

The Role of Synchronized Calling, Ambient Light, and Ambient Noise, in Anti-Bat-Predator Behavior of a Treefrog

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Received March 8, 1982 / Accepted July 16, 1982

Summary. Male treefrogs, *Smilisca sila* (Hylidae), produce calls of varying complexity and demonstrate a remarkable ability to synchronize their calls with those of neighbors. The bat *Trachops cirrhosus* eats frogs and uses the frogs' advertisement calls as locational cues. The bats are less likely to respond to synchronous calls than to asynchronous calls, and when given a choice prefer complex calls to simple calls.

Experiments with bat models indicate that, like other frogs, *S. sila* probably uses visual cues to detect hunting bats. In response to bat models the frogs decreased both the number and the complexity of their calls. The calling behavior of the frogs was sampled in the field during periods with and without artificial illumination. The frogs produced fewer and less complex calls, and they tended to call from more concealed sites, during the period without illumination, when presumably it would have been more difficult for the frogs to detect hunting bats.

S. sila tended to call from sites with higher ambient noise level, the noise primarily originating from waterfalls. The frequencies of the dominant energies in the waterfall sounds completely overlapped the frequency range of the *S. sila* call; thus waterfalls might mask the frog calls. When given a choice between calls produced near and away from waterfall sounds, bats preferred the latter.

Introduction

The fringe-lipped bat, *Trachops cirrhosus*, preys on frogs and uses their advertisement calls as loca-

tional cues. The bats typically fly along streams and capture frogs that are calling on the ground or the water's surface. Bat capture success is dependent upon frog calling behavior, and variation in such call parameters as intensity, complexity and repetition rate influence the frogs' bat predation risk (Tuttle and Ryan 1981; Ryan et al. 1982). Since these call parameters might also affect a calling frog's ability to attract a mate (e.g. Whitney and Krebs 1975; Ryan 1980, 1982; Rand and Ryan 1981), it is not surprising that bat predation seems to have influenced anuran male sexual display behavior (e.g. Ryan et al. 1982; Tuttle et al. 1982).

Bat predation on a species of frog that calls from aggregations (i.e. choruses), *Physalaemus pustulosus*, has been studied in detail (Tuttle and Ryan 1981; Ryan et al. 1982; Tuttle et al. 1982). Although hunting bats are attracted to the acoustic stimuli produced by the *P. pustulosus* chorus, we have shown that males in larger choruses are relatively safer from bat predation due to the selfish herd effect (Ryan et al. 1981). However, most neotropical frogs do not form aggregations when acoustically advertising for mates. To determine the potential influence of bat predation on sexual advertisement of a non-chorusing frog, we investigated the calling behavior of *Smilisca sila* (Hylidae).

S. sila breeds during the dry season, which is from December to April on Barro Colorado Island (BCI), Panama, where this study was conducted. Our previous observations revealed that the daily peak of calling activity of this species was usually at dusk. But subsequent calling activity was influenced by ambient light level, and calling activity remained high during clear, moonlit nights. Males usually called from streams and seemed to be more abundant near areas where noise from waterfalls and riffles was most intense. Males also were ob-

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served calling from bushes and trees overhanging the streams. Males did not form aggregations and usually were well spaced along the stream, but they showed a remarkable ability to synchronize their calls with those of their neighbors.

In this study we examined how bat predation might influence aspects of male *S. sila* reproductive behavior, especially the amount of calling, call complexity, call synchronization, and calling site selection. We were especially interested in how the interactions between the bats and frogs were mediated by ambient noise and light.

Materials and Methods

We conducted field experiments on BCI and the adjacent mainland on Bohio from January to April, 1981. Field experiments and stream censuses were conducted along the Lutz, Nemesia and Bohio streams. Call playback experiments were conducted on 18, 20, 21, 27, and 28 January and on 3 and 7 February. Visibility of calling frogs under varied light conditions was quantified on 2, 4, 5, 15, and 16 March. Frog distribution vs stream sound levels was sampled on 19 February (Lutz) and on 18 (Nemesia), and 20 (Bohio) March. Responses of *T. cirrhosus* to varied call types and conditions were tested from 7 February to 21 March.

Analysis of Call Synchronization. Calls of male *S. sila* were recorded with a Nagra IV-D tape recorder and a Sennheiser MKH 104 microphone. The temporal and spectral properties of the calls were analyzed with a Nicolet 444A spectrum analyzer and a Kay Sonograph model 6079A.

We investigated the ability of males to synchronize their calls using call playback experiments. A PearlCorder model SD2 microcassette recorder with a tape of either a simple (1 note) or complex (4 note) *S. sila* advertisement call was placed 1 m from a male. A Sennheiser MKH 104 microphone from a Nagra IV-D tape recorder was placed 0.5 m from the frog on the opposite side from the cassette recorder, and recorded the stimulus call and the frog's response at a tape speed of 15 ips. The observer was 5–10 m away with the tape recorder and a long microphone cable; a remote control lead was used to activate the cassette recorder.

The male's response to simple and complex calls was determined by broadcasting a single call from the cassette recorder and recording the stimulus call and the male's response for the following 5 s. Stimulus calls were broadcast at ca 75 dB SPL at 0.5 m (Realistik SPL meter, fast response). Although we were not able to measure the intensity of a male's call, it was louder than 75 db SPL at 0.5 m, and was probably about 90 dB SPL. Each male was presented with a stimulus call once every 1–3 min until the male was tested with 10 calls of each type, first one call type, then the other. The initial call type tested was alternated between successive males. The complete set of each call type (i.e. 10 stimulus calls) was not always tested because several males hopped away or amplexed females during the experiments.

The male's response and its temporal relation to the stimulus call were analyzed by playing the call at 1/4 speed (3.75 ips) into a General Radio type 1521 graphic level chart recorder.

Frog Responses to Bat Models. In each test a 10 m monofilament line was stretched directly over a male *S. sila*. After the

frog resumed normal calling, we observed it for 5 min with a Javelin model 221 night vision scope. We counted the number of calls, number of notes per call, and whether the frog called alone or immediately before or after another frog. At the end of the 5 min observation period, a model *T. cirrhosus* was released at the upper end of the sloping line about 6 m from the frog. The model passed over the frog at a height of about 20 cm (see Tuttle et al. (1982) for details of bat model experiments). We then repeated our observations of calling behavior for an additional 5 min. During all testing a rheostat-controlled, diffuse-filtered headlight, held stationary on a tripod, was used to maintain constant illumination between 0.17 and 0.35 lux. This eliminated light level changes due to moving clouds and held light constant within the range normally produced by a partial moon. Ten frogs were tested, once each, and their calling behavior before and after model passes was compared with a sign test.

Calling Sites and Ambient Noise. Two streams on BCI, Lutz and Nemesia, and one on a nearby peninsula, Bohio, were censused for male *S. sila*, and ambient noise level was recorded to determine if males were located preferentially at noisier sites. All males present along each stream were counted, and their location recorded in exactly 10 m intervals. Ambient noise was recorded at the same 10 m intervals with a Sennheiser MKH 104 microphone and a Nagra IV-D tape recorder. The microphone and tape recorder have a fairly flat frequency response curve up to at least 15 kHz. The microphone was approximately 3 cm off the ground, which is within the range of heights that males in the stream call. The microphone always was pointed directly upstream regardless of the location of sources of ambient noise (i.e. waterfalls and riffles). Microphone input level was kept constant and never was overloaded. Most of the ambient noise was from waterfalls and riffles.

The recordings of ambient noise level were then played into a General Radio graphic level chart recorder type 1521 to determine sound pressure level. The graphic level chart recordings were calibrated for absolute sound pressure level by recording a waterfall of known sound pressure level (70 dM SPL at 1 m, Realistik SPL meter, C-weighted) at the identical microphone input level and then analyzing this sound of known intensity with the graphic level chart recorder. It should be emphasized that the relative differences in ambient noise level among sites were determined with the General Radio level chart recorder. The Realistik sound level meter was only used to determine the absolute values of the readings. The mean sound pressure level over each 10 m interval was determined by averaging the dB SPL reading at the beginning and end of each 10 m interval. The frequency-energy spectrum of the ambient noise (in this case predominated by a waterfall) was determined with a Nicolet 444A spectrum analyzer.

Visibility of Frogs and Ambient Light. Nights that were either moonless and dark, or moonlit and bright were selected for behavioral comparisons of calling male frogs. Each evening's observations were begun as soon after 18:30 h as the *S. sila* began calling, and continued until 19:00 h. In that time period we briefly used recorded *S. sila* calls every few meters to elicit responses, enabling us to rapidly locate as many calling frogs as possible.

Each frog's visibility was determined from 30 cm directly above and from 30 cm out on four opposite sides at a height of 20–30 cm (the average height at which *T. cirrhosus* hunts). We viewed each frog from these five points and for each point we estimated the proportion of the frog's surface area facing us that was visible. The frog's mean visibility was determined

by averaging the visibility from all five points. After we measured the visibility of the frog, we marked the site with a numbered flag to facilitate our location of the frog for the next census. At 19:00 h observations were terminated, and we waited out of sight until our return census at 19:30 h. From 19:30–20:00 h we relocated as many of our marked frogs as possible, repeating our previous measurements of the visibility of each one.

Frog Calling Behavior and Ambient Light. The influence of artificially increased light intensity on frog calling behavior was determined on dark nights between 19:15 and 21:00 h, when crepuscular calling had nearly ceased. Locations where 3–5 *S. sila* were heard calling at dusk were selected.

During 10 min sampling periods, we recorded numbers of simple (1 note) and complex (>1 note) calls produced by frogs located within a radius of 10 m from a pre-chosen central point. In the first 10 min period we simply recorded normal calling behavior without artificial illumination. Two minutes prior to beginning the second 10 min period we aimed a rheostat-controlled headlight with a diffuse lens 4 m above and across the stream and adjusted light intensity so that light within the area of observation ranged from 0.17–0.35 lux. A Gossen Lunasix light meter was used to measure reflected light. The third sample was begun after the light had been turned off for two minutes. This procedure was repeated until three pairs of dark and light samples had been obtained at each of four widely separated locations on the Nemesia and Lutz streams.

Bat Preference of Call Types and the Effect of Ambient Noise. We tested preference among frog calls by *T. cirrhosus* in an outdoor flight cage according to the procedures described by Tuttle and Ryan (1981) and Ryan et al. (1982). All recordings used in the experiments were made with a Nagra IV-D tape recorder and a Sennheiser MKH 104 microphone. The call repetition rate of all frog calls used in the experiments was 1 call/1.6 s, and the call intensity was 70 dB SPL at 1 m from the speaker. Frog calls were played on Stellovox tape recorders using tape loops and small extension speakers. A Nagra IV-D tape recorder with a continuous tape loop was used for playbacks of the waterfall sounds at a tape speed of 15 ips.

Bats were tested individually in a flight cage 4.5 m on each side and 2.3 m high. The observer sat in one corner and the bat perched in the opposite corner. Speakers were located in the remaining corners, each speaker was 4 m from the perched bat. Stimuli were discontinued as soon as the bat flew toward a speaker to avoid habituation. A response was recorded only when the bat passed within 1 m of a speaker (see Table 1 in Ryan et al. (1982) for typical approach distances of bats to speakers during playback experiments). A no response was recorded if a bat did not respond during the 60 s of stimuli presentation. Trials were conducted once every several minutes. There were no rewards. Speaker cables were switched between trials so that the stimuli were presented from opposite corners in successive trials.

In experiments with waterfall sounds, two identical tape loops of a single 4-note call were played simultaneously from speakers in opposite corners of the flight cage. Two Nagra tape recorders were placed between the two speakers which were broadcasting frog calls. Each tape recorder was 1 m from one frog call speaker and 5 m from the other frog call speaker. During each trial one tape recorder broadcast waterfall sounds while the other tape recorder was silent. The waterfall sound recording was switched between Nagra tape recorders after each trial, so the speaker playing the frog call that was nearest to the waterfall noise changed between successive trials. Frog calls

were broadcast at an intensity of 70 dB SPL at 1 m. Waterfall sounds were broadcast at 65 dB SPL at 1 m.

Bat preferences for synchronous versus asynchronous *S. sila* calls were tested using two identical tape loops of a 4-note call. The tape loops were adjusted to play synchronously versus asynchronously (ca 0.5 s apart) in successive trails, regardless of whether or not the bat responded. Preference for simple versus complex calls was tested similarly (also see Ryan et al. (1982)). A 1-note call from one speaker and a 4-note call from the opposite speaker were broadcast simultaneously, and the bat's response was recorded.

Results

Call Synchronization

S. sila produce calls of varying complexity (sensu lato Rand and Ryan (1981)); that is, the number of notes per call is variable. The temporal and spectral properties of a 1-note and 3-note call are shown in Fig. 1A–C. A single note is about 0.16 s in duration (Fig. 1A, B). The note (or a simple call) contains two frequency peaks of energy at about 1,300 Hz and 2,500 Hz (Fig. 1C). Males produced calls with as many as 4 notes. The temporal and spectral structures of the notes were similar whether they were part of a single note call or a multi-note call (Fig. 1A).

Male *S. sila* called relatively infrequently, an average of only 1.7 calls/min. Although calling rates were low, the calls of males often overlapped temporally. In fact, the calls often overlapped to such an extent that it was not possible for an observer to be sure of how many calls were produced. This could only be determined by acoustic analysis.

The males' responses to the simple stimulus call in the playback experiments demonstrate that males vocally respond to neighbors in such a way that synchronized calling results. The temporal duration of the simple stimulus call was about 0.2 s. A male's response was recorded during the stimulus call and for the following 5 s. If a male called randomly during this test period (i.e. 5.2 s), we would expect the beginning of his call to overlap the stimulus call in only 3.8% of the responses (i.e. $100\% \times 0.2/5.2$). 96.2% of his responses would not overlap the stimulus call if his response was random with respect to the stimulus. As is shown in Table 1, 20 of the 29 responses overlapped the simple stimulus call. Thus when presented with a simple call, males are more likely to produce a synchronous, rather than an asynchronous, response ($\chi^2 = 26.9$, $P < 0.001$).

Male *S. sila* were more likely to respond to complex stimulus calls than to simple calls (Table 1). Although most responses to simple (69%)

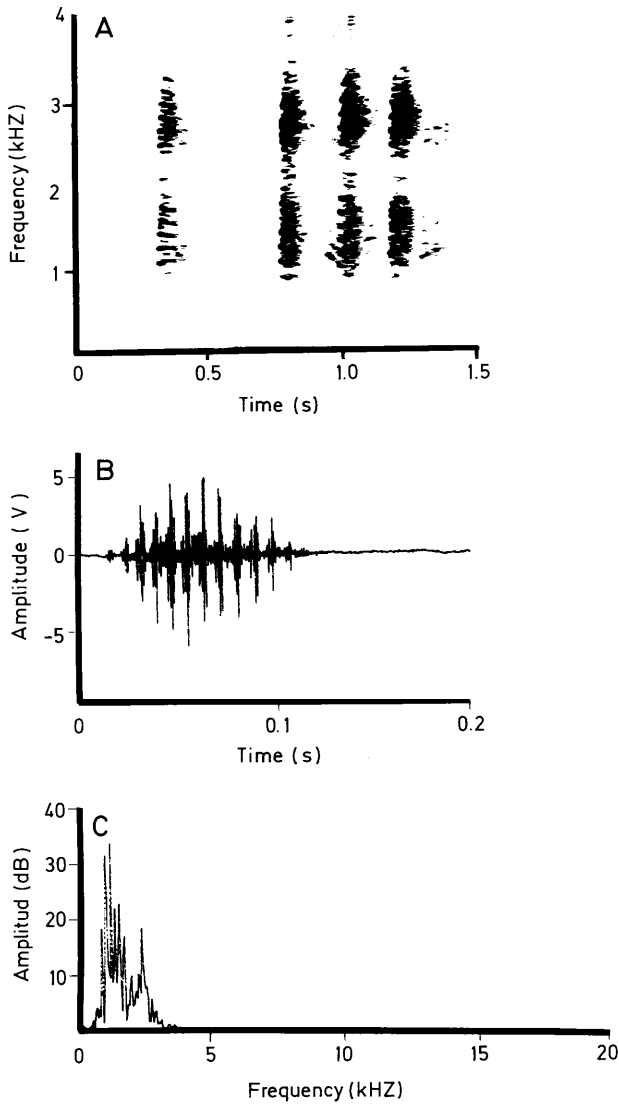


Fig. 1. **A** A sonographic representation of a simple (1 note) and complex (3 note) advertisement call of *Smilisca sila*; **B** a time-amplitude representation of one note of the advertisement call; **C** a power spectrum of one note of the advertisement call

and complex (99%) calls overlapped the stimulus calls, responses were more likely to be synchronized with complex stimulus calls (Table 1). The mean time from stimulus presentation to response was 0.20 s (SD=0.05, range=0.15–0.35) for simple stimulus calls and 0.31 s (SD=0.16, range=0.13–0.66) for the complex call. The longer duration (ca. 0.84 s) of the complex stimulus call facilitates call synchronization, since the mean response time to the complex stimulus call would not have overlapped the shorter (ca. 0.2 s) simple call. Male frogs also produced more complex calls (i.e. more notes per call) in response to the complex stimulus call than to the simple stimulus call.

Table 1. Responses of male *Smilisca sila* to playbacks of simple (1-note) and complex (4-note) advertisement calls

Stimulus	No re- sponse	Re- sponse	Calls over- lapped	Calls not over- lapped	\bar{x} (SD) number of notes/call
Simple	37	29	20	9	1.45 (0.69)
Complex	15	68	67	1	2.28 (2.21)
Test statistic	$\chi^2=212$		$\chi^2=191$		$U=0.212$
Probability	$P<0.001$		$P<0.001$		$P=0.015$

Table 2. The spatial distribution of male *Smilisca sila* in relation to ambient noise. Sound pressure level (dB SPL) between intervals with and without frogs for each stream was compared with a Mann Whitney *U*-test

Site	Number of inter- vals	$\bar{x} \pm$ SD dB	Total range in dB SPL	<i>P</i>
Lutz				
with frogs	6	64 ± 5.1	57–71	0.019
without frogs	20	59 ± 2.7		
Nemesia				
with frogs	9	55 ± 1.1	53–57	0.496
without frogs	15	55 ± 1.1		
Bohio				
with frogs	15	55 ± 3.1	51–66	0.002
without frogs	49	53 ± 1.7		

Frog Responses to Bat Models

The calling behavior of *S. sila* changed in response to the overhead flight of a *T. cirrhosus* model. In the 5 min observation period prior to the bat model pass, calling males made an average of 8.5 calls (SD=3.8, range=4–14), and these calls contained an average of 1.29 notes (SD=0.2, range=1–4). Fewer calls ($\bar{x}=1.9$, SD=0.2) with fewer notes ($\bar{x}=1.1$, SD=0.2) were produced in the 5 min period following the model pass. A sign test showed that both the number of calls ($P=0.001$) and the number of notes ($P=0.008$) decreased significantly following the model pass.

Calling Sites and Ambient Noise

On two of the three streams censused, Lutz and Bohio, the 10 m intervals that contained frogs had a higher ambient noise level than did the intervals without frogs (Table 2). The range in ambient noise level on Lutz (57–71 dB SPL) and Bohio (51–66 dB SPL) was greater than the range of noise

level on Nemesia (53–58 dB SPL) where the sound levels of intervals with and without frogs were not significantly different (Table 2). The variance of the sound levels was not different between Lutz and Bohio ($F=1.59$, $P>0.05$), but it was significantly different between Lutz and Nemesia ($F=6.01$, $P<0.005$) and Bohio and Nemesia ($F=4.33$, $P<0.005$).

The frequency-energy spectrum of the waterfall noise, the dominant ambient noise on the streams, is shown in Fig. 2. The frequency response of the tape recording system is not reliable above 20 kHz. Therefore, we do not know if the waterfalls produce significant energy in the ultrasonics. However, within the subsonic range virtually all of the energy is concentrated within a frequency band of 550–4,550 Hz with the dominant peak at 550 Hz. As can be seen by comparing Figs. 1C and 2, the dominant energy in the waterfall covers the entire frequency range of the *S. sila* call.

Visibility of Frogs and Ambient Light

The location and visibility of frogs were more likely to change between the first and second sample (i.e. from 18:30–19:30 h) on dark nights than on moonlit nights. On dark nights frogs were more likely to have moved up to vegetation overhanging the stream between samples than on moonlit nights (10 of 19 on dark nights, 0 of 24 on light nights; $\chi^2=10.1$, $P<0.001$). Also, on dark nights frogs were less likely to be located during the second sample (9 of 19 on dark nights, 4 of 24 on light nights; $\chi^2=6.0$, $P<0.05$). On moonlit nights frogs were more likely to maintain their visibility between samples than on dark nights (19 of 24 on light nights, 2 of 19 on dark nights; $\chi^2=8.6$, $P<0.01$).

Frog Calling Behavior and Ambient Light

S. sila called more frequently, and those calls had more notes in the 10 min sample with artificial illumination than in the 10 min sample without artificial illumination. Frogs produced 122 calls in the dark sample and 570 calls in the light sample ($\chi^2=290$, $P<0.001$). There were both more simple calls (474 vs 121; $\chi^2=209$, $P<0.001$) and complex calls (96 vs 1; $\chi^2=94$, $P<0.001$) during the light sample than during the dark sample.

Bat Preference of Call Types and the Effect of Ambient Noise

T. cirrhosus preferred calls that were 5 m from the waterfall sounds to calls that were only 1 m from

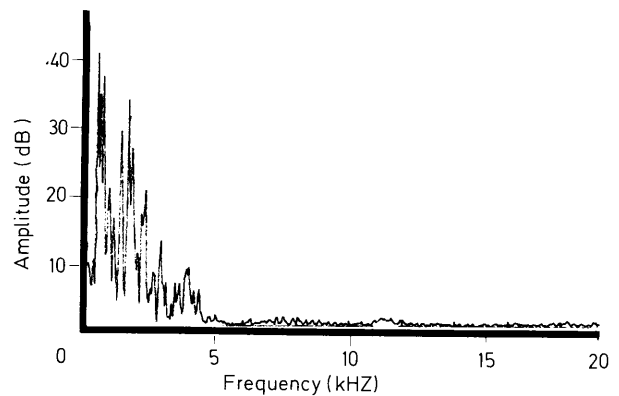


Fig. 2. A power spectrum of waterfall sounds, which were the predominant abiotic noise on the streams

the sounds. Four bats responded 25 times in these playback experiments (10 no responses) and 19 responses were to the calls 5 m from the waterfall sounds ($\chi^2=6.8$, $P<0.001$).

The bats also preferred calls that were broadcast asynchronously to synchronous calls. Five bats were more likely to respond to asynchronous calls (14 responses in 19 trials) than to synchronous calls (10 responses in 28 trials; $\chi^2=6.5$, $P<0.02$). When the bats did respond, they did so sooner to asynchronous calls ($\bar{x}=15.4$ s, $SD=13.1$) than they did to synchronous calls ($\bar{x}=22.0$ s, $SD=13.2$; $t=1.76$; $P<0.05$).

Five bats were given a choice between simple and complex calls. There was a significant preference for the complex call (36 vs 4, 17 no responses; $\chi^2=25.6$, $P<0.005$).

Discussion

Bat Predation and *S. sila* Calling Behavior

The most remarkable aspect of *S. sila* reproductive behavior, and one of the reasons we studied this species, is their ability to synchronize their calls with those of their neighbors. Some species of frogs have been classified as synchronous or near-synchronous callers (Wells 1977). But in most cases these are merely animals that are acoustically active at the same time. Here, we prefer the more strict definition of synchrony proposed by Otte (1977) and Greenfield and Shaw (in press). They suggest that individual signal elements are temporally related in true synchronous signalling, as opposed to random acoustic activity with signal elements temporally independent. By this definition we think that *S. sila* can be classified as a synchronous caller. Synchronous callers, in the strict sense, are rare among anurans.

Male *S. sila* that produce calls synchronously should suffer less bat predation. Bats are less likely to respond to synchronous vs asynchronous calls, and when they do respond, they do so more quickly to the latter. The mechanism of localization of subsonic acoustic cues by bats has not been investigated adequately. It is assumed, however, that localization of sounds by most mammals is accomplished by some sort of binaural cross-correlation (Konishi 1977). Therefore, it would not be surprising if it were more difficult for bats to locate synchronous frog calls as opposed to asynchronous calls.

The role of sexual selection in the production of synchronous signals has been confusing. Otte (1974) suggested that synchronization may be a strategy to interfere with a competing male, but Alexander (1975) pointed out that neither male would benefit from such a strategy. Regardless of the selective force responsible for the evolution of synchronous signalling, it has been assumed that signal interference does occur during synchronization (e.g. Wells 1977). Therefore, it is significant that Passmore and Telford (1981) have shown that painted reed frog females are able to locate synchronous calls as accurately as they locate asynchronous calls.

Our study shows that for *S. sila* there probably is some selective advantage in producing synchronous calls – it should reduce bat predation risk. However, we have no idea how this might affect a male's ability to attract females.

S. sila produce calls of varying complexity, and our results show that the complexity of their calls is mediated by vocal interactions with other males; they increase call complexity in response to complex calls. These complex calls probably increase a male's predation risk, because *T. cirrhosus* preferentially responded to complex vs simple calls.

This parallels the situation in *Physalaemus pustulosus*. These frogs also increase the complexity of their calls during vocal interactions (Rand and Ryan 1981), and *T. cirrhosus* prefer complex *P. pustulosus* calls to simple calls (Ryan et al. 1982). Female *P. pustulosus* also prefer complex calls (Rand and Ryan 1981), probably, at least in part, because complex calls provide the female with some information about male body size which she uses in mate selection (Ryan 1980, 1982). There is little known about the reproductive behavior of *S. sila*, especially about female preference for call complexity. Males do increase call complexity during vocal interactions, and these calls increase predation risk. We would expect some selective advan-

tage, such as female preference, which results in males producing the more dangerous complex calls.

Bat Predation and Ambient Light and Noise

As with *P. pustulosus* (Tuttle et al. 1982), *S. sila* use visual cues to detect hunting bats. In response to bat models, males change their calling behavior in such a way that they reduce their vulnerability to bat predation; they call less frequently and their calls are less complex. Because the frogs seem to rely on visual cues to detect bats, their vulnerability to bat predation should be inversely related to ambient light level. We have shown that frogs behave more cautiously at lower light levels: they call less frequently, they call from more concealed sites, or they call from sites above the streams. Most *T. cirrhosus* on BCI hunt at ground level and rarely land in pursuit of prey. Such pauses likely would increase their own risk of predation. Thus frogs that climb or perch in the protection of foliage probably avoid more *T. cirrhosus*.

The ambient noise level also influences bat-frog interactions. Frogs tended to call from sites that had higher ambient noise levels, usually near waterfalls. The bats preferred calls that were farther away from waterfall sounds. We do not know why the bats avoided calls near waterfall sounds. The *T. cirrhosus* echolocation call has its energy in the 50–100 kHz frequency range (Barclay et al. 1981). Since we do not know what energy the waterfalls produce in this frequency range, it would be pure speculation to suggest that the bats avoided these calls because the waterfall sounds interfered with their ability to echolocate. However, the acoustic analysis has shown that the frequencies in the waterfall sound completely overlap the frequency range of the *S. sila* advertisement call. It seems at least probable that bats prefer calls on a background of less ambient noise, because it increases their ability to locate the sounds. Although the resistance of bat echolocation calls to noise jamming has been studied extensively (see review in Schnitzler and Henson 1980), the importance of noise jamming in the perception of subsonic acoustic signals by bats needs to be investigated.

We do not know if bat predation has been the selective force responsible in call site selection by *S. sila*. There is not enough known about the reproductive biology of this frog to speculate what the other advantages or disadvantages of different calling sites might be.

Concluding Remarks

Studies of the anuran advertisement call have been concerned primarily with its role as a species isolation mechanism. However, it is now clear that predation (this study and others cited here), as well as other factors (e.g. sexual selection, Ryan 1980, 1982), probably have played an important role in the evolution of anuran vocalizations. In this study we show that the influence of predation on frog reproductive behavior must be considered in a proper ecological context, especially against the background of abiotic factors such as ambient light and noise. A clear understanding of the evolution of anuran vocalizations must integrate the roles of species recognition, sexual selection, predation, and the abiotic environment.

Acknowledgements. This research was supported by a grant from the National Geographic Society, and we are grateful to them for their continued interest in this study. MJR was supported by a Smithsonian Institution predoctoral fellowship and National Science Foundation Grant DEB-79-08893. We thank the Smithsonian Tropical Research Institute for the opportunity to continue our studies of bat-frog interactions on Barro Colorado Island.

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