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FORMS OF CALL OVERLAP AND THEIR IMPACT ON ADVERTISEMENT CALL ATTRACTIVENESS TO FEMALES OF THE GRAY TREEFROG, *HYLA VERSICOLOR*

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ABSTRACT

Male gray treefrogs, *Hyla versicolor*, advertise for females in choruses in which calls often overlap. Previous research has demonstrated that such acoustic interference among conspecifics can impair the ability of a male to attract a mate. However, the stimulus set used in those studies was quite limited. Here we performed single-speaker and two-speaker tests of phonotaxis with female *Hyla versicolor* to explore the impact of different degrees and forms of call overlap on the relative attractiveness of male signals. We found that: (1) overlapped calls are recognized as acceptable signals by females, although they are less attractive than calls that are not overlapped; (2) the relative phase of the overlapping calls matters. When calls were time-shifted by 50% of their pulse-period (180 degree offset), attractiveness of overlapped calls was reduced relative to non-overlapped calls as much as it would be by a reduction in intensity of about 12 dB SPL or a drop in call duration of between one third to one half. A 90 degree phase offset was equivalent to a 3 dB drop in SPL; (3) partial call overlap may not impair call attractiveness if one third or less of the call is overlapped; (4) if the ending portion of a call is overlapped it may impair attractiveness less than if previous segments of a call are obscured; (5) if most (three fourths or more) of a male's calls are free of interference, overlap of his remaining calls does not significantly impair his attractiveness.

Keywords: communication, treefrogs, chorusing, acoustic interference, female choice

INTRODUCTION

Males of many species of frogs advertise vocally for mates in dense assemblages (Zelick *et al*. 1999; Gerhardt & Huber 2002). Although this behaviour can improve opportunities for the exchange of information

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(Grafe 2005; Wells & Schwartz 2006), the ability to communicate may also be impaired. On the one hand, the ability of females to assess potential mates may be improved because of the propinquity of males and elevated levels of male-male vocal competition (Wiley & Poston 1996). On the other hand, background noise levels can be high due to the advertisement displays of conspecific and heterospecific individuals (Narins & Zelick 1988; Gerhardt & Schwartz 1995; Schwartz 2001) and so the detection, localization, discrimination, and interpretation of acoustic signals may be compromised (Schwartz & Gerhardt 1989; Wollerman & Wiley 2002a, b).

In anuran species in which calls are organized into pulses, the fine-temporal structure of the call may be obscured from receivers during acoustic interference. These call features can play a critical role in call recognition and discrimination (Gerhardt & Huber 2002 for review) and so interference may affect receiver responses to calls. For example, females of the grey treefrog, *Hyla versicolor* discriminated against conspecific calls that were subjected to overlap in favour of non-overlapping calls in arena-based tests of phonotaxis (Schwartz 1987; Schwartz *et al*. 2001). Males that exhibited lower levels of call overlap were also approached by females more often than other males during tests of phonotaxis in an artificial pond (Schwartz *et al*. 2001). In *H. versicolor*, the pulse and pulse interval duration as well as the shape of pulses within calls are “static” features (sensu Gerhardt 1991) and, in areas of syntopy they mediate discrimination (Gerhardt & Doherty 1988; Schul & Bush 2002; Gerhardt 2005) by females of conspecific males from males of the putative diploid progenitor of *H. versicolor*, *H. chrysoscelis* (Ptacek *et al*. 1994). Call overlap also may impact on male-male communication and inter-male spacing because it reduces the ability of males to judge the amplitude of neighbours’ calls (Narins 1992). For example, males responded with aggressive calls at lower playback intensities to stimulus calls timed to alternate with their own calls than they did to stimulus calls timed to overlap their own calls (Schwartz 1987). High levels of call overlap are a reality in choruses of *H. versicolor*. Male timing of calls is ineffective in reducing call overlap in all but pair-wise vocal interactions, and acoustic interference among males increases with chorus size (Schwartz *et al*. 2002). Moreover, selective attention resulting in reduced signal overlap of nearest neighbours, as has been reported in some species of insects and frogs (Brush & Narins 1989; Schwartz 1993; Snedden *et al*. 1998; Greenfield & Rand 2000), seems to be absent in gray treefrogs (Schwartz *et al*. 2002).

In the arena-based phonotaxis tests described above with *H. versicolor*, the entire duration of overlapping signals was subject to interference. In addition, unless precisely in phase, the overlapping calls were always time shifted by 50% of the pulse period (i.e. 180 degrees out of phase) such that the constituent pulses of the two calls alternated rather then overlapped. However, in natural choruses of this species because of the dynamic and non-uniform distribution in time and space of callers and their vocalizations (Wells & Taigen 1986; Schwartz *et al*. 2001; Schwartz personal observations), the calls of males are subject to overlap to varying degrees. Therefore, neither the phase relationship nor the amount of overlap nor the amplitude of interfering calls is a constant. In the experiments described herein, we have explored the degree to which partial overlap, phase and relative amplitude impact on the attractiveness to females of interfering conspecific advertisement calls. Our findings significantly augment those obtained in earlier studies employing a much more limited stimulus set and also complement those from our recent work on the consequences of call overlap between *H. versicolor* and *H. chrysoscelis* (Marshall *et al*. in press).

METHODS

We performed our experiments at the University of Missouri (Columbia, Mo., USA; UMC) and Pace University (Pleasantville, NY, USA; PU). For tests at the former venue, we obtained gravid females of *Hyla versicolor* from a pond at the Thomas Baskett Wildlife Area in Boone County, Missouri during May and June of 2000-2003. For tests at the latter venue, we obtained females at a pond in the Blue Mountain Reservation in Peekskill, NY during May and June of 2004. Females were captured during the evening in amplexus, separated from their mates and held until testing (usually the following day) in plastic containers either in an ice-filled cooler or refrigerator in order to postpone oviposition. Following tests of phonotaxis, we released females at their site of capture. The handling and use of study animals were approved by the University of Missouri IACUC (Protocol No. 1910) and the Pace University IACUC (Protocol No. 8).

The testing environments at UMC and PU were similar. At both UMC and PU, we conducted playbacks in a temperature-controlled (~ 20 ^{0} C) chamber floored with waterproof low-pile carpet and walled with echo-attenuating acoustic foam (for UMC see Gerhardt 1994 for additional details; PU: chamber inner dimensions – 255 cm long × 225 cm wide × 195 cm high, Ultimate Walk-Ins, Inc., foam – Silent Source TFW-4). The testing chambers were illuminated in the infrared, and we observed female phonotaxis on a video monitor nearby following their release (via an externally-controlled pulley) from an acoustically-transparent cage on the floor of each arena.

Our tests utilized synthetic stimulus advertisement calls (8-bits per sample; 20 KHz sampling rate) that were modelled after the natural calls of *H. versicolor* calling at our testing temperature (Schwartz, unpublished software). Synthetic calls (50 ms rise time) consisted of trains of individual pulses (20 ms linear rise, 5 ms concave down fall; pulse duty cycle = 50%) with each pulse formed by combining and then shaping a 2200 Hz and a 1100 (- 6 dB relative amplitude) Hz sinusoid (0^o phase offset). Earlier work has demonstrated that females do not discriminate between natural and synthetic analogues of advertisement calls (Gerhardt 1978). The temporal relationships of our stimuli were adjusted using sound editing features of our playback software packages. At UMC, the calls were delivered from a computer running under DOS and using sound output software and hardware from SiliconSoft Inc. (San Jose, California). Amplified calls (Nagra DSM) were delivered via ADS 200-C speakers and sound amplitudes adjusted using a Larson-Davis Precision Integrating Sound Level Meter (Model 800B; flat-weighting, fast response). At PU, we used a Commodore Amiga 600 computer running FutureSound software, a Realistic SA-10 amplifier and Realistic Minimus 0.3 speakers. We adjusted sound amplitudes with a Gen Rad 1982 Precision Sound Level meter (flat weighting, fast response). In all tests, stimulus rates were 15/min per speaker.

We performed phonotaxis tests using both two-speaker and single-speaker designs with overlapped signals originating from a single source. Thus we simulated a situation in which fine temporal, spectral and directional information could not enhance the call-recognition abilities of our test subjects (Schwartz & Gerhardt 1995). In two-speaker choice tests, stimulus calls were broadcast in alternating fashion from speakers at opposites sides of the arena (1 m from the central release point) and test subjects displayed a discrimination by moving to one of the speakers. Each female was exposed to the call stimuli for 30 seconds prior to release from the cage and a choice recorded if she came within 10 cm of a speaker within ten minutes. To assess the strength of preferences for particular stimuli, we sequentially completed a series of tests in which (usually) the preferred stimulus was selectively attenuated (typically in decrements of 3 dB) relative to the stimulus that was not preferred until and often beyond the level at which no significant discrimination was first evident using a two-tailed binomial test. We conducted single-speaker tests at MU within a circular arena (diameter 1.5 m) bordered with acoustically transparent hardware cloth (height = 25 cm) inside the larger testing chamber described above. The face of the playback speaker was located just outside the arena facing the release point at the centre of the arena. Females were given five presentations of the stimulus prior to release and allowed ten minutes to reach the speaker. In these tests, the time of approach to the source of an experimental stimulus was compared to the time of approach to the source of a standard (i.e. control) stimulus (a non-overlapped 18-pulse call). We tested each female with the standard stimulus immediately before and after exposure to the experimental stimulus. We used a "phonotaxis score"

(Bush *et al*. 2002) to quantify the attractive strength of call stimuli in the single-speaker tests. We calculated the score by forming the ratio of the average approach time to the standard stimulus and the approach time to the experimental stimulus (T_{av}stand / Texp) for each female. A phonotaxis score of one indicates an equivalent response to the experimental stimulus and the standard call, a score greater than one indicates that the experimental stimulus was more attractive than the standard, and a score of less than one indicates that the experimental stimulus was less attractive than the standard. Subjects that did not reach the broadcast speaker within 10 min were to receive a score of "0". However, all females made contact with the speaker within the allotted time period.

Experiments 1, 2

In Experiment 1, we offered females a choice between an 18-pulse "standard" call and a pair of overlapped calls (Figure 1, upper pair of overlapped calls). The pulses of the overlapped calls were timed so that they alternated (i.e. they were 180 degrees out-of-phase and thus time-shifted by 50% of the pulse period; pulse duration = 25 ms, pulse period = 50 ms). In this experiment, and those described below, initial playback levels were 85 dB SPL (fast root-mean-square, dB re 20 µPa) and the levels from the speakers were adjusted using non-overlapped calls so that the SPL of each of the overlapped calls would equal (unless otherwise noted; see Experiments 3 and 4 below) that of the non-overlapped calls presented from the opposite speaker. In successive tests we lowered the relative amplitude of the non-overlapped stimulus. Because the amplitude of a call at a receiver declines with increased separation of signaller and receiver (6 dB decrease with each doubling of separation assuming spherical sound spread and no excess attenuation), the experiment allowed us to estimate the relative distance over which the calls of a non-overlapped male would be more attractive than those of an overlapped male.

Experiment 2 was identical to Experiment 1 except that that the overlapped calls were phase shifted by 90 rather than 180 degrees (Figure 1, lower pair of overlapped calls).

Experiments 3, 4

Experiments 3 and 4 were identical to Experiments 1 and 2 except that we lowered the relative intensity of the leading overlapped call in successive tests (Figure 2). Thus the experiments allowed us to estimate the relative distance over which an overlapping male could impact negatively on the ability of another male to attract a female.

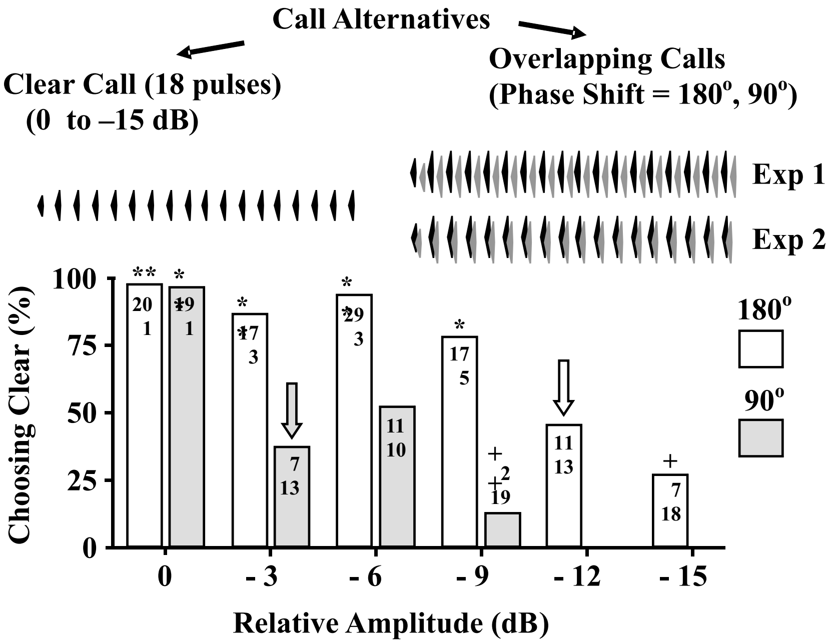

Figure 1. Top. Representation of call alternatives offered to females in Experiment 1 and 2. Overlapped calls (180° phase offset for Experiment 1, 90° phase offset for Experiment 2) are shown in black and gray and vertically out of alignment so that they may be more easily distinguished. Bottom. Choice results of females in Experiment 1 and 2 (number of females choosing each alternative given inside or above bins). 'Relative Amplitude' gives the attenuation of the clear call (dB re. to each overlapped call). Arrow indicates relative amplitude at which females first failed to show significant discrimination for the clear call. Asterisks or pluses indicate a significant preference for the clear call (* $p < 0.05$, ** $p < 0.01$, two-tailed binomial test) or overlapped call (+ $p < 0.05$, ++ $p < 0.01$).

Experiment 5

In Experiment 5, we used single speaker presentations to time the approach of females to overlapped calls with either a 180 degree or 90 degree phase shift. Calls were broadcast at 85 dB SPL at the release point of the females. Time of approach of the same females to single-speaker broadcasts of non-overlapped calls were used to calculate phonotaxis scores.

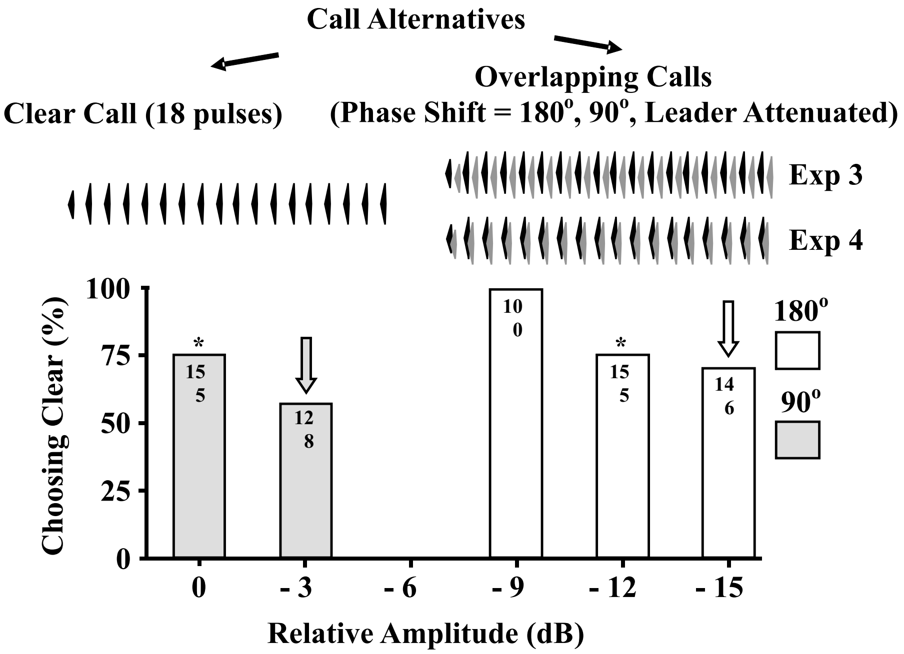

Figure 2. Top. Representation of call alternatives offered to females in Experiment 3 and 4. Bottom. Choice results of females in Experiment 3 and 4. 'Relative Amplitude' gives the attenuation of the leading overlapped call (dB re. to the trailing overlapped call illustrated in grey). Additional symbols are as described for Figure 1.

Experiment 6

In Experiment 6, we systematically varied the duration of the overlapping stimulus (16 – 4 pulses long) in order to examine whether there was a threshold degree of overlap that resulted in females discriminating against overlapped calls (180 degree pulse phase shift). Thus the number of normal interpulse intervals in the 18-pulse overlapped call was varied in the successive tests (range: 2-14 intervals). In these tests, the uninterrupted intervals of the 18-pulse call were present at the leading portion of the call and the pulses of the shorter overlapping call trailed those of the 18-pulse call such that the last pulse of the shorter call fell after the last pulse of the longer call (Figure 3). The partially overlapped calls were tested against an 18-pulse call free of overlap.

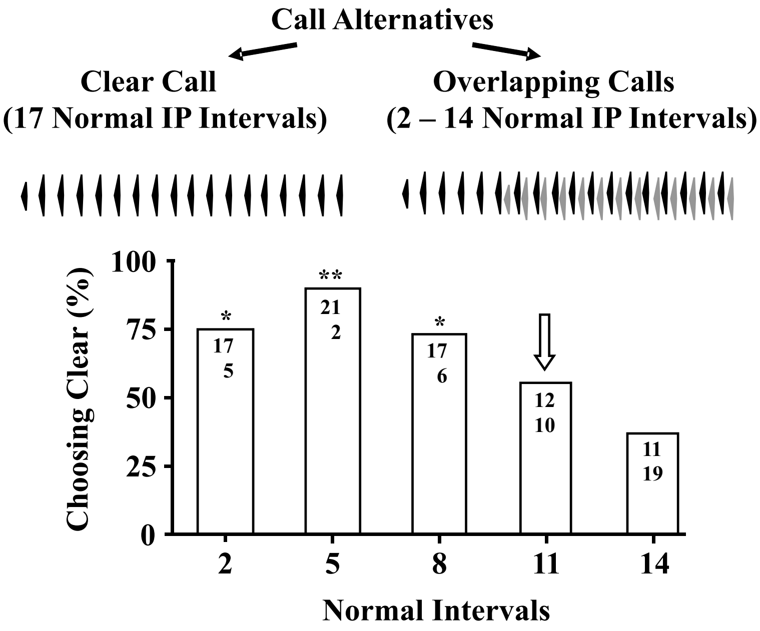

Figure 3. Top. Representation of call alternatives offered to females in Experiment 6. Bottom. Choice results of females in Experiment 6. 'Normal Intervals' gives the number of uninterrupted interpulse intervals in the leading overlapped call. Additional symbols are as described for Figure 1.

Experiment 7

In Experiment 7, we offered females a choice between two overlapped calls (180 degree phase shift) and a non-overlapped stimulus of variable duration (6, 9, 12, and 15 pulses in successive tests; Figure 4). This experiment provided another way to gauge the relative attractiveness of the alternative stimuli because females discriminate in favour of longer relative to shorter calls (Gerhardt 2001; Schwartz *et al.* 2001).

Experiment 8

In Experiment 8, we offered females a choice between a non-overlapped 18-pulse call and one in which we varied the section (beginning, middle, end) that was overlapped (180 degree pulse phase shift). The shorter overlapping call was nine pulses in length and timed so that there were eight normal interpulse intervals in the longer overlapped call (Figure 5).

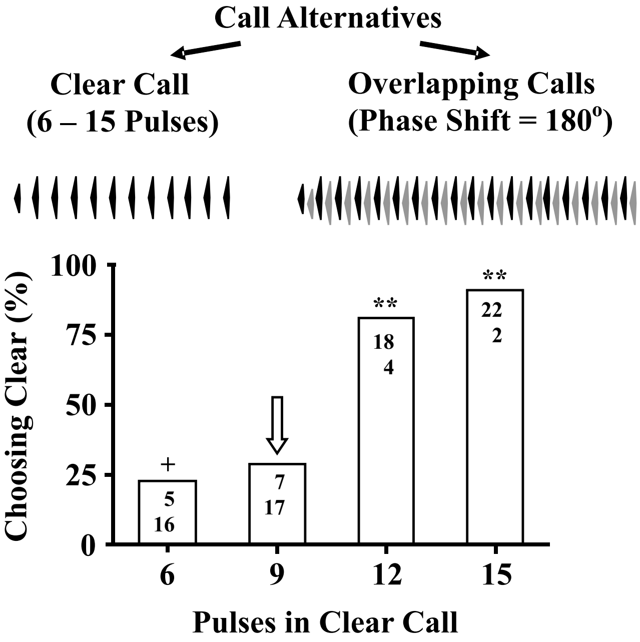

Figure 4. Top. Representation of call alternatives offered to females in Experiment 7. Bottom. Choice results of females in Experiment 7. 'Pulses in Clear Call' gives the number of pulses in the non-overlapped call. Additional symbols are as described for Figure 1.

Experiment 9

Experiment 9 was conducted to test whether overlap (180 degree pulse phase shift) at the beginning or the end of a call was more detrimental. Alternative call stimuli were overlapped by a 9-pulse call such that there remained eight normal interpulse intervals in each.

Experiment 10

Experiment 10 was identical to Experiment 8 except that the non-overlapped call was only nine pulses long. Thus, in each of three tests, we allowed females to choose between non-overlapped calls and partially overlapped calls with equal numbers of normal interpulse intervals (i.e. 8 intervals; Figure 6).

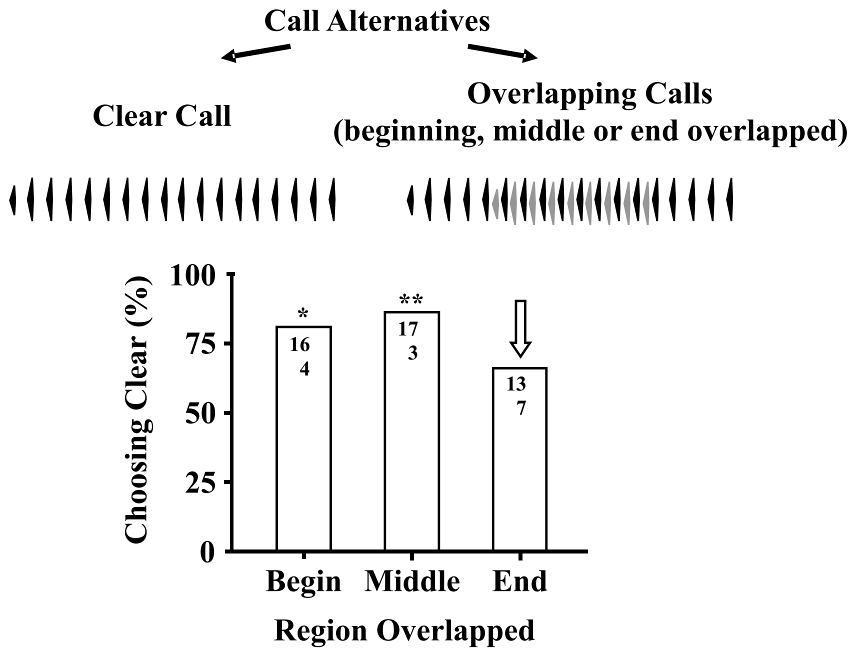

Figure 5. Top. Representation of call alternatives offered to females in Experiment 8. Bottom. Choice results of females in Experiment 8. 'Region Overlapped' gives the section of the 18-pulse call alternative that was overlapped by a 9-pulse call. Additional symbols are as described for Figure 1.

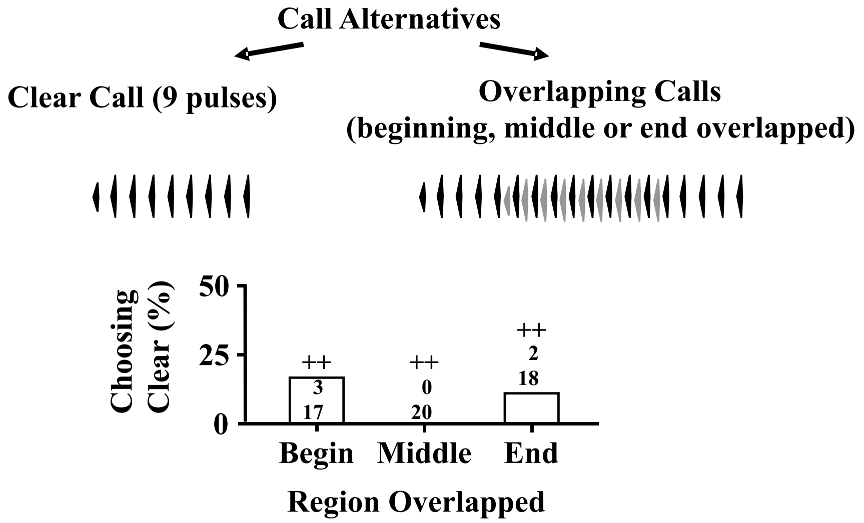

Figure 6. Top. Representation of call alternatives offered to females in Experiment 10. Bottom. Choice results of females in Experiment 10. 'Region Overlapped' gives the section of the 18-pulse call alternative that was overlapped by a 9-pulse call. Additional symbols are as described for Figure 1.

Experiment 11

In the final experiment, we offered females a choice between non-overlapped calls and trains of calls in which just a subset of calls were overlapped (full overlap, 180 degree phase shift). In one test, every other call in the latter stimulus was overlapped. In a second test, only 25% of the calls were overlapped (Figure 7).

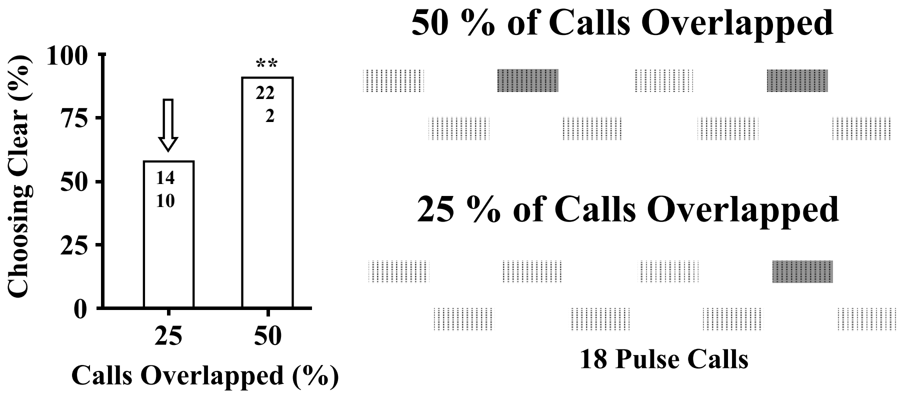

Figure 7. Right. Representation of call alternatives offered to females in Experiment 11 when 50% (top right) of calls were overlapped (shaded calls) or when 25% (bottom right) of calls were overlapped. Left. Choice results of females in Experiment 11. Additional symbols are as described for Figure 1.

RESULTS

Experiments 1-4

When overlapping calls were time-shifted by 50% of the pulse period (180 degree phase shift), a speaker broadcasting non-overlapping calls had to be attenuated by 12 dB to abolish discrimination against the overlapping calls and by 15 dB to reverse the pattern of discrimination (Figure 1). However, when the overlapping calls were time shifted by 25% of the pulse period (90 degree phase shift) such that the pulses only partially overlapped, discrimination was abolished following just a 3 dB reduction in amplitude of the non-overlapping calls. Discrimination in favour of the overlapping calls occurred at a relative amplitude difference of 9 dB (Figure 1).

When we attenuated one of the overlapping calls, it was necessary to lower its relative amplitude by 15 dB to eliminate discrimination when the phase shift was 180 degrees (Figure 2). When the phase shift between the overlapping calls was just 90 degrees, a relative amplitude drop of just 3 dB elicited a loss of discrimination (Figure 2). Note that in these experiments, further attenuation of overlapping calls would not be expected to reverse the preference because at best the alternative stimuli would be indistinguishable.

Experiment 5

When we presented calls from a single speaker in order to calculate phonotaxis scores we found that (1) irrespective of their phase shift (90, 180 degrees), overlapped calls were inherently attractive to females. That is, all females approached the source of overlapped calls in both tests. However, females moved more slowly to overlapping calls than they did to non-overlapping calls when the former were phase shifted by 180 degrees (mean phonotaxis score = 0.69, median = 0.64, n = 10 females). When the phase shift was only 90 degrees, females actually approached the overlapping calls more rapidly than they did to the non-overlapping calls (mean phonotaxis score = 1.44, median = 1.34, n = 9; Wilcoxon 2-sample test: Z = 2.74, p = 0.0062).

Experiments 6 and 7

When we varied the amount of overlap, discrimination in favour of the non-overlapping calls was eliminated when approximately 2 / 3 of the interpulse intervals within the longer overlapped calls were normal (i.e. 11 intervals; Figure 3). When we varied the duration of the non-overlapping calls (Experiment 7, Figure 4), discrimination against overlapping 18-pulse calls was eliminated when the alternative had been reduced in length to just nine pulses.

Experiments 8 – 10

Tests in which we offered females a choice between non-overlapped calls and calls in which different sections had been overlapped revealed significant discrimination against calls with the leading or middle sections overlapped (Figure 5). Although there was a bias against calls with the trailing section overlapped, this result was not significant. Note that in Experiment 6, we obtained a significant result using call alternatives identical to these (clear call versus overlapped call with eight normal intervals; Figure 3). Therefore, we performed Experiment 9 to confirm the suggested asymmetry in relative attractiveness in overlapped calls obtained in Experiment 8. When call alternatives were subjected to overlap in either their leading or trailing sections, females discriminated against the former stimulus type (7: 16; p = 0.047, 1-tailed binomial test). We also found that when non-overlapped and overlapped calls had equivalent numbers of clear pulses and intervals, independent of the region of overlap, discrimination occurred in favour of the overlapped call (Experiment 10, Figure 6).

Experiment 11

Relative to non-overlapped trains of calls, females discriminated against trains of calls when 50% of them were overlapped (full overlap, 180 degree phase shift) but not when only 25% were subjected to interference (Figure 7).

DISCUSSION

Our results confirm those of earlier studies (Schwartz 1987; Schwartz & Gerhardt 1995; Schwartz *et al.* 2001) indicating that call overlap between males of *H. versicolor* reduces the relative attractiveness of advertisement calls. However, not all forms of overlap are equally deleterious. For example, when the pulses within overlapped calls alternate with a 180 degree phase shift and so would be expected to alter a female's perception of a call's pulse interval duration (and double the pulse duty cycle), attractiveness is reduced relative to "clear" calls by as much as a drop in amplitude of about 12 dB (equivalent to a quadrupling of male-female separation; Experiment 1) or a drop in call duration by 1/3 – 1/2 (i.e. between 6 – 9 pulses, Experiment 7) for an 18-pulse call. When the pulses within overlapped calls themselves overlap (90 degree phase shift), the effect is equivalent to a drop of no more than 3 dB in relative amplitude of a clear call (equivalent to an increase in signaller-receiver separation of ~ 1.4 times). Although the second timing pattern disrupts the perceived shape of a call's pulses, it shortens the interval between pulses to a lesser degree. Recent work has highlighted the importance of pulse and pulse interval duration, acting independently, in call recognition of *H. versicolor* (Schul & Bush 2002). Female responses during the single speaker tests indicate that, in the absence of non-overlapped calls, overlapped calls remain a potent stimulus for female phonotaxis. In fact, although calls that were phase shifted by 180 degrees retarded female approach speed, calls that were shifted by 90 degrees actually accelerated females. This curious result is not inconsistent with results of a recent study that mapped out the call “recognition space” of *H. versicolor* by presenting females with calls in which pulse duration and interpulse interval were independently varied. Schul & Bush (2002) found that females of *H. versicolor* exhibit a fairly broad phonotactic response field bounded by pulse durations of about 12 and 75 ms and interpulse intervals of 0 (abutting pulses) and about 60 ms (see their Figure 2b). Moreover, some stimuli with anomalous pulse durations and intervals elicited elevated phonotaxis scores.

When the call alternatives were a non-overlapped call and overlapped calls for which one had been attenuated, our results supported the conclusion that a 180 degree phase shift among overlapping males is more problematic than a shift of 90 degrees. In the former case, a drop in relative amplitude of 15 dB for the leading overlapped call was necessary to eliminate discrimination as opposed to just 3 dB in the latter case. A decline of 15 dB is equivalent to an increase in signaller-receiver separation of ~ 5.6 times.

Partial call overlap does not entirely eliminate the attractive attributes of the overlapped call section (Experiment 10) and may not even impair call attractiveness if one third or less of the call is overlapped (Experiment 6). However, the region of a call which is obscured differentially impacts on a call’s relative attractiveness. The results from Experiments 8 and 9 indicate that overlap of the trailing half of a call can be less detrimental than overlap of the leading or middle section of a call. We can only speculate as to why this should be the case. If neurons that are selective for the temporal features of calls (e.g. Edwards *et al.* 2002) have a brief refractory period following exposure to inappropriately timed call elements, as would occur during overlap, this would provide a possible mechanistic explanation. This refractory period would harmlessly extend into an intercall interval when a call’s lagging section is disrupted but extend into the remaining portion of a call when a call’s earlier sections are overlapped. Elevated firing rates of auditory neurons coupled with superior coding of fine-temporal call features (Klump *et al.* 2004) during the leading portion of a call may also be relevant. This might render the trailing sections of a call less potent phonotactic stimuli than leading sections. In any event, it is interesting to note that our results are consistent with those of Gerhardt & Schul (1999) who found that the leading portion of the call of *H. versicolor* is probably more important in transmitting information on pulse shape than the trailing portion of a call (see their figure 5). A more influential role of the leading rather than lagging portion of a call is also suggested by both neurophysiological (Klump *et al.* 2004) and behavioural data (Klump & Gerhardt 1992) on females of *H. cinerea*. However, we also must note that choice tests in which females of *H. versicolor* were offered alternatives that partially overlapped (inter-call delays of 225-675 ms) revealed no leader preference (Marshall 2004).

A particularly interesting finding was that females appear to ignore call overlap as long as at least 75% of calls are not obscured by such interference (Experiment 11). This result and those of Experiment 6 suggest that if a sufficient percent of perceived call elements fall within species-specific ranges, females discount call anomalies. However, female behaviour may to some extent depend on the precise nature of signal disruption. In dense choruses, where high levels of call overlap are both common and probably unavoidable by males (Schwartz *et al*. 2002), such tolerant behaviour could facilitate assessment of male vocal performance by females.

Within a chorus, intermale call timing relationships are dynamic and it is likely that the calls of individual males suffer a wide range of call overlap patterns during an evening. This statement is consistent with call timing records obtained in choruses of males monitored within an artificial pond (Schwartz *et al*., 2002). However, given that a female's mate choice decision is likely based on acoustic events that occur in only the last minute or two prior to pairing (Schwartz *et al*. 2004), the results of this study indicate that the precise form of call overlap during such brief periods could have an impact on a male's mating success. Nevertheless, unless some males are more adept than others in timing their calls in a beneficial (or less problematic) way, such situations will be fortuitous and so inter-male asymmetries should diminish over longer periods of time. Thus, on average, the location of males relative to sources of interference (see Schwartz & Gerhardt 1989, 1995) may exert a more profound effect on male reproductive success than call timing in a dense assemblage of *H. versicolor*. Because acoustic differences among overlapping signals can help receivers group signals into separate auditory streams (Bregman 1990; Bee & Klump 2005), inter-male differences in call frequency and pulse structure might also influence the ability of female gray treefrogs to discriminate among overlapped calls and assess the relative attractiveness of particular males during call overlap. Our experiments, which utilized overlapping calls that were identical with respect to spectral and fine-temporal attributes, were designed to simulate a worst case scenario in which such information could not be used by the female auditory system to help segregate the interfering signals. Assessing the importance of these factors to communication in choruses remains an important goal of future research.

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