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Review Paper

Geographic variation in acoustic communication in anurans and its neuroethological implications

Nelson A. Velásquez *

Laboratorio de Neuroetología, Programa de Fisiología y Biofísica, ICBM, Universidad de Chile, Independencia 1027, 8380453 Independencia, Santiago, Chile
Facultad de Ciencias Básicas, Universidad Católica del Maule, San Miguel 3605, 3480112 Talca, Chile

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ABSTRACT

Geographic variation of traits may represent the first step for evolutionary divergence potentially leading to speciation. Signals are behavioral traits of particular interest for the study of variation at a geographic scale. The anuran acoustic communication system represents an excellent model for studies of this kind, because their vocalizations play a main role in reproduction and the extant variation in this system may determine the evolution of this group. This review is committed to studies on geographic variation of acoustic communication systems in anurans, focusing on temporal and spectral characteristics of signals, environmental constraints affecting them and sound producing and receiving organs. In addition to the review of the literature on these topics, I highlight the deficit of investigation in some areas and propose alternative directions to overcome these drawbacks. Further, I propose the four-eyed frog, *Pleurodema thaul*, as an excellent model system to study geographic variation using a wide spectrum of approaches.

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1. Introduction

Darwin proposed that species diverge by means of natural selection favoring individuals having fitter traits over other individuals less adapted to compete for limited resources (Darwin, 1859). However, it has been widely recognized that this process is not a generator of variation, but operates on pre-existing trait variation (Jablonka and Lamb, 2002, 2005; Endler, 1986). After Darwin, diverse processes such as mutation, genetic drift and hybridization have been proposed as sources of variation (Futuyma, 2013). The combined action of these factors produces divergence among populations, causing speciation as a potential final outcome (Butlin et al., 2012; Coyne and Orr, 1998; Coyne and Orr, 2004). Speciation could arise as the consequence of dispersion and colonization phenomena, by which members of a population migrate and settle in new environments (e.g. Bonacum et al., 2005). Also vicariance phenomena have been proposed to produce geographic barriers that isolate and expose populations to different environmental conditions (e.g. Hoskin et al., 2005). Individuals of populations exposed to such conditions may establish distinct behavioral dynamics of interaction between themselves and with their environment, yielding variation of behavioral characters at geographical scales (see Freeman and Herron, 2007 or Turelli

* Address: Facultad de Ciencias Básicas, Universidad Católica del Maule, San Miguel 3605, 3480112 Talca, Chile. Tel.: +56 71 2203370.
E-mail address: nelson.velasquez@gmail.com

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et al., 2001 for mechanisms of speciation). This kind of variation has provided an excellent model to investigate possible initial stages of speciation and the factors responsible for these divergences. The main factors that have been attributed to generate geographic variation are natural and sexual selection and genetic drift, which have been studied for different kinds of traits (Bush and Schul, 2010; Butlin et al., 2012; Funk et al., 2009).

Animal communication, understood as the transmission of a signal between a sender and a receiver across an environment causing a behavioral change in the second actor (see Bradbury and Vehrencamp, 2011; Hauser, 1997 for a complete discussion on the definition of animal communication), is a widely studied phenomenon that plays a significant role in species divergence (Endler and Basolo, 1998; Ryan and Rand 1990; Boughman, 2002; Wilkins et al., 2013). Because signals travel across an environment as they are transmitted from sender to receiver, the evolution of the communication system may be affected by particular environmental conditions to which different populations are exposed (Narins, 2001; Gridi-Papp and Narins, 2009). Acoustic communication has been an excellent model to study the effects of environmental factors on the structure of signals, the morphology of the sound-producing structures, and auditory sensitivities (Morton 1975; Hermida and Farías, 2009; Schwartz and Gerhardt, 1998).

Anurans possess important features that make them particularly interesting from a bioacoustic standpoint. Anurans spend their first stages in the aquatic environment, depending totally on this resource (Vitt and Caldwell, 2014). The auditory sensitivity of anurans starts developing from premetamorphic stages (Boatright-Horowitz and Simmons, 1997) and some larvae are even capable of emitting acoustic signals in certain contexts (Natale et al., 2011; Salgado Costa et al., 2013). In adult life, anurans become partially independent of the aquatic medium, returning there to complete their reproduction. The change from aquatic to terrestrial life causes modifications at morphological, physiological and behavioral levels in both senders and receivers (Vitt and Caldwell, 2014; Wells and Schwartz, 2007; Vidal and Labra, 2008). Therefore, anurans also represent an excellent model for studies on development, influences of environmental conditions, morphological and physiological changes.

In most anuran species males aggregate in chorusing ensembles, producing advertisement calls which attract females (Gerhardt and Huber, 2002; Ryan, 2001), in a reproductive system called lek, widely used by birds and mammals (Bradbury and Vehrencamp, 2011; Alcock, 2005). Furthermore, males of some species set territories by means of their calls (Gerhardt and Huber, 2002; Ryan, 2001). Various structures including lungs, larynx, mouth and vocal sac participate in the production of these calls (Martin, 1971; Martin, 1972; Martin and Gans, 1972; see Walkowiak, 2007 for a review of vocal production in anurans). By contracting the flank muscles air is forced to flow through the larynx, which contains a series of muscles (e.g. dilator, constrictor), cartilage (e.g. arytenoid, cricoid) and folds (vocal cords). As the air flows the vocal cords vibrate, determining the fundamental frequency of frog vocalizations. After its passage through the larynx, the different frequencies of the sound produced are amplified or attenuated in the mouth cavity and vocal sac, determining the final spectral content of the vocalizations produced. The temporal structure of the vocalizations may be modulated in active or passive modes (Martin, 1971; Gerhardt and Huber, 2002). In the active mode, the contraction of the flanks determines the number of pulses, the duration of each pulse and the duration of the interpulse interval. In contrast, in passive control the amplitude modulations exerted by both laryngeal muscles and arytenoid valves are responsible for the fine temporal properties of vocalizations such as the number and depth of intra-pulse modulations (i.e. ratio of the difference between the maximum and minimum envelope amplitude within a pulse, expressed as a percentage). Sound reception in anurans has peculiar characteristics because at the auditory periphery the frequency sensitivity is segregated in two different organs. The low and mid frequencies are processed by the amphibian papilla and the high frequencies by the basilar papilla (Feng et al., 1975). These two structures represent the first filter in the auditory system, in contrast with temporal filters that are located upstream in the anuran auditory system (Narins et al., 2007).

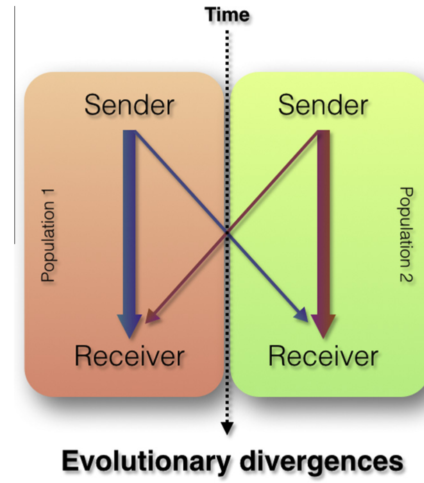

Fig. 1. Schematic diagram of geographic variation in the anuran acoustic communication system. In each population, a signal travels from a sender to a receiver, but the signal emitted by a sender from population 1 is perceived or triggers behavioral responses mainly from receivers of the population 1 compared to receivers of population 2 and vice versa. Over time and by means of different evolutionary mechanisms (e.g. genetic drift, natural and sexual selection), the signals emitted and the sound producing-receptor structures diverge between the populations.

Geographic variation of the acoustic communication system in anurans may generate evolutionary divergences, representing the initial stages of speciation. If the signals emitted by senders differ between populations, and if the receivers from different populations perceive them as distinct, different behavioral responses may be triggered. In addition, if the environments across which these signals travel are different between populations, different conditions for propagation and degradation may be generated. Thus the main evolutionary forces (e.g. genetic drift, natural and sexual selection) may act with different intensities in each population, producing their divergence (Fig. 1).

Signal variation at a geographic scale represents an excellent model to investigate the factors that influence signal divergence between populations at both sender and receiver levels. Several studies in anurans have undertaken efforts in this direction. In addition, since behavior is the expression of structure and organization of the nervous system in a particular environment (Maturana-Romesin and Varela, 2003), the neurobiological mechanisms underlying this behavioral variation at a geographic scale are also relevant to be understood. The receptor responses are so important that these may induce drastic changes in the configuration of certain signal parameters, which could in turn generate important evolutionary changes. For this reason it is crucial to consider the geographic variation of both morphology and physiology of the sound receptor structures. However, few investigators have carried out studies on the neurobiological implications of the geographic variation of the communication system and these efforts have received considerably less attention than behavioral studies. Thus the aim of this review is to comment on studies regarding geographic variation in the acoustic communication systems of anurans from behavioral and neurobiological approaches, and to