



Lack of phonotactic preferences of female frogs and its consequences for signal evolution



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ABSTRACT

Sexual selection is one of the main evolutionary forces that drive signal evolution. In previous studies, we have found out that males of *Pleurodema thaul*, a frog with an extensive latitudinal distribution in Chile, emits advertisement calls that show remarkable variation among populations. In addition, this variation is related to intense inter-male acoustic competition (intra-sexual selection) occurring within each population. However, the extent to which female preferences contribute to the signal divergence observed is unclear. To study the responsiveness of females in each population, we stimulated females with synthetic calls designed with the acoustic structure of their own population and subsequently responsive females were subjected to a two-choice experiment, where they were stimulated with synthetic calls of their own population versus a call of a foreign population. Females do not show phonotactic preferences for calls of their own or foreign populations as measured with both linear and circular variables. The lack of phonotactic preferences suggests an absence of participation of inter-sexual selection processes in the divergence of the acoustic signals of *P. thaul*, highlighting the importance of intra-sexual selection for the evolution of these signals. These results concur with studies in other vertebrates emphasizing the relevance of interactions among males for the evolution of acoustic communication systems.

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1. Introduction

Sexual selection plays a fundamental role in the evolution of sender and receiver features in communicating organisms. According to this theory, males produce conspicuous signals by means of which they compete for access to females (intra-sexual selection), and/or females exert preferences for these displays resulting in mate choice (inter-sexual selection) (Darwin, 1871; Andersson, 1994; Searcy and Nowicki, 2009). When sexual selection operates in disjunct populations of a same species, reproductive isolation and consequent evolutionary divergence and speciation are likely outcomes (Coyne and Orr, 2004). These selective mechanisms may generate geographic variation of the signals emitted by senders and/or the responses displayed by receivers, affecting directly the appropriate matching between these two components and potentially altering conspecific recognition and breeding (Wilczynski and Ryan, 1999). The study of geographic variation in communication

systems can therefore shed light on the evolutionary processes promoting the divergence between populations.

Anurans use acoustic communication extensively during their breeding seasons. Males produce advertisement calls that attract females and promote the establishment of territories (Gerhardt and Huber, 2002). Geographic variation of these signals has been reported to occur in various cases (e.g., Nevo and Capranica, 1985; Pröhl et al., 2006, 2007; Wilczynski and Ryan, 1999; Velásquez et al., 2013) and has been attributed to different factors such as environmental conditions affecting signal propagation (Wilczynski and Ryan, 1999), genetic or geographic distances (Bernal et al., 2005; Pröhl et al., 2006, 2007; Velásquez et al., 2013), and/or sexual selection processes (Boul et al., 2007; Velásquez et al., 2014). However, few studies on the geographic variation of female preferences in response to male calls from populations of different geographical origin have been carried out. Pröhl et al. (2006) reported discrimination experiments (i.e., two-choice) showing female preferences in *Engystomops* (= *Physalaemus*) *pustulosus* for male calls from their own population relative to those of foreign populations. In this case, inter-sexual selection would lead to stabilizing selection would contribute to pre-zygotic barrier preventing hybridization and males of about average size are preferred. In contrast, Ryan

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Table 1

Values of the acoustic parameters used to build the synthetic calls used in the phonotaxis experiments.

Acoustic parameter	Totoral	Los Maitenes	Osorno	Om (T)	Om (LM) ^a	Om (O) ^a
Call duration (s)	3.8	4.3	1.8	3.7	4.2	4.2
Number of pulses per call	29	39	14	29	33	33
Pulse duration (ms)	57	58	65	65	65	65
Interpulse interval (ms)	75	53	65	64	64	64
Modulation depth (%)	91	88	58	58	58	58
Dominant frequency (Hz)	1870	2140	1790	1790	1790	1790
Rise time functions	$f(t) = 101.42 - 59.991 \exp(-2.1926 \cdot t)$	$f(t) = 101.87 - 54.358 \exp(-2.3209 \cdot t)$	$f(t) = 98.915 - 70.592 \exp(-3.0621 \cdot t)$	$f(t) = 98.915 - 70.592 \exp(-3.0621 \cdot t)$	$f(t) = 98.915 - 70.592 \exp(-3.0621 \cdot t)$	$f(t) = 98.915 - 70.592 \exp(-3.0621 \cdot t)$

^a Om (LM) and Om (O) have the same structure. See the text for details.

et al. (1992) reported discrimination experiments with females of *Acris crepitans* showing strong preferences for calls with low frequency contents relative to population averages. These results have been mostly interpreted in terms of the sensory exploitation model, implying that receivers have pre-existing biases in their sensory systems that are subsequently used advantageously by senders (see Endler and Basolo, 1998 and Ryan, 1998 for general discussions on receiver biases and sensory exploitation). In these conditions, larger-than-average males producing relatively low frequency calls are favored by inter-sexual selection.

Pleurodema thaul (Leiuperidae) is an anuran broadly distributed in Chile, ranging from the Atacama Desert (27°06'S, 69°53'W) to the Patagonian region (45°24'S, 72°42'W); (Correa et al., 2007; Veloso, 2006). This species has a prolonged breeding season, from May to December. During this period, males congregate in chorusing assemblages, producing advertisement calls while perching on low vegetation or floating on the water surface of pools and slow-flowing streams. A recent study of geographic variation of the advertisement calls of this species has revealed the existence of three bioacoustic groups, differing in the structure of both temporal and spectral components, corresponding to northern, central and southern populations (Velásquez et al., 2013) (Velásquez, 2014). In addition, a study of evoked vocal responses (i.e., vocal responses that are elicited by a stimulus and do not correspond to spontaneous vocal activity) revealed that males of this species exhibit different vocal activity when confronted with local or foreign stimuli, implying intra-sexual selection in the origin of advertisement call divergence (Velásquez et al., 2014).

In the current study, we examine the phonotactic preferences of female frogs *P. thaul* of different geographic origin for signals having local and foreign features, in order to explore the extent to which inter-sexual selection is involved in the generation of the observed geographic variation in the advertisement calls of this species. Preferences of this kind would denote the action of past selective pressures originating the contemporary divergence patterns observed. The comparison of the status of variation in signals and preferences is meant to provide evidence on the precedence order of the evolutionary divergence of components of the sound communication system along the geographical distribution of this species.

2. Methods

2.1. Subjects

We conducted phonotaxis experiments with females from three localities within the distribution range of *P. thaul*. The tests were conducted in the localities from which the frogs were native (Totoral, northern population: 27°54'S, 70°56'W, 136 m a.s.l.; Los Maitenes, central population: 34°41'S, 71°26'W, 140 m a.s.l. and Osorno, southern population: 40°35'S, 73°03'W, 70 m a.s.l.). The experiments in Totoral and Los Maitenes were conducted during

September and October 2009 and in Osorno during September 2010. In each population, females were captured during daytime, under stones or low vegetation in the vicinity of breeding sites: pools or slow flowing creeks. The subjects were maintained in individual containers until tests were carried out at nighttime, within 12 h of capture.

2.2. Synthetic stimuli

The advertisement call of *P. thaul* has a remarkable variation along the latitudinal range of the species (Velásquez et al., 2013). We used the analysis carried out in that previous study, which corrected the acoustical parameters for the morphological and environmental parameters measured in each population to build the synthetic stimuli (see Velásquez et al., 2013 for details on the analysis of the advertisement calls used for the synthesis of the stimuli used in the current study). Briefly, in Velásquez et al. (2013) advertisement calls of 27, 17 and 23 males from the localities of Totoral, Los Maitenes and Osorno, respectively, were recorded. Based on the mean values of the acoustic parameters, we built standard synthetic calls for each population, imitating the natural calls emitted by local males, using Adobe Audition 3.0. The acoustic parameters to build the Standard synthetic calls for Totoral, Los Maitenes and Osorno are listed in Table 1. In addition, the gradual amplitude increase of the 10 first pulses was modeled with different rise curves for the standard synthetic calls of each population (Table 1, Fig. 1a). These stimuli were also used to explore the geographic variation of the evoked vocal responses in males of this species in a subsequent study (Velásquez et al., 2014). Because the standard stimulus of Osorno had a short call duration and a small number of pulses relative to the synthetic calls of the other two populations, additional stimuli were built to compensate for the low values of these variables of stimulus and for potential biases produced by call duration and number of pulses on females preferences. Thus, in addition to the standard synthetic calls of each population, we built three different synthetic calls having the same pulse duration, modulation depth and dominant frequency as the standard synthetic call of Osorno, but having the approximate call duration, number of pulses and inter-pulse interval duration of the standard synthetic call of each population studied (Osorno modified synthetic calls, Om). For the tests with females from Totoral and Los Maitenes, these calls had durations of 3.8 and 4.2 s, and number of pulses of 29 and 33 pulses, respectively. Similarly, an Osorno modified call was synthesized for tests with females from the Osorno population, and in this case the characteristics of the stimulus having the longer duration and larger number of pulses (e.g., Los Maitenes: 4.2 s and 33 pulses, respectively) were chosen. These stimuli are shown in Fig. 1 and the acoustic parameters used to build them are also summarized in the Table 1. These sounds were saved as WAV files (44.1-kHz sampling rate, 16-bit resolution) and used to generate the stimulation schedules employed in the control and two-choice experiments.

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