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The Adaptive Significance of a Complex Vocal Repertoire in a Neotropical Frog

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With one figure

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Abstract

Male frogs, *Physalaemus pustulosus*, produce an advertisement call of varying complexity. Males increase call complexity in response to vocal competition from other males, and females are preferentially attracted to complex calls. The role of female choice and predation in the evolution of the advertisement call's complexity series is discussed.

Introduction

The importance of the anuran advertisement call as a species recognition signal is well known (Bogert 1960). This function probably accounts for most of the stereotypy within a species' call. However, in many species there is considerable intra-individual variation within the advertisement call and there has been little attention given to how this variation functions in mate attraction and male-male competition. In this paper we describe what is, to our knowledge, the most complex communication system reported for an anuran. We experimentally demonstrate the relationship between advertisement call complexity and both vocal competition and female mate choice and suggest a role for predation in the evolution of the call repertoire.

The Species

Male *Physalaemus pustulosus* (Leptodactylidae) call from small pools of water throughout the year. Breeding activity is concentrated during the wet

season, approximately from April to December on Barro Colorado Island (BCI), Panama, where most of this study was conducted. Females usually come to the breeding site only on the night they oviposit, but males are present on many nights. Therefore, the sex ratio at the breeding site is heavily skewed toward males and there is intense male-male competition for mates (RYAN 1980).

Materials and Methods

All *P. pustulosus* advertisement calls were recorded with a Nagra III tape recorder and a Sennheiser MKH 104 microphone. Sonagrams were made on a Kay Sonagraph model 6061-B.

We conducted male playback experiments by broadcasting a stimulus (whine-only) with a Uher 4000 tape recorder and a small extension speaker and simultaneously recording the male's response with a Nagra III and a Sennheiser MKH 104 microphone. We determined the complexity of one male's response (i. e. the number of chucks) in the presence of the stimulus by recording the male's response during 18 no stimulus — stimulus alternations. We also determined the effect of the distance of a neighboring calling male, and the number of males calling on the complexity of a male's response. 10 males were presented with a soft (more distant) and a loud (closer) call stimulus. The mean complexity of responses during soft-loud-soft-loud-soft presentations was determined, and response complexities among sequential presentations were compared. Male *P. pustulosus* have a fairly constant calling rate (1 call/2 s). We presented 11 males with a slow (1 call/2 s) and a fast (1 call/1 s) stimulus, which the male should perceive as one and two calling males, respectively. We then compared the mean complexities of the responses during slow-fast-slow-fast-slow presentations.

In the female choice experiments, a female was placed in a small cage in the center of an octagonal arena. Stimuli were broadcasted on two Uher 4000 tape recorders with small extension speakers, opposite each other, just outside the cloth wall of the arena. The intensities of the stimuli at the center of the arena were equalized, and the speakers were 150 cm apart. As the stimuli were presented alternately, the cage was removed and the female's initial direction and where she contacted the wall were recorded. 15 females were tested.

Results

The advertisement call of *P. pustulosus* consists of two components, onomatopoetically referred to as the "whine" and "chuck". All males produce calls of varying complexity, always containing the introductory whine followed by 0—6 chucks (Fig. 1).

Soloing males usually produce the simplest call: the whine-only. There is a tendency for call complexity to increase with chorus size, suggesting that males alter their call complexity due to vocal interactions with other males. To test this hypothesis, the vocal responses of males to playbacks of advertisement calls were examined. The results of these experiments showing the relationship between call complexity and vocal interactions are summarized in Table 1.

Initially, we determined the response of soloing males to the simple call: whine-only. Table 1a shows that a male gives a more complex call in the presence of the call stimulus ($\chi^2 = 455.8$, $p < .005$). We also tested the effect of distance between interacting males. Males responded with more complex calls to the closer (louder) advertisement call than to the more distant (softer)

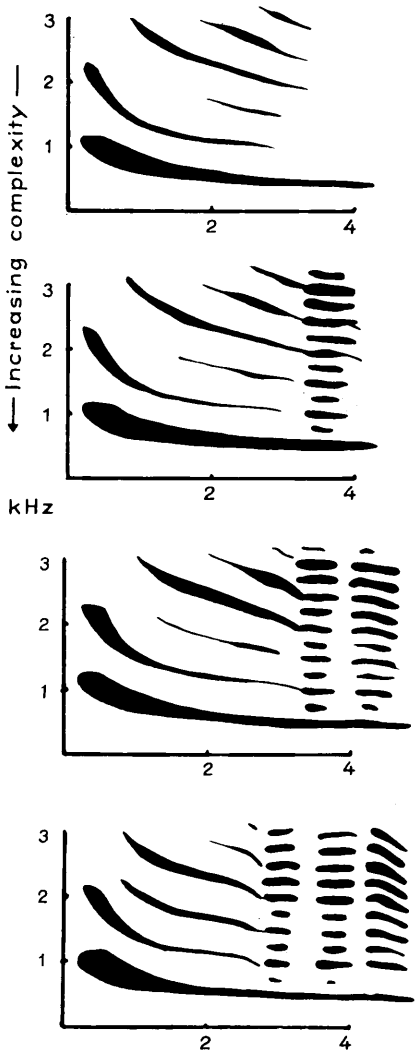

Fig. 1: Sonagraphs of the *Physalaemus pustulosus* calls of increasing complexity, from top to bottom

call ($\chi^2 = 40.0$, $p < .005$, Table 1b). Because call complexity increased with chorus size, we predicted that a male would produce a more complex call to a playback of two rather than one male. As predicted, males gave a more complex response to the faster repetition rate of two males (faster) than to the repetition rate of one male (slower) ($\chi^2 = 28.1$, $p < .005$, Table 1c).

Since vocalizations are the primary means of sexual advertisement in *P. pustulosus,* then increased call complexity should have some relationship to mate-attraction ability. We tested the response of females to simple and complex calls. Females readily approached speakers producing either a whine or a whine-chuck but not a chuck-only (which had been dissected from a normal call). This suggests that an advertisement call of any complexity produced by

Table 1: Responses of male *Physalaemus pustulosus* to various stimuli presentations

	Stimulus presented	Response			
		whine - only	whine + 1 chuck	whine + 2 chucks	
A.	with stimulus	15	239	46	
	without stimulus	276	24	0	
					$\chi^2 = 455.8$
					$p < .005$
		>complexity	<complexity	no change	
B.	loud	20	0	2	
	soft	0	20	2	
					$\chi^2 = 40.0$
					$p < .005$
C.	fast	15	2	3	
	slow	0	18	2	
					$\chi^2 = 28.1$
					$p < .005$

an isolated male is capable of attracting a female. We also tested female preference of call complexity by simultaneously presenting a female with a whine and a whine-chuck. Females showed a significant preference for the more complex call (14 vs 1, $\chi^2 = 11.3$, $p < .005$).

Discussion

We have experimentally demonstrated that males increase their call complexity due to vocal interactions with other males and that females prefer more complex calls. This suggests that the call complexity series is a form of vocal competition and that males alter call complexity to increase mate-attraction ability. Two questions become apparent: Why do females prefer more complex calls? and, Why do males not maximize mate attraction ability by always producing the most complex calls?

RYAN (1980) showed that larger males have higher reproductive success. There is a significant negative correlation between male size and fundamental frequency of the chuck component and playback experiments demonstrated that females choose calls with lower frequency chucks. By preferring a more complex call to the simple whine females are choosing calls which contain information about male body size. Since females are present at the breeding site only on the night they ovoposit, it is not surprising that females will respond to a whine-only in the absence of more complex calls.

A calling male risks being located by acoustically foraging predators. JAEGER (1976) suggested that the toad *Bufo marinus* uses acoustic cues to locate calling male *P. pustulosus* on BCI and TUTTLE and RYAN (1981), also working on BCI, demonstrated that the carnivorous bat, *Trachops cirrhosus*, uses acoustic cues to locate a number of its prey items, including *P. pustulosus*. *Philander opossum* also use the mating call as a locational cue when hunting *P. pustulosus* (TUTTLE et al. 1981).

We suggest that by adding chucks to the call, males increase predation risk. RYAN et al. (1982) showed that the bat *Trachops cirrhosus* is preferentially attracted to the more complex call. The increased predation risk might be because the chuck increases the locatability of the call. Chucks increase the duration, frequency range and total energy of the call and add abrupt transients over a wide frequency range, perhaps making the call more apparent to a number of predators. In fact, the whine bears a close structural resemblance to the alarm calls of birds, which are difficult to locate, while the chuck is similar to the locatable avian alarm calls (MARLER 1955 but see SHALTER 1978). Regardless of the mechanism involved, we show that both females (this study) and some predators (RYAN et al. 1982) are attracted preferentially by complex calls.

Therefore, we propose that the call complexity series of the *P. pustulosus* advertisement call allows a male to adjust call complexity to effect a compromise between maximizing mate attraction ability and minimizing predation risk.

Summary

Male *P. pustulosus* produce an advertisement call of varying complexity; the call containing one whine and 0—6 chucks. Soloing males tend to produce the whine-only but males increase call complexity in response to vocal competition from other males. Females are preferentially attracted to calls with chucks as opposed to calls without chucks. We suggest that females prefer complex calls because the chucks provide information about male body size. But more complex calls increase predation risk. Thus, the advertisement call seems to have evolved to allow a male to effect a compromise between maximizing mate attraction ability and minimizing predation risk.

Zusammenfassung

Männchen von *P. pustulosus* haben einen Ruf, der verschieden kompliziert sein kann. Er besteht aus einem langgezogenen Laut und 0—6 Schnalzern. Einzeln rufende Männchen äußern meist nur den langen Laut; hören sie andere Männchen rufen, dann äußern sie auch die Schnalzlaute.

Die Weibchen bevorzugen Rufe mit Schnalzern. Wir vermuten, daß die Weibchen komplizierte Rufe bevorzugen, weil die Schnalzer Auskunft geben über das Körpergewicht der Männchen. Andererseits erhöhen komplizierte Rufe für die Männchen das Risiko, von Raubfeinden gefaßt zu werden. Die variable Form des Rufes scheint also ein Kompromiß zwischen maximaler Anlockung von Weibchen und minimaler Anlockung von Raubfeinden zu sein.

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