

## Do Green Treefrogs (*Hyla cinerea*) Eavesdrop on Prey Calls?

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**ABSTRACT.**—Efficient foraging may be facilitated by attending to the signals produced by potential prey items. Such predatory eavesdropping is taxonomically widespread, yet there is currently a dearth of information for amphibians. Anuran amphibians, with their highly developed auditory system and robust phonotaxis toward advertisement calls when searching for mates, seem predisposed to use this hearing capability in other behavioral contexts such as foraging. We conducted playback experiments to test whether Green Treefrogs (*Hyla cinerea*) eavesdrop on sexual signals of prey (House Cricket [*Achaeta domestica*] song), or whether the presentation of acoustic prey stimuli in addition to a live cricket improved prey localization. We found that frogs did not use acoustic prey signals to guide their foraging movements. Frogs were not indifferent to acoustic stimuli, however, because they moved away from the sound source in some treatments.

The signals used by many animals to attract mates are often crucial for mating success (Andersson, 1994), yet they can also be taken advantage of by unintended receivers (McGregor, 2005; Peake, 2005). Frequently, such eavesdroppers are predators and parasites that use the signals of advertising males to locate their prey or hosts (Zuk and Kolluru, 1998; Peake, 2005). Predatory eavesdropping occurs in a wide range of taxa. Insects (Zuk et al., 2006), reptiles (Sakaluk and Belwood, 1984), birds (Iguane et al., 2008), and mammals (Tuttle and Ryan, 1981) have been reported to locate their prey in this way. Although all sensory modalities can be involved in eavesdropping (Lloyd and Wing, 1983; Stowe et al., 1995; Stoddard, 2002; Laumann et al., 2007), most reported examples involve acoustic signals (Zuk and Kolluru, 1998). Thus, animal taxa that are oriented acoustically are prime subjects for studies involving questions about eavesdropping.

Anuran amphibians (frogs and toads) constitute one of the major study groups for investigating the ecology and evolution of acoustic communication (Ryan, 2001; Gerhardt and Huber, 2002). Males produce conspicuous advertisement calls; females use these calls to select and locate mates (Ryan, 2001; Gerhardt and Huber, 2002; Wells, 2007), and other males use them for spacing within a chorus, territory maintenance, and male–male competition (e.g., Wilczynski and Brenowitz, 1988; Wagner, 1989; Bee and Gerhardt, 2002). The wealth of information on anuran acoustic behavior associated with reproduction is in contrast to the dearth of information on whether or how anurans respond to acoustic cues in the environment outside the reproductive context (but see Grafe et al., 2002). Although eavesdropping on vibrational and chemical cues (e.g., kairomones, alarm cues) has been well documented in anuran larvae (Warkentin, 2005; Fraker, 2009; Schoeppner and Relyea, 2009), few studies have investigated whether adult anurans eavesdrop on signals or cues associated with approaching predators (Schwartz et al., 2000; Bernal et al., 2007; Llusia et al., 2010; Bonachea and Ryan, 2011), or whether they use the signals of potential prey items to facilitate foraging (Jaeger, 1976; Taylor, 2001).

During routine feeding of captive frogs, we observed a frog that appeared to turn, listen, and then approach a singing

cricket. This observation posed the question for the investigation here. We conducted playback experiments to test whether Green Treefrogs (*Hyla cinerea*) eavesdrop on the acoustic advertisement signals of prey (House Cricket [*Achaeta domestica*] song). We predicted that frogs would show phonotaxis toward acoustic stimuli from potential prey. Because many amphibians are visually oriented predators (Ingle, 1968; Ewert, 1987; Freed, 1988; Buchanan, 1998), we also tested the hypothesis that auditory eavesdropping may improve prey localization. We predicted that frogs would orient faster or more directly to the prey if an acoustic stimulus from the prey was also present.

### MATERIALS AND METHODS

*Experimental Animals.*—Frogs used in this study came from a captive colony of Green Treefrogs maintained at the University of Wisconsin–Milwaukee (UWM). All test frogs were female. We chose to focus on female frogs because they have been shaped by selection to respond to auditory stimuli, and because we did not have sufficient males available for a meaningful comparison between the sexes. Timing of experiments did not correspond to the species' breeding season, and none of the frogs were in reproductive condition (no eggs or large follicles visible through venter).

Frogs were housed in glass terraria under 12 : 12 h; light : dark cycle and fed live crickets once a week ad libitum (Fluker's Cricket Farm, Baton Rouge, LA). The cricket colony was housed in the same room as the frogs, so frogs could hear crickets sing throughout the day. We fed frogs by placing crickets into the terraria, and there were frequently some crickets that sang during feeding time.

We chose the House Cricket as our model prey. Although Green Treefrogs may not encounter these crickets in the wild, they readily accept them as food in captivity, and all tested frogs were familiar with the House Cricket's appearance and song because they were the frogs' staple diet in this captive colony. Crickets are part of the prey spectrum of wild anurans (Freed, 1982; Mahon and Johnson, 2007), and House Crickets are used commonly as prey in studies on food preferences and prey capture behavior in anurans (Roster et al., 1995; Taylor, 2001). Crickets use songs to attract mates (Gerhardt and Huber, 2002), and a variety of auditory eavesdroppers take advantage of these

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songs (Sakaluk and Belwood, 1984; Zuk et al., 2006); the frequencies of cricket songs (Riede, 1998) overlap broadly with the anuran hearing range (Schoffelen et al., 2008). For example, the carrier frequency of our House Cricket song was 4.6 kHz, and the Green Treefrog hearing range extends from 0.3 to 5.4 kHz (Moss and Simmons, 1986).

*Experimental Design.*—To test whether frogs eavesdrop on a prey song, we set up two experimental conditions, without a visual cue or with a cricket in jar as a visual cue, with three treatments each: 1) playback of a cricket (prey) song; 2) playback of white noise that served as a control of whether an acoustic stimulus unrelated to prey affected the frogs' behavior; and 3) silence. The experimental protocol was approved by the Animal Care and Use Committee of the UWM (protocol 07-08#38). In the first experimental condition, we provided only auditory stimuli to test whether auditory prey signals alone elicit a phonotactic response. Because many amphibians are visually oriented predators, we included a second experimental condition in which we tested whether an auditory stimulus improved prey localization; here we provided a live female cricket ( $21.2 \pm 1.6$  mm [mean  $\pm$  SD]; size equalized among trials) in a jar in addition to the auditory stimulus. Female crickets do not sing, and the glass jar was sealed so as not to provide olfactory or additional acoustic cues. Frogs could see the cricket inside the jar, and some frogs did try to eat it when they approached the jar.

We used a 7.6-s-long recording of an *A. domesticus* song (downloaded from <http://entnemdept.ufl.edu/walker/buzz/index.htm>) as the auditory stimulus. It consisted of a series of 11 song syllables (2 or 3 pulses/syllable) that were repeated about every 700 ms and that had a dominant frequency peak at 4.6 kHz. The white noise stimulus was a continuous signal generated using Audition 2.0 software (Adobe Systems, San Jose, CA).

We randomly assigned each frog to one experimental condition, tested the frog with the three treatments on the same day, and then retested the frog in the other experimental condition 1–4 mo later. We aimed to test each frog in each experimental condition, but some frogs died before the study was completed. Consequently, most (85%) of the 52 frogs that participated in the study were tested in six trials (two experimental conditions with three treatments each), but we tested additional frogs from our colony to keep sample sizes even.

*Test Procedure.*—We fed frogs one cricket 48 h before being tested to standardize satiation levels; after this amount of time, frogs would not be starved but would be ready to feed again if presented with another cricket.

We tested frogs in a no-choice paradigm, presenting one signal at a time and assessing orientation and response time as measures of phonotactic behavior. All trials were conducted under simulated moonlight (dim lighting provided by a light-emitting diode lamp [7200LED-BN, 5 lux at center of arena; Lights of America]). This allowed frogs to see the prey when it was present (experiment 2). Between the three trials of a given experimental condition, frogs were kept in plastic containers ( $10 \times 10 \times 5$  cm); light entering the milky container walls created a dim interior that afforded the frogs some dim-light adaptation before entering the trials. Treatment stimuli were presented in random order with a minimum of 5 min rest between consecutive trials.

Experiments took place in a circular arena (2 m in diameter) set up inside an anechoic chamber at UWM. An infrared video

camera (EQ150, EverFocus USA, Duarte, CA) was placed centrally above the arena to monitor the frog's behavior. The arena was delimited by cloth-covered wire mesh and divided into 24 arcs that were each 15°. The speaker broadcasting the stimuli (JBL Control 1Xtreme, Harman International Industries, Inc., Stamford, CT) was located on the floor just outside the arena, centered in one of the 15° arcs and 1 m away from the arena center. For testing, we placed one frog in a wire release cage at the center of the arena. Once the trial commenced (playback of cricket song, noise stimulus, or silence), we removed the lid of the release cage by pulling a string remotely. We broadcast stimuli using Audacity Version 1.2.5 software (Carnegie Mellon University, Pittsburgh, PA) and a Pyle Pro PT1200 amplifier. Before each trial, we adjusted the sound pressure level (SPL) of the stimuli (cricket song and noise) to 85 dB using a sound level meter (Extech Instruments 407764). Stimuli were presented in a playback loop that lasted up to 20 min. We terminated a trial once the frog touched the arena wall anywhere in the test arena, or after 20 min had elapsed.

We obtained the following data during each trial: 1) initial orientation, the direction relative to the speaker at which the frog left the release cage; 2) final orientation, the direction relative to the speaker at which the frog touched the arena wall; and 3) response time, the time elapsed between opening the release cage and the frog making contact with the arena wall. To minimize handling time and disturbance, we waited until a frog had completed the last of the three trials of the day, and then we measured snout–vent length (SVL) to the nearest 0.1 mm with calipers as a proxy for size, and we determined mass to the nearest 0.1 g using a digital scale. From these values, we calculated body condition using the residuals of a linear regression of length and mass (Schulte-Hostedde et al., 2005). Size and body condition were entered as covariates in the statistical models (see below).

*Statistical Analysis.*—First, we tested which factors affected the orientation of approach. A frog touching the arena wall at 30° or 330° relative to a speaker situated at 0° is numerically different, but equivalent in terms of phonotactic precision, because they are equally close to the target stimulus. We therefore transformed the orientation angles into absolute angular deviations from the location of the target sound (i.e., 30° remained 30°, but 330° was transformed to 30°). We calculated test statistics using a mixed model (REML) implemented in JMP 7.0.1 (SAS Institute, Cary, NC) that provides *P*-values for fixed factors and confidence intervals for random factors; confidence intervals overlapping zero indicate nonsignificant effects. We used models with initial orientation or final orientation, respectively, as test variables, and we entered experiment (without cricket in jar, with cricket in jar), treatment stimulus (cricket, noise, silence), their interaction, frog SVL, and frog body condition as fixed factors in the model. To account for multiple testing of frogs and the fact that trials were conducted by different experimenters (DSK, DN), we also entered frog identity and observer as random factors in the model. To further explore orientation during the trials, we calculated regressions between angular deviation values of initial and final orientation to test whether a once chosen orientation was maintained or updated during approach.

For visual comparison, we provide an analysis of approach orientation using circular statistics (for final orientation only, because results of initial orientation were similar). We tested the null hypothesis that orientation angles were distributed uniformly using Rayleigh tests. If frogs attend to the presented

TABLE 1. Analysis of orientation of Green Treefrogs in relation to variation in experimental condition and playback stimulus. Significant factors are in bold. Only the stimulus type affected orientation angles.

	Initial orientation			Final orientation		
	df	F	P	df	F	P
Experiment (presence or absence of cricket in jar)	1,193.1	0.6301	0.43	1,162.3	2.5947	0.11
Stimulus (Cr, N, S)	2,179.8	2.3955	0.09	2,151.1	5.3007	<b>0.006</b>
Stimulus × experiment	2,179.3	0.5337	0.59	2,151.8	0.9806	0.38
SVL	1,41.93	1.38	0.25	1,42.19	2.3842	0.13
Body condition	1,51.4	0.0192	0.89	1,47.25	0.5764	0.45
Observer & random		Overlap 0			Overlap 0	
Female ID & random		Overlap 0			Overlap 0	

stimuli, orientation angles should not be uniformly distributed, but instead should be directed toward the stimulus. In cases where Rayleigh tests indicated nonuniform distribution, we used V-tests to test for distribution in a specified mean direction. After visual inspection of the polar histograms, we set the expected mean for the V-tests at either 0° (toward the speaker)

or 180° (away from the speaker). We used Oriana 3.21 (Kovach Computing Services, Anglesey, Wales, U.K.) to calculate test statistics.

We further tested which factors affected the speed of approach using a mixed model with response time as test variable; experiment, treatment stimulus, their interaction, frog SVL, and frog body condition as fixed factors; and frog identity and observer as random factors.

RESULTS

Frogs did not approach playbacks of prey sound, nor did the prey sound appear to aid frogs in finding prey. We did not find support for the predatory eavesdropping hypothesis. Frogs did not ignore acoustic stimuli, however, because they moved away from the sound source in some trials.

Across all treatments, 75% of frogs left the release cage and contributed to the initial orientation data set, and 62.2% of frogs reached the arena wall and contributed to the final orientation and response time data set.

Orientation was affected by treatment stimulus (Table 1; Fig. 1A,B). However, in the cricket song and noise treatments, frogs tended to walk away from the source of the stimulus. Furthermore, adding an acoustic stimulus to the presentation of a live cricket did not improve orientation (Table 1). Analysis using circular statistics corroborate these results (Fig. 2); orientation angles were distributed uniformly in the silent treatments in both experiments (absence or presence of cricket in jar; in both cases,  $r < 0.21$ ; Rayleigh test:  $Z < 1.34$ ,  $P = 0.27$ ) and in the noise treatment of the experiment that presented the auditory stimuli together with a live cricket ( $r < 0.21$ ; Rayleigh test:  $Z < 1.18$ ,  $P = 0.31$ ). Orientation angles were nonuniform in response to the noise treatment in the experiment that only presented auditory stimuli ( $r < 0.29$ ; Rayleigh test:  $Z < 3.196$ ,  $P = 0.04$ ) and to the cricket song treatment in both experiments (absence or presence of cricket in jar; in both cases,  $r < 0.29$ ; Rayleigh test:  $Z < 2.52$ ,  $P = 0.08$ ); however, in all cases in which orientation angles were nonuniform, they were directed away from the location of the speaker (in all cases,  $V > 0.203$ ,  $\mu > 1.57$ ,  $P = 0.058$ ).

Angular deviation values of initial and final orientation were highly correlated (Table 2), suggesting that orientation was decided largely once the frogs left the release cage.

For response time, there was an interaction between experiment and stimulus treatment (Table 3; Fig. 1C). Frogs moved at similar, intermediate speeds in both silent treatments, but they moved faster during presentation of the noise stimulus in the experiment without the cricket in a jar, and faster during presentation of the cricket stimulus during the experiment that did present a cricket in jar.

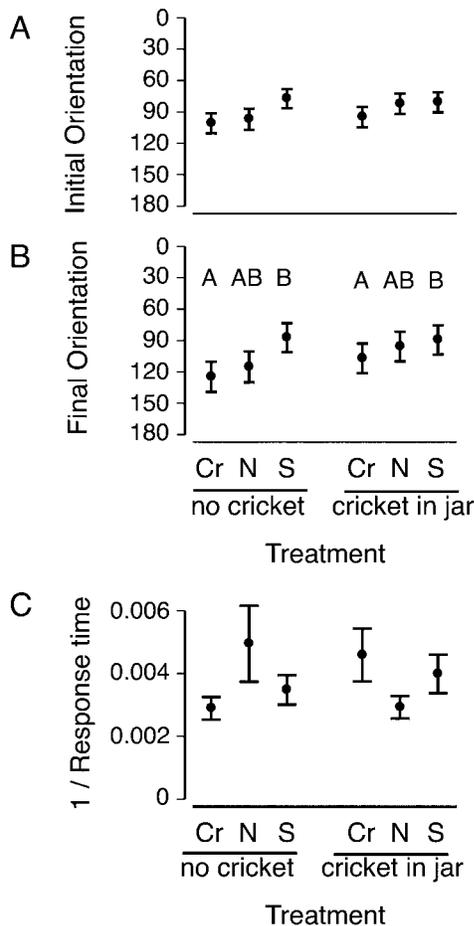


FIG. 1. Responses of Green Treefrogs when presented with cricket song (Cr), noise (N), and silence (S), in the absence (left) and presence (right) of a cricket in jar. Initial (A) and final (B) orientation was never directional toward the speaker presenting treatment stimuli. Speaker position at 0°; orientation measured as angular deviation (least square means ± SE). Post hoc Tukey's honestly significant difference tests indicate that final orientation during playbacks of cricket song and silence was significantly different from each other, whereas orientation during playback of noise was intermediate and not significantly different from the behavior in response to either cricket song or silence. (C) Response time differed across treatments; response time data are inverse transformed such that higher values indicate faster speed.

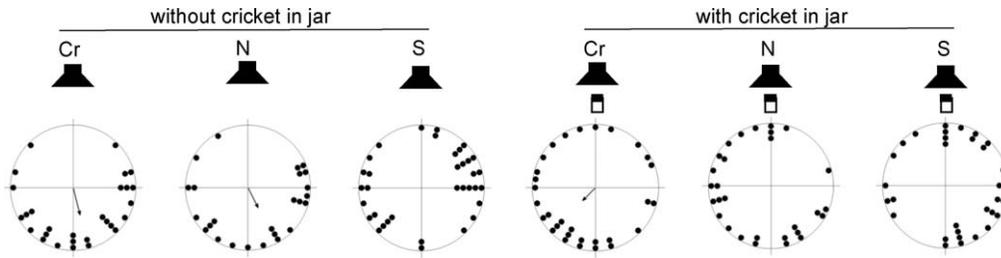


FIG. 2. Polar diagrams showing the final orientation angles in relation to the position of the speaker (at 0°; top of diagram); each dot represents one frog; treatments in which orientation angles were significantly clustered are indicated by an arrow denoting the length and direction of the mean vector. Note that frogs moved randomly in the silent treatments but oriented away from the sound source in most trials involving acoustic playback.

DISCUSSION

Most foraging in frogs is visually mediated (Ingle, 1968; Ewert, 1987; Freed, 1988; Buchanan, 1998); yet, it seems intuitive that they might take advantage of their highly developed auditory system (Schoffelen et al., 2008) to aid in prey acquisition. Studies investigating the importance of anuran hearing outside the contexts of mate choice are rare, however, and there is mixed support for the use of hearing in other behavioral contexts. In our experiments, female Green Treefrogs did not show phonotaxis to prey sounds, but they were not indifferent to acoustic stimuli, because they moved away from the sound source in two cricket song treatments (in both experimental conditions) and in one noise treatment (in experimental condition in which no visual cue was provided).

Although predatory eavesdropping is taxonomically widespread (Zuk and Kolluru, 1998), not all species take advantage of such sources of information; or if used, they do not use them all the time. For example, predators with a sit-and-wait foraging strategy may be less prone to use eavesdropping compared with active foragers that could use prey signals to guide their foraging movements. We are aware of only one additional study that conducted experiments that can be interpreted for testing the predatory eavesdropping hypothesis in anurans: Taylor (2001) tested the role of visual and auditory senses involved in prey detection in Southern Toad (*Bufo terrestris*) using live crickets and cricket songs played from a loudspeaker. Neither the active forager *B. terrestris* (Taylor, 2001) nor the sit-and-wait predator *H. cinerea* (this study) approached sounds of potential prey; thus, there is no evidence of a relationship between predatory eavesdropping and foraging strategy in anuran amphibians.

Although anurans do not seem to eavesdrop on sounds associated with prey, several studies have found that they eavesdrop on sounds associated with animals that may prey on them (Bernal et al., 2007; Llusia et al., 2010; Bonachea and Ryan, 2011; but see Schwartz et al., 2000). This pattern of attention to

predator cues, but inattention to prey signals is in line with the life-dinner principle (Dawkins and Krebs, 1979) that suggests that selection for prey avoiding predators is stronger than selection for predators to eavesdrop on prey. Prey incur a lethal cost when preyed upon, but a failed predation attempt only results in a relatively small fitness loss for the predator (Dawkins and Krebs, 1979).

As expected, frogs did not show directional preferences during silent control trials. In contrast, during trials involving either acoustic stimulus, frogs frequently moved away from the sound source. The fact that frogs reacted the same way to cricket song and to white noise (i.e., with avoidance) suggests that they may not have perceived the cricket song stimulus as being associated with prey. Furthermore, frogs moved faster during some cricket song and noise trials compared with trials in which no sound was presented, indicating that the noise or cricket song stimuli may have elicited an escape response. However, even the “fast” response times associated with acoustic playbacks were around 200 sec, much slower than the frogs would need to cover the 1-m distance from release cage to arena wall (the shortest recorded time in our trials was 5 sec). It is also about 3 times slower than the average time females of this species take to approach speakers during trials testing preferences for conspecific advertisement calls (Höbel, 2010). Thus, rather than a directed escape response, frogs showed a more generalized avoidance of sound. Whether this is an adaptive response, for example, to avoid areas of high ambient noise where they cannot hear approaching predators remains to be tested.

Confidently documenting the absence of a behavioral response is challenging. To identify species of anurans for which this behavior is truly absent, additional studies on predatory eavesdropping are required. Testing different types of stimuli (e.g., prey calls, prey movement cues, chemical and

TABLE 2. Regression of initial and final orientation of Green Treefrogs inside the testing arena. Significant comparisons are in bold. Initial orientation was always a good predictor of final orientation, suggesting that frogs maintained the directions they had chosen when leaving the release cage.

Treatment stimulus	Experiment 1 (no cricket in jar)		Experiment 2 (with cricket in jar)	
	Slope	P	Slope	P
Cricket song	0.529	<b>&lt;0.0001</b>	0.581	<b>0.0005</b>
Noise	0.491	<b>0.004</b>	0.540	<b>0.003</b>
Silence	0.501	<b>0.0005</b>	0.533	<b>0.004</b>

TABLE 3. Analysis of response time of Green Treefrogs in relation to variation in experimental condition and playback stimulus. Significant factors are in bold. The significant stimulus × experiment term indicates that it was a different stimulus that elicited the fastest responses in each of the two experiments.

	df	F	P
Experiment	1,140.1	0.047	0.83
(absence or presence of cricket in jar)			
Stimulus (Cr, N, S)	2,136.4	0.0495	0.95
Stimulus × experiment	2,139.7	4.72	<b>0.01</b>
SVL	1,8.91	1.3075	0.28
Body condition	1,44.19	1.5815	0.22
Observer & random	No overlap 0		
Female ID & random	Overlap 0		

visual cues) from a range of potential prey items might help identify prey cues to which frogs attend. It would also be good to test males and females and to conduct trials both outside and during the breeding season. Reproductive state seems to influence the ability of acoustic signals to stimulate the auditory system in frogs (Arch and Narins, 2009), and the lack of response to prey signals that we observed during our study may be a consequence of the auditory system being down-regulated outside the breeding season (when our study was conducted). Finally, it is possible that responses of anurans to certain acoustic cues are context specific. For example, toads only flee from otter sounds during the hours of highest predator activity (Llusia et al., 2010), and Reedfrogs (*Hyperolius nitidulus*) only flee from the sound of brushfires during the peak of the fire season (Grafe et al., 2002). Such context specificity would make it more difficult to document eavesdropping because it would require additional information on predator or prey activity patterns to test the eavesdropping hypothesis under the most relevant ecological conditions. The hint at context-specific behavior suggests new and interesting avenues for research on anuran communication.

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