

## Communicative Significance of the Two-Note Call of the Treefrog *Eleutherodactylus coqui*

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**Summary.** Male treefrogs, *Eleutherodactylus coqui*, on the island of Puerto Rico produce a two-note “Co-Qui” advertisement call throughout most of the year. To determine the communicative significance of two notes in this species’ call, natural and synthetic acoustic stimuli were broadcast to calling males in the rain forest.

1. When the playback intensity of the natural or synthetic two-note call exceeds a threshold level, males answer by uttering just a “Co” note about 42% of the time.

2. Reversing the stimulus note sequence, namely “Qui-Co”, is as effective as the normal “Co-Qui” sequence in evoking the male’s one-note response.

3. Playback of the “Qui” note alone has relatively little effect on male calling behavior.

4. The “Co” note presented alone is equally effective as the complete natural call in evoking the one-note response from a male.

5. The duration and frequency content of the “Co” note in a natural call are optimal in evoking a male’s one-note response.

ing males are classed as territorial calls (Bogert, 1960) or encounter calls (McDiarmid and Adler, 1974); these calls presumably function to maintain spacing between males by warning an intruder that he is approaching another male.

On the other hand, evidence is beginning to accumulate which indicates that in some species a particular vocalization might serve more than one function. For instance, Emlen (1968) and Wiewandt (1969) found that playback of a recorded “mating call” elicited approach of territorial male bullfrogs (*Rana catesbeiana*). One possible interpretation of these observations is that in ranids the mating call might also serve a territorial function. A more recent experimental study by Whitney and Krebs (1975) has shown that the mating call of the Pacific treefrog, *Hyla regilla*, also functions in maintaining spacing; more males settled in an unoccupied area than in one in which recorded mating calls were broadcast through loudspeakers.

The calls of many neotropical anurans consist of a sequence of different notes. These notes are distinct and often highly stereotyped (Narins and Capranica, 1977). Is it possible that each note within a call conveys a separate behavioral significance? In our study we have investigated this question in one particular species, *Eleutherodactylus coqui* (Thomas).

The geographic range of this leptodactylid frog is restricted to the island of Puerto Rico and to several small introduced populations in Miami, Florida and also in St. Thomas and St. Croix, U.S. Virgin Islands (Austin and Schwartz, 1975; Schwartz and Thomas, 1975). Males emit a two-note call (“Co-Qui”) from sunset until midnight or shortly thereafter (Narins and Capranica, 1977). The first note, “Co”, is a constant-frequency tone of about 1100 Hz lasting approximately 100 ms. It is followed by a variable-length pause of between 250–300 ms. The second note, “Qui”, lasts nearly 170 ms and sweeps upward in

### Introduction

Most studies of anuran vocal behavior have suggested that different vocalizations in a species’ repertoire have a distinct communicative significance. For example, calls made by males at appropriate breeding sites during the reproductive season are termed mating (advertisement) calls since they have been shown, at least in some species, to attract females (Martof and Thompson, 1958; Blair, 1958). Other vocalizations occurring in close-range encounters between neighbor-

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frequency from about 1800 Hz to approximately 2100 Hz. The call is repeated once every three to four seconds. Each male typically calls from the same site for many nights in succession. Preferred calling sites for *E. coqui* are the trunks and branches of *Heliconia* and *Musa*, vertical mud banks along roadsides, fallen tree trunks or, frequently, within the folds of dead *Cecropia* trees. Although males have been reported to call from heights of 15 m above the ground (Drewry, 1970), rarely was a male heard calling from a height greater than about 5 m during our study.

Male *E. coqui* do not aggregate to form breeding choruses, but rather spread themselves out within a forested area; neighbouring males are usually separated by at least three meters. In our study we noted that whenever one calling male approached another, so that the received intensity of the intruding male's call reached a sufficient level, then the resident male typically changed his vocal pattern. Instead of continuing to produce the two-note call, the resident oriented toward the intruder and uttered only the Co note, omitting the Qui note. Further interaction resulted in a "bout" in which both males emitted only the Co note. Previous studies have reported that if a calling male was physically removed from his perch and placed within about 0.6 m of a second calling male, the resident initiated a biting, butting attack on the intruder (Reyes Campos, 1971). In some cases, males have been observed to travel 10–15 feet to attack another calling male (Drewry, 1970). Thus the Co note alone is used during male-male encounters which suggests that it plays a role in territorial maintenance.

We conducted acoustic playback experiments in order to determine the features of the two-note call of *E. coqui* which evoke the one-note response during male-male calling interactions. These experiments involved playback of natural and synthetic calls to males while simultaneously monitoring their vocal responses.

## Materials and Methods

This study was conducted near El Yunque Peak (altitude 900 m) and Pico de Este (alt. 1075 m) in the Luquillo National Rain Forest, Puerto Rico in May, 1973 and in August, 1974. Calling male *E. coqui* were located in their natural habitat and their calls were recorded using a Nagra IV-D or a Nagra IV-S tape recorder and a Sennheiser MKH 815 directional condenser microphone. During May, 1973 a second tape recorder (Nagra IV-D) was used to present pre-recorded acoustical stimuli through a Nagra DH speaker-amplifier, while during August, 1974 acoustic stimuli were delivered from a portable animal sound synthesizer (see Appendix I).

Males chosen for study were relatively isolated from other

calling frogs to ensure that their vocal behavior was selectively affected by our playbacks. A further consideration in a choice of a particular male was the presence of a reasonably direct path between the recording microphone and his calling site. The speaker-amplifier was placed no closer than one meter to the calling male and directed toward him. The intensity of the acoustic stimulus was measured with an impulse precision sound-level meter (Bruel and Kjaer 2204) and was adjusted to a level typical of a calling male (80 dB SPL at a distance of two meters).

### Acoustic Stimuli

A series of natural and synthetic sounds were played back to calling males; the use of synthetic sounds permitted precise manipulation of individual stimulus parameters. Five stimuli, selected from 7 pre-recorded stimulus tapes or generated by the sound synthesizer, were presented in random order to each male and the responses evoked by these stimuli were recorded. The stimuli consisted of: (1) the natural call of a male *coqui*; (2) a synthesized version of the natural call; (3) a "sequence-reversed" synthetic call in which the order of the two notes was inverted; (4) a "duration-reversed" synthetic call in which the durations of the two notes were interchanged; (5) a "sequence and duration reversed" synthetic call; (6) the Co note alone; and (7) the Qui note alone.

Normally the spontaneous calling of each male was recorded for a period of 2.5 min, followed by a 3-min stimulus presentation period during which one of the stimuli was presented once every 4 s. Following this stimulus presentation, the spontaneous calling was again recorded for 2.5 min and then another stimulus was presented. This procedure was continued until all five stimuli had been tested and a concluding 2.5 min of spontaneous calling recorded. If a male showed a particularly high level of responsiveness, the entire sequence was presented again, either repeating the stimuli from the first sequence or substituting new ones. The height of the male above the ground, the distance of the microphone and speaker-amplifier from the animal, the orientation of the animal, a short description of the calling site, air temperature, time, altitude and weather conditions were noted during each playback experiment.

### Response Criteria

In general, the acoustic stimuli elicited two classes of vocal responses: 1) a two-note Co-Who call which tended to alternate with the stimulus and 2) a one-note Co response which appeared to be time-locked to the stimulus. The responses for all of the acoustic playback experiments were scored as follows, unless otherwise stated: the percentage  $p_1$  of one-note responses elicited by playback of a typical natural call during its 3-min presentation to each male was determined. Then,  $p_1$  values for all of the individuals tested with this same call were averaged, obtaining  $\bar{p}_1$ . In a similar fashion,  $\bar{p}_2, \bar{p}_3 \dots \bar{p}_7$  were obtained for the remaining stimuli. These values were then pair-wise tested for differences with  $\bar{p}_1$  using a  $2 \times 2$  Chi-square test for homogeneity (Snedecor and Cochran, 1971).

### Additional Acoustic Playback Experiments

Several additional acoustic playback experiments were performed to determine the role of the following parameters in eliciting the one-note Co response: 1) the frequency within the Co note, 2) the duration of the Co note, and 3) the interval between the Co and the Qui notes.

To observe the role of the Co-note frequency on male responsiveness, a frequency audiogram was obtained for 2 males as fol-

lows. After locating an appropriate calling male, 50 presentations of a Co note from the sound synthesizer were played to him (repetition interval: 4 s; duration: 100 ms; frequency: adjusted by ear before the stimulus presentation to match the frequency of the Co note of the calling male; initial playback intensity: <40 dB SPL measured at the animal's position). The number of one-note calls given in response to the 50 stimulus presentations was recorded. Ten one-note responses out of 50 stimulus presentations was arbitrarily designated as the threshold for the male's vocal response. The intensity of the stimulus was increased by either 2 or 4 dB increments from its initial level until the male's threshold was reached. The process was then repeated, changing only the frequency of the Co-note stimulus in 100-Hz steps above and below the calling male's Co frequency. In this way, a threshold response curve as a function of stimulus frequency and intensity was obtained for each male.

The effect of changing the Co-note duration, while its spectral frequency remained constant, was also measured. For 7 males this was done at stimulus intensities (80 dB SPL at 2 m) to which the animals seemed to readily respond; in addition for 2 males the effect of changing the Co-note duration was determined at "threshold" intensities. These threshold measurements were used to derive a duration audiogram, namely a behavioral measure of a calling male's sensitivity to the duration of an acoustic stimulus. The duration audiograms were obtained in a manner similar to the frequency audiograms, except the frequency in the Co-note stimulus was fixed at the animal's calling frequency (adjusted by ear before the playback experiments began). The durations of the Co-note stimulus were 30, 50, 75, 100, 150, 200, and 300 ms; they were presented in random order. Threshold was defined in the same way as for the frequency audiograms.

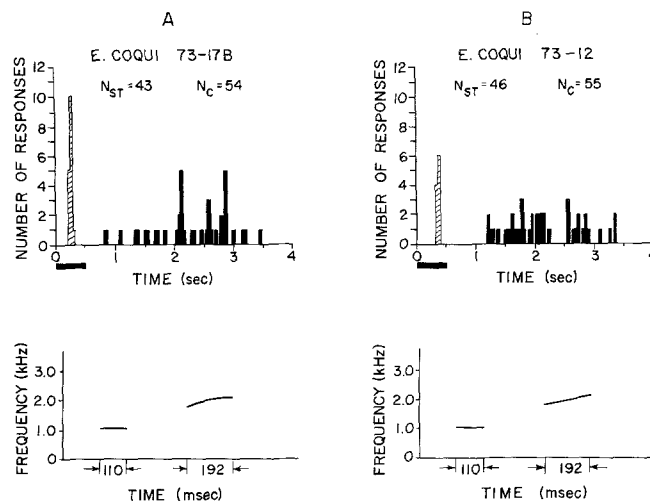
Finally, the inter-note interval was varied using the natural call-note sequence (Co-Qui) as well as the reverse call-note sequence (Qui-Co), and the number of one-note Co responses to these stimuli were recorded from 3 males. The stimuli were presented at 80 dB SPL and repeated every 4 s.

## Results

The acoustic playback experiments were designed to determine the features of the two-note call of *E. coqui* which elicited the one-note responses observed during male-male calling interactions.

### *Effectiveness of Various Stimuli in Evoking Calling*

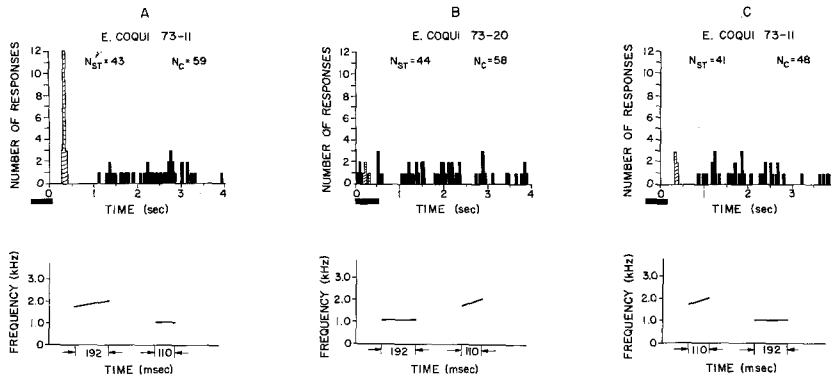
The first stimulus tested was the natural call of a male *E. coqui* from the El Yunque population. The results from this playback presentation to a responsive male (Number 73-17b) are shown in Figure 1A. 43 playback repetitions were presented during the 3-min test period and 16 of the male's responses during this period were one-note Co responses. The Co responses were time-locked to the stimulus and are presented in the PST histogram by the striped vertical bars. These single Co-note responses always occurred within 100 ms of the termination of the Co-note component in the stimulus. On the other hand, the Co-Qui



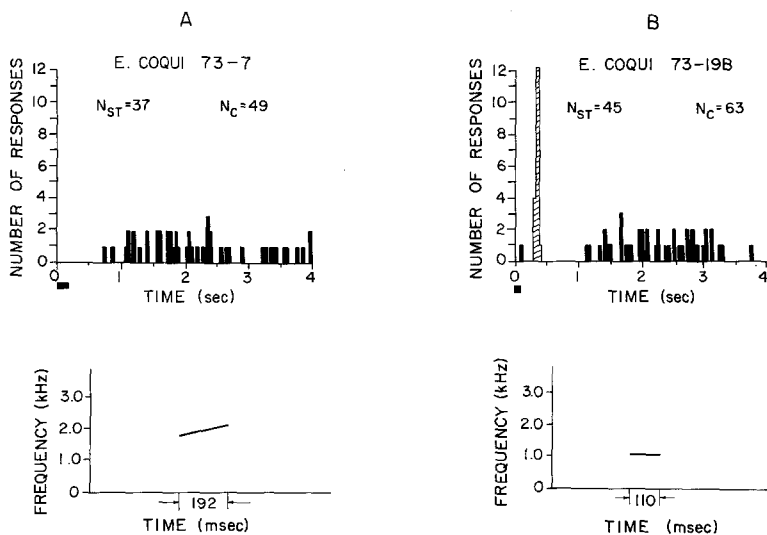
**Fig. 1.** A Vocal response to a natural call. *Above:* Post-stimulus-time histogram of the vocal responses of a representative male during a 3-min trial. The duration of each stimulus is indicated by the black bar below the histogram. The onset of the Co note in each playback presentation served as the time reference in compiling the histogram. The two classes of responses are represented by the striped bars (one-note Co responses) and the solid bars (two-note Co-Qui responses). The bin width in the histogram is 50 ms.  $N_{st}$  refers to the number of stimuli presented during the trial;  $N_c$  refers to the total number of calls (Co responses plus Co-Qui responses) given by the test male during the stimulus presentation period. For animals which called more often than once per stimulus period (4s),  $N_c$  was greater than  $N_{st}$ . *Below:* Sonagram tracing of the acoustic stimulus. **B** Vocal response to a synthetic two-note call. *Above:* the response of a male to synthetic version of the natural call. *Below:* Sonagram tracing of the stimulus. The inter-note interval for all of the two-note stimuli was fixed at 250 ms

responses tended to alternate with the stimulus and are represented in the histograms by the solid vertical bars. This male was particularly responsive; consequently the stimulus tape was repeated. During the second playback sequence, he gave 21 Co responses to the 43 presentations of the natural call. Therefore,  $p_1$  for this male was  $(16+21)/(43+43)=0.430$  or 43.0%. This value was averaged with the  $p_1$  values for the other males tested to obtain the mean one-note response rate to the natural call,  $\bar{p}_1=42.2\%$  ( $N=4$ ).

Figure 1B shows the vocal response of a different male (no. 73-12) to a synthetic version of the natural call. The difference between the linear sweep of the synthetic Qui note and the approximately exponential sweep of the natural Qui note was shown to be non-significant for evoking a one-note response;  $p_2$  (the percentage of this synthetic call which evoked a one-note Co response) for this male was 21.7% and  $\bar{p}_2$  (the average  $p_2$  values for all males tested) was 35.5% ( $N=10$ ). The mean one-note Co response rate to this stimulus was not significantly different from that for the natural call, using the  $2 \times 2$  Chi-



**Fig. 2.** **A** The response of a male *coqui* to a "Sequence-Reversed" synthetic call and the sonagram tracing of the corresponding stimulus. The stimulus bar is displaced to the left since the computer was triggered by the onset of the Co note, which occurred in the later portion of the stimulus. **B** The response of a male *coqui* to a "Duration-Reversed" synthetic call and the sonagram tracing of the corresponding stimulus. **C** The response of a male *coqui* to a "Sequence and Duration-Reversed" synthetic call and the sonagram tracing of the corresponding stimulus. As in **A** the horizontal stimulus bar is displaced to the left



**Fig. 3.** **A** The response of a male *coqui* to the 192 ms synthetic Qui note alone and the sonagram tracing of this stimulus. **B** The response of a male *coqui* to the 110 ms synthetic Co note alone and the sonagram tracing of this stimulus

square test for homogeneity. It may be concluded, therefore, that the synthetic version of the natural call was as effective as the natural call in evoking the single Co response.

We then attempted to determine if the natural call-note sequence (Co followed by Qui) was necessary to evoke the time-locked Co response. Reversing the note sequence, as shown in the bottom portion of Figure 2A, resulted in the responses seen in the top portion of the Figure. These data are for male no. 73-11 for which  $p_3 = 44.2\%$ . After obtaining the mean response rate for all the males tested with this stimulus ( $\bar{p}_3 = 49.6\%$ ,  $N = 11$ ), the "Sequence-Reversed" call was found to be as effective in evoking the Co response as either the natural or synthetic call.

Next, the durations of the two notes comprising the natural call sequence were interchanged; that is, the Co note was lengthened to 192 ms and the Qui

note was shortened to 110 ms. This stimulus was not as effective as the ones previously tested in evoking the Co response. Figure 2B shows a typical response pattern to a "Duration-Reversed" stimulus. The  $p_4$  for this male was 9.1% and  $\bar{p}_4$  ( $N = 5$ ) was found to be 9.0% which is significantly lower ( $p < 0.0005$ ) than  $\bar{p}_1$ . The note sequence was then reversed and the note durations were interchanged simultaneously, producing a "Sequence and Duration-Reversed" call, shown in the lower portion of Figure 2C. The upper portion of this figure shows the responses of male no. 73-11. For this male  $p_5$  was 12.2% but  $\bar{p}_5$  based on several males ( $N = 9$ ) was only 6.2%. This value is significantly lower ( $p < 0.0005$ ) than  $\bar{p}_1$  for the natural call stimulus. In other words, when the note durations were reversed, the percentage of Co note responses was significantly reduced compared to the natural call, regardless of the note sequence.

The individual notes were then tested separately

**Table 1.** Summary of altered call playback experiments with the Puerto Rican coqui

Stimulus	Animal no.	"Co" resp.	No. stim.	Percent "Co" resp.	$p(\chi^2)^a$	
Natural call	16	3	11	27.3		
	17	37	86	43.0		
	18	21	45	46.7		
	20	17	43	39.5		
Totals	78	185		Mean 42.2	—	
Synthetic call	2	17	45	37.8		
	3	17	42	40.5		
	4	16	44	36.4		
	7	13	39	33.3		
	8	10	40	25.0		
	9	12	40	30.0		
	12	10	46	21.7		
	13	19	46	41.3		
	14	9	47	19.1		
	15	31	45	68.9		
	Totals	154	434		Mean 35.5	ns.
	Sequence-Rev. call	1	31	40	77.5	
		2	20	40	50.0	
3		21	63	33.3		
4		9	35	25.7		
6		29	41	70.7		
7		27	48	56.3		
8		9	23	39.1		
9		10	43	23.3		
11		19	43	44.2		
13		38	45	84.4		
14		17	43	39.5		
Totals		230	464		Mean 49.6	ns.
Duration-Rev. call		15	5	44	11.4	
		16	3	36	8.3	
	17	8	43	18.6		
	19	3	88	3.4		
	20	4	44	9.1		
	Totals	23	255		Mean 9.0	<0.0005

to determine whether a two-note sequence was necessary in evoking the one-note response. Figure 3A shows the response of male no. 73-7 to just the 192 ms Qui note ( $p_6=0$ ;  $\bar{p}_6=0.9\%$ ,  $N=10$ ). This mean response rate is significantly lower than  $\bar{p}_1$  for the natural call ( $p<0.0005$ ). Although the Qui note evoked a very low mean one-note response rate, the test males did not produce the two-note Co-Who call (or any call) in the first 500 ms immediately following the

**Table 1** (continued)

Stimulus	Animal no.	"Co" resp.	No. stim.	Percent "Co" resp.	$p(\chi^2)^a$	
Seq. and Dur.	1	1	42	2.4		
Rev. Call	2	8	41	19.5		
	3	1	40	2.5		
	4	0	36	0		
	7	0	44	0		
	11	5	41	12.2		
	12	0	43	0		
	13	8	43	18.6		
	14	0	43	0		
	Totals	23	373		Mean 6.2	<0.0005
	Qui alone	1	0	44	0	
2		0	44	0		
3		1	45	2.2		
4		0	44	0		
7		0	37	0		
9		0	47	0		
11		0	46	0		
12		2	46	4.3		
13		1	46	2.2		
14		0	45	0		
Totals		4	444		Mean 0.9	<0.0005
Co alone		2	16	40	40.0	
		3	24	45	53.3	
		4	18	45	40.0	
	7	11	45	24.4		
	11	28	46	60.9		
	12	8	46	17.4		
	13	32	47	68.1		
	14	7	42	16.7		
	15	15	45	33.3		
	16	9	39	23.1		
	17	45	86	52.3		
	19	16	45	35.6		
	20	16	45	35.6		
	Totals	245	616		Mean 39.8	ns.

<sup>a</sup>  $p(\chi^2)$  is the Chi-square significance level for the difference between the mean percentage of "Co" responses for the natural call and the mean percentage of "Co" responses for the other stimuli

Qui note stimulus. Thus, they appear to be actively avoiding overlap with the stimulus, with a minimum response latency of the order of 500 ms, suggesting that the Qui note is *perceived* by the males.

The response of male no. 73-19B to just the 110 ms Co note is shown in Figure 3B. In this case,  $p_7=35.6\%$ , and  $\bar{p}_7=39.8\%$  ( $N=13$ ). Thus,  $\bar{p}_7$  does

not differ significantly from  $\bar{p}_1$ , indicating that the 110 ms Co note alone and the natural call were equally effective in evoking the one-note response.

The results of these experiments are presented in Table 1, and may be summarized as follows:

1) The natural call (or its synthetic equivalent) is capable of evoking a one-note Co response from a calling male *E. coqui* about 42% of the time. Reversing the note sequence does not change the average response rate.

2) Interchanging the note durations, regardless of the note sequence, significantly reduces the Co response rate.

3) The 110 ms Co note alone and the natural, two-note Co-Qui call are equally effective in evoking the one-note Co response, whereas the 192 ms Qui note alone is almost completely ineffective.

Therefore, the Co note in a male's call is responsible for evoking the one-note vocal responses from other males.

#### *Effect of Inter-Note Interval in Evoking One-Note "Co" Responses*

Two series of two-note stimuli in which the interval between the notes was varied were presented to one male. In the first series of stimuli, the natural call note sequence was preserved; in the second case, the sequence was reversed. The results were qualitatively the same (Figure 4A); the percentage of one-note Co responses is independent of the inter-note interval for either note sequence.

#### *Effect of Note Duration in Evoking One-Note "Co" Responses*

A series of experiments was performed in which the duration of the Co-note stimulus was varied and the percentage of one-note responses was determined for 7 males (Figure 4B). The graph clearly shows a maximum number of Co responses for a stimulus duration of 100 ms, which corresponds closely with the duration of the natural Co note. The playback intensity was adjusted in each case to a level at which the calling male readily responded.

#### *Behavioral Audiogram Determination*

##### 1. Spectral Sensitivity

A frequency audiogram was measured for one animal and the results are shown in Figure 5A. The audio-

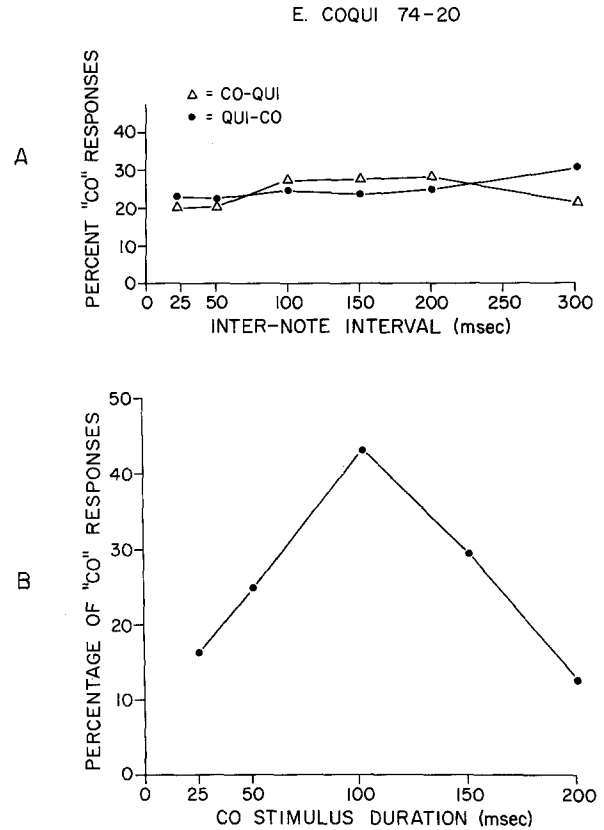
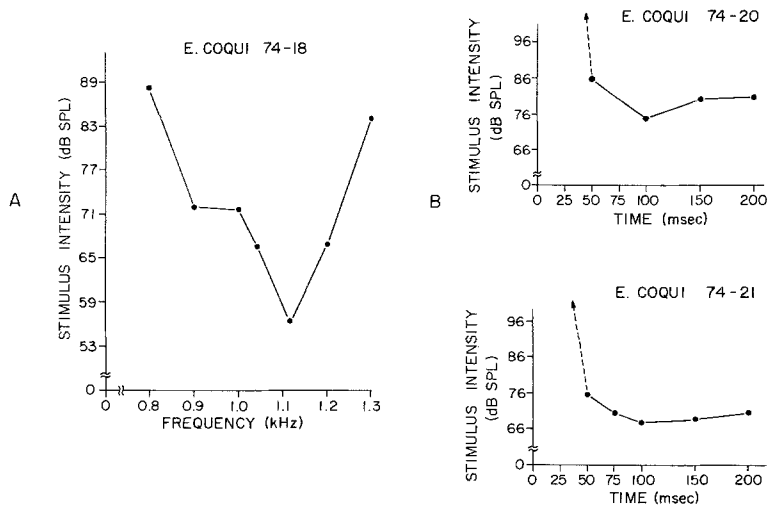


Fig. 4. **A** The percentage of time-locked Co responses from a male *coqui* as a function of the inter-note interval in the stimulus. The triangles represent responses to the Co-Qui sequence and the filled circles represent responses to the Qui-Co sequence. **B** The percentage of one-note Co responses as a function of the duration of the synthetic Co note alone, presented once every 4 s. Each point on the curve was derived by averaging the percentage of one-note responses from 7 different males

gram indicates maximal sensitivity around 1100 Hz for a playback threshold of 56 dB SPL. This curve indicates that the male has a minimum threshold in the range of frequencies containing his own Co note.

##### 2. Temporal Sensitivity

A duration audiogram was measured for two animals and the results are shown in Figure 5B. For both animals, the duration of the Co-note stimulus which evoked a 20% response level with a minimum intensity was about 100 ms. For animal no. 74-20 this intensity was 75 dB SPL, and for animal no. 74-21 it was 68 dB SPL. In neither animal could a 20% response level be evoked using a 25-ms Co-note stimulus, even with intensities measured at the animal of 105 dB SPL which represented the upper intensity limit of the stimulus generator.



**Fig. 5.** **A** Frequency audiogram based on 20% response level (see text for details) for male no. 74-18. The stimulus frequency for which the 20% response level could be evoked with minimum intensity was about 1.1 kHz, which corresponds to the frequency of the natural Co note in a male's call. The synthetic Co-note stimulus had a duration of 100 ms and was presented once every 4 s. The dependence of the audiogram on stimulus repetition rate was not investigated. **B** Duration audiogram determined behaviorally for two different males. The stimulus duration for which the 20% response level could be evoked with minimum intensity was around 100 ms, which corresponds to the duration of the Co note in a male's natural call. The frequency of the Co-note stimulus was adjusted to be that of the Co note of the calling male; the stimuli were presented once every 4 s

## Discussion

In our present study we have found that male *E. coqui* produce a species-specific two-note call. The Co note serves as a species-specific signal by which calling males indicate their presence to nearby male conspecifics. Closely spaced male *coqui* often engage in acoustic "bouts" consisting of quickly alternating Co notes. These "bouts" terminate either in the retreat of the "intruder" or in a biting, butting attack initiated by the "resident" (Reyes Campos, 1971).

The results of our acoustic playback experiments suggest that the first note (Co) of the male *E. coqui* call is a necessary and sufficient stimulus to evoke the one-note Co response from a neighboring conspecific male (Fig. 3B). Furthermore, its effectiveness in evoking the one-note response is unchanged whether or not it is followed or preceded by the Qui note of the male's call (Fig. 2A and B respectively). Moreover, the Qui note is relatively ineffective in evoking this response (Fig. 3A).

The effect on an individual male of a small variation in two of the call parameters—the frequency and duration of the Co note—was experimentally demonstrated. The frequency audiogram shown in Figure 5A indicates that the frequency at which the threshold response rate could be evoked at minimum intensity corresponds closely to the frequency of the Co note in the natural call. In addition, the threshold intensity increases rather rapidly for stimulus fre-

quencies above and below the optimal frequency. This result shows that a male *E. coqui* is selectively responsive to a narrow frequency range around 1120 Hz.

One may reasonably ask how the bandwidth,  $\Delta F$ , of the frequency audiogram at 10 dB above threshold compares with the inter-individual variation in the Co-note frequency. Systematic measurements of these parameters (Narins and Capranica, 1977) revealed that  $\Delta F$  for male no. 74-18 was about 160 Hz, while  $\pm 2$  standard deviations about the mean Co frequency (based on a sample of 16 males) was about 120 Hz, confirming that indeed the great majority of males in this population would be capable of evoking a one-note response from this presumed typical male. Similar calculations were made for the duration audiograms in Figure 5B and the conclusions were comparable, namely the inter-individual variation of the Co-note duration was less than the bandwidth of the duration audiogram, in this case at 3 dB above threshold.

The duration audiogram in Figure 5B indicates that the stimulus duration for which the threshold response rate could be evoked at minimum intensity corresponds to the duration of the Co note in the natural call. Although this audiogram is much broader than the frequency audiogram in Figure 5A, it nevertheless exhibits some tuning. These results suggest that males of this species are most sensitive to call-note durations of 100 ms. Likewise, Figure 4B illustrates that, for intensities above threshold, the

highest one-note response rates were recorded for Co-note stimuli whose durations were 100 ms, the natural Co-note duration.

What selective pressures in the animal's environment have been instrumental in bringing about this frequency and duration selectivity of the males' Co response? It has been observed that *E. coqui* produces the lowest call-note frequency of the 14 known eleutherodactylid frogs in Puerto Rico (Drewry, 1970). The sympatric species which produce call notes containing energy closest in frequency to the Co note are *E. portoricensis* (1300 Hz) and *E. antillensis* (1900 Hz). Furthermore, the durations of the call notes of these sympatric species are shorter than the Co note. One of the characteristic aspects of the shape of the duration audiograms in Figure 5B is the relatively steep slope for short durations. This shape is adaptive since vocalizations of sympatric congeners would fall on the steep side of the curve, which results in reduced interspecific responsiveness. These observations imply, then, that a "resident" male *coqui* will more likely respond to an approaching male *coqui* than to an "intruder" of another species. Thus, the male-male vocal interaction is probably species-specific.

Moreover, if one assumes that an "intruding" male *coqui* stops his approach upon engaging in a Co-note calling bout with the "resident", then the distance between the males at this point will be a function of the Co-note frequency and duration (see Figs. 5A and B). Since it is known that the minimum intensity of the Co note to which a male responds has a frequency and duration similar to that of his own Co note, and furthermore that the frequency and duration of the Co note are highly stereotyped (Narins, 1976; Narins and Capranica, 1977), it follows that a male will respond to a calling *coqui* at a greater distance than he will to a male of another species (assuming that sympatric males are calling at roughly the same intensity). One might therefore predict that the distance at which a male-male Co-note "bout" would start with another male *E. coqui* would be greater than the distance for an interspecific interaction, for example with a male *E. portoricensis*. Vocal interactions between these two species have been reported (Drewry, 1970).

In conclusion, the spectral and, to a lesser extent, the temporal dependence of the male-male vocal interaction, coupled with the stereotyped nature of the male's call, result in greater spacing between conspecifics than between heterospecifics. This, in effect, provides the male *coqui* with a mechanism to selectively exclude conspecifics from his "calling space" which thus may reduce agonistic interactions that could interfere with courtship.

Preliminary results from orientation and discrimination experiments with females (Narins and Capranica, 1976b) suggest that the two-note call of the male is attractive to females<sup>1</sup>. Furthermore, if given the choice, a female is more likely to orient toward a loudspeaker broadcasting a Qui note than one emitting a Co note. In a related neurophysiological study, we have found that the peripheral auditory nervous system of the male is more specialized for detection of the Co note whereas the female's peripheral auditory system is more specialized for detection of the Qui note (Narins and Capranica, 1976a, b).

These results, coupled with those from the acoustic playback experiments, imply that each note of the male's call has a separate function. The first note plays a role during male-male encounters whereas the second note serves to attract females. Such a separate function of the individual notes in animal sound communication may be more general than we suspect. For example, many bird songs consist of a sequence of different syllables. It may be that some syllables have significance for males and other syllables have a different significance for females. Further studies of this sort might reveal some intriguing strategies employed in animal sound communication.

## Appendix I

The acoustic stimuli for the playback experiments in 1974 were delivered by a portable animal sound synthesizer of integrated circuit design, capable of delivering a one or two-note sequence of variable frequency, repetition rate, note duration, note sequence, inter-note interval and sweep rate (Land, in preparation). In addition, provisions were made for selection of either a linear or exponential sweep of the Qui note. Furthermore, a switch on the instrument enabled attenuation of the Co note by 10 dB with respect to the Qui note, to more closely approximate the natural call. The synthesizer was housed in a acrylic case and moisture sealed with bathtub caulking. It was calibrated in the laboratory before and after field use to ensure that none of the parameters had changed significantly. Stimulus intensity was variable in 2 or 4 dB steps, by using different combinations of the intensity switches on the synthesizer and on the Nagra DH speaker-amplifier. The frequency response of the overall acoustic delivery system was flat ( $\pm 5$  dB) from 100–5000 Hz.

<sup>1</sup> The sex of an adult can be readily determined since males are smaller than females (Thomas, 1966). Furthermore, adult males possess a prominent subgular vocal pouch which is absent in females. Little is known about female *E. coqui* other than that they are cryptically colored, nocturnal and generally silent. Collection of a large number of females is therefore extremely difficult.

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