

The Sounds of Silence as an Alarm Cue in Túngara Frogs, *Physalaemus pustulosus*

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ABSTRACT

In many species males vocally advertise for mates in choruses and these choruses serve as acoustic beacons to conspecific females as well as to eavesdropping predators and parasites. Chorusing will often cease in response to disturbances, such as the presence of predators. In some cases the cessation is so rapid and over such a large area that it seems improbable that males are all responding directly to the same local disturbance. Here, we demonstrate experimentally in Neotropical túngara frogs, *Physalaemus pustulosus*, that the cessation of calling by males spreads rapidly through the chorus. The cessation of chorusing in response to the cessation of playbacks of three calling males is more effective in inducing chorus cessation than is the cessation of one male calling. When three males are calling, the cessation of complex calls is more effective in inducing chorus cessation than simple calls. There is no main effect on whether the final call of the male is complete or is interrupted. We thus conclude that the sudden lack of signals—the ‘sounds of silence’—becomes an alarm cue that can explain the rapid cessation of choruses that are common in many chorusing species.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: anuran; chorus; communication; Panama; predation; public information; sexual selection.

IN MANY ANIMAL SPECIES MALES GATHER INTO CONGREGATIONS during the breeding season to advertise acoustically for mates. Such choruses are especially common in insects and anurans (Ryan 2001, Gerhardt & Huber 2002, Greenfield 2002, Grafe 2005, Wells 2007). These choruses act as acoustic beacons to conspecific females, but they also often attract eavesdroppers, predators, and parasites, who prey upon the calling males (Cade 1975, 1984; Tuttle & Ryan 1981; Zuk 1992; Hedrick & Dill 1993; Zuk & Kolluru 1998; Zuk *et al.* 2006). In response to the presence of predators and parasites (Ryan *et al.* 1981, Tuttle *et al.* 1982, Spangler 1984, Jennions & Backwell 1992, Luchzkovich *et al.* 2000, Zuk *et al.* 2006, Phelps *et al.* 2007), as well as other disturbances (Sun & Narins 2005), chorusing ceases, thus momentarily depriving eavesdroppers of acoustic cues to localize callers. In frog-eating bats, for example, bats are less able to localize calls of male túngara frogs that are discontinued as the bat approaches compared with calls that continue to be broadcast (Page & Ryan 2008). Curio (1976) referred to this phenomenon as adaptive silence. Call cessation also has consequences for male mating success because females engaged in mate choice are also influenced by call cessation (Akre & Ryan 2010, Baugh & Ryan 2010).

In this study, we consider cessation of calling that is known to occur as an alarm response to predators as a cue that induces the same alarm response in others. Specifically, we test the hypothesis that the alarm response (the cessation of calling) of some callers serves as an alarm cue for others which in turn results in the same alarm response (the cessation of calling). In numerous taxa animals detect predators vicariously through alarm signals or cues of others

(*e.g.*, Sherman 1977, Seyfarth *et al.* 1980, Templeton *et al.* 2005). We address this same question about túngara frog choruses, but we ask if it is the absence of a behavior, ‘the sounds of silence,’ rather than the presence of one that induces the alarm response. Although there are other reasons why a frog might stop calling, such as vocal fatigue (Schwartz 1991), we already know from extensive field observations (Ryan *et al.* 1981) and controlled experiments (Tuttle *et al.* 1982) that male túngara frogs stop calling and show additional changes in behavioral posture in response to the presence of frog-eating bats. Here we explore the details as to how this occurs at the level of chorus cessation.

The túngara frog, *Physalaemus pustulosus*, is a leptodactylid frog common throughout much of the lowland tropical forests in Middle America, a small part of Colombia and throughout the llanos of Venezuela (Ryan *et al.* 1996). The acoustic communication system of this species has been the focus of numerous studies (reviewed in: Ryan 1985, Ryan & Rand 2003, Ryan in press), including how the sexual communication system is influenced by a predator, the frog-eating bat, *Trachops cirrhosus* (Tuttle & Ryan 1981; Ryan *et al.* 1981, 1982; Page & Ryan 2008), and parasites, the blood-sucking fly species of the genus *Corethrella* (Bernal *et al.* 2006).

The basic mating call of the male túngara frog is a whine, a frequency sweep with a fundamental frequency that extends from *ca* 1000 to 400 Hz in 350 ms. Males can produce whines alone or they can add up to seven chucks to a whine (Ryan 1985, Bernal *et al.* 2007). The chuck has *ca* 15 harmonics, is *ca* 45 ms in duration, and has a dominant frequency of *ca* 2500 Hz. Females are attracted preferentially to calls with chucks (complex calls) compared with calls without chucks (simple calls).

Túngara frogs can call in small groups of just a few males, or they can be found in much larger choruses of hundreds (Ryan *et al.*

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1981). When males are in such large choruses, we can be certain that they do not attend to the calls of all males whose locations can span tens of meters (Marsh *et al.* 2000, Greenfield & Rand 2001). Experiments suggest that males vocally interact with a neighborhood of nearby males and that these neighborhoods overlap (Greenfield & Rand 2001). Thus what we perceive as a chorus is probably an emergent property of overlapping social networks.

Many naturalists who encounter frog choruses are often struck by the near simultaneity in which the cacophony of boisterous males advertising for sex suddenly ceases. Túngara frogs cease calling in response to the approach of frog-eating bats, as well as other disturbances, and they adjust the severity of their behavioral response based on the perceived predation risk, increasing the duration of noncalling behavior when predation risk is perceived to be high (Tuttle *et al.* 1982, Jennions & Backwell 1992, Phelps *et al.* 2007). They detect the bats using visual cues as males fail to respond to a bat model on moonless nights with heavy cloud cover but respond quickly if there is light overhead. In many cases, however, a chorus seems to cease almost simultaneously in situations in which it is clear that all of the frogs did not observe the approaching bat (Ryan 1985, Fig. 8.1, p. 166). Males give no alarm or warning calls in response to perceived predation. Thus this observation suggests that males attend to the calling of neighbors and when neighbors cease calling the result is call cessation, and this pattern spreads through the chorus in rapid succession. Lahanas (1995) and Phelps *et al.* (2007) showed that male túngara frogs are more likely to resume calling if they hear other male túngara frogs call, and Phelps *et al.* (2007) showed that a decrease in latency to calling also can be induced by the calling of sympatric heterospecific males. Here we test the hypothesis that call cessation by a male in the chorus, 'the sounds of silence,' can spread quickly through a chorus thus causing a rapid cessation of chorusing over a greater area.

METHODS

GENERAL METHODS.—We tested the general hypothesis that sounds of silence are perceived as an alarm cue. We designed experiments to test the specific prediction that a male ceases calling in response to his neighbor doing the same thing. In addition, we tested the hypothesis that calling cessation is dependent on three states: (1) the number of males calling, (2) the complexity of the calls in the chorus, and (3) the nature of the final call heard.

We predicted that cessation of calling by more males compared with fewer males would be more likely to induce chorus cessation. The cessation of more males calling could indicate greater predation risk or it could be more likely to be detected by other frogs.

We predicted that the cessation of complex calls will be more alerting to calling males than the cessation of simple calls. This could be for at least two reasons. Males increase and decrease chuck number in a stepwise manner (Bernal *et al.* 2009). In an analysis of call bouts by 92 males, 48 percent of the bouts ended with a simple whine, 41 percent with a whine and one chuck, and 11 percent with a whine and two chucks. No bouts ended with a whine and three chucks. As it is more common for a male to cease calling after a whine then after a whine and three chucks, the latter signifies a

more unusual condition, such as the presence of a predator. Another reason for a greater effect of complex calls vs. simple calls is that the transition from a call to no-call is a larger change in acoustic energy when a whine with chucks rather than a whine without chucks is the last call, and thus might be more likely to be detected by males. Our study was not designed to determine which of these causes might be responsible for an increased alerting effect of chorus cessation.

We also predicted that a chorus that ends with an interrupted call will be more alerting than a chorus that ends with a completed call. Our extensive field observations suggest that males always complete a call unless they are startled or forced to cease calling by a predator. We also used a call that was truncated but the truncated section was replaced with noise. If there was a difference in response to a full call vs. a truncated call, the call with noise would allow us to determine if the effect resulted from an interruption of salient features of a call or a shorter acoustic signal.

Calls were broadcast to calling males in the field. Males called back to the playback, and after some period of time the playback ceased. We compared the number of calls before and after playback cessation. We also determined how the response of focal males varied in different treatments to compare the effects of: (1) fewer or more males; (2) simple or complex calls; and (3) complete or truncated calls (the latter with or without noise at the ending). As a control we compared the number of calls before and after the same time point in naturally occurring choruses. We feel this control is most appropriate because it is a more accurate measure of how the animals behave under situations in which they are not disturbed by experimental manipulations. Since the more interesting results derive from comparing the response variables between treatments, as noted above, the control has little influence on how we determine these main results.

FIELD EXPERIMENTS.—Experiments were conducted between 2000 and 2400 h during July and August 2007 near facilities of the Smithsonian Tropical Research Institute in Gamboa, Panama (9° 07' 00" N, 79° 41' 51" W). We chose focal choruses in which all of the calling males could be identified in order to gauge the size of the chorus, and also which tended to be physically and acoustically isolated from other choruses in order to reduce any potential effects of the response of nearby choruses.

The call used for playback was the median whine-chuck call of this population based on the analysis of 300 calls of 50 males (call M in Fig. 3 Ryan & Rand 2003). Each playback was 60 sec.

We varied several parameters of the playbacks: (1) *number of males*: either one or three calling males were simulated. In the one-male treatment a call was broadcast every 2 sec, the typical calling rate of túngara frogs. We simulated three males calling by broadcasting three calls every 2 sec. (2) *Call complexity*: playbacks consisted of either simple calls (whines) or complex calls (whines with three chucks). The simple call was synthesized by excising the single chuck from the test call, and the complex call was synthesized by copying the call's chuck and adding it in duplicate to the original whine-chuck call with a 4 ms inter-chuck interval. (3) *Ending call*: in the wild when males are startled they sometimes do not complete

the final call. Thus in the playbacks the final call was either complete (F) or truncated (T). The truncated calls were either simply cut short at 0.116 ms (T), or the call from 0.116 ms onwards was replaced by 'green noise' (N). Green noise is white noise that is filtered to match the frequency characteristics of a túngara frog chorus. These three parameters were varied to result in 12 playback treatments (Fig. 1).

The playback experiments were conducted with eight natural túngara frog choruses. Chorus sizes ranged from two to six males with an average size of 3.42 (SD = 1.16). We used a repeated measures design in which each chorus was tested with all 12 playback treatments sequentially with approximately 1 min between trials. The order of the treatments was varied randomly among choruses. Once a chorus was identified we used a random-number generator in Microsoft Excel[®] to determine the order of the 12 playback treatments. We did not initiate a playback during ongoing chorusing. We began to record the chorus as we initiated the playback, which continued for 60 sec, and we then continued the recording for an additional 30 sec after the playback ceased. We recorded choruses with a Marantz PMD 420 digital recorder and Sennheiser ME 80 microphone. We broadcast playbacks with an Apple iPod[®] and a Minneroff field speaker. The speaker was positioned 1 m from the center of the chorus and standardized to 60 dB SPL (re. 20 μ Pa) at 1 m away using a digital sound pressure level meter (RadioShack, Fort Worth, Texas, U.S.A.).

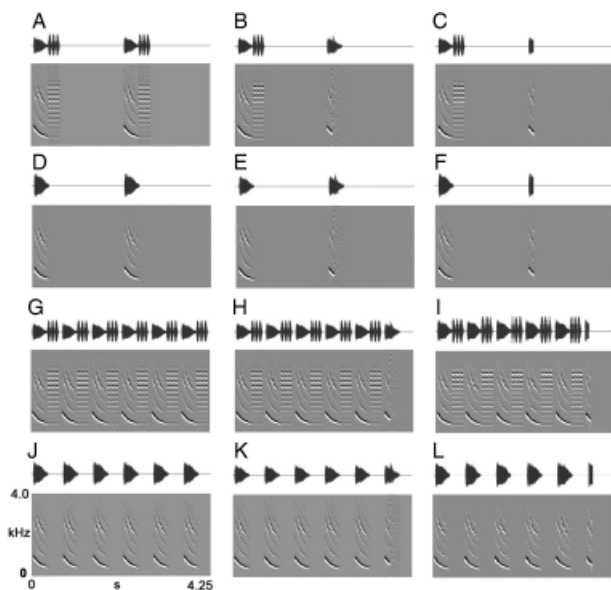


FIGURE 1. Stimuli used in this study. We represent the waveform (top) and spectrogram (bottom) of the last 4 sec for each of the 60-sec treatments. For each stimulus we indicate Number of males (M), number of chucks (C), and how the final call ended, F, full (normal) ending; N, green noise ending; T, truncated ending. (A) 1M, 3C, F; (B) 1M, 3C, N; (C) 1M, 3C, T; (D) 1M, 0C, F; (E) 1M, 0C, N; (F) 1M, 0C, T; (G) 3M, 3C, F; (H) 3M, 3C, N; (I) 3M, 3C, T; (J) 3M, 0C, F; (K) 3M, 0C, N; (L) 3M, 0C, T.

DATA ANALYSIS.—For each playback we quantified calls for the 20 sec immediately before and after the playback cessation. We also measured the latency from the end of the playback (60 sec following beginning of trial) to chorus cessation, which was defined as the absence of calls for more than 5 sec.

We used two variables in the statistical analysis: (1) *call ratio* is the ratio of the number of calls in the 20 sec immediately before and after playback cessation; the ratio is > 1.0 if calls increased after the playback ceased and < 1.0 if calls decreased after the playback ceased. (2) *Latency to cessation* is the time from cessation of the playback to chorus cessation. If a chorus did not cease calling after playback cessation, we arbitrarily assigned a value of 20 sec for latency. Out of 96 playbacks (12 playbacks \times 8 choruses) the chorus failed to cease in a total of seven instances across three different choruses.

We tested each data set for normality with a Kolmogorov–Smirnov test. We analyzed the data with a repeated measures analysis of variance (ANOVA). There were three within-subject factors: (1) number of calling males (two levels: 1, 3); (2) number of chucks (two levels: 0, 3); and (3) ending call (three levels: complete [F], truncated [T], truncated-noise [N]).

We analyzed only the eight choruses, which responded in all 12 treatments. We did not analyze samples in which choruses ceased before the end of the playback during any of the 12 treatments or did not receive all 12 treatments. The α criterion applied in all analyses was 0.05. All analyses were conducted in SPSS (version 16.0).

In order to compare our experimental results with an unmanipulated control, we analyzed chorus recordings from the study by Bernal *et al.* (2007). We selected recordings that were collected from choruses in the same area where we conducted this study, and that were small enough and with low enough background noise to allow us to count individual calls accurately. These criteria yielded recordings from 12 unique choruses. We then followed the same protocol used to analyze the experimental data. We counted the number of calls 20 sec before and 20 sec after the 60-sec time point of the chorus recording and used these data to calculate the call ratios and latencies. Because this control group was not a repeated measures extension of the experimental treatments, we report the results graphically. For the control group, only three of the 12 recordings exhibited call cessation greater than 5 sec following the 60 sec mark, thus we analyzed only call ratio results for the control data sets.

RESULTS

The call ratio responses of the choruses ($N=8$) to each of the 12 treatments as well as the control are shown in Fig. 2.

CONTROL.—The average call ratios are compared with the call ratios of the control choruses in Fig. 2. In all cases the call ratios were substantially lower for the treatments than for the controls; there was no overlap between the standard error of the control and that of any of the treatments. Thus the number of calls in the experimental treatments in the 20 sec before playback cessation was greater than

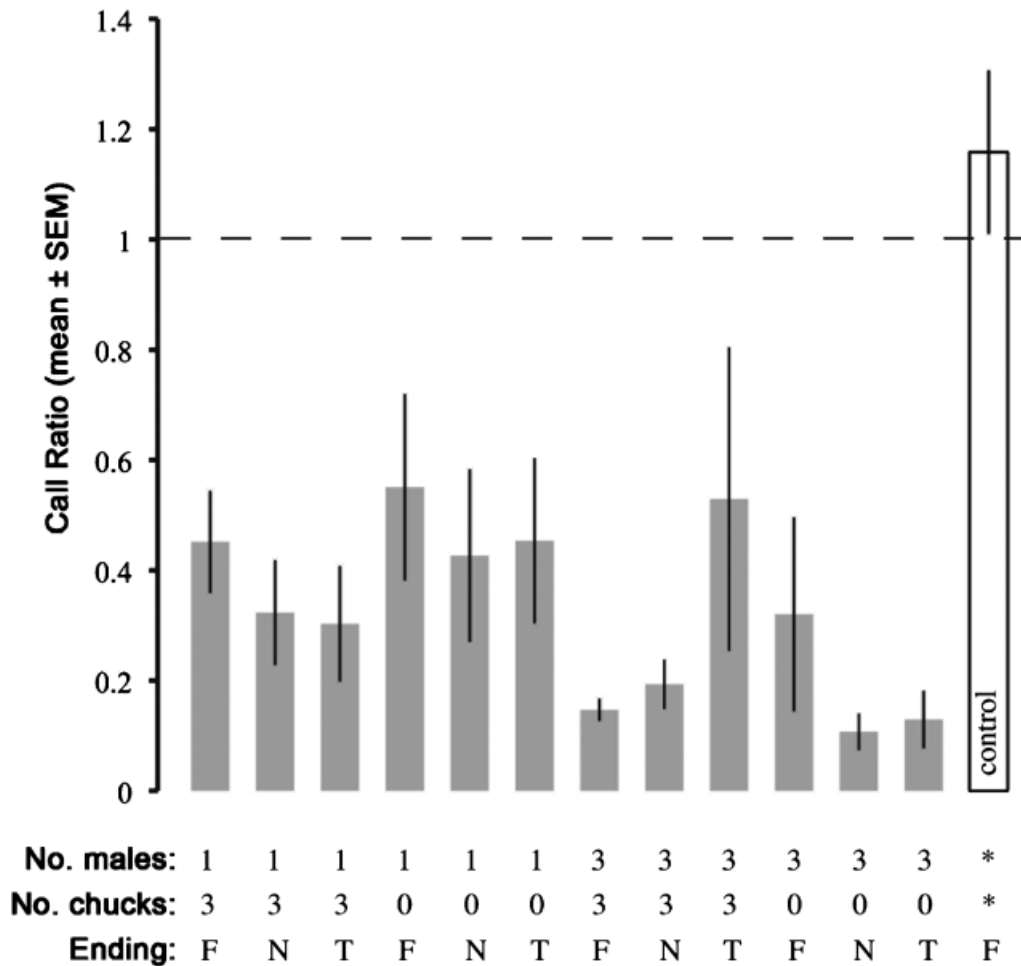


FIGURE 2. Mean (\pm SE) call ratio for each of the 12 experimental treatments ($N=8$) and the natural, unmanipulated control group ($N=12$). The parameters identifying each of the treatments are: Ending type: F, full (normal) ending; N, green noise ending; T, truncated ending. Dashed line indicates the null expectation of no change.

the number of calls in the 20 sec after playback cessation compared with what occurs in the natural choruses. The call ratios of the natural choruses were close to the null expectation.

CALL RATIO.—The Kolmogorov–Smirnov test for normality showed that the distributions for all 12 experimental treatments and the control met the assumption of normality ($P > 0.05$).

The ratio of calls before and immediately after playback cessation can be used to test two hypotheses. The first is that the treatments influenced the calling of the males. The null hypothesis is that the ratio of calls before and after the treatment should be approximately 1.0. The prediction of a cessation effect is that the ratio should be significantly less than 1.0. The data in Fig. 2 show that the call ratios for all the experimental treatments were significantly less than 1.0. This contrasts with the unmanipulated control group, which had an average call ratio close to 1.0 (mean = 1.15, SEM = 0.148, Fig. 2).

We also asked if experimental treatments differed in their effectiveness in inducing chorus cessation (Fig. 2). The repeated measures ANOVA shows that there was a significant main effect of the number

of males in the simulated chorus ($F = 38.49$, $df = 1,7$, $P = 0.00044$), as three males were more effective in inducing chorus cessation than was one male. There was also a significant interaction between the number of males and the number of chucks in the playback ($F = 7.92$, $df = 1,7$, $P = 0.026$) and a significant interaction between the number of males and the ending type of the final call ($F = 7.88$, $df = 2,6$, $P = 0.021$). The remaining main effects and interactions were not significant: main effect of the number of chucks ($F = 0.01$, $df = 1,7$, $P = 0.92$), main effect of call ending ($F = 1.59$, $df = 2,6$, $P = 0.278$), interaction effect of number of chucks-by-call ending ($F = 0.37$, $df = 2,6$, $P = 0.71$), interaction of number of males-by-number of chucks-by-call ending ($F = 1.63$, $df = 2,6$, $P = 0.273$).

LATENCY.—The Kolmogorov–Smirnov test for normality showed that the distributions of two of the eight experimental treatments failed to meet the assumption of normality. These two treatments included the one male/0-chucks/truncated ending ($P = 0.05$) and the three males/three chucks/truncated-noise ending ($P = 0.03$). The remaining 10 distributions met the assumption of normality ($P > 0.05$).

We analyzed the latency data only to compare differences in the effects among treatments on latency. The repeated measures ANOVA showed that there was a significant main effect of the number of males in the playback ($F = 10.96$, $df = 1,7$, $P = 0.013$). The remaining main effects and interactions were not significant: main effect of the number of chucks ($F = 0.075$, $df = 1,7$, $P = 0.792$), main effect of the ending call ($F = 2.15$, $df = 2,6$, $P = 0.19$), interaction effect of number of males-by-number of chucks ($F = 0.46$, $df = 1,7$, $P = 0.52$), interaction of number of male-by-call ending ($F = 1.78$, $df = 2,6$, $P = 0.25$), interaction of number of chucks-by-call ending ($F = 0.072$, $df = 2,6$, $P = 0.93$), interaction of number of male-by-number of chucks-by-call ending ($F = 3.48$, $df = 2,6$, $P = 0.099$).

DISCUSSION

The results of our experiments strongly support the hypothesis that chorus cessation can be initiated when a few males cease calling as this behavior spreads through the chorus. More specifically, we show that for all treatments males decrease the number of calls in response to the cessation of a simulated male calling. This effect is more pronounced in response to a larger chorus, and when there is a larger chorus the effect is further enhanced when the males are producing complex calls compared with simple calls. Furthermore, the time to which all calling ceases is more pronounced in response to a larger simulated chorus than to a smaller one. Thus males are able to respond vicariously to a disturbance, such as the presence of a predator, without directly experiencing it. Because female túngara frogs are sensitive to call cessation during mate choice, the choice to cease advertising is not a cost free solution (Baugh & Ryan 2010). To summarize these results, we show that male túngara frogs respond to sounds of silence as an alarm cue.

In túngara frogs, as well as many other chorusing insects (Greenfield 2002) and anurans (Gerhardt & Huber 2002), we know that male vocal interactions are regulated socially. In this species, males call in response to calls of other males and their call complexity is also modulated by the complexity of calls of other males (Ryan 1985, Bernal *et al.* 2009, Goutte *et al.* 2010). We also know that male túngara frogs will alter their calling behavior and other behaviors associated with calling, such as posture and vocal sac inflation, in response to the presence of models of a frog-eating bat (Tuttle *et al.* 1982), and that the duration of chorus cessation can be influenced by chorus size (Jennions & Backwell 1992). Finally, the duration of chorus cessation is shorter when males are exposed to calls of conspecifics (Lahanas 1995) or sympatric heterospecifics but not allopatric heterospecifics (Phelps *et al.* 2007).

In the above examples, calling in male túngara frogs is influenced by signals or cues from conspecific males, predators, and heterospecific males. In this study, however, it is the lack of a conspecific call that triggers an alarm response within neighborhoods of calling males. The strength of this alarm response is also context dependent. If the silence follows more calling, *e.g.*, more males making more complex calls, the effect on chorus cessation is greater. This might be because the information about the presence of a predator is more reliable when it is indicated by more males.

Also, as males do not often transition from a whine with three chucks to no calls, when such a transition does occur this might also be more likely to be due to the presence of a predator. The same point holds when the final call is not a complete one. On the mechanistic side, the cessation of male calling might be more extreme when there is a greater change in the overall sound level. The ultimate and proximate causes need not be mutually exclusive.

In chorusing frogs and insects diel patterns in chorusing are rather common (Greenfield 2002, Gerhardt & Huber 2002, Wells 2007). Most of the studies that investigate this phenomenon have not tested the hypothesis that the cessation of choruses can result from disturbance. In the most detailed analysis of this problem, Schwartz (1991) tested three hypotheses as to why male *Hyla microcephala* cease calling: (1) females prefer males that call cyclically; (2) males cease calling because of acoustic interference; and (3) males cease calling to reduce the high cost of calling. His data supported the third hypothesis. Energy conservation also could interact with widespread response to the sounds of silence. One or a few males could cease calling for energy concerns and their cessation of calling could be perceived as an alarm cue that leads to widespread chorus cessation. As noted in the introduction, however, we have already shown that túngara frogs respond to predators with cessation of calling as well as other changes in behavioral postures that indicate an alarm response (Tuttle *et al.* 1982). Here we show how the alarm response serves as a cue that induces alarm behavior in other túngara frogs.

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