

# Calls of Recently Introduced Coquí Frogs Do Not Interfere with Cricket Phonotaxis in Hawaii

Marlene Zuk<sup>1</sup> · Jessie C. Tanner<sup>1</sup> ·  
Elizabeth Schmidtman<sup>1</sup> · Mark A. Bee<sup>1</sup> ·  
Susan Balenger<sup>1,2</sup>

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**Abstract** Acoustically-signaling animals such as crickets may experience interference from environmental noise, a particular concern given the rise in anthropogenic or other novel sources of sound. We examined the potential for acoustic interference of female phonotaxis to calling song in the Pacific field cricket (*Teleogryllus oceanicus*) by invasive coquí frogs (*Eleutherodactylus coqui*) in Hawaii. The frogs were introduced to Hawaii from Puerto Rico in the 1980s. When female crickets were exposed to male calling songs with and without simultaneous broadcast of a coquí chorus, they were equally likely to move toward the cricket song, regardless of the location of the frog sound (ground level or above ground). Unlike some species of frogs and birds, *T. oceanicus* do not appear to experience acoustic interference from an introduced signaler, even though the introduced species' calls subjectively seem to be masking the crickets' songs.

**Keywords** Acoustic interference · introduced species · phonotaxis

Animals that signal acoustically run the risk of interference from other noises in the environment, both abiotic (traffic, running streams) and biotic (conspecific or heterospecific signals) (Brumm 2013). Interest in the effect of anthropogenic sound on animal signaling has been growing, with discoveries of underwater anthropogenic noise potentially interfering with a wide range of activities in both vertebrates and invertebrates

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✉ Marlene Zuk  
mzuk@umn.edu

<sup>1</sup> University of Minnesota, Department of Ecology Evolution, and Behavior, 1479 Gortner Avenue, Saint Paul, MN 55108, USA

<sup>2</sup> Present address: Department of Biology, University of Mississippi, 214 Shoemaker Hall, University, MS 38677, USA

(Sabet et al. 2016). Alterations of bird vocalizations in the face of traffic noise have been shown to reduce reproductive success (Halfwerk et al. 2011), and urban noise can make certain bird song frequencies harder to detect at a distance (Pohl et al. 2009). In transmission of black-capped chickadee vocalizations, ambient noise depressed both signal-to-noise ratios and detection of signal features (LaZerte et al. 2015). Even aspects of habitats that do not appear overtly noisy can cause sound interference; LaZerte et al. (2015) found that open urban green spaces were noisier than rural forested areas.

Invasive species have been a particular subject of scrutiny for their potential to interfere with the signals of resident species. Several studies have examined the role of introduced frogs and toads on native amphibian reproductive behavior. An invasive frog in Brazil appears to have caused changes in the call structure of native frogs (Both and Grant 2012), and Llusia et al. (2013) found that invasive American bullfrog (*Rana catesbeiana*) calls propagated more efficiently than the calls of native species in the Iberian Peninsula, potentially interfering with the native species' communication. Invasive cane toads (*Rhinella marina*) in the Australian tropics appeared to cause shifts in the call structure of one, but not another, species of native frog (Bleach et al. 2015).

Much of the work on interference with acoustic communication has focused on vertebrates, which are generally more plastic in their signaling behavior than invertebrates and hence more likely to alter individual calling behavior in response to noise. Little work has been done, however, on the potential for anthropogenic or other novel forms of noise to interfere with the calls of invertebrates such as singing insects (but see Lampe et al. 2012 and Costello and Symes 2014). Singing insects do, of course, contend with ambient noise, and many species call in mixed-species groups, where the potential for interference is great (Schmidt and Römer 2011). Insects' relative inflexibility compared with vertebrates may even put them at greater risk of not being able to accommodate such interference. Schmidt and Römer (2011) suggest that orthopterans may be able to overcome such interference through sharply tuned frequency selectivity, spatial release from masking (in which the location of noise can ameliorate its likelihood of interfering with signal reception or processing), and a neuronal gain control mechanism that enhances the contrast between responses to the potential interference and the signaler. However, this ability has not been tested in the context of introduced or anthropogenic noise.

Here we take advantage of the opportunity to examine the potential for interference in cricket acoustic communication by an introduced frog. The coqui frog, *Eleutherodactylus coqui*, was introduced to Hawaii from Puerto Rico in the 1980s, and has since spread to over 275 sites (Woolbright et al. 2006). The frogs emit two-part calls, with a “co” syllable and a “qui” syllable. Woolbright et al. (2006) found that population densities of *E. coqui* on the island of Hawaii were three times greater than those in Puerto Rico, producing sound pressure levels of more than 70 dB within a chorus in some areas. The Pacific field cricket, *Teleogryllus oceanicus*, was introduced to Hawaii by humans at least 140 years ago (Kevan 1990), where it occurs in some of the same disturbed habitats more recently occupied by *E. coqui*. Like other crickets, *T. oceanicus* females find their mates by orienting to their calling song, and we were interested in whether noise from *E. coqui* interfered with cricket phonotaxis. Because *E. coqui* call from locations 1–15 m above the ground in bushes and trees (Drewry and Rand 1983), while crickets call from ground level, we tested the ability of female crickets to orient to male calling song with and without simultaneous broadcast of *E. coqui* calls from both ground level and 1 m above

the ground. If coqui frog choruses interfere with phonotaxis by *T. oceanicus* females, we expected the crickets to exhibit successful phonotaxis less often and more slowly in the presence of frog chorus noise compared with quiet conditions.

## Methods

### Colony Maintenance and Cricket Selection

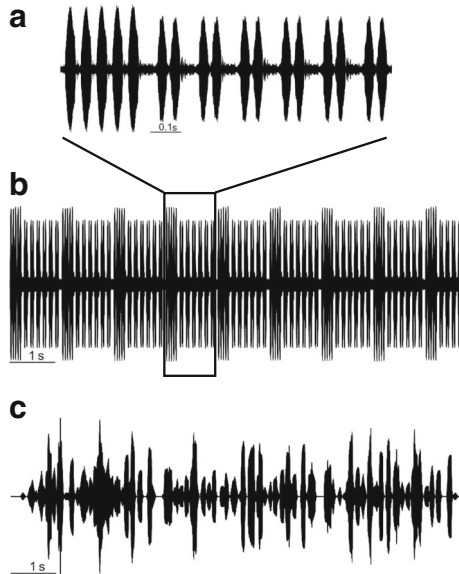
Virgin female *T. oceanicus* descendants from a population originating from Hilo, HI, were used in this experiment. The lab colony was established in 1991 and is supplemented annually with offspring from eggs of field-caught females. The sites where we collect eggs now also have populations of the frogs. A minimum colony size of 100 breeding pairs is maintained at all times. To control for maternal effects, we bred two generations of crickets in the lab, that is, we used F2 offspring of the most recent field-caught females. Crickets are housed in 15-L containers and stored in insect growth chambers (Caron model 6025–2, Marietta, OH, USA) that maintain 26 °C, 75% relative humidity, and a photo-reversed 12 L:12D light cycle.

Once juveniles had visible ovipositors and could be sexed, females were separated from the colony and housed together in a group enclosure. Juveniles were checked daily for eclosions. Newly eclosed adult females were isolated and housed in individual cups until behavioral testing. All behavioral testing occurred during the scotoperiod, the time of increased cricket activity, between days 6 and 8 after eclosion.

### Acoustic Stimuli

The calling song of *T. oceanicus* consists of a trill-like “long chirp” segment of between 3 and 9 pulses, followed by a sequence of two-pulse “short chirps” (Fig. 1a). We constructed calling song models following the methods of Simmons et al. (2001). Briefly, the calling song of a *T. oceanicus* male was recorded in the field near Hilo, HI, at 25 °C, and a single pulse was excised from each of the long chirp and short chirp segments of the calling song. We then concatenated pulses to generate an entire “standard” calling song with constant carrier frequency (4810 Hz) and mean pulse number and temporal call properties measured in the Hilo population (Zuk et al. 2008). This single calling song (representing one average male) was repeated for the duration of all behavior trials.

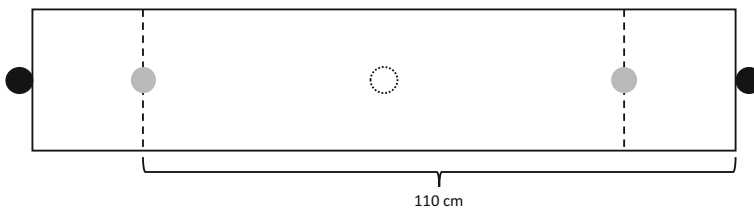
We created an artificial chorus of *E. coqui* using synthetic calls having spectral and temporal values similar to those reported in the study of Hawaiian *E. coqui* by Benevides and Mautz (2014). We first used Adobe Audition 3.0 (Adobe Systems, Inc., San Jose, CA, USA) to create a single synthetic version (16 bit, 44.1 kHz sampling rate) of the two-note “co-qui” call in which the “co” and “qui” notes were 115 ms and 133 ms in duration, respectively, and were separated by an inter-note interval of 273 ms. The “co” note consisted of a frequency-modulated tone that swept downward and linearly in frequency from 1525 Hz to 1470 Hz and had a center frequency of 1497 Hz. The “qui” note was also a frequency modulated tone, but it swept upward and linearly in frequency from 2561 Hz to 2843 Hz and had a center frequency of 2702 Hz. The amplitude envelopes of both notes were shaped to visually approximate those of



**Fig. 1** Waveforms of stimuli used in phonotaxis trials. **a** A single *T. oceanicus* song. **b** A 10-s sample of *T. oceanicus* song. **c** A 10-s sample of the artificial *E. coqui* chorus

the calls depicted in Fig. 2 of Benevides and Mautz (2014). The envelope of the “co” note was symmetrical and linear, with rise and fall times of 57 ms. The “qui” note had a rise time of 53 ms that reached 50% amplitude within 4 ms of the onset of the note, and a fall time of 60 ms that declined to 50% amplitude 46 ms prior to the offset of the note. The peak amplitude of the “co” note was attenuated so that it was 10 dB lower than that of the “qui” note. We used Audition to create two additional “pitch-shifted” versions of this call in which the temporal properties were the same but all frequencies were shifted either upward or downward by 5%. The resulting frequencies correspond to approximately  $\pm 1$  standard deviation around the mean frequency.

The artificial chorus was created using Matlab® R2014a and consisted of a 5-min sequence of 24 simulated calling males, each producing its own sequence of randomly timed calls. For each simulated male, the timing of the onset of each successive call in his sequence was determined by drawing a random call repetition period from a normal distribution based on the mean and standard call repetition period reported by



**Fig. 2** Diagram of testing arena, overhead view. *Solid black circles* indicate speakers placed on the semi-anechoic chamber floor, from which we broadcast cricket song and, in the co-located condition, the artificial frog chorus. *Dashed circle* indicates speaker mounted 1 m above the arena floor, from which we broadcast the artificial frog chorus in the separated condition. *Solid grey circles* indicate release points for test subjects

Benevides and Mautz (2014). A randomly chosen inter-call interval was used to offset the first call in each simulated male's sequence of calls. Thus, all 24 sequences had randomly timed calls. Sequences for three subgroups of eight simulated males were produced using one of the three versions of the synthetic call differing in frequency (i.e., pitch shifts of  $-5\%$ ,  $0\%$ ,  $+5\%$ ). Within each subgroup of eight males, two males each had their entire sequence of calls attenuated by 0,  $-4$  dB,  $-8$  dB, or  $-12$  dB to simulate males calling from different distances.

## Experimental Design

Phonotaxis trials were conducted in a rectangular cardboard arena (155 cm length  $\times$  34 cm width  $\times$  32 cm height; Fig. 2) placed in a temperature-controlled, semi-anechoic sound chamber (2.8 m  $\times$  2.3 m  $\times$  3.1 m, length  $\times$  width  $\times$  height; Industrial Acoustics Company, IAC, Bronx, NY, USA). Trials were conducted at  $24 \pm 1$  °C. Each end of the arena contained an acoustically transparent window (10 cm  $\times$  7.5 cm, width  $\times$  height) immediately outside of which a speaker (Mod1, Orb Audio, New York, NY, USA) was placed on the floor of the anechoic chamber. A second, overhead speaker was suspended 1 m above the center of the arena floor.

We broadcast signals using Adobe Audition 3.0, running on a Dell Optiplex 980 PC (Dell Computer Corporation, Round Rock, TX, USA). Sounds were output through a MOTU model 16A 16-channel sound card (MOTU, Inc., Cambridge, MA, USA) and then amplified using Crown XLS1000 High-Density Power Amplifiers (HARMAN Professional, Northridge, CA, USA). We calibrated the playback sound pressure levels (SPL, re 20 uPa, RMS, C-weighted) of cricket song and artificial frog choruses on the arena floor at a distance of 1 m from the playback speaker using a Bruël and Kjær 2250-L sound level meter (Bruël and Kjær, Norcross, GA, USA). We presented cricket song at an overall playback level of 80 dB SPL ( $LCF_{max}$ ), which approximates the level of a male's calling song (Bailey and Zuk 2008). The two spectral peaks of the artificial frog choruses were calibrated separately in software using the 1.6 kHz and 2.5 kHz bands of a 32-band graphic equalizer. Using the 1/3-octave filter of the sound level meter, the 1.6 kHz band ("co") was adjusted to 80 dB SPL ( $LCF_{max}$ ) and the 2.5 kHz band ("qui") was adjusted to 90 dB ( $LCF_{max}$ ). These 1/3-octave sound levels approximate the sound levels of spectral bands corresponding to the "co" and "qui" notes of natural choruses (Narins 1982).

In all behavioral trials, *T. oceanicus* calling song was broadcast from a speaker on the arena floor. In the control condition, *T. oceanicus* calling song was broadcast in the absence of an artificial frog chorus, simulating allopatry with *E. coqui*. In the co-located condition, *T. oceanicus* calling song was broadcast simultaneously with an artificial *E. coqui* chorus, from the same speaker. In the separated condition, the artificial *E. coqui* chorus was broadcast from 1 m overhead.

We used a within-subjects design in which female *T. oceanicus* were tested in one trial per day for three consecutive days, until all three treatments had been completed. We controlled for presentation order by randomizing trial order; we controlled for side bias by randomizing which side of the arena was used for playback of cricket song. Most females ( $n = 28$ ) experienced all three treatments, six females experienced two of three treatments, and eight females experienced one treatment. A total of 104 trials were run, representing data from 42 individual females.

## Trial Procedure

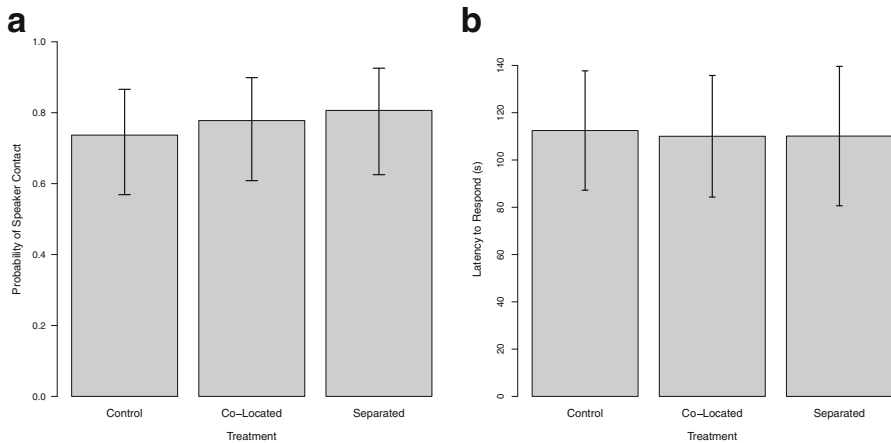
To begin each trial, a female cricket was placed under a cup at one of two possible release points, each located at a distance of 110 cm from a playback speaker. Test subjects were given two minutes in which to acclimate to the testing arena in silence. Playback began at the end of the acclimatization period; simultaneously, the subject was released from the cup by means of a rope-and-pulley system operated from outside the chamber. All trials were carried out under infrared (IR) light (Tracksys, Ltd., Nottingham, England) and observed using an IR-sensitive video camera (Panasonic WV-BP334; Panasonic Corporation of North America, Secaucus, NJ, USA) mounted from the ceiling of the sound chamber, directly above the test arena. Trials were broadcast via closed-circuit television system to an observer outside the sound chamber, who scored the trials in real time by hand. Trials ended when the subject made antennal contact with the speaker (“speaker contact”) or else at the end of five minutes. We recorded the response latency as the number of seconds that elapsed between releasing the subject from the cup and speaker contact. If a female did not make contact with the speaker before the end of the trial, she was assigned a latency value of 300 s.

## Analyses

All analyses were carried out in R version 3.2.3 (R Foundation for Statistical Computing, Vienna, Austria). We used generalized estimating equations (GEE; Hardin and Hilbe 2012) to model the effect of acoustic treatment on two measures of female responsiveness: probability of making speaker contact and response latency. For both models, we used exchangeable correlation structures, which assume that the correlations between repeated measurements are homogenous. We validated our choice of correlation structure using the Quasi-Likelihood under the Independence Model Criterion (QIC; Pan 2001). The probability of making speaker contact was modeled as a binomial variable (logit link function), while response latency was modeled as a Gaussian response (identity link function). Statistical inference for model parameters was based on Wald  $\chi^2$  statistics calculated using the *geepack* package in R (Halekoh et al. 2006).

## Results

Compared to the cricket-only control condition, subjects were no less likely to make contact with the speaker in the co-located condition (Fig. 3a;  $\beta = 0.19$ ,  $\chi^2 = 0.35$ ,  $p = 0.67$ ) or the separated condition (Fig. 3a;  $\beta = 0.35$ ,  $\chi^2 = 0.57$ ,  $p = 0.43$ ). Response latencies for the subset of subjects that made contact with the speaker are shown in Fig. 3b ( $n = 81$  tests, 39 unique subjects). There was no difference in response latencies between the cricket-only control condition and either the co-located ( $\beta = -3.36$ ,  $\chi^2 = 0.04$ ,  $p = 0.85$ ) or separated ( $\beta = -0.461$ ,  $\chi^2 = 0.00$ ,  $p = 0.98$ ) conditions. There was no qualitative difference in the results of the analysis when we modeled the full dataset (including females that did not touch, but were assigned a latency of 300 s) rather than the subset.



**Fig. 3** **a** The probability that a subject made contact with a speaker by acoustic treatment. Error bars show 95% Clopper-Pearson (“exact”) binomial confidence intervals. **b** Mean response latency in seconds by acoustic treatment. Error bars show 95% confidence intervals

## Discussion

Unlike some species of frogs and birds, *T. oceanicus* do not appear to experience acoustic interference from an introduced signaler, even though the introduced species’ calls subjectively seem to be masking the crickets’ songs. Female crickets were able to locate a conspecific calling song equally well, regardless of the presence or location of a competing chorus of *E. coqui* frogs.

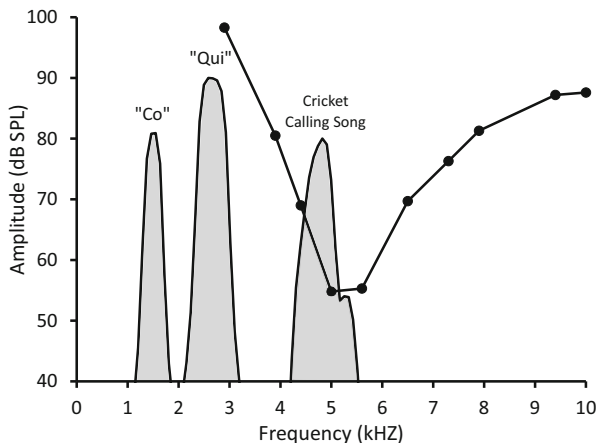
Why might this be the case? As Römer (2013) notes, unlike katydids and other tettigoniids, crickets in the subfamily Gryllinae have pure-tone calling songs at frequencies from 2 to 9 kHz (Bennet-Clark 1998). Their hearing is particularly sensitive between the ranges of 4 to 5 kHz and 25 to 50 kHz (Moiseff et al. 1978); Boyd and Lewis (1983) found that the best frequency for *T. oceanicus* hearing was 4.74 kHz. Despite both the *T. oceanicus* and *E. coqui* calls being easily audible to humans, cricket phonotaxis does not appear to be disrupted by the calling frequencies of the *E. coqui*, which range from 1.5 to 2.7 kHz when in sympatry with the cricket population tested (O’Neill and Beard 2011; Benevides and Mautz 2014). Throughout most of the range of *T. oceanicus*, there are few or no acoustic competitors with calls in their most sensitive frequency range (Otte and Alexander 1983), suggesting that little selection on this species’ ability to discern their own calling song from that of other organisms is likely to have occurred.

The lack of coqui-generated noise interfering with the reception of *T. oceanicus* calling song can be explained by a sensory mechanism called the “matched filter” (von der Emde and Warrant 2016). A matched filter reduces interference or masking by any sound outside of the frequency range(s) of interest (Römer 2016; Narins and Clark 2016). In many gryllines, sensitivity peaks occur both near the major frequency component of the calling song as well as in the ultrasonic range to detect echolocation signals of bats (Popov and Shuvalov 1977, Moiseff et al. 1978). The introduction of environmental sounds by invasive species therefore will not necessarily interfere with communication in a species using a narrow frequency channel for communication that



is already outside the range of the introduced signal before the invasive's introduction (Schmidt and Römer 2011). Matched filtering by the *T. oceanicus* auditory system can explain why the sounds of the frogs had no discernible impact on cricket behavior. For example, although a nominal signal-to-noise ratio of  $-10$  dB (cricket song relative to the artificial chorus) might be expected to generate substantial auditory masking, the animal's audiogram must also be considered. The cricket song, which we presented at 80 dB SPL at the animal's release point, was approximately 25 dB above the animal's behavioral threshold at the frequency of the cricket song (Fig. 4). In contrast, the frequencies of the "co" and "qui" notes in our artificial chorus were almost certainly 10 dB or more below the animal's behavioral threshold at the animal's release point, which means that the spectral peaks of the frogs' calls fall well below both the frequency of the cricket's songs and the range of its most sensitive hearing, which is tuned to its own song (Fig. 4). Interestingly, *Chorthippus biguttulus* grasshoppers collected in noisy roadside habitats had higher calling frequency than those collected in quieter areas, although the main frequency peak of the traffic noise was much lower than that of typical male calling songs; it is possible that the grasshoppers, unlike our crickets, could still hear the road noise (Lampe et al. 2012).

Our results offer a more optimistic perspective on the increasingly popular notion that introduced species will interfere with the communication of native acoustically-signaling organisms. As Schmidt and Römer (2011) note, "without knowledge of the receiver properties and the spatial release mechanisms the detrimental effect of noise may be strongly overestimated." They were referring to the "cocktail party" phenomenon, in which individual sounds can be difficult to discern in a group of signalers, and were cautioning against assuming that crowded environments necessarily make signal detection more difficult (Bee and Micheyl 2008), but the same conclusion can be applied to our system. It is possible that the narrow frequency tuning by many singing insects provide better abilities to cope with the potential for interference than their vertebrate counterparts.



**Fig. 4** Behavioral audiogram showing the average frequency sensitivity (black circles) of *Teleogryllus oceanicus*, measured as the threshold sound amplitude for eliciting steering response behavior (adapted from Moiseff et al. 1978, Fig. 2). Also shown are the power spectra for the artificial frog chorus ("co" and "qui" notes) and the *T. oceanicus* calling song plotted at the calibrated amplitudes used in this study (areas shaded in gray)



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