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THE INFLUENCE OF BACKGROUND NOISE ON THE BEHAVIOR OF A NEOTROPICAL TREEFROG, HYLA EBRACCATA

JOSHUA J. SCHWARTZ AND KENTWOOD D. WELLS

ABSTRACT: Hyla ebraccata males reduce their calling rates and proportion of multi-note calls when exposed to choruses of *H. microcephala*. The calls of these species overlap spectrally. We presented calling male *H. ebraccata* with filtered one-third octave noise centered at 2, 3, 4 and 6 kHz to assess their responses to acoustical stimuli shifted from the dominant frequency of their calls (3 kHz). The 3 kHz noise was most effective in reducing calling rate and multi-note calling. Our results suggest that the latter shift in behavior is due to the masking of the vocalizations of nearby males which elicit multi-note calls. Since all frequencies of noise except 6 kHz reduced calling rates in most frogs, these animals are potentially responsive to background noise generated by a number of anuran species in their environment. Calling by *H. ebraccata* also is inhibited by choruses of *H. phlebodes*. There is less frequency overlap between the calls of *H. ebraccata* and *H. phlebodes* than between *H. ebraccata* and *H. microcephala*. We demonstrate that male *H. ebraccata* that shift the timing of their calls in response to background noise have a selective advantage. In a two-choice experiment, female *H. ebraccata* discriminated against conspecific advertisement calls which were overlapped by a recorded chorus of *H. microcephala*.

Key words: Amphibia; Anura; Hylidae; Hyla; Background noise; Communication; Acoustic interference; Behavior

IN multi-species assemblages of synchronously breeding anurans, background noise levels often are very high. If the spectral features of the calls of different species are similar, both conspecific and heterospecific calls may be a significant source of acoustic interference which masks the vocalizations of male frogs (Ehret and Gerhardt, 1980; Gerhardt, 1982; Littlejohn, 1977). If such interfering noise occurs sporadically or fluctuates in intensity, an effective way to minimize masking would be to partition the broadcast period by calling when noise levels subside. This should enhance a male's ability to advertise ownership of a territory to other males or to attract females.

Males of the neotropical treefrog Hyla ebraccata are inhibited from calling by nearby choruses of *H. microcephala*. Playbacks of recorded *H. microcephala* choruses, and of filtered noise centered at 3 kHz, had a similar effect (Schwartz and Wells, 1983). This frequency corresponds to the dominant frequency of the *H. ebraccata* call and the lower band of energy in the *H. microcephala* call. In addition to reducing call rates during noisy periods, *H. ebraccata* males also reduce the proportion of multi-note and aggressive calls given during calling bouts (Schwartz and Wells, 1983). Since multinote advertisement calls and aggressive calls are given mainly in response to the calls of other individuals (Wells and Greer, 1981), these results suggest that background noise masks the calls of nearby conspecifics.

Anuran peripheral auditory systems that have been studied are selectively tuned to the frequency spectra of conspecific calls (Capranica, 1977). Acoustic interference should be most pronounced when the distribution of energy in background noise is concordant with that of a species' calls. Narins (1982) found that artificial noise was most effective in masking the simulated "Co" note of *Eleutherodactylus coqui* when the noise was narrowly focussed around the dominant frequency of the call. Zelick and Narins (1982) also found that calling was suppressed in this species by 100 ms pure tones over a wide range of frequencies, and peak suppression did not occur at the dominant frequency of its advertisement call. *E. coqui* males therefore may respond to the sounds of many species in their environment.

The main purpose of this study was to assess the behavioral responses of H. ebraccata males to background noise outside the frequency range of their own calls. We presented males with filtered noise centered at 2, 4 and 6 kHz. The 6 kHz noise corresponds to the upper frequency band of *H. microcephala* calls (Schwartz and Wells, 1983) while the 4 kHz noise is close to the dominant frequency of *H. phlebodes*, another species which calls in the same area. For comparison, we include data from Schwartz and Wells (1983) on responses to 3 kHz noise at the same intensities. In that study, we presented H. ebraccata males with filtered noise solely at 3 kHz over a wider range of playback intensities. We also report data on natural interactions between H. ebraccata males and choruses of H. phlebodes which indicate that species other than H. microcephala can inhibit calling by *H. ebraccata*. Finally, we report the results of an experiment designed to test the effect of noise generated by *H. microcephala* choruses on the ability of female H. ebraccata to select mates.

METHODS AND MATERIALS

We conducted noise playback experiments in a flooded field in Gamboa, Panama, during July and August 1982. A more detailed description of this study site is given in Schwartz and Wells (1983). Field work was performed between 1930 and 2400 h. We worked with male *H. ebraccata* isolated from natural *H. microcephala* choruses, but within 10 m of calling conspecific males. This was done so that we could evaluate the effect of noise on the vocal behavior of frogs which were interacting with other *H. ebraccata* males without significant acoustic interference contributed by *H. microcephala*.

We presented 14 males with filtered one-third octave noise centered at 2, 4 and 6 kHz. Data on responses to 3 kHz noise are from experiments performed the previous year and reported in more detail elsewhere (Schwartz and Wells, 1983). The noise was synthesized with a Gen Rad random noise generator (P390 B) and filtered with a #125 Bruel and Kjaer graphic spectrum analyzer. Each noise stimulus was presented in two 30 s noise bursts, each followed by 30 s of silence. Before each playback, we recorded the frog calling spontaneously for 1 min. For playbacks and recording, we used two Uher 4200 Report Stereo IC tape recorders. A University 4401 horn speaker mounted on a wooden baffle and placed 1 m from the frog was used to broadcast stimuli. The amplitude-frequency response of this speaker is $\pm 3 \text{ dB}$ from 1.1– 14.5 kHz. The frog's calls were recorded with a Sennheiser MKE 802 microphone on the right channel of one Uher. The stimulus was simultaneously recorded on the left channel of the same machine through a patch cord to the other Uher. Playback intensities were predetermined with a Gen Rad 1982 precision sound level meter set for flat weighting and calibrated with a Gen Rad 1562A sound level calibrator. We measured Peak SPL at 1 m with a random incidence microphone. Sound pressure levels are expressed in dB SPL (dB re 20 μ Pa). Playbacks were made at 90 and 100 dB SPL (±1 dB). We counted the number and type of calls given by *H. ebraccata* males during the noise playback and silent intervals and analyzed these data using non-parametric statistical tests (Siegel, 1956).

We recorded two natural vocal interactions between a small group of *H. phlebodes* males and nearby *H. ebraccata*. These interactions were recorded on one channel of a stereo Uher with a cardioid microphone (Uher M517). We played the recordings back through a real-time spectrum analyzer (Uniscan Model 4500) and obtained a hard copy from a linescan recorder (Honeywell Model LS-8). The number of calls given by *H. ebraccata* males during bouts of *H. phlebodes* calling and during quiet periods was determined and analyzed with the *G*-test for goodness of fit (Sokal and Rohlf, 1969).

Female choice experiments were performed in a darkened apartment in Gamboa at natural field temperatures (about 26 C) between 2230 and 0300 h. Two Heppner mid-range horn speakers (amplitude-frequency response: ±4 dB, 1.1-10.5 kHz) mounted on wooden baffles were placed 2.8 m apart at opposite ends of an arena delimited by uniformly colored blankets. Large cushions were placed along the wall behind each speaker to minimize the reflection of sound. The arena was approximately 3 m long, 1.6 m wide, and 1 m high. It served to shield test animals from extraneous light and movements of the experimenters, but it did not restrain the movements of the frogs. The only light was provided by a 25 W red bulb suspended 1 m above the center of the arena.

Females were captured in amplexus between 2230 and 0100 h and were transported to the arena in individual plastic food boxes. Each female was placed in the center of the arena in the box. The lid was replaced with a piece of cardboard which could be lifted off of the box with a string from outside the arena. Most females remained immobile when placed in the arena, so testing began within 1 min. After stimulus playbacks were started, the lid was carefully lifted off the box. A positive response was scored if a female approached to within 10 cm of one speaker: most females moved directly toward a speaker and made contact with it. If a female hopped onto the arena walls or showed extensive undirected wandering, her response was scored as an escape. Females exhibiting this behavior were tested one more time later in the evening. All females showing a positive response did so within 8 min; females that failed to respond within 10 min were removed and retested later.

For all tests, stimulus calls were syn-

thetic one-note advertisement calls (200 ms long) produced according to methods described in Gerhardt (1974). Calls were recorded on two tracks of the same tape and played in alternation through the two speakers at 6 s intervals. Playback intensities for each speaker were regulated by separate Realistic L-pads and were equalized at 85 dB $(\pm 1 \text{ dB})$ (Peak SPL) using the Gen Rad sound level meter held 2.5 cm above the floor. A University midrange horn speaker connected to a second tape recorder was placed at the center of one side of the arena 1.5 m above the floor and directed at a 45° angle toward the central release box. This third speaker played 6 s bursts of recorded H. *microcephala* chorus at a playback intensity of 90 dB SPL (±5 dB). In natural choruses, *H. microcephala* calls are 6 dB louder than *H. ebraccata* calls at the same distance (Schwartz and Wells, 1983). The chorus playback was manually regulated with a pause switch so that it overlapped all of the calls produced by one speaker but none of the calls produced by the other. The speaker that was overlapped was alternated between trials. The experiment was designed to determine whether female H. ebraccata approach conspecific calls given during quiet periods rather than during chorusing bouts of nearby H. microcephala.

RESULTS

Noise Tests

At 90 dB SPL, both 3 kHz and 4 kHz noise inhibited calling by *H. ebraccata* males (Table 1), but the effect was most pronounced with 3 kHz noise (Fig. 1). The percent decrease in calling during noise playback relative to the silent intervals was significantly greater at 3 kHz than at 2 kHz or 6 kHz (P = 0.042 and P = 0.0075respectively; two-tailed Mann-Whitney *U* Test). At 100 dB, all noise frequencies but 6 kHz inhibited calling (Table 2). The percent decrease in calling with noise differed significantly from the results at 90 dB SPL only at 2 kHz (P = 0.029). The



FIG. 1.—The percentage decrease in number of calls given by *Hyla ebraccata* males when exposed to noise centered at different frequencies relative to the number of calls given during silent intervals. Playbacks were at intensities of 90 and 100 dB SPL. Data are presented at medians with approximate 95% confidence intervals (2, 4, 6 kHz, n = 14; 3 kHz, n = 12).

only significant differences among frequencies at 100 dB occurred between 2 kHz and 6 kHz (P = 0.0019).

At both 90 and 100 dB, multi-note calling was most effectively reduced during playback of the 3 kHz noise (Tables 3 and 4; Fig. 2). At 90 dB, this reduction was significantly greater at 3 kHz than at 6 kHz; at 100 dB, it was significantly greater at 3 kHz than at each of the other three frequencies (two-tailed Mann-Whitney *U* Test). At 100 dB, only the 3 kHz noise caused males to significantly reduce their proportion of multi-note calls (Table 4), whereas at 90 dB, both 2 kHz and 3 kHz did so (Table 3).

H. phlebodes-H. ebraccata Interaction

In our study site, *H. phlebodes* is not nearly as abundant as *H. ebraccata* or *H*.



FIG. 2.—The decrease in percentage of multi-note calls given by *Hyla ebraccata* males when exposed to noise centered at different frequencies relative to the percentage of multi-note calls given during silent intervals. Data are presented as medians with approximate 95% confidence intervals (2, 4, 6 kHz, n = 14; 3 kHz, n = 12).

microcephala, and sustained choruses are rare. However, when interacting vocally with conspecific males, individuals often add over 20 click notes to the primary note of their calls (Fig. 3) or alternate many single notes synchronously. Therefore, a few frogs can generate a considerable amount of noise. We recorded two interactions between *H. ebraccata* and *H. phlebodes* lasting 356 s and 229 s. In both of these, *H. ebraccata* males gave significantly fewer calls than expected during *H. phlebodes* calling bouts (Table 5).

Female Choice Experiment

Fifteen of the 23 female *H. ebraccata* tested responded positively by moving to a speaker. Thirteen of these approached the speaker that was broadcasting calls not overlapped by the recording of the *H*.

	Total calls 2 kHz			Total calls 4 kHz		Total calls 6 kHz			Total calls 3 kHz			
Frog	N	S	Sign	N	S	Sign	N	S	Sign	N	S	Sign
29	13	16		14	16	_	16	13	+	13	15	
30	5	17	-	6	22		17	17	0	4	14	
31	16	11	+	12	15	-	10	15	-	12	17	-
32	6	20	-	6	10	-	9	15		7	15	_
33	15	14	+	12	8	+	11	11	0	7	11	-
34	15	15	0	13	17	-	16	18		12	17	_
35	16	16	0	14	14	0	12	13	-	20	17	+
36	24	23	+	3	5	-	20	15	+	5	14	_
37	21	14	+	18	27	_	25	21	+	11	13	_
38	28	26	+	20	16	+	15	25	-	12	19	—
39	14	16	-	4	11		11	12	-	8	9	
40	14	8	+	8	15	-	15	11	+	11	15	_
41	11	26	_	18	17	+	13	11	+			
42	14	15	-	17	15	+	14	15	-			
All												
frogs	212	236		165	208		198	213		122	176	
P _s	0	.61		0	.13		C).39		0	.003	
P_w	0	.31		C	.03		0).38		0	.003	

TABLE 1.—Number of calls given by Hyla ebraccata males during playback of 2, 3, 4 and 6 kHz noise at 90 dB SPL and during silent periods. P_s and P_w are significance levels for a one-sided sign test and Wilcoxon signed-ranks test. Data shown for 3 kHz are from Schwartz and Wells (1983) and were obtained from different frogs. Noise (N) and Silent (S) periods each lasted a total of 60 s for each frequency.

TABLE 2.—Number of calls given by Hyla ebraccata males during playback of 2, 3, 4 and 6 kHz noise at 100 dB SPL and during silent periods. P_s and P_w are significance levels for a one-sided sign test and Wilcoxon signed-ranks test. Data shown for 3 kHz are from Schwartz and Wells (1983) and were obtained from different frogs. Noise (N) and Silent (S) periods each lasted a total of 60 s for each frequency.

	Total calls 2 kHz				Total calls 4 kHz		Total calls 6 kHz			Total calls 3 kHz		
Frog	N	S	Sign	N	S	Sign	N	S	Sign	N	S	Sign
29	6	17		10	12	_	10	16	_	13	18	_
30	2	17	-	4	21	-	12	17	-	2	19	_
31	8	18	-	6	15	-	13	16	_	15	13	+
32	4	19	-	2	18	-	9	11	_	3	15	
33	6	16	_	6	8	_	11	9	+	9	15	_
34	16	15	+	13	17	-	24	20	+	7	19	_
35	12	15	-	10	7	+	13	15	_	19	20	-
36	12	18	_	5	10	_	24	22	+	2	14	_
37	15	13	+	18	28	_	18	19	-	11	12	_
38	10	26	_	20	15	+	15	16	_	15	16	_
39	6	13	-	10	13	_	19	13	+	8	7	+
40	9	17	_	7	6	+	13	9	+	9	17	_
41	13	14	_	11	16	_	13	15	_			
42	14	16	_	17	13	+	15	16	-			
All												
frogs	133	234		139	199		209	214		113	185	
P _s	0.0	006		0	.09		(0.21		0.0	019	
P_w	0.0	001		0	0.02		0).35		0.0	007	



FIG. 3.—Sonagram of a portion of a vocal interaction between *Hyla ebraccata* and *H. phlebodes*. The calls of higher frequency are those of 3 to 4 *H. phlebodes*. The calls of lower frequency are those of 2 *H. ebraccata*. The sonagram was made with a linescan recorder linked to a real-time spectrum analyzer.

microcephala chorus (P = 0.008; twotailed binomial test). Choice of calls was independent of speaker position (G =1.35, P > 0.10).

DISCUSSION

The calling of *H. ebraccata* was inhibited by one-third octave noise centered

at the dominant frequency of their vocalizations and 1 kHz on either side of it. However, 6 kHz noise had no significant effect on any aspect of their vocal behavior. Therefore, it is unlikely that the 6 kHz component of *H. microcephala* calls contributes significantly to inhibiting the calling of *H. ebraccata* males. Since the

TABLE 3.—Frequency of multi-note calls (FMC) given by $Hyla\ ebraccata$ males during playback of 2, 3, 4 and 6 kHz noise at 90 dB SPL and during silent periods. P_s and P_w are significance levels for a sign test and a Wilcoxon signed-ranks test, respectively. Data shown for 3 kHz are from Schwartz and Wells (1983) and were obtained from different frogs. Noise (N) and Silent (S) periods each lasted a total of 60 s for each frequency.

		FMC 2 kHz			FMC 4 kHz			FMC 6 kHz			FMC 3 kHz	
Frog	N	S	Sign									
29	0.15	0.75	-	0.14	0.69	-	0.94	0.77	+	0.23	0.00	+
30	0.20	0.35	-	0.17	0.09	+	0.77	0.65	+	0.00	0.57	-
31	0.25	0.55	-	0.42	0.47	-	0.50	0.67	~	0.33	0.76	-
32	0.33	0.75		0.50	0.90	-	0.67	0.87	-	0.14	0.87	~
33	0.33	0.07	+	0.25	0.13	+	0.36	0.55		0.57	0.82	_
34	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00	0.06	
35	0.94	0.81	+	0.71	0.93	~	0.58	0.62		0.65	0.47	+
36	0.00	0.00	0	0.00	0.20	-	0.05	0.00	+	0.20	0.00	+
37	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.36	0.46	-
38	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.50	0.79	-
39	0.21	0.56	~	0.75	0.09	+	0.46	0.33	+	0.38	0.67	-
40	0.36	0.38	-	0.25	0.13	+	0.73	0.45	+	0.55	0.80	_
41	0.36	0.54	~	0.28	0.41	-	0.46	0.27	+			
42	0.36	0.73	-	0.53	0.80	-	0.64	0.80	-			
All												
frogs	0.22	0.37		0.26	0.32		0.40	0.36		0.37	0.52	
P.,	0.0	55		0	.27		0.	.50		0.	.07	
Pw	0.0	2		0	.12		0.	.40		0.	.02	

		FMC 2 kHz			FMC 4 kHz			FMC 6 kHz			FMC 3 kHz	
Frog	N	S	Sign									
29	0.00	0.71	_	0.20	0.33	_	0.80	0.81	0	0.15	0.72	
30	0.50	0.18	+	0.25	0.00	+	0.58	0.41	+	0.00	0.47	-
31	0.00	0.56	-	0.17	0.27		0.46	0.75	-	0.27	0.77	-
32	0.00	0.58		0.00	0.50		0.56	0.91		0.00	0.53	-
33	0.17	0.00	+	0.17	0.00	+	0.55	0.44	+	0.67	1.00	
34	0.00	0.00	0	0.15	0.00	+	0.08	0.05	+	0.00	0.63	
35	0.67	0.93	-	0.20	0.29	-	1.00	1.00	0	0.42	0.50	-
36	0.00	0.00	0	0.40	0.20	+	0.08	0.05	+	0.00	0.29	-
37	0.00	0.00	0	0.00	0.00	0	0.00	0.05	-	0.27	0.33	-
38	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.27	0.75	-
39	0.17	0.15	+	0.00	0.15	-	0.74	0.85	~	0.25	0.14	+
40	0.00	0.41		0.00	0.00	0	0.62	0.78	_	0.33	0.94	-
41	0.08	0.14	-	0.27	0.38	-	0.77	0.53	+			
42	0.50	0.50	0	0.53	0.15	+	0.80	0.69	+			
All												
frogs	0.14	0.30		0.17	0.16		0.45	0.48		0.28	0.63	
P_s	0.2	5		0	.50		0	.50		0.0	03	
P_w	0.0	55		0	.07		0	.44		0.0	05	

TABLE 4.—Frequency of multi-note calls (FMC) given by $Hyla\ ebraccata$ males during playback of 2, 3, 4 and 6 kHz noise at 100 dB SPL and during silent periods. P_s and P_w are significance levels for a sign test and a Wilcoxon signed-ranks test, respectively. Data shown for 3 kHz are from Schwartz and Wells (1983) and were obtained from different frogs. Noise (N) and Silent (S) periods each lasted a total of 60 s for each frequency.

data demonstrate that *H. ebraccata* males are behaviorally responsive to a range of filtered noise frequencies, our results are qualitatively similar to those of Zelick and Narins (1982) and indicate that calling inhibition of *H. ebraccata* may be elicited by the vocalizations of a number of other anuran species in its environment. Our data indicate that *H. ebraccata* males do reduce call rate during bouts of calling by nearby *H. phlebodes*, which have a dominant frequency shifted up slightly from that of *H. ebraccata*. This response is what one would predict based on the inhibition elicited by 4 kHz filtered noise. We also have conducted playback experiments demonstrating that *H. ebraccata* males will respond vocally to the individual calls of several species of frogs, including those mentioned here and *H. boulengeri* (Schwartz and Wells, unpublished data).

Our results support the hypothesis that the reduction in multi-note calling with noise is due to masking of the vocalizations of neighboring males. Detection of a call should be most difficult when most of the sound energy contributed by the noise overlaps that contributed by the vocalization. Filtered noise shifted from the

TABLE 5.—Number of calls given by <i>Hyla ebraccata</i> in natural interactions with chorusing <i>H. phlebodes</i> .
Expected values are equal to the average call rate during both the chorus and no-chorus periods multiplied
by the duration of the chorusing period.

	Tin	ne (s)	Total ca during H. phl		
Interaction	Chorus	No chorus	Observed	Expected	G
I	92	264	20	33	6.79*
II	130	99	33	58	23.48*

dominant frequency of the calls should be a less effective masker, based on our understanding of the anuran auditory system (Capranica, 1977; Ehret and Capranica, 1980).

Both H. microcephala and H. phlebodes respond to conspecific males by producing long series of click notes which are alternated with those of other individuals. One factor that might favor the evolution of this type of vocal behavior is that it effectively monopolizes portions of the broadcast period. That is, such behavior makes communication by individuals of certain other species difficult and may select for partitioning of signalling time. H. microcephala, which choruses in dense aggregations in our study site. is particularly effective in inhibiting calling by *H. ebraccata* (Schwartz and Wells, 1983). While H. ebraccata has an advertisement call with a longer primary note than either H. phlebodes or H. microcephala, it rarely gives calls with more than four notes. In our study site, aggregations of calling male H. ebraccata generally are much less dense than those of H. microcephala, and H. ebraccata does not appear to appreciably inhibit the calling of the other species. However, we have not tested this experimentally.

In other animals, species with long calls or long calling bouts can inhibit calling by species with shorter calls. Samways and Broughton (1976) and Samways (1977a,b) described a number of pairwise interactions among orthopteran species in which this was the case. Ficken et al. (1974) reported that the red-eved vireo, Vireo olivaceus, a species with a long song, inhibits singing in the least flycatcher, Empidonax minimus, which has a shorter song. The Australian frog Geocrinia victoriania has calls consisting of a primary note followed by nearly 100 shorter secondary notes. This species inhibits calling by *Pseudophryne semimarmorata*, which has short, single-note calls (Littlejohn and Martin, 1969). In two other Australian frogs, Ranidella signifera and R. parinsignifera, there is an asymmetry in the response of males to playbacks of congeneric calls. The longer calls of *R. parinsignifera* cause some *R. signifera* males to stop calling entirely and retreat. The shorter calls of *R. signifera* cause *R. parinsignifera* males to shift the timing of their calls to avoid overlap, but overall call rates are not altered relative to basal call rates before the stimulus presentation (MacNally, 1982).

The results of the female choice experiment indicate that noise generated by a chorus of *H. microcephala* can influence the behavior of female *H. ebraccata*. This could be due to masking of the vocalizations of conspecific males. Because females move toward advertisement calls that are not overlapped by a heterospecific chorus, males that reduce calling during *H. microcephala* chorusing bouts and increase calling rates during quiet intervals should be those most likely to attract females. Hence, our results suggest a selective advantage for the behavior exhibited by males in the field.

This study demonstrates that background noise can have profound effects on the behavior of both male and female H. ebraccata. Although the vocal behavior of males was most effectively modified by filtered noise centered at the dominant frequency of their vocalizations, noise with less overlap also elicited responses. The sensitivity of the frogs to noise may reflect both the tuning of their peripheral auditory system and the masking potential of the background noise. Our results underscore the potential complexity of vocal interactions among frogs in multi-species assemblages and suggest that specific patterns of vocal behavior are related to the phenomenon of acoustic interference.

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