



Finding a mate at a cocktail party: spatial release from masking improves acoustic mate recognition in grey treefrogs

MARK A. BEE

Department of Ecology, Evolution, and Behavior, University of Minnesota, Twin Cities

(Received 13 July 2007; initial acceptance 2 September 2007;
final acceptance 9 October 2007; published online 3 April 2008; MS. number: A10816)

The ‘cocktail party problem’ refers to the difficulty that humans have in recognizing speech in noisy social environments. Many nonhuman animals also communicate acoustically in noisy social aggregations, and thus also encounter and solve cocktail-party-like problems. Relatively few studies, however, have investigated the processes by which nonhuman animals solve sound source segregation problems in the behaviourally relevant context of acoustic communication. In humans, ‘spatial release from masking’ contributes to sound source segregation by improving the ability of listeners to recognize speech that is spatially separated from other sources of speech or ‘speech-shaped’ masking noise. Using a phonotaxis paradigm, I tested the hypothesis that spatial release from masking improves the ability of female grey treefrogs, *Hyla chrysoscelis*, to discriminate between conspecific and heterospecific calls that were spatially separated from two sources of ‘chorus-shaped’ masking noise by either 15° or 90°. As the signal-to-noise ratio (SNR) was decreased from +3 dB to –15 dB (by decreasing the signal level in 6-dB steps), fewer females made a choice, and the likelihood of a female choosing the heterospecific call also increased. At a SNR of –3 dB, females oriented towards and chose the conspecific call in the 90° separation condition, but not when signals and maskers were separated by 15°. These results support the hypothesis that a well-known solution to the cocktail party problem in humans, spatial release from masking, also plays a role in acoustic signal recognition in animals that communicate in biological equivalents of cocktail-party-like environments.

© 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Keywords: acoustic communication; cocktail party problem; communication; gray treefrog; grey treefrog; *Hyla chrysoscelis*; sound source segregation; spatial release from masking; spatial unmasking; vocal communication

Understanding what one person is saying in a large and noisy group of talking people is a difficult, but not impossible, perceptual challenge to overcome. Over the last several decades, one important goal of research on human hearing and speech communication has been to understand how the healthy human auditory system solves this so-called ‘cocktail party problem’ (Cherry 1953; Bronkhorst 2000; Bee & Micheyl, *in press*). Much of the interest in the human cocktail party problem stems from the observations that both people with hearing

impairments and computer algorithms for automated speech recognition have difficulties understanding target speech in the presence of masking or interfering speech or speech-like noise (Bee & Micheyl, *in press*).

Acoustic communication in many diverse nonhuman animal species also occurs in large social aggregations, such as a crèche or a chorus, in which the signals of unattended signallers may be a source of auditory masking or interference (Aubin & Jouventin 1998; Gerhardt & Huber 2002; Greenfield 2002; Brumm & Slabbekoom 2005; Langemann & Klump 2005). For these animals, perceiving acoustic signals is equivalent to the human cocktail party problem (Bee & Micheyl, *in press*). To understand the magnitude of the computational problems that many animals encounter and solve in cocktail-party-like acoustic

Correspondence: M. A. Bee, Department of Ecology, Evolution and Behavior, University of Minnesota, 100 Ecology, 1987 Upper Buford Circle, St Paul, MN 55108, U.S.A. (email: mbee@umn.edu).

conditions, it is important to appreciate that acoustic signals and other environmental noises are composed of sound pressure waves that add together to form a single complex pressure waveform that impinges on a receiver's hearing organs. Hence, in noisy social environments, receivers face a fundamental problem known as 'sound source segregation', which involves perceptually segregating behaviourally relevant acoustic signals from the numerous sources of masking and interfering noise in the environment (Klump 1996; Hulse 2002; Brumm & Slabbekoorn 2005; Bee & Micheyl, *in press*). In comparison to the human hearing and speech communication literature, surprisingly few studies have investigated sound source segregation in the context of animal acoustic communication (Feng & Ratnam 2000; Hulse 2002; Bee & Micheyl, *in press*). Hence, we still know relatively little about how animals solve their own cocktail-party-like problems.

Human listeners experience stark improvements in speech recognition when a speech signal and a 'speech-shaped' masking noise (i.e. noise with the frequency spectrum of speech) originate from different locations (e.g. Bronkhorst & Plomp 1992; Arbogast et al. 2002; Culling et al. 2004; Hawley et al. 2004). This phenomenon, known as 'spatial release from masking' or 'spatial unmasking', contributes to human sound source segregation in noisy social environments (Bronkhorst 2000; Shinn-Cunningham et al. 2005). Nonhuman animals experience spatial release from masking in the detection of relatively simple signals (e.g. pure tones) that are spatially separated from sources of masking noise (reviewed in Bee & Micheyl, *in press*). Whether spatial release from masking might function in acoustic signal recognition in behaviourally relevant contexts, such as mate choice, social recognition or eavesdropping, has thus far received little attention in the animal behaviour literature.

Acoustic communication in frogs is a biological equivalent of the human cocktail party problem. In many frog species, males aggregate in large, multispecies choruses in which they produce loud advertisement calls that are both necessary and sufficient for species recognition by females (reviews in Ryan 2001; Gerhardt & Huber 2002; Gerhardt & Bee 2006). The high levels of background noise in a chorus can mask the perception of acoustic signals in frogs (Gerhardt & Klump 1988; Wollerman 1999; Schwartz et al. 2001; Wollerman & Wiley 2002; Bee 2007; Bee & Swanson 2007). Thus, we might expect sound source segregation to be important for communication in this taxonomic group (Feng & Ratnam 2000; Hulse 2002; Feng & Schul 2006; Bee & Micheyl, *in press*).

In this study, I investigated the potential role of spatial release from masking in acoustic mate recognition by females of Cope's grey treefrog, *Hyla chrysoscelis*. The grey treefrog species complex comprises two cryptic species, *H. chrysoscelis* (a diploid) and the eastern grey treefrog (*Hyla versicolor*), which is a tetraploid (Gerhardt 1994; Ptacek et al. 1994; Holloway et al. 2006). Both species breed syntopically throughout much of their common range in North America, and a great deal is already known about the acoustic properties that mediate species recognition by females of both species (reviewed in Gerhardt

2001). Importantly, hybrid offspring can be found in syntopic breeding populations of the two species (Gerhardt et al. 1994), which suggests that females might sometimes make mistakes in choosing a conspecific male in the cocktail-party-like conditions of a mixed-species chorus. Such mistakes, while generally rare, are costly in terms of evolutionary fitness, because hybrids are infertile (Gerhardt et al. 1994). Perceptual mechanisms for sound source segregation might play some role in reducing the risk of costly mating mistakes in a mixed-species chorus. Here, I report results from a series of two-choice phonotaxis experiments that were designed to test the hypothesis that spatial release from masking improves a female's ability to discriminate between conspecific (*H. chrysoscelis*) and heterospecific (*H. versicolor*) calls in the presence of 'chorus-shaped' noise.

METHODS

Subjects and Study Sites

Nightly collections of gravid females were made between 25 May and 15 June 2007 from ponds and marshes at three field sites located within 80 km of the Saint Paul campus of the University of Minnesota. These field sites included a pure population of *H. chrysoscelis* (Carver Park Reserve, Carver County, MN) and two populations in which *H. chrysoscelis* breeds syntopically with *H. versicolor* (Carlos Avery Wildlife Management Area, Anoka County, MN; Tamarack Nature Center, Ramsey County, MN). For females collected from mixed-species populations, I always tested the female in an initial two-choice discrimination experiment in which I alternated broadcasts of synthetic *H. chrysoscelis* and *H. versicolor* calls (see below) to confirm the female's species identity. At the completion of all testing (typically within 1–3 days of collection), I released females with their mates at their original location of capture.

General Testing Procedures

I collected females in amplexus between 2130 and 0100 hours, stored the pairs in small plastic containers and returned them to the laboratory where they and their mates were maintained at 2°C to delay egg deposition prior to testing. On the day of testing, the pair was transferred to a 20°C incubator until their body temperatures had reached $20 \pm 1^\circ\text{C}$. For testing, the female was separated from her mate, used as a subject in a phonotaxis test and then returned to her mate in the incubator where they remained until the female was used in a subsequent test.

I tested females in a custom-built, hemi-anechoic sound chamber (Industrial Acoustics Company, IAC, Bronx, New York, U.S.A.; inside dimensions: $3.0 \times 2.8 \times 2.2$ m, $L \times W \times H$). The floor of the chamber was covered with dark grey carpet, and the inside walls and ceiling were constructed from acoustic insulation covered by dark grey perforated metal to reduce reverberations (IAC's Planarchoic™ panel system). The temperature inside the chamber was maintained at $20 \pm 2^\circ\text{C}$. With the chamber ventilation unit running, the baseline sound pressure

levels (SPL re. 20 μ Pa) inside the chamber ranged from 2 to 12 dB SPL (LZF) over the 500-Hz to 4-kHz 1/3-octave bands, which span the frequency range of interest here. The frequency response of the playback system was flat (± 3 dB) over this same range of frequencies. I used a Larson-Davis System 834 sound level meter to measure sound levels and to calibrate the playback levels of acoustic stimuli. Sound level measurements were made by placing the microphone of the sound level meter at the approximate position of a female's head at the location from which females were released. Acoustic stimuli were calibrated at least twice daily.

I tested females under infrared (IR) illumination using two IR light sources (Noldus Information Technology Inc., Leesburg, VA, U.S.A.) that were mounted near the ceiling at the centre of opposite walls of the sound chamber. Behavioural responses were observed using an overhead IR-sensitive video camera (Panasonic WV-BP334; Panasonic Corporation of North America, Secaucus, NJ, U.S.A.) mounted from the centre of the chamber ceiling and a video monitor located outside the chamber. Acoustic signals were broadcast through A/D/S L210 speakers (Vista, CA, U.S.A.) using a Dell Optiplex GX745 computer (Dell Computer Corporation, Round Rock, TX, U.S.A.) 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 (San Jose, CA, U.S.A.) interfaced with an M-Audio FireWire 410 multichannel soundcard (M-Audio USA, Irwindale, CA, U.S.A.). Output from the soundcard was amplified using a Sonamp1230 multichannel amplifier (Sonance, San Clemente, CA, U.S.A.).

I conducted phonotaxis tests in a circular test arena (2 m diameter) located on the floor of the sound chamber. The walls of the arena were constructed from hardware cloth (60 cm high) and covered by visually opaque, but acoustically transparent, black cloth. The perimeter of the arena floor was divided into 24 bins of 15° (Fig. 1). Two speakers for broadcasting conspecific and heterospecific signals were positioned on the chamber floor just outside the wall of the test arena and aimed towards the centre of the arena, where females were released during a test. The signal speakers were placed 2 m and 180° apart on opposite sides of the test arena at the centre of one of the 15° bins around the edge of the arena (Fig. 1). Speakers for broadcasting masking sounds were also placed 2 m and 180° apart on the floor just outside the arena wall and centred in one of the 15° bins, but the absolute positions of the masker speakers depended on the design of a particular test (Fig. 1; see below).

At the beginning of a test, the female was placed in an acoustically transparent release cage (9 cm diameter) located on the floor and positioned at the centre of the test arena. Females were free to move about and reorient inside the release cage and I did not quantify a female's orientation before her release. Following a 1 min acclimation period, I started broadcasts of the alternating signals, which were broadcast as a continuous loop during a test. After a female had heard four presentations of both signals, I remotely released her using a rope and pulley system that could be operated from outside the chamber.

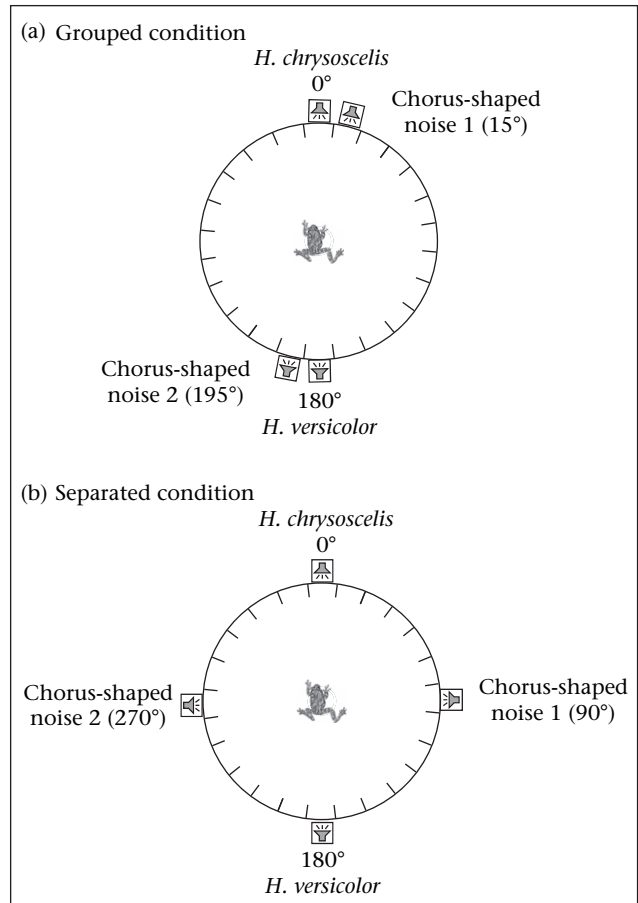


Figure 1. Schematic diagram illustrating the circular test arena divided into 15° bins along the perimeter and the positions of speakers broadcasting signals and chorus-shaped noises in (a) the grouped condition and (b) the separated condition. Note that the frog and speakers are not drawn to scale.

Females were given up to 5 min to make a choice, which consisted of touching the wall of the test arena inside the 15° arc directly in front of either of the two signal speakers. Responsive females typically initiate phonotaxis within seconds of their release and show directed patterns of zigzag hopping or walking towards the speaker (Gerhardt 1995); they typically do not initially go to some location along the arena wall and follow the wall to a speaker. I tested females individually and gave them a 'timeout' of at least 5 min between consecutive tests. I periodically switched the outputs from the amplifier going to each signal speaker or switched the positions of the two signal speakers to control for directional response bias in the chamber. No such bias was detected.

Acoustic Stimuli

I conducted two-choice discrimination tests (Gerhardt 1995; Ryan & Rand 2001) in which females were given a choice between a synthetic conspecific (*H. chrysoscelis*) call and a synthetic heterospecific (*H. versicolor*) call broadcast in an alternating fashion between the two signal speakers. Both of these signals had average temporal

and spectral properties that were based on recordings of the two species at my field sites and corrected to a temperature of 20°C (M. A. Bee, unpublished data; Fig. 2). The signals were composed of a series of pulses that I synthesized using a custom-made program (courtesy of J. J.

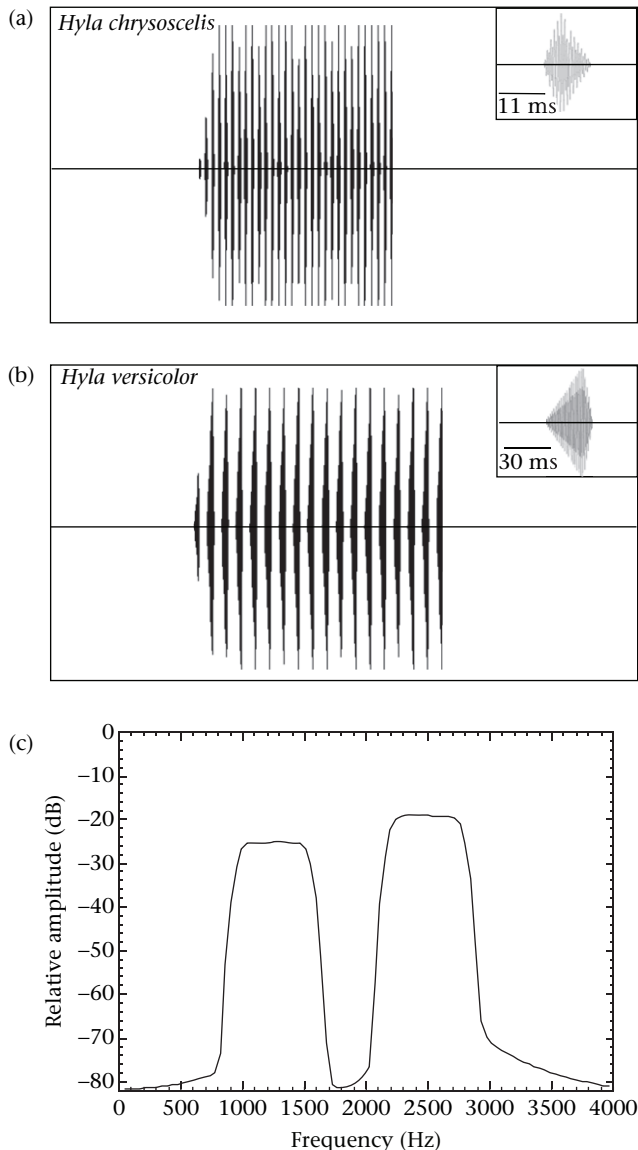


Figure 2. Oscillograms of the (a) conspecific (*H. chrysoscelis*) signal and (b) the heterospecific (*H. versicolor*) signal depicting a temporal window of 1.5 s around each call. Insets in (a) and (b) depict a single pulse from the corresponding call. The pulses in the *H. chrysoscelis* call (a) were 11 ms in duration and separated by 11 ms interpulse intervals (pulse period = 22 ms; pulse duty cycle = 50%) and were shaped with onsets (4 ms) and offsets (7 ms) that had half-amplitude times that were 43% and 53% of the duration of the onset and offset times, respectively. The pulses in the *H. versicolor* call (b) were 30 ms in duration and separated by 30 ms interpulse intervals (pulse period = 60 ms; pulse duty cycle = 50%) and were shaped with onsets (20 ms) and offsets (10 ms) that had half-amplitude times that were both 55% of the duration of the respective envelope ramp. Note that this *H. versicolor* call was effective at eliciting phonotaxis from females of *H. versicolor* (M. A. Bee, unpublished data). (c) Power spectrum of the chorus-shaped noise.

Schwartz). Each pulse consisted of two harmonically related spectral peaks that had frequencies (and relative amplitudes) of 1.3 kHz (−9 dB) and 2.6 kHz (0 dB) in the *H. chrysoscelis* call and 1.2 kHz (−5 dB) and 2.4 kHz (0 dB) in the *H. versicolor* call. The *H. chrysoscelis* call (Fig. 2a) consisted of 30 pulses (11 ms pulse duration) delivered at a pulse rate of 45.5 pulses/s (649 ms total call duration), and the *H. versicolor* call (Fig. 2b) consisted of a series of 18 pulses (30 ms pulse duration) delivered at a pulse rate of 16.7 pulses/s (1050 ms total call duration). Both calls repeated with a period of 5 s, and the two calls were presented so that there were equal intervals of silence preceding and following each call. The SPLs of the two signals were equalized at the female release site, but the absolute levels were varied in different tests to create different signal-to-noise ratios (SNRs; see below).

I constructed two artificial 'chorus-shaped' noises (i.e. noise with a spectrum approximating that of a grey treefrog chorus) using the Adobe Audition software to filter each of two separate white noises into two spectral bands, each with a bandwidth of 600 Hz (Fig. 2c). The low-frequency band had a centre frequency of 1.25 kHz and a relative amplitude that was −6 dB in relation to the high-frequency band centred at 2.5 kHz. Each spectral band, therefore, was centred at a frequency that was the arithmetic mean between the corresponding spectral peaks in the synthetic calls of the two species. These masking noises simulate the frequency spectrum of a natural mixed-species breeding chorus of grey treefrogs (Bee 2007; Bee & Swanson 2007; Swanson et al. 2007). During phonotaxis tests that included broadcasts of the chorus-shaped noise, the level of each masker was calibrated to be 70 dB SPL (LC_{eq}) at the female release site; therefore, the overall level of both maskers together was 73 dB SPL at the female's release site. This level falls within the range of background noise levels in natural grey treefrog choruses (Schwartz et al. 2001; Swanson et al. 2007). Note that my use of 'chorus-shaped noise' as a masker parallels the use of 'speech-shaped noise' in studies of the cocktail party problem and spatial release from masking in humans (Bronkhorst 2000).

Experimental Design

I attempted to test all females ($N = 40$) in a complete series of 10 two-choice tests. The first and last tests in this series were considered 'reference conditions' and they involved broadcasting the alternating conspecific and heterospecific calls at 76 dB SPL (at 1 m, LCF) with no masking noise. In the intervening eight tests, I varied the SNR and the spatial configuration between signals and maskers using a 4 (SNR) \times 2 (spatial configuration) factorial design and a different random order for each subject.

I tested females at nominal SNRs of +3 dB, −3 dB, −9 dB and −15 dB, expressed as the level of each signal in relation to the overall level of both maskers at the female release site (73 dB SPL). These four SNRs, therefore, correspond, respectively, to absolute signal levels of 76 dB, 70 dB, 64 dB and 58 dB SPL (at 1 m, LCF). It is worth making explicit that these were the nominal SNRs at the female's release

site and that actual SNRs obviously varied as females moved about in the arena. Allowing subjects to move about under free-field listening conditions is an important departure from traditional psychoacoustic studies of auditory masking, in which stimuli are typically presented over headphones, or the positions of listeners and speakers are fixed in tests conducted under free-field listening conditions. The use of traditional psychoacoustic methods is difficult and rare in studies of frog hearing and communication (Gerhardt 1995; Simmons & Moss 1995; Gerhardt & Huber 2002); therefore, most previous studies of auditory masking in frogs have used a phonotaxis paradigm (e.g. Ehret & Gerhardt 1980; Gerhardt & Klump 1988; Wollerman 1999; Schwartz et al. 2001; Wollerman & Wiley 2002; Bee 2007; Bee & Swanson 2007). Phonotaxis represents an ecologically valid behavioural measure of spatial release from masking in frogs because it takes advantage of the natural behaviour of females in response to acoustic signals.

I tested females with two spatial configurations of the signal and masker speakers (Fig. 1). In the 'grouped' conditions (Fig. 1a), masking noises were displaced 15° laterally from the signals. Approximately half of females were tested with the maskers displaced either to the left or the right of the signals. In the 'separated' conditions (Fig. 1b), the two maskers were displaced from the signals by 90°, so that each one was presented 90° from both signals on opposite sides of the arena. In both conditions, approximately half of females were tested with a particular chorus-shaped noise (i.e. noise 1 or noise 2 in Fig. 1) displaced either to the left or the right of each signal.

If a female failed to make a choice within 5 min in two consecutive tests with masking noise, then the next test of that female was another reference condition to ensure that the female was still responsive. If the female made a choice in this reference condition, then the previous two 'no-response' results were considered valid and testing with that female continued. If the female did not make a choice in this reference condition, then the data from the two previous 'no-response' tests were discarded from all analyses and the female was not tested further. Of the 40 females tested in this study, 30 females were tested in all 10 discrimination tests; the remaining 10 females were tested in three ($N = 1$), four ($N = 2$), five ($N = 2$), six ($N = 2$) or seven ($N = 3$) tests.

Hypotheses and Data Analysis

I made two predictions according to the hypotheses that the chorus-shaped noise would mask a female's perception of advertisement calls and that spatial unmasking would improve a female's ability to discriminate between conspecific and heterospecific calls. First, I predicted that the proportion of females responding to one of the two signals would decrease as a function of decreasing SNR. I tested this prediction using Cochran's Q tests (Sokal & Rohlf 1995) to compare the proportion of females that chose one of the two signals across the four SNRs ($N = 30$ females that completed all tests).

My second prediction was that, among the females that responded to one of the two signals at a particular SNR, a greater proportion of females would chose the conspecific call in the separated condition compared with the grouped condition. The data did not meet the requirements for using the McNemar test for significant changes (Sokal & Rohlf 1995; Zar 1999) to compare the proportions of responsive females that changed their response between the grouped and separated conditions at a particular SNR. Therefore, I used separate binomial tests for each combination of SNR and spatial configuration to test the null hypothesis that 50% of females would choose each call against the one-tailed alternative hypothesis that greater than 50% of females would choose the conspecific call. This use of binomial tests is quite common in analyses of results from two-choice discrimination experiments with frogs (Gerhardt 1992, 1995). The rationale behind these analyses was two-fold. First, if females were able to discriminate between the conspecific and heterospecific calls in a particular condition, then significantly more than 50% of females should choose the conspecific call. Second, if spatial unmasking improved signal recognition at a particular SNR, then we might expect the proportion of females choosing the conspecific call in the separated condition to be significantly greater than 50%, whereas females in the grouped condition might be expected to choose the two signals in similar proportions. These analyses were based on the number of responsive females in each test that chose one of the two signals. I used one-tailed tests based on the a priori expectation that females would choose conspecific calls (Gerhardt 2001) and computed power for nonsignificant results following Zar (1999).

As a second measure of female phonotaxis behaviour, I used the angle at which females first touched the wall of the circular test arena to assess directional orientation. I designated the *H. chrysoscelis* call as originating from 0° and the *H. versicolor* call as originating from 180°. For each two-choice experiment, I used a V test (Zar 1999) to test the null hypothesis that the angles at which females first touched the arena wall were uniformly distributed against the alternative hypothesis that females significantly oriented in the direction of the conspecific call at 0°. If, at a particular SNR, females showed greater orientation towards the conspecific call in the separated condition compared with the grouped condition, I interpreted this result as evidence in favour of the spatial unmasking hypothesis.

For all statistical analyses, I used a significance criterion of $\alpha = 0.05$. Descriptive and nonparametric statistics were computed either by hand or using Statistica 7.1 (Statsoft, Tulsa, OK, U.S.A.) and circular statistics were computed using Oriana 2.02 (Kovach Computing, Anglesey, U.K.).

RESULTS

In both the first and last reference conditions, in which females were given a choice between calls of *H. chrysoscelis* and *H. versicolor* with no masking noise, 100% of responsive females chose the conspecific call (one-tailed binomial tests: first reference, $P < 0.001$, $N = 40$; second reference,

$P < 0.001$, $N = 34$). In addition, females first touched the wall of the arena in the reference conditions at locations that were significantly oriented in the direction of the conspecific call (Table 1). In these conditions, the length of the mean vector (r) was near 1.0 (Table 1). Thus in my experimental set-up, all females oriented towards, and chose, the conspecific call in the absence of chorus-shaped noise.

In the presence of the chorus-shaped noise, the proportion of females that responded by choosing one of the two signals in both the grouped and separated conditions decreased as the SNR decreased from +3 dB to -15 dB (Cochran's Q tests: grouped: $Q_3 = 24.1$, $N = 30$, $P < 0.001$; separated: $Q_3 = 31.2$, $N = 30$, $P < 0.001$; Fig. 3). Thus, at lower SNRs, the signals were more effectively masked for a larger proportion of females. Yet even at the lowest SNRs of -9 dB and -15 dB, some females were responsive and showed unequivocal phonotaxis (e.g. zigzag patterns of directed walking) towards one of the two signals, thus indicating that these responsive females were clearly able to detect one or both of the signals.

As the SNR decreased from +3 dB to -15 dB, there was also a decrease in the proportion of responsive females that chose the conspecific call (Fig. 3) and a concomitant increase in the proportion of females that made a mistake by choosing the heterospecific call. For example, of the females that responded to one of the two signals when the SNR was +3 dB, 94% and 97% of females chose the conspecific call over the heterospecific call in the grouped and separated conditions, respectively (one-tailed binomial test: grouped: $P < 0.001$, $N = 35$; separated: $P < 0.001$, $N = 32$; Fig. 3). At a SNR of -3 dB, significantly more females (92%) chose the conspecific call in the

separated condition (one-tailed binomial test: $P < 0.001$, $N = 25$), but the proportion of females (68%) that chose the conspecific call in the grouped condition was not significantly greater than 50% (one-tailed binomial test: $P = 0.067$, $N = 22$, power ≥ 0.60) (Fig. 3). When the SNR was either -9 dB or -15 dB, fewer females responded to one of the two signals and the proportions that chose the conspecific and heterospecific calls did not differ significantly from the null expectation of 50:50 (Fig. 3). In the grouped conditions at SNRs of -9 dB and -15 dB, 59% and 67% of females, respectively, chose the conspecific call (one-tailed binomial test: -9 dB: $P = 0.315$, $N = 17$, power ≥ 0.60 ; -15 dB: $P = 0.194$, $N = 12$, power ≥ 0.63). In the separated conditions, 45% and 55% of females chose the conspecific call at SNRs of -9 dB and -15 dB, respectively (one-tailed binomial test: -9 dB: $P = 0.500$, $N = 11$, power ≥ 0.61 ; -15 dB: $P = 0.500$, $N = 11$, power ≥ 0.62).

In the presence of the chorus-shaped noise presented at a SNR of +3 dB, female phonotaxis was significantly oriented towards the conspecific call in both the grouped and the separated conditions (Table 1) and orientation in these conditions was quite strong ($r \geq 0.89$; Table 1). At a SNR of -3 dB, females significantly oriented in the direction of the conspecific call in the separated condition (Table 1), and orientation in this condition was still fairly strong ($r = 0.57$; Table 1). In contrast, while the mean vector was also in the direction of the conspecific call in the grouped condition at a SNR of -3 dB, orientation was weaker ($r = 0.21$; Table 1) than in the separated condition at this SNR and was not directed significantly towards the conspecific call. When the SNR was -9 dB or -15 dB, female responses were not significantly directed towards

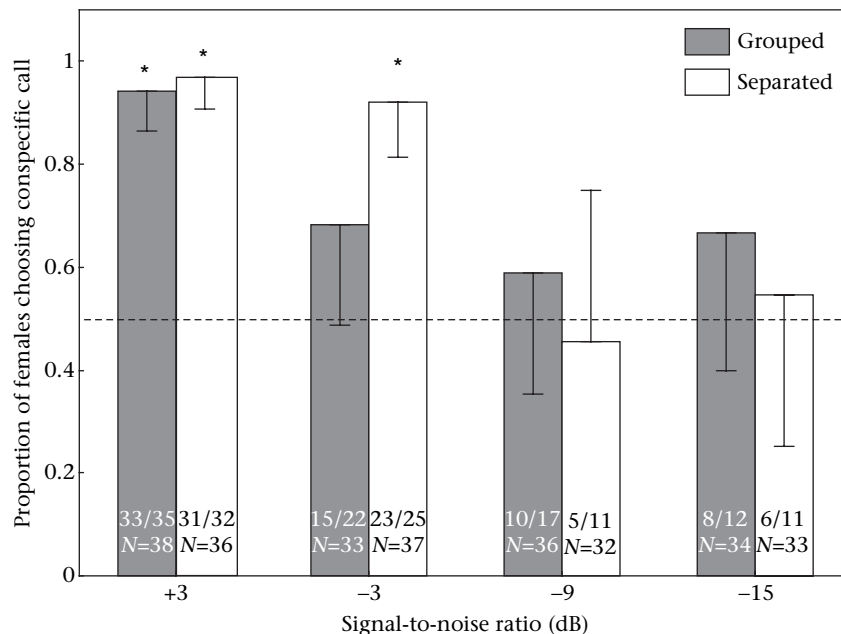


Figure 3. Histograms showing the proportion of responsive females that chose the conspecific call as a function of SNR in each condition. The numbers associated with each bar depict the ratio of the number of females that chose the conspecific call to the number of females that actually made a choice in that condition; N represents the total number of females that were tested in that condition. The error bars depict either the upper or lower 95% confidence interval around the proportion of females choosing and the horizontal dashed line depicts the expected proportion according to the null hypothesis that females would choose the conspecific and heterospecific calls in a 50:50 ratio. Asterisks indicate that significantly more females than expected by chance chose the conspecific call (one-tailed binomial $P < 0.05$).

Table 1. Results from circular statistical analyses of orientation angles for females that touched the arena wall in each condition

Parameter	Reference condition		Grouped conditions				Separated conditions			
	First	Last	+3 dB	-3 dB	-9 dB	-15 dB	+3 dB	-3 dB	-9 dB	-15 dB
Number of females	40	34	36	28	29	26	33	29	22	30
Mean vector (μ)	0.0°	0.9°	0.4°	5.5°	46.9°	283.0°	2.6°	12.3°	319.4°	227.9°
Length of mean vector (r)	0.99	0.99	0.90	0.21	0.17	0.29	0.89	0.57	0.13	0.17
Circular standard deviation	7.5°	8.1°	26.2°	101.1°	107.5°	90.6°	27.2°	60.4°	116.8°	107.5°
V test (u)	8.9	8.2	7.6	1.6	0.9	0.5	7.3	4.3	0.6	-0.9
V test (P)	<0.001	<0.001	<0.001	0.058	0.187	0.323	<0.001	<0.001	0.266	0.813

V tests were used to test the null hypothesis that female responses were randomly distributed against the alternative hypothesis that responses were oriented in the direction of the conspecific call (0°).

the conspecific call in either the grouped or the separated condition (Table 1).

DISCUSSION

Spatial release from masking is one important phenomenon that contributes to sound source segregation in humans, and thus functions as one solution to problems associated with speech recognition in cocktail-party-like listening conditions (Bronkhorst 2000). Noisy social environments for acoustic communication are also common among nonhuman animals and include many well-known examples, such as frog and insect choruses (Gerhardt & Huber 2002; Greenfield 2005), dawn choruses of songbirds (Amrhein et al. 2004; Gorissen & Eens 2004; Liu 2004), and large crèches of juvenile bats (Balcombe 1990; Balcombe & McCracken 1992) and penguins (Aubin & Jouventin 1998, 2002). Relatively few previous studies have directly investigated mechanisms of sound source segregation and solutions to cocktail-party-like problems in the context of animal acoustic communication (but see e.g. Schwartz & Gerhardt 1989, 1995; Hulse et al. 1997; Aubin & Jouventin 1998). The aim of the present study was to investigate spatial release from masking as a potential mechanism that contributes to improved sound source segregation in frogs.

Spatial Release from Masking in Grey Treefrogs

In a previous study of grey treefrogs (Bee 2007), results from single-stimulus phonotaxis tests suggested that females experienced a release from masking in the detection of a conspecific signal presented against a background of chorus-shaped noise when the signal and noise were separated by 90° compared with a separation of 7.5°. Spatial release from masking was significant at SNRs of 0 dB and -6 dB, but not at SNRs of +6 dB and -12 dB. The primary aim of the present study was to extend these initial findings by testing the hypothesis that spatial release from masking also plays a role in mate recognition by improving a female's ability to discriminate between conspecific and heterospecific calls under noisy conditions simulating a breeding chorus.

At SNRs of +3 dB, -9 dB and -15 dB, there was little evidence to suggest that females experienced spatial unmasking when the maskers were in the separated configuration. At the highest SNR of +3 dB, nearly all females chose the conspecific call in both the grouped and separated conditions, and the orientation of female responses was directed towards the conspecific stimulus in both conditions. At the two lowest SNRs (-9 dB and -15 dB), most females failed to make a choice and failed to show phonotaxis-related behaviours. It seems almost certain that these unresponsive females failed to detect the signals. At these relatively low SNRs (-9 dB and -15 dB), however, some females showed unequivocal phonotaxis towards one of the two signals. Clearly, this subset of responsive females was able to detect one or both of the signals. Importantly, these responsive females chose the conspecific and heterospecific calls in similar proportions. In neither the grouped nor the separated condition at SNRs of -9 dB and -15 dB was there any evidence to suggest that female phonotaxis was significantly oriented towards the conspecific call. These results are important in that they indicate that some females could still detect the signals at SNRs of -9 dB and -15 dB, but that auditory masking interfered with their ability to discriminate between conspecific and heterospecific calls.

Evidence supporting the hypothesis that spatial unmasking improved the ability of females to discriminate between conspecific and heterospecific calls was found at a SNR of -3 dB. At this SNR, females chose the conspecific call significantly more often than expected by chance in the separated condition, but in the grouped condition there was only a nonsignificant tendency for females to more often choose the conspecific call. In the separated condition, females first touched the wall of the arena at locations that were significantly oriented in the direction of the conspecific call, but this was not the case in the grouped condition. In fact, at a SNR of -3 dB, the strength of orientation (r) was more than twice as great in the separated condition ($r = 0.57$) compared with the grouped condition ($r = 0.21$; Table 1). Thus, at a SNR of -3 dB, the ability of females to choose a conspecific call over a heterospecific call was improved when the signals and the two sources of chorus-shaped noise were spatially separated by 90° compared with a separation of just 15°. These results provide support for the hypothesis that

spatial release from masking not only improves signal detection in grey treefrogs (Bee 2007), but also improves signal recognition.

Could Spatial Unmasking Contribute to Sound Source Segregation in a Frog Chorus?

Previous studies of the problem of auditory masking in frog choruses have elucidated various behavioural strategies that signallers use to increase the likelihood that their signals are detected by receivers (reviewed in Narins & Zelick 1988; Gerhardt & Huber 2002; Wells & Schwartz 2006). These strategies include (1) partitioning the frequency spectrum or the time of day by calling in locations or at times when other species with spectrally overlapping calls are not calling, (2) precise call timing interactions to avoid call overlap with nearby males in the chorus, (3) spacing out within the available breeding habitat to avoid calling too closely to other signalling males and (4) increasing calling effort in dense social conditions by calling more frequently or producing longer calls. While these strategies clearly function to improve signal transmission in a chorus, the efficacy of these behavioural strategies might be diminished in particularly dense choruses, for example, because of unavoidable increases in call overlap (e.g. Brush & Narins 1989; Schwartz et al. 2002) and decreases in intermale distances (e.g. Gerhardt et al. 1989; Murphy & Floyd 2005). Effective communication under such listening conditions, therefore, should depend at least in part on the perceptual mechanisms of receivers.

Historically, the selectivity of the frog auditory system for the spectral and temporal properties of conspecific calls has often been viewed as analogous to a template-matching process for call detection and recognition that could ameliorate masking interference, at least by heterospecifics (e.g. the 'matched filter' hypothesis; Capranica & Moffat 1983; reviewed in Gerhardt & Huber 2002). For the two grey treefrog species, spectral selectivity for conspecific calls might provide little such benefit in syntopic breeding populations because the calls of both species are spectrally quite similar (Gerhardt 2001, 2005). More generally, template-matching processes alone might contribute little towards separating the overlapping calls of conspecific males from each other or from the general din of background noise in a dense chorus. This follows because all conspecific males in a chorus would have signals approximating a receiver's spectrotemporal template. Moreover, as the results of this and other laboratory studies show, background noise can impair a female frog's ability to detect and discriminate among calls (Ehret & Gerhardt 1980; Gerhardt & Klump 1988; Wollerman 1999; Schwartz et al. 2001; Wollerman & Wiley 2002; Bee 2007; Bee & Swanson 2007). Hence, in addition to auditory selectivity for conspecific calls, we might expect the operation of other perceptual mechanisms to contribute to signal detection and recognition under the noisy conditions of a breeding chorus. Spatial release from masking is likely to be one such mechanism.

In an earlier study of green treefrogs, *Hyla cinerea*, females were given the choice between an attractive

conspecific advertisement call and a less attractive conspecific aggressive call (Schwartz & Gerhardt 1989). Females experienced spatial release from masking in signal detection when the signals and two sources of broadband noise (0.1–10 kHz) were presented at angular separations of either 45° or 90° compared with conditions in which the signal and masker speakers were adjacent to each other. In that study, however, there was little evidence that spatial release from masking improved the ability of females to discriminate between the two types of conspecific calls. Neurophysiological studies of northern leopard frogs, *Rana pipiens*, have also revealed spatial release from masking in the signal detection thresholds of auditory nerve fibres (Lin & Feng 2001) and neurons in the auditory midbrain (torus semicircularis; Ratnam & Feng 1998; Lin & Feng 2003). Together with these earlier studies, the results of the present study suggest that in frogs, the auditory system may exploit spatial separation between signals and noise to improve not only the detection of mating signals (Schwartz & Gerhardt 1989; Bee 2007), but also the ability to recognize the signals of appropriate mates.

The contribution of spatial release from masking to mate recognition might be important under the listening conditions of natural breeding choruses. In this study, the manipulations of SNR and spatial configuration simulated males signalling at different distances and locations in relation to fixed sources of masking noise, with lower SNRs simulating more distant males. Female treefrogs typically enter a chorus from the periphery and spend several minutes assessing different nearby males as potential mates (Murphy & Gerhardt 2002; Schwartz et al. 2002, 2004). It is not unreasonable to expect that females may often encounter situations during mate assessment in which the signals of multiple conspecific and heterospecific males and the general background noise of the chorus originate from different locations and distances. Under such listening conditions, spatial release from masking might improve a female's ability to detect and recognize the calls of conspecific males, such as those calling near the edge of a breeding pond. In real breeding choruses, of course, the acoustic scene is composed of many sound sources located in different directions and at different distances from a receiver. Therefore, some caution is necessary in extending to the real world the findings from controlled laboratory experiments like the one reported here and elsewhere (Schwartz & Gerhardt 1989; Bee 2007). Nevertheless, experiments on spatial release from masking in frogs almost certainly engage perceptual mechanisms that benefit receivers under some listening conditions in natural choruses.

Conclusion

The mechanisms underlying spatial release from masking contribute to sound source segregation in humans and to our ability to solve the cocktail party problem (Bronkhorst 2000). Compared to the large number of studies of spatial release from masking in humans, however, only a few studies have investigated spatial unmasking in

animals. In addition to frogs, behavioural studies have reported spatial release from masking in signal detection tasks in fish (Chapman & Johnstone 1974; Hawkins & Sand 1977), birds (Dent et al. 1997), ferrets (Hine et al. 1994), mice (Ison & Agrawal 1998), harbour seals (Turnbull 1994; Holt & Schusterman 2007) and California sea lions (Holt & Schusterman 2007). Ronacher & Hoffmann (2003) failed to find strong evidence for spatial release from masking in a study of a grasshopper. Together, these studies indicate that spatial release from masking might be a general and taxonomically widespread phenomenon that contributes to sound source segregation in a diversity of animals, at least among vertebrates. Our understanding of the perceptual mechanisms of sound source segregation, and their potentially important roles in animal acoustic communication in noisy social environments, would be greatly improved by investigating these processes in a greater diversity of animals and behavioural contexts. Such investigations have considerable potential to increase our understanding of the evolved sensory mechanisms that allow humans and other animals to perceptually organize the complex acoustic scenes associated with noisy social aggregations (Feng & Ratnam 2000; Hulse 2002; Bee & Micheyl, in press).

Acknowledgments

I thank John Moriarty and the Ramsey County Parks Department for access to the Tamarack Nature Center, Madeleine Linck and the Three Rivers Park District for access to the Carver Park Reserve, and Daniel Rhode and the Minnesota Department of Natural Resources for access to the Carlos Avery Wildlife Management Area. Laura Corcoran, Laura Cremin, Michael Kuczynski, Reid Olsen, Kasen Riemersma, Nathan Rogers, Eli Swanson, Sandra Tekmen and Alejandro Velez provided helpful assistance in collecting and testing frogs. Alejandro Velez provided helpful comments on an earlier version of the manuscript. This research adhered to the Association for the Study of Animal Behaviour/Animal Behavior Society *Guidelines for the Use of Animals in Research*, the legal requirements of the U.S.A. and all institutional guidelines, and was approved by the University of Minnesota's IACUC (No. 0510A76966) on 14 November 2006. Animal collections were made under Special Permit 14278 from the Minnesota Department of Natural Resources. This work was supported by a Grant-in-Aid from the Dean of the Graduate School of the University of Minnesota and NIDCD DC008396.

References

- Amrhein, V., Kunc, H. P. & Naguib, M. 2004. Non-territorial nightingales prospect territories during the dawn chorus. *Proceedings of the Royal Society of London, Series B*, **271** (Supplement), S167–S169.
- Arbogast, T. L., Mason, C. R. & Kidd, G. 2002. The effect of spatial separation on informational and energetic masking of speech. *Journal of the Acoustical Society of America*, **112**, 2086–2098.
- Aubin, T. & Jouventin, P. 1998. Cocktail-party effect in king penguin colonies. *Proceedings of the Royal Society of London Series B*, **265**, 1665–1673.
- Aubin, T. & Jouventin, P. 2002. How to vocally identify kin in a crowd: the penguin model. *Advances in the Study of Behavior*, **31**, 243–277.
- Balcombe, J. P. 1990. Vocal recognition of pups by mother Mexican free-tailed bats, *Tadarida brasiliensis mexicana*. *Animal Behaviour*, **39**, 960–966.
- Balcombe, J. P. & McCracken, G. F. 1992. Vocal recognition in Mexican free-tailed bats: do pups recognize mothers? *Animal Behaviour*, **43**, 79–87.
- Bee, M. A. 2007. Sound source segregation in grey treefrogs: spatial release from masking by the sound of a chorus. *Animal Behaviour*, **74**, 549–558.
- Bee, M. A. & Micheyl, C. In press. The 'cocktail party problem': what is it, how can it be solved and why should animal behaviorists study it? *Journal of Comparative Psychology*.
- Bee, M. A. & Swanson, E. M. 2007. Auditory masking of anuran advertisement calls by road traffic noise. *Animal Behaviour*, **74**, 1765–1776.
- Bronkhorst, A. W. 2000. The cocktail party phenomenon: a review of research on speech intelligibility in multiple-talker conditions. *Acustica*, **86**, 117–128.
- Bronkhorst, A. W. & Plomp, R. 1992. Effect of multiple speech-like maskers on binaural speech recognition in normal and impaired hearing. *Journal of the Acoustical Society of America*, **92**, 3132–3139.
- Brumm, H. & Slabbekoorn, H. 2005. Acoustic communication in noise. *Advances in the Study of Behavior*, **35**, 151–209.
- Brush, J. S. & Narins, P. M. 1989. Chorus dynamics of a neotropical amphibian assemblage: comparison of computer-simulation and natural behavior. *Animal Behaviour*, **37**, 33–44.
- Capranica, R. R. & Moffat, J. M. 1983. Neurobehavioral correlates of sound communication in anurans. In: *Advances in Vertebrate Neuroethology* (Ed. by J. P. Ewert, R. R. Capranica & D. J. Ingle), pp. 701–730. New York: Plenum.
- Chapman, C. J. & Johnstone, A. D. F. 1974. Some auditory discrimination experiments on marine fish. *Journal of Experimental Biology*, **61**, 521–528.
- Cherry, E. C. 1953. Some experiments on the recognition of speech, with one and with two ears. *Journal of the Acoustical Society of America*, **25**, 975–979.
- Culling, J. F., Hawley, M. L. & Litovsky, R. Y. 2004. The role of head-induced interaural time and level differences in the speech reception threshold for multiple interfering sound sources. *Journal of the Acoustical Society of America*, **116**, 1057–1065.
- Dent, M. L., Larsen, O. N. & Dooling, R. J. 1997. Free-field binaural unmasking in budgerigars (*Melopsittacus undulatus*). *Behavioral Neuroscience*, **111**, 590–598.
- Ehret, G. & Gerhardt, H. C. 1980. Auditory masking and effects of noise on responses of the green treefrog (*Hyla cinerea*) to synthetic mating calls. *Journal of Comparative Physiology A*, **141**, 13–18.
- Feng, A. S. & Ratnam, R. 2000. Neural basis of hearing in real-world situations. *Annual Review of Psychology*, **51**, 699–725.
- Feng, A. S. & Schul, J. 2006. Sound processing in real-world environments. In: *Hearing and Sound Communication in Amphibians* (Ed. by P. A. Narins, A. S. Feng, R. R. Fay & A. N. Popper), pp. 323–350. New York: Springer.
- Gerhardt, H. C. 1992. Conducting playback experiments and interpreting their results. In: *Playback and Studies of Animal Communication: Problems and Prospects*. NATO Advanced Research Workshop (Ed. by P. K. McGregor), pp. 59–77. New York: Plenum.

- Gerhardt, H. C. 1994. Reproductive character displacement of female mate choice in the grey treefrog *Hyla chrysoscelis*. *Animal Behaviour*, **47**, 959–969.
- Gerhardt, H. C. 1995. Phonotaxis in female frogs and toads: execution and design of experiments. In: *Methods in Comparative Psychoacoustics* (Ed. by G. M. Klump, R. J. Dooling, R. R. Fay & W. C. Stebbins), pp. 209–220. Basel: Birkhäuser-Verlag.
- Gerhardt, H. C. 2001. Acoustic communication in two groups of closely related treefrogs. *Advances in the Study of Behavior*, **30**, 99–167.
- Gerhardt, H. C. 2005. Acoustic spectral preferences in two cryptic species of grey treefrogs: implications for mate choice and sensory mechanisms. *Animal Behaviour*, **70**, 39–48.
- Gerhardt, H. C. & Bee, M. A. 2006. Recognition and localization of acoustic signals. In: *Hearing and Sound Communication in Amphibians* (Ed. by P. M. Narins, A. S. Feng, R. R. Fay & A. N. Popper), pp. 113–146. New York: Springer.
- Gerhardt, H. C. & Huber, F. 2002. *Acoustic Communication in Insects and Anurans: Common Problems and Diverse Solutions*. Chicago: University of Chicago Press.
- Gerhardt, H. C. & Klump, G. M. 1988. Masking of acoustic signals by the chorus background noise in the green treefrog: a limitation on mate choice. *Animal Behaviour*, **36**, 1247–1249.
- Gerhardt, H. C., Diekamp, B. & Ptacek, M. 1989. Inter-male spacing in choruses of the spring peeper, *Pseudacris (Hyla) crucifer*. *Animal Behaviour*, **38**, 1012–1024.
- Gerhardt, H. C., Ptacek, M. B., Barnett, L. & Torke, K. G. 1994. Hybridization in the diploid-tetraploid treefrogs *Hyla chrysoscelis* and *Hyla versicolor*. *Copeia*, **1994**, 51–59.
- Gorissen, L. & Eens, M. 2004. Interactive communication between male and female great tits (*Parus major*) during the dawn chorus. *Auk*, **121**, 184–191.
- Greenfield, M. D. 2002. *Signalers and Receivers*. New York: Oxford University Press.
- Greenfield, M. D. 2005. Mechanisms and evolution of communal sexual displays in arthropods and anurans. *Advances in the Study of Behavior*, **35**, 1–62.
- Hawkins, A. D. & Sand, O. 1977. Directional hearing in the median vertical plane by the cod. *Journal of Comparative Physiology*, **122**, 1–8.
- Hawley, M. L., Litovsky, R. Y. & Culling, J. F. 2004. The benefit of binaural hearing in a cocktail party: effect of location and type of interferer. *Journal of the Acoustical Society of America*, **115**, 833–843.
- Hine, J. E., Martin, R. L. & Moore, D. R. 1994. Free-field binaural unmasking in ferrets. *Behavioral Neuroscience*, **108**, 196–205.
- Holloway, A. K., Cannatella, D. C., Gerhardt, H. C. & Hillis, D. M. 2006. Polyploids with different origins and ancestors form a single sexual polyploid species. *American Naturalist*, **167**, E88–E101.
- Holt, M. M. & Schusterman, R. J. 2007. Spatial release from masking of aerial tones in pinnipeds. *Journal of the Acoustical Society of America*, **121**, 1219–1225.
- Hulse, S. H. 2002. Auditory scene analysis in animal communication. *Advances in the Study of Behavior*, **31**, 163–200.
- Hulse, S. H., MacDougall-Shackleton, S. A. & Wisniewski, A. B. 1997. Auditory scene analysis by songbirds: stream segregation of birdsong by European starlings (*Sturnus vulgaris*). *Journal of Comparative Psychology*, **111**, 3–13.
- Ison, J. R. & Agrawal, P. 1998. The effect of spatial separation of signal and noise on masking in the free field as a function of signal frequency and age in the mouse. *Journal of the Acoustical Society of America*, **104**, 1689–1695.
- Klump, G. M. 1996. Bird communication in the noisy world. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsmas & E. H. Miller), pp. 321–338. Ithaca, New York: Cornell University Press.
- Langemann, U. & Klump, G. M. 2005. Perception and acoustic communication networks. In: *Animal Communication Networks* (Ed. by P. K. McGregor), pp. 451–480. Cambridge: Cambridge University Press.
- Lin, W. Y. & Feng, A. S. 2001. Free-field unmasking response characteristics of frog auditory nerve fibers: comparison with the responses of midbrain auditory neurons. *Journal of Comparative Physiology A*, **187**, 699–712.
- Lin, W. Y. & Feng, A. S. 2003. GABA is involved in spatial unmasking in the frog auditory midbrain. *Journal of Neuroscience*, **23**, 8143–8151.
- Liu, W. C. 2004. The effect of neighbours and females on dawn and daytime singing behaviours by male chipping sparrows. *Animal Behaviour*, **68**, 39–44.
- Murphy, C. G. & Floyd, S. B. 2005. The effect of call amplitude on male spacing in choruses of barking treefrogs, *Hyla gratiosa*. *Animal Behaviour*, **69**, 419–426.
- Murphy, C. G. & Gerhardt, H. C. 2002. Mate sampling by female barking treefrogs (*Hyla gratiosa*). *Behavioral Ecology*, **13**, 472–480.
- Narins, P. M. & Zelick, R. 1988. The effects of noise on auditory processing and behavior in amphibians. In: *The Evolution of the Amphibian Auditory System* (Ed. by B. Fritzsche, M. J. Ryan, W. Wilczynski, T. E. Hetherington & W. Walkowiak), pp. 511–536. New York: J. Wiley.
- Ptacek, M. B., Gerhardt, H. C. & Sage, R. D. 1994. Speciation by polyploidy in treefrogs: multiple origins of the tetraploid, *Hyla versicolor*. *Evolution*, **48**, 898–908.
- Ratnam, R. & Feng, A. S. 1998. Detection of auditory signals by frog inferior collicular neurons in the presence of spatially separated noise. *Journal of Neurophysiology*, **80**, 2848–2859.
- Ronacher, B. & Hoffmann, C. 2003. Influence of amplitude modulated noise on the recognition of communication signals in the grasshopper *Chorthippus biguttulus*. *Journal of Comparative Physiology A*, **189**, 419–425.
- Ryan, M. J. 2001. *Anuran Communication*. Washington, D.C.: Smithsonian Institution Press.
- Ryan, M. J. & Rand, A. S. 2001. Feature weighting in signal recognition and discrimination by túngara frogs. In: *Anuran Communication* (Ed. by M. J. Ryan), pp. 86–101. Washington, D.C.: Smithsonian Institution Press.
- Schwartz, J. J. & Gerhardt, H. C. 1989. Spatially mediated release from auditory masking in an anuran amphibian. *Journal of Comparative Physiology A*, **166**, 37–41.
- Schwartz, J. J. & Gerhardt, H. C. 1995. Directionality of the auditory system and call pattern recognition during acoustic interference in the gray treefrog, *Hyla versicolor*. *Auditory Neuroscience*, **1**, 195–206.
- Schwartz, J. J., Buchanan, B. W. & Gerhardt, H. C. 2001. Female mate choice in the gray treefrog (*Hyla versicolor*) in three experimental environments. *Behavioral Ecology and Sociobiology*, **49**, 443–455.
- Schwartz, J. J., Buchanan, B. W. & Gerhardt, H. C. 2002. Acoustic interactions among male gray treefrogs, *Hyla versicolor*, in a chorus setting. *Behavioral Ecology and Sociobiology*, **53**, 9–19.
- Schwartz, J. J., Huth, K. & Hutchin, T. 2004. How long do females really listen? Assessment time for female mate choice in the grey treefrog, *Hyla versicolor*. *Animal Behaviour*, **68**, 533–540.
- Shinn-Cunningham, B. G., Ihlefeld, A., Satyavarta & Larson, E. 2005. Bottom-up and top-down influences on spatial unmasking. *Acta Acustica United with Acustica*, **91**, 967–979.
- Simmons, A. M. & Moss, C. F. 1995. Reflect modification: a tool for assessing basic auditory function in anuran amphibians. In: *Methods in Comparative Psychoacoustics* (Ed. by G. M. Klump, R. J. Dooling, R. R. Fay & W. C. Stebbins), pp. 197–208. Basel: Birkhäuser-Verlag.

- Sokal, R. R. & Rohlf, F. J.** 1995. *Biometry*. New York: W. H. Freeman.
- Swanson, E. M., Tekmen, S. M. & Bee, M. A.** 2007. Do female anurans exploit inadvertent social information to locate breeding aggregations? *Canadian Journal of Zoology*, **85**, 921–932.
- Turnbull, S. D.** 1994. Changes in masked thresholds of a harbor seal (*Phoca vitulina*) associated with angular separation of signal and noise sources. *Canadian Journal of Zoology*, **72**, 1863–1866.
- Wells, K. D. & Schwartz, J. J.** 2006. The behavioral ecology of anuran communication. In: *Hearing and Sound Communication in Amphibians* (Ed. by P. M. Narins, A. S. Feng, R. R. Fay & A. N. Popper), pp. 44–86. New York: Springer.
- Wollerman, L.** 1999. Acoustic interference limits call detection in a Neotropical frog *Hyla ebraccata*. *Animal Behaviour*, **57**, 529–536.
- Wollerman, L. & Wiley, R. H.** 2002. Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog. *Animal Behaviour*, **63**, 15–22.
- Zar, J. H.** 1999. *Biostatistical Analysis*. Upper Saddle River, New Jersey: Prentice Hall.