific wood frog chorus and a heterospecific mink frog chorus from opposing speakers. All 11 males tested in Experiment 1 were also tested in Experiment 2, and seven of these males also met the response criterion in Experiment 2. In total, 16 of the 27 males (59%) tested in Experiment 2 met the response criterion during either their first test ($N=12$) or a second test ($N=4$); eleven males did not respond during either test. In addition, the 16 responsive males required an average of 5.1 min (standard deviation=3.3 min) to meet the response criterion. Thus, the males tested in Experiment 2 appeared to be somewhat less responsive than males tested in Experiment 1. This is the reason a larger sample of males was tested in this experiment. One likely explanation for this observation is that Experiment 2 was conducted after the completion of Experiment 1, and motivation to respond declined the longer frogs were held in captivity. Alternatively, lower responsiveness in Experiment 2 might have arisen because discriminating between two simultaneous sounds with overlapping spectra is probably a more difficult perceptual task than the simple detection and recognition task of Experiment 1. I cannot distinguish

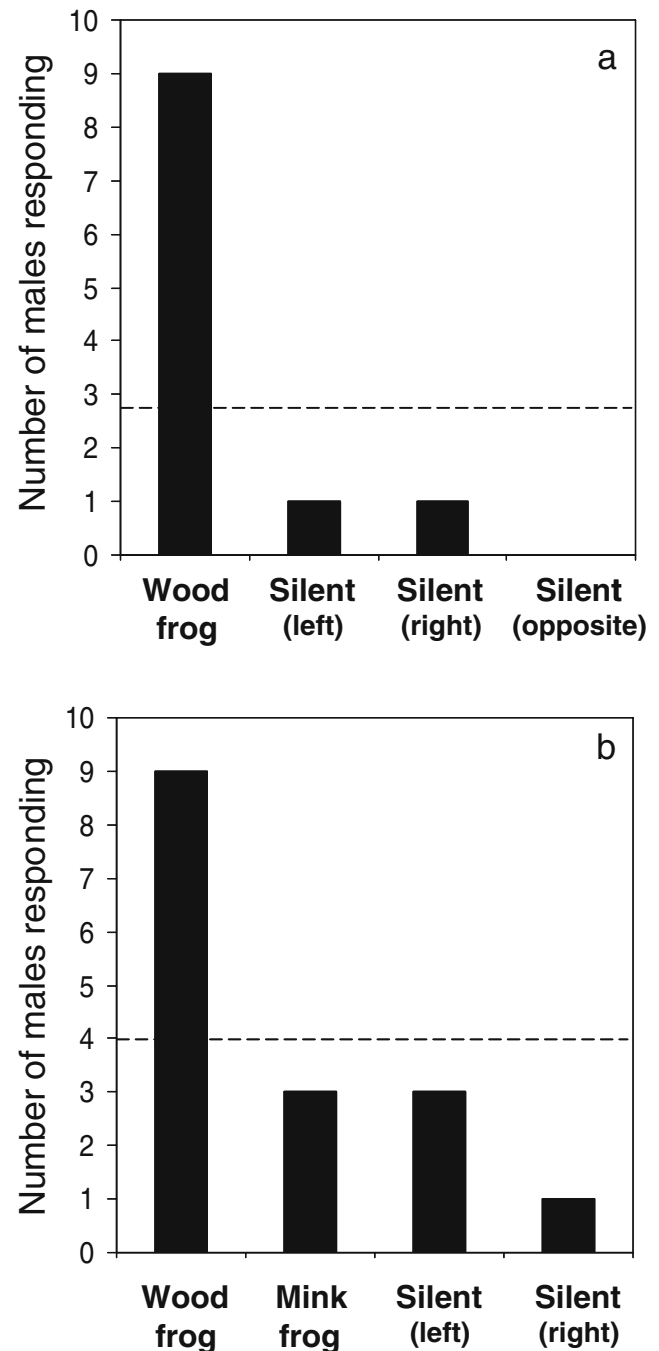


Fig. 4 Results of male phonotaxis tests: **a** number of males that approached to within 10 cm of a speaker broadcasting the sounds of a wood frog chorus or one of three silent speakers that was located in the corner of the sound chamber to the left or right of the target speaker (when facing the target speaker) or in the corner of the sound chamber opposite from the target speaker; **b** number of males that approached to within 10 cm of a speaker broadcasting the sounds of a wood frog chorus or a mink frog chorus from the opposite corner of the sound chamber, or one of two silent speakers that were located in the corners of the sound chamber to the left or right of the target speaker (when facing the target speaker). In each plot, the horizontal dashed line represents the number of males that was expected to approach each speaker according to the null hypothesis that responses would be distributed randomly across the four speakers

between these two alternatives because Experiment 2 was conducted after the completion of Experiment 1.

As in Experiment 1, the number of males that responded to each speaker differed significantly from the null expectation that responses would be distributed evenly across the four speakers ($\chi^2=9.0$, $P<0.03$, $df=3$, $N=16$; Fig. 4b). Nine of 16 males (56%) approached the speaker broadcasting the conspecific chorus. Three males (19%) approached the heterospecific mink frog chorus. Three males (19%) approached the silent speaker located to the left of the target (wood frog) speaker, and one male (6%) approached the silent speaker located to the right of the target speaker. Two of the four males that initially approached a silent speaker went on to approach to within 10 cm of the target speaker in a total elapsed time under 7 min. If a more relaxed response criterion is adopted that considers these two responses as valid approaches to the wood frog chorus, then 69% of males (11 of 16) approached the wood frog chorus, 19% (3 of 16) approached the mink frog chorus, and 12.5% (2 of 16) approached a silent speaker. These results, of course, also differ significantly from the null expectation that 25% of males would approach each speaker ($\chi^2=17.0$, $P<0.01$, $df=3$, $N=16$).

An alternative approach to analyzing the results of this experiment considers the design as a traditional two-choice discrimination task (wood frog chorus vs mink frog chorus) and treats the outcome of each replicate test as a simple Bernoulli trial. Approaches to silent speakers are ignored. Only approaches to within 10 cm of one of the two active speakers are considered valid behavioral responses. The null expectation for a two-choice discrimination test, then, is that 50% of males would choose each of the two alternative stimuli. The one-tailed alternative hypothesis of interest is that significantly more males approached the conspecific chorus. In this experiment, 11 of the 14 males (79%) that eventually approached to within 10 cm of an active speaker approached the wood frog chorus. This result is significantly different from the null expectation (one-tailed binomial test: $P=0.029$).

Discussion

The general aim of this study was to experimentally test the hypothesis that male wood frogs—an explosive breeder—exhibit selective phonotaxis to the sound of a conspecific chorus under controlled laboratory conditions. In Experiment 1, in which males were tested with three silent speakers and one speaker broadcasting a conspecific chorus, 82% of males approached the speaker broadcasting the sound of a wood frog chorus. Only 25% of males were expected to do so by chance alone. Although consistent

with the hypothesis that male wood frogs exhibit positive phonotaxis to the sound of a chorus, this result alone would not rule out the possibility that males exhibit phonotaxis to any sound. Therefore, in Experiment 2, males were tested with a wood frog chorus from one speaker, a spectrally overlapping mink frog chorus from the opposite speaker, and two silent speakers in the adjacent corners of the chamber. Again, the null expectation was that 25% of males would approach the one speaker out of four that was broadcasting a wood frog chorus. In contrast to this null expectation, 56% of males approached the wood frog chorus. If the results of this experiment are considered from the perspective of a traditional two-choice discrimination task, then 11 of 14 males (79%) chose the conspecific chorus over the heterospecific chorus. These results are consistent with the hypothesis that male wood frogs exhibit selective phonotaxis to conspecific sounds in the form of a breeding chorus. Before discussing the possible adaptive value of phonotaxis to a chorus in this species, a number of caveats are worth considering.

First, it is worth being explicit here about the fact that a chorus is comprised of the calls of many individual males. Hence, my results cannot rule out the possibility that male wood frogs responded to the calls of an individual male in the chorus stimulus as opposed to the sound of the chorus per se. In contrast to males (e.g., Pfenning et al. 2000) and females (e.g., Gerhardt and Klump 1988b) of some lek-breeding frog species, however, there are few compelling a priori reasons to expect that explosively breeding male wood frogs, which engage in scramble competition for access to females (Howard 1980; Berven 1981; Howard and Kluge 1985), should exhibit positive phonotaxis toward a particular calling male in the chorus. Moreover, I used a single exemplar for each chorus stimulus and did not test for whether male wood frogs respond to conspecific choruses as a general class of stimuli (e.g., Kroodsmas 1989). Therefore, the conclusions of this study should be qualified by stating that male wood frogs exhibited selective phonotaxis to a conspecific sound (in this case, a chorus), which is consistent with the stated aim of the study.

Second, an important question that was not addressed in this study, and one that is related to the use of a single chorus exemplar, is over what spatial scale could male wood frogs use chorus sounds to locate breeding aggregations of conspecifics? An answer to this question depends on the sensitivity of the wood frog auditory system under natural acoustic conditions and on the propagation of chorus sounds as a function of distance in the species' natural habitat. Two limitations of the present study is that the chorus stimulus was recorded at a height of 1 m, and the stimulus levels used for playback tests were determined

based on my own subjective experiences while collecting frogs and making acoustic recordings of the chorus. No data are presently available on the relationship between the amplitude of chorus noise and the number of males in a chorus, which can vary over two orders of magnitude (Stevens and Paszkowski 2004), nor do we know how the levels and frequency spectrum of a wood frog chorus vary with recording height (e.g., Gerhardt and Klump 1988b) or change over distance and as a result of propagation in different microhabitats at ground or water level or through the water (e.g., Boatright-Horowitz et al. 1999). Incidentally, Gerhardt and Klump (1988b), in their study of chorus attraction in *H. gratiosa*, report that chorus sound levels were 2–4 dB lower when measured at a height of 1 m compared to measurements made at ground level at one of their field sites. At their other site, there was no difference between ground level and 1 m high measurements. Nevertheless, quantifying these relationships in the field, and then testing frogs with stimuli that simulate chorus noise propagating over various distances and through different habitats, will be important next steps toward understanding the spatial extent over which the sounds of a chorus might effectively elicit phonotaxis in wood frogs. In addition, we currently lack data on wood frog auditory thresholds under natural noise conditions. Therefore, it is currently impossible to estimate the spatial extent over which the sounds of a wood frog chorus might be attractive to individuals of this species.

Finally, the acoustic stimuli used in my experiments were actually recordings of mixed-species choruses and not pure wood frog and mink frog choruses. For example, the calls of chorus frogs represented a prominent component of the acoustic scene simulated by broadcasts of the wood frog stimulus. In this preliminary study, I chose not to filter out these elements of the natural acoustic scene. Hence, the interesting possibility remains that the sounds of a different, syntopically breeding frog species actually provide additional acoustic cues that wood frogs could use to orient to a suitable breeding site. A widely held view of anuran hearing suggests, however, that frog ears function as “matched filters” because they are most sensitive to the sound frequencies emphasized in the frequency spectrum of conspecific calls (Capranica and Moffat 1983; Zakon and Wilczynski 1988; Gerhardt and Huber 2002). This feature of the anuran auditory system is thought to be an adaptation for ameliorating the potential masking effects of the calls of other species. Given that the range of frequencies emphasized in the calls of chorus frogs fall approximately an octave above the dominant frequencies emphasized in wood frog calls (Fig. 3a), it seems almost certain that the sounds of the wood frogs were the more salient aspect of the wood frog chorus stimulus. Future work will be required to confirm this.

Taking at face value the main finding of the present study—that male wood frogs exhibited selective phonotaxis to the sound of a conspecific chorus—it is worth considering possible reasons for why reliance on chorus noise as an acoustic orientation cue might be adaptive. The breeding phenology and ecology of this species, and aspects of its mating system, suggest several hypotheses for why attraction to the sounds of a group of calling males might be evolutionarily advantageous for male wood frogs.

One such hypothesis is that the phenology of the wood frog’s explosive breeding has favored frogs that exploit the sounds of a chorus to locate temporally unpredictable breeding sites. Wood frogs reproduce in the early spring of the northern temperate zone of North America (Howard 1980; Berven 1981; Waldman 1982; Howard and Kluge 1985). Both sexes overwinter in terrestrial hibernacula that tend to be located within 100 m of suitable breeding habitat (Regosin et al. 2003). Thus, each spring, males and females must migrate over some distance to a breeding site. Chorusing and mating occur soon after the ice on a pond melts or after the first spring rains fill the pond (e.g., Howard 1980). Thus, the temporal availability of suitable breeding sites can be highly unpredictable due to a dependence on localized and variable climatic factors. Moreover, once initiated, breeding is typically completed within a few days, with most mating events occurring within a single 24-h period after females arrive at the pond (e.g., Howard and Kluge 1985). This high degree of temporal unpredictability, combined with the synchrony of female reproduction, suggests that a male wood frog that failed to exploit all available cues—including acoustic cues—to the timing of an unpredictable and short-lived breeding aggregation could fail to mate. Following this reasoning, we might also expect that unpaired female wood frogs would also be selected to orient to the sounds of a chorus, although this remains to be tested. Gerhardt and Klump (1988b) provided a similar explanation for their finding that females of the barking tree frog (*H. gratiosa*) exhibited selective phonotaxis to the sounds of a conspecific chorus, whereas females of the closely related green tree frog (*H. cinerea*) did not. Barking tree frogs more often breed in unpredictable and ephemeral aquatic habitats, whereas green tree frogs tend to use more permanent bodies of water for breeding; therefore, females of the barking tree frog might benefit more from relying on acoustic cues to locate an unpredictable breeding aggregation (Gerhardt and Klump 1988b; but see Murphy 2003).

To be sure, frogs can use other nonacoustic sensory cues to locate suitable breeding habitat (e.g., olfactory cues; Oldham 1967). Likewise, numerous environmental variables, such as temperature and rainfall, influence the onset of migration into the pond, chorusing behavior, and breeding activity (Henzi et al. 1995; Brooke et al. 2000;

Oseen and Wassersug 2002; Murphy 2003; Hauselberger and Alford 2005; Vaira 2005). Interestingly, a recent investigation by Oseen and Wassersug (2002) failed to identify any environmental factors that were correlated with wood frog chorus activity over a 10-day period when calling was observed. The only significant predictor of male calling activity was the observation of calling in the previous hourly sample. Thus, in wood frogs, acoustic cues associated with the sound of a breeding aggregation might be exploited as an additional sensory cue to the location or timing of breeding or both.

Other advantages to male wood frogs of acoustically orienting to the sounds of a breeding aggregation might stem from the fact that amplexed females of this species lay their eggs at a communal oviposition site, which can be both temporally and spatially unpredictable (Howard 1980; Waldman 1982; Howard and Kluge 1985). Egg masses deposited earliest are located near the center of a growing communal clump of eggs, and they have greater hatching success than eggs added 1–2 days later (Waldman 1982). Delayed oviposition also renders the fertilized eggs and tadpoles of later-reproducing individuals more vulnerable to cannibalism by tadpoles that hatch from the communal egg mass earlier (Petranka and Thomas 1995). Hence, males that arrived relatively late at a breeding site could be at a disadvantage compared to males that arrived earlier. Using the sounds of a forming chorus as an additional cue to the timing or location of breeding activity, therefore, might increase the likelihood that a male could avoid costs associated with mating later than other males. These same advantages would be expected to accrue also to females that exploited acoustic cues to avoid late arrival to the breeding pond.

An alternative to the hypothesis that males exploit the sounds of a chorus as an acoustic orientation cue to ensure timely and accurate migration to suitable breeding sites is the hypothesis that unpaired males within the breeding pond use the sounds of a chorus to locate and join groups of calling males. The wood frog mating system is scramble competition polygyny, and there is intense male–male competition for direct access to females (Howard 1980; Berven 1981; Howard and Kluge 1985). Unpaired males vocalize as they actively search for unpaired, receptive females, and they attempt to clasp any that they encounter. In addition, relatively large males are often successful at dislodging smaller males already in amplexus with a female (Howard 1980; Berven 1981; Howard and Kluge 1985). Howard (1980) reported that both males and females were widely distributed in his study pond at the beginning of the short breeding period. Over time, amplexant pairs congregated near the south-central bank of the pond, and unpaired males clustered in the same area soon thereafter. This was the same area where the communal oviposition site was

later established. Furthermore, both the chorus activity level and the frequency of male–male contests over amplexed females increased in the area where unpaired males and amplexant pairs congregated (Howard 1980). Phonotaxis toward the sounds of a group of unpaired calling males within the breeding pond would allow an unpaired male to join just such an aggregation. This, in turn, might increase his chances of obtaining a mate by dislodging an already paired male or perhaps by finding an unpaired female if they are also attracted to such an aggregation.

The importance of acoustic communication in the context of sexual selection by male–male competition is well established in frogs (reviewed in Gerhardt and Bee 2006, Wells and Schwartz 2006). Phonotaxis to the calls of an individual male is commonly used as a measure of aggressive responsiveness and acoustic discrimination in field playback studies of male frogs (e.g., Wagner 1989; Bee et al. 2000; Bee and Gerhardt 2001a, 2002; Narins et al. 2003). Few previous studies, however, have used the laboratory methods pioneered for studying auditory perception, species recognition, and sexual selection in female frogs (reviewed in Gerhardt 1995) to investigate the phonotaxis behavior of male frogs (Bush et al. 1996; Pfenning et al. 2000). Moreover, few studies have investigated the importance of acoustic signals to male frogs outside the contexts of inter-male spacing in a chorus (e.g., Brenowitz 1989; Marshall et al. 2003) or aggressive male–male contests over calling sites or territories (e.g., Wagner 1989; Bee et al. 1999, 2000; Bee and Gerhardt 2001a,c, 2002). The results of this study suggest that male wood frogs may exploit the acoustic signals of groups of other males to join those groups. This finding highlights a function of auditory perception in male frogs that falls outside the usual contexts of chorus spacing and male–male aggression. This finding also raises a number of basic but important questions that should be addressed in future field and laboratory studies. For example, over what spatial extent could the sounds of a chorus function as an acoustic orienting cue in wood frogs and other species? Do males and females differ in the use of chorus noise as an acoustic orientation cue? How common among frogs is acoustic orientation to the sounds of a chorus, and how is the evolution of acoustic orientation related to a species' mating system and breeding ecology? In other words, is the ability to acoustically orient to breeding aggregations more likely to evolve in explosively breeding species and species that breed in unpredictable habitats? Additional work will be needed to answer these and other open questions regarding the chorus attraction hypothesis in frogs. Addressing these questions will be important for understanding the roles of acoustic communication in a wider diversity of frog mating systems and in broader behavioral contexts.

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