

Interference Risk and the Function of Dynamic Shifts in Calling in the Gray Treefrog (*Hyla versicolor*)

Joshua J. Schwartz, Robert Brown, Sarah Turner, Kola Dushaj, and Marisol Castano
Pace University

Male gray treefrogs call to attract females under challenging acoustic conditions. At higher chorus densities, there is considerable background noise and a good chance that a male's calls will often be overlapped by calls of other individuals. Call overlap may reduce the probability of mating because females prefer calls with internal pulse structure that is not obscured. With increases in acoustic stimulation, males lengthen call duration while simultaneously reducing call rate such that "pulse effort" changes little. In our study, we tested the "interference risk hypothesis." This proposes that males change call duration so that, on average, there will be a sufficient number of pulses and interpulse intervals clear of acoustic interference per call to attract a female. However, female choice experiments employing call alternatives of different durations, rates, intensity levels, and degrees of call overlap refuted this hypothesis. Our results leave open the possibilities that the dynamic shift in the two components of pulse effort are related to the problem of call detection in a noisy environment or are responses by males to the perceived threat of competition for females.

Keywords: frog, acoustic, communication, interference

Hyla versicolor is a relatively common treefrog in the north-eastern and central United States. In evenings in the late spring and early summer males call at or near wetland venues from trees, bushes, shorelines, and the water surface. Although advertising males may be diffusely distributed, in some areas that evidently possess a suite of appropriate habitat characteristics, aggregations can be quite dense (e.g., 100 + males per hectare) and generate high levels of background noise. The advertisement call consists of a series of individual pulses, the structure, number, and timing of which have been shown to be critically important in eliciting positive phonotaxis (i.e., movement to a sound source) from gravid females (Gerhardt, 2001). Such receptive females are typically found at breeding aggregations at considerably lower densities than are advertising males. Accordingly, males at choruses usually face extremely high levels of competition for potential mates. This is not an exceptional situation for many species of treefrogs (Gerhardt & Huber, 2002), and the calling behavior of males responds to the dynamic changes in the acoustic environment in ways that may help males maintain their relative attractiveness (Wells & Schwartz, 2006).

In *H. versicolor*, males respond to calls of neighboring males by appending pulses to their calls. An extensive experimental data set has demonstrated that females find longer calls (i.e., those with more pulses) a more potent stimulus for phonotaxis than shorter calls (see Figure 15 in Gerhardt, 2001). This preference can, in some larval environments, confer a genetic benefit on the offspring of females choosing males using longer calls (Welch, 2003; Welch, Semlitsch, & Gerhardt, 1998). Intriguingly, when males lengthen calls they simultaneously reduce the rate at which the calls are delivered such that the average long-term rate at which pulses are produced (pulse effort) remains about the same (Schwartz, Buchanan, & Gerhardt, 2002; Wells & Taigen, 1986). A question that remains unresolved is why male gray treefrogs shift the two components of pulse effort (call rate and pulses per call) in opposite directions in response to acoustic changes that accompany changes in chorus size.

Wells and Taigen (1986) speculated that at equal pulse efforts, producing longer calls could utilize more glycogen (relative to lipid) than producing shorter calls and so confer a degree of honesty on the signaling pattern. Their observations that males giving longer calls ceased calling sooner in the evening were consistent with the hypothesis. However, Grafe's (1997) measurements of respiratory quotients in calling males were inconsistent with the hypothesis. The Wells and Taigen hypothesis that, at equal pulse efforts, longer calls should be more attractive to female gray treefrogs than shorter calls was subsequently confirmed in two-stimulus choice tests performed in an acoustic chamber (Gerhardt, Dyson, & Tanner, 1996; Klump & Gerhardt, 1987; Schwartz, Buchanan, & Gerhardt, 2001). However, in eight-speaker choice tests conducted at the edge of a pond there was little discrimination against all but the shortest call alternative (a six-pulse call), and choice tests with calling males in an artificial pond indicated that call duration accounted for less than 10% of the variance in male "mating success" (Schwartz et al., 2002).

Joshua J. Schwartz, Robert Brown, Sarah Turner, Kola Dushaj, and Marisol Castano, Department of Biology and Health Sciences, Pace University.

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Correspondence concerning this article should be addressed to Joshua J. Schwartz, Department of Biology and Health Sciences, Pace University, 861 Bedford Road, Pleasantville, NY 10570. E-mail: jschwartz2@pace.edu

Moreover, during experimental manipulations of choruses in the enclosed pond, males changed their call durations but maintained their relative rank in a hierarchy based on call duration. Thus in smaller choruses, males gave shorter calls than they were capable of giving and so sacrificed a higher position in the hierarchy. This behavior seems inconsistent with the notion that adjustments by males in their call duration and rate are directly associated with the inherent attractiveness of calls and threat of being out competed by other males.

Based on the above findings, Schwartz et al. (2001, 2002) proposed that shifts in call duration and rate were tied to the problem posed for communication by environments replete with potential sources of acoustic interference and thus increased risk of call overlap among neighboring males. Some other solutions to the problem of call overlap do not appear to be utilized by gray treefrogs. Although a pair of males may alternate their calls, with increases in chorus size and density the chance that such a strategy is entirely successful declines (Schwartz et al., 2002). Moreover, selective timing of signals (Brush & Narins, 1989; Greenfield & Rand, 2000; Schwartz, 1993; Snedden, Greenfield, & Jang, 1998) whereby males shift their call-timing in response to their closest neighbors while allowing their calls to overlap those of more distant callers and thus less potent sources of acoustic interference, appears to be absent. In fact, males of *H. versicolor* were more likely to overlap the calls of closest neighbors than those of more distant individuals (Schwartz et al., 2002). Finally, work in progress in our laboratory indicates that females seem incapable of significant temporal induction (Warren, 1999), a process that could enable their brains to “reconstruct” segments of calls that were masked or otherwise acoustically degraded by overlapping calls.

The “interference risk hypothesis” (IRH) posits that males of *H. versicolor* change their calling in a way that significantly improves the chances that within individual calls there will be a sufficient number of call pulses and interpulse intervals clear of interference to attract a female (see Figure 8 in Schwartz et al., 2001). Essential to the argument is that overlapped calls are less attractive than nonoverlapped calls and very short calls are particularly unattractive relative to longer calls. Both of these requirements are met. In addition to the significant bias against only the shortest calls in the pond-based choice test (Schwartz et al., 2001), in two-stimulus choice tests, the strength of the female bias against short calls increased dramatically for the shortest calls (Gerhardt, Tanner, Corrigan, & Walton, 2000). Female gray treefrogs also exhibit strong discrimination against advertisement calls that are overlapped by the calls of other males relative to nonoverlapped calls in arena-based choice tests (Marshall, Schwartz, & Gerhardt, 2006; Schwartz, 1987; Schwartz & Marshall, 2006). Moreover, choice experiments with calling males in the artificial pond demonstrated that males with fewer overlapped call pulses had a significantly greater chance of attracting a female than other males (Schwartz et al., 2001). The degradation of important fine-temporal attributes of the call (pulse shape, pulse duration, interpulse interval) accompanying overlap likely accounts for much of the observed bias (Marshall et al., 2006; Schwartz & Gerhardt, 1995; Schwartz & Marshall, 2006).

In a preliminary test of the IRH, Schwartz et al. (2001) examined levels of call overlap in the enclosed artificial pond. In support of the hypothesis, in pairwise comparisons of males in the same choruses who had nearly equivalent (within about 10%; \bar{x} =

4.6%) pulse efforts but very different call durations (> 25%; \bar{x} = 57.1%), the male producing longer calls had a greater total number of nonoverlapped pulses in his calls (beyond a six pulse putative attractiveness threshold) than the male producing shorter calls significantly more often (19:7; p = .029, two-tailed binomial test). The goal of the present study was to determine whether patterns of female discrimination are consistent with expectations of the IRH using a set of choice stimuli and acoustic background environments specifically designed to rigorously test the hypothesis.

Method

During evenings in May and June of 2005, we obtained amplexed females of *H. versicolor* at a pond in the Blue Mountain Reservation in Peekskill, New York. The females were separated from their mates, returned to our laboratory, and held until testing (usually the next day) in plastic containers in a refrigerator (1 to 2°C) to postpone oviposition. We returned each group of frogs to the pond within a day of completing our tests with them. We conducted phonotaxis experiments within a temperature-controlled (~ 20°C) chamber floored with waterproof low-pile carpet and walled with echo-attenuating acoustic foam at the Pleasantville, New York campus of Pace University (chamber inner dimensions: 255 cm long × 225 cm wide × 195 cm high, Ultimate Walk-Ins, Inc., Monsey, NY, USA foam: Silent Source TFW-4). The “choice arena” was illuminated using infrared LEDs (part #1165OP, Marlin P. Jones & Assoc. Inc., part #11665OP) and the movements of the females monitored from outside the chamber with a closed circuit video security system (item #49-2511, #49-2513; Radio Shack, Fort Worth, TX, USA). During each test, females were held briefly in and then released (via an externally controlled pulley) from an acoustically transparent cage on the floor of the arena.

We used a Commodore Amiga 600 computer (Commodore Business Machines; West Chester, PA, USA) running Future-Sound software (Applied Visions, Cambridge, MA, USA), a Realistic SA-10 amplifier (RadioShack, Fort Worth, TX, USA) and RCA PRO-X33AV speakers (AudioVox Electronics Corp., Hauppauge, NY, USA) to broadcast synthetic stimulus calls (synthesized using custom software written by Schwartz; eight-bits per sample; 20 kHz, low-pass filtered at ~ 6 kHz) that were modeled after the natural calls of *H. versicolor* (Schwartz, unpublished software). We adjusted sound amplitudes with a calibrated Gen Rad, 1982 Precision Sound Level meter (IET Labs; Westbury, NY, USA; flat weighting, fast RMS response). These adjustments were made using broadcasts of calls identical in form and duration (i.e., 18-pulse calls without overlapped sections) from both speakers so that we could be sure that the amplitude of the pulsed sections of our test stimuli would have equal Sound Pressure Levels (SPLs). SPL for calls was 85 dB SPL (re 20 μPa) unless otherwise indicated (relative attenuation values are given below). In all tests, we equalized the pulse efforts of the call alternatives offered from two speakers. Stimulus calls were broadcast in alternating fashion from speakers on the floor at opposite sides of the arena (1 m from the central release point) and each subject was exposed to the call stimuli for 60 s prior to lifting of the release cage. Females displayed discrimination by moving to within 10 cm of one of the speakers within 10 min or less.

In some tests, using a second Amiga 600 and Realistic SA-10 amplifier, we simultaneously broadcast (Realistic Minimus 0.3 speaker) either calls or filtered noise from an elevation 63 cm above the release point. This elevated arrangement was chosen so that test females would orient to the floor speakers. The SPL was adjusted at the release point to 83 dB (flat weighting, fast RMS response). The software used to broadcast the sounds was written by the senior author and was designed so that one could specify the amount of broadcast time that would be occupied by calls and intervening silent intercall intervals. The duration of each call (or noise burst) and subsequent interval were individually chosen using a random number routine (a different starting "seed" was used to begin each playback; Knuth's algorithm, see pp. 212–213 in Press, Flannery, Teukolsky, & Vetterling, 1988) with the restriction that either (a) both durations fell within those of calls 12 to 24 pulses long (inclusive durations: 575 ms to 1,175 ms) yielding a long-term sequence in which calls (or noise) filled 50% of the broadcast time or (b) calls were 12 to 24 pulses long and intervals half as long yielding a long-term sequence in which calls filled ~ 67% of the broadcast time. Therefore, these broadcasts simulated the calling activity of other neighboring individuals in a chorus that, on average, would overlap either 50% or ~ 67% of the pulses broadcast from the floor speakers. In the tests of Schwartz et al. (2002) within an artificial pond, these levels of overlap are similar to those that occurred in choruses of four and eight males, respectively. Because the temporal relationship between the calls from the floor and ceiling speakers was not static, the amount and timing of the overlap between the background calls and call alternatives varied as would be expected in a natural chorus (Schwartz et al., 2002).

Experiment 1

In these tests, females were presented with call alternatives of either (a) 12 pulses and 24 pulses or (b) 6 pulses and 12 pulses. The shorter call was presented at twice the rate of the longer call so that the stimulus alternatives had identical pulse efforts (e.g., 240 pulses per min for stimulus pair "a"). Each of the longer pulsed calls was timed to fall midway between two shorter pulsed calls so that there was no acoustic interference between these call alternatives. In tests with the 12-pulse and 24-pulse calls, randomly timed calls from above the arena occupied 50% of the broadcast time. Therefore, as indicated previously, by chance, equal proportions of the pulses in the 12-pulse and 24-pulse calls were eventually overlapped. However, unobscured segments of the long call were, on average, twice the length of those of the short call. Based on previous data (e.g., Klump & Gerhardt, 1987; Schwartz et al., 2001), we predicted that females would discriminate in favor of the long calls. To determine the strength of this preference, the relative intensity of the 24-pulse call was to be lowered (in 3 dB steps) until the preference was abolished.

We also ran two tests without the overlapping calls to obtain results to which the results of the aforementioned tests could be compared. In one of these tests, we used 12- and 24-pulse calls. In the second test, we broadcast 6- and 12-pulse calls. Again, we determined the relative intensity difference that abolished the preference for the longer call in each of these tests. Because females have previously shown very strong discrimination in choice tests against extremely short calls (e.g., 6-pulses long), we

anticipated that the intensity difference that abolished the preference should be greater in the second test than the first (see Gerhardt et al., 2000). The IRH predicts that when the interfering chorus was broadcast, the strength of the preference against the 12-pulse call when offered against the 24-pulse call should be comparable to the strength of the preference against the 6-pulse call in the second test without the interfering chorus.

Experiment 2

In this and subsequent experiments we made modifications to the acoustic background and or the call alternatives to increase our confidence in the generality of the results we had obtained with Experiment 1. Our results were such that we did not need to run additional tests to determine preference strength as described above. In Experiment 2, we offered females a choice between 12- and 24-pulse calls and doubled the ratio of calls relative to silent intercall intervals from above the arena. Accordingly, on average, ~ 67% of the pulses of the short and long call alternatives would be overlapped. We expected that this would more heavily skew any female bias for the 24-pulse call.

Experiment 3

In Experiment 3, we again offered females a choice between 12- and 24-pulse calls. However, rather than broadcast calls from above, we used bursts of filtered noise and silent interburst intervals following protocol "a" above (50% noise:50% silent). The noise was computer-generated white noise that had been digitally filtered to resemble the spectrum of a chorus of gray treefrogs (spectral peaks at 1100 and 2200 Hz; 10 dB bandwidth ~ 750 Hz for each).

Experiment 4

In Experiment 4, we gave females a choice between long and short calls both without background calls as well as with background calls with the two calls:silent ratios (i.e., 50:50, 67:33). However, in the three tests we conducted, the call alternatives were 20-pulse calls and 10-pulse calls (pulse effort of each alternative = 200 pulses per min).

Experiment 5

One test of Experiment 5 was run without and one test with background calls broadcast from above the arena (50% calls:50% silent). However, in these two tests, we offered females alternatives with a less extreme difference in call pulse number (18-pulse calls vs. 24-pulse calls). To equalize the pulse efforts of the call alternatives (240 pulses per min), the call period of the 24-pulse call was set to 6 s and the call period of the short call to 4.5 s. Therefore, the relative timing of the long and short call shifted during the course of playback and the calls often overlapped to varying degrees. These tests, then, not only provided for a more conservative test of the IRH (because any long-call preferences should be less pronounced) but also offered a dynamic pattern of call timing between the call alternatives. Both of these characteristics of the tests simulated situations that females in actual choruses would be expected to frequently encounter (Schwartz et al., 2002).

Experiment 6

In a final test, we gave females a choice between 12-pulse calls and 24-pulse calls (pulse effort = 240 pulses per min). However, rather than create a dynamic pattern of call overlap using call broadcasts from above the arena, we incorporated the call overlap within the individual call alternatives. The pulses of the first 50% of each call were interleaved with pulses of either a 12-pulse call (for the 24-pulse alternative) or a 6-pulse call (for the 12-pulse alternative). This was the least conservative test of the IRH (which predicts a strong preference for the 24-pulse call) because the alternatives are always overlapped and overlap occurs in the section of the call most likely to negatively influence female attraction (Gerhardt & Schul, 1999; Schwartz & Marshall, 2006).

Results

Experiments 1 to 3

Without background calls, females exhibited significant discrimination in favor of the 24-pulse call relative to a 12-pulse call (see Table 1). However discrimination was absent when the 24-pulse call was attenuated by 3 dB. When we offered females a choice between a 6-pulse and a 12-pulse call, females discriminated in favor of the longer call until the intensity of the longer call was lowered by 6 dB.

In contrast to the predictions of the IRH, with the background calls broadcast from above, females either failed to discriminate in favor of the longer call (calls:silent = 50:50) or discriminated in favor of the shorter call (Experiment 2, calls:silent = 67:33). Females did not discriminate when we broadcast noise bursts from above (Experiment 3, noise:silent = 50:50). Rather, as with the overlapping call broadcasts, there was a response bias favoring the 12-pulse call alternative.

Experiments 4 to 6

In Experiment 4, in which we offered females a choice between 10-pulse and 20-pulse calls, subjects failed to significantly discriminate with or without background calls (see Table 2). Signif-

Table 1
Choice Results of Females in Experiments 1 to 3

Overlap	Relative amplitude ^a	Females' choices (Short Call:Long Call)	<i>p</i>
12 pulse versus 24 pulse			
No	0	9:21	.043
No	3	17:13	<i>ns</i>
Calls (50:50)	0	19:11	<i>ns</i>
Calls (67:33)	0	21:9	.043
Noise (50:50)	0	21:11	<i>ns</i>
6 pulse versus 12 pulse			
No	0	5:15	.041
No	3	9:21	.043
No	6	17:13	<i>ns</i>

Note. The *p* values are for a two-tailed binomial test. Overlap = whether the alternatives were offered without (no) or with broadcasts of background calls (calls:silent ratio) or noise bursts (noise:silent ratio); amplitude = attenuation of the longer call alternative; *ns* = not significant.

^aGiven in dB.

Table 2
Choice Results of Females in Experiments 4 to 6

Overlap	Females' choices (Short Call:Long Call)	<i>p</i>
10 pulse versus 20 pulse ^a		
No	11:19	<i>ns</i>
Calls (50:50)	12:18	<i>ns</i>
Calls (67:33)	12:18	<i>ns</i>
18 pulse versus 24 pulse ^a		
No	18:12	<i>ns</i>
Calls (50:50)	15:15	<i>ns</i>
12-pulse versus 24-pulse ^a		
Fixed	18:12	<i>ns</i>

Note. The *p* values are for a two-tailed binomial test. Call alternatives were presented at equal intensity. Overlap = whether the alternatives were offered without (no) or with broadcasts of calls (calls:silent ratio) or incorporated a fixed overlapped section; *ns* = not significant.

^aCall alternatives: 10-pulse versus 20-pulse call (Experiment 4); 18-pulse versus 24-pulse call (Experiment 5); 12-pulse versus 24-pulse call (Experiment 6).

icant discrimination was also absent in Experiment 5 (18-pulse vs. 24-pulse calls with and without background calls) and Experiment 6 (12-pulse vs. 24-pulse calls each with fixed 50% overlap).

DISCUSSION

We had hypothesized that by lengthening calls under more competitive and thus noisier conditions, males could maintain the relative attractiveness of their advertisement signals. Specifically, males would add pulses to calls to compensate for the increased probability that critical fine-temporal information would be obscured by the vocalizations of others. Without such adjustments in vocal behavior, acoustic overlap could result in the perception by females of individual calls lacking a sufficient number of attractive elements to elicit phonotaxis.

To test the IRH, we offered females call alternatives of different duration with and without broadcasting sources of acoustic interference. In most tests, the interference was in the form of bouts of calling or filtered noise alternating with blocks of silence to produce a pattern of stimulus overlap comparable to that occurring in a natural chorus. Previous results had demonstrated that discrimination against a shorter call alternative is accentuated when call alternatives are selected from the short end of the distribution of male call durations (Gerhardt et al., 2000). Therefore, we predicted that we would observe an increased bias against the shorter call alternatives in the presence of acoustic interference. To obtain data on bias strength for comparison, we tested females with shorter call alternatives in the absence of acoustic interference. Selective attenuation of the preferred stimulus alternatives was used to gauge the strength of discrimination.

Our results constitute a solid refutation of the IRH. Under no circumstances did we observe an increase in preference strength or significant bias for a longer call alternative in the presence of acoustic interference. We are extremely confident in this finding because we employed a range of call alternatives under conditions of interference: 24-pulse versus 12-pulse calls, 20-pulse versus 10-pulse calls, and 24-pulse versus 18-pulse calls. Moreover, in our tests we used two types of acoustic background that had

different average probabilities of overlapping with the call alternatives (calls:silent ratios of 50:50, 67:33, noise:silent ratio of 50:50) as well as 24- and 12-pulse calls with a fixed and overlapping timing relationship. According to the IRH, interfering backgrounds with a more extreme (67:33) ratio of calling to quiet intervals should have elicited a stronger bias in favor of longer calls than either the 50:50 backgrounds or the choice tests using call alternatives half as long without an acoustic background. This did not happen. Most surprisingly, females actually showed an increased likelihood of approaching the source of the shorter call alternative when calls were subjected to the possibility of overlap. This unexpected result was even statistically significant using 24-versus 12-pulse call alternatives with background calls presented in a calls:silent ratio of 67:33. A potential criticism is that most of these tests, although they may resemble the situation in the wild, are too conservative because over the relatively brief time windows during which different females may have compared call alternatives, we do not know the actual pattern of overlap with the background calls or noise—although we can calculate confidence intervals for particular time intervals (or for the number (n) of call broadcasts from a floor speaker; CI around the mean expected overlap of 50% in Experiment 1, $T_{test} = \pm (\sqrt{1/24}) \times (Z/\sqrt{n})$, assuming independence of call overlap proportions). For this reason, in particular, we conducted Experiment 6 in which half of each call alternative was always overlapped. Again, the results refuted the IRH.

Our data also confirm that the female preference for long calls is quite weak (and stimulus specific) when choice alternatives are of equal pulse effort. In the case of 24-pulse versus 12-pulse calls, the female preference for the longer call was eliminated when it was attenuated by just 3 dB. Consistent with our qualitative expectation based on earlier work (Gerhardt et al., 2000), when offered 12-pulse versus 6-pulse calls it was necessary to attenuate the longer call to a greater degree (6 dB) to eliminate significant discrimination by females. Gerhardt et al. found a mean preference strength of 2 dB for a 27-pulse call paired against an 18-pulse call but a mean preference strength of 7 dB for a 12-pulse call paired against an 8-pulse call (unequal call effort stimuli). In the tests using the other pairs of call alternatives (24-pulse vs. 18-pulse calls, 20-pulse vs. 10-pulse calls), females failed to discriminate. Using alternative stimuli with nearly equal pulse efforts, Klump and Gerhardt (1987) also found that females discriminated in favor of longer calls under some circumstances (24-pulse vs. 12-pulse calls) but not others (18-pulse vs. 12-pulse calls). In the latter case, the relative timing of the call alternatives shifted and so there were periods of overlap and alternation as was the case with our test using 24-pulse and 18-pulse calls. In contrast, Schwartz et al. (2001) found a significant preference for 18-pulse as opposed to 12-pulse calls using a static timing relationship with partial overlap among call alternatives. It therefore seems that choice results with females in such tests are idiosyncratic, depending on the pulse disparity among call alternatives, the nature and stability of call timing as well as the presence of background calls or noise.

Our study leaves unresolved the question of why males shift call duration and call rate in opposite directions as their acoustic environment changes. It is possible that using longer calls facilitates call detection under conditions of especially high ambient noise (Brumm & Slabbekoorn, 2005). Our playback test using filtered noise did not explicitly test this hypothesis because our

noise background was structured into relatively brief on and off periods and was presented at a background intensity that was insufficient to mask the call alternatives. The viability of this idea depends on the integration time of the female's auditory system because the vulnerability of calls to masking is mediated, in part, by the time period over which the female auditory system sums sound energy (Brumm & Slabbekoorn, 2005). Tests underway may provide a behavioral estimate of the maximum integration time for female gray treefrogs as well as assess the susceptibility of calls of different duration to masking.

Another hypothesis proposes that call duration and rate are adjusted by males in response to the perceived threat of competition for females (Wells & Taigen, 1986). Although the preference for longer calls under conditions of equal pulse effort are conditional and, even then, relatively weak, it may be that on average males' chances of attracting a mate are improved by dynamically modulating call rate and pulse number. The tendency for males to maintain their rank among neighbors for call duration seems, on its face, to be inconsistent with the male competition hypothesis. However, the threat of enhanced vocal competition by high ranked males may explain this behavior. According to this scenario, if a male who is not top-ranked fails to drop pulses from his calls in response to a decline in chorus size (or background noise), other, formerly higher ranking males, detect this and shift back to giving calls longer than the "cheater." Thus a cheater might gain only a momentary and insignificant, advantage. A test of whether such a constraint operates is planned.

Finally, shifts in call duration and call rate may have communicative significance in male-male communication. Perhaps there is an agonistic message conveyed in advertisement calls that increases with duration. According to this hypothesis, addition of pulses to calls represents a graded response that may ultimately transition to aggressive calls. Although males of *H. versicolor* append pulses to their calls in response to broadcasts of individual calls simulating an individual neighbor, re-examination of data from an earlier study (Schwartz, 1987) indicated that there was only a small effect of stimulus intensity or stimulus duration on response duration. However, the effect of stimulus duration on aggressive call responses was not explicitly tested. Accordingly, considerable work remains before one of most intriguing aspects of the communication system of this fascinating anuran is understood.

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