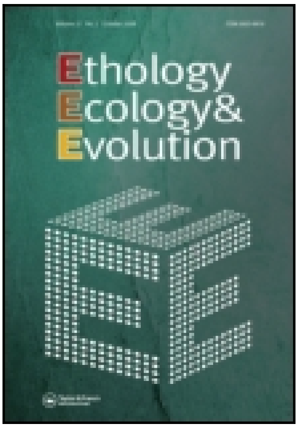

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Environmental effects on anuran call design: what we know and what we need to know

L.K. Erdtmann [a] & A.P. Lima [a]

[a] Graduate Program in Ecology, Instituto Nacional de Pesquisas da Amazônia - INPA, Caixa Postal 478, CEP 69011-970, Manaus, Amazonas, Brazil

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Environmental effects on anuran call design: what we know and what we need to know

L.K. Erdtmann [1,2] and A.P. Lima [1]

[1] *Graduate Program in Ecology, Instituto Nacional de Pesquisas da Amazônia - INPA, Caixa Postal 478, CEP 69011-970 Manaus, Amazonas, Brazil*

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Long-range acoustic signals are subject to a variety of evolutionary pressures, such as sexual selection, species recognition, body-size constraints, physiological constraints, and natural selection by environmental constraints. Anuran advertisement calls are long-range acoustic signals with two essential functions: to attract females, and to defend a territory against other males. However, the environment offers obstacles to sound transmission. The call can be attenuated and degraded, and the surrounding environment might impose a strong constraint on it by means of sound refraction, reflection, and absorption along the transmission path. The Acoustic Adaptation Hypothesis (AAH) predicts that the acoustic signal could be adapted in order to maximise transmission distance by minimising call attenuation and degradation. The predictions of the AAH have been reviewed twice for birds, and once for mammals and anurans. This study extends the anuran review, focusing on the environmental effects on anuran call design, and their conformity to the AAH predictions. A small number of studies were found, and the results were conflicting. These studies were carefully analysed, and we report a lack of standardised methodology to test for environment effects. We discuss in detail the diverse methodologies and point out how the matter has been treated. We highlight the importance of improving the project design by increasing the sample size, controlling for phylogenetic and body size effects, and using a quantitative representation of vegetation structure.

KEY WORDS: bioacoustics, acoustic communication, advertisement call, adaptation, Anura.

INTRODUCTION

Acoustic signals are primordial for communication in a variety of animal groups. They may contain information about the informer's identity, physical location, body size, species, and sexual status (Gerhardt & Huber 2002). However, a

[2] Corresponding author: Luciana Kreutz Erdtmann, Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia - INPA, Caixa Postal 478, CEP 69011-970, Manaus - AM, Brazil (E-mail: luciana.erdtmann@gmail.com).

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communication system is only efficient when the signal emitted by an individual travels through the environment and influences the perceiver (Bradbury & Vehrencamp 1998; Ruxton & Schaefer 2011). Acoustic signal evolution can be shaped by several selective pressures, e.g., sexual selection, morphology, physiology, phylogeny, predation, parasitism, and environment (Endler 1992; Forrest 1994). These selective pressures could act in isolation or integrated with each other, sometimes even in opposite directions; for instance, when the signal production attracts both mates and predators (Ryan 1986). The local environment, i.e., described by the environmental characteristics around the calling site or along the call propagation path, may represent a strong selective force on acoustic signals, because they are particularly affected by the environmental characteristics of their propagation path, such as temperature, vegetation structure, and background noise. The environmental pressures on signals are often studied as background noise effects or in relation to signal attenuation and degradation patterns. Sound attenuation is usually greater than expected in spherical spreading conditions, due to sound absorption, scattering, reflection, and refraction caused by the environment, and this additional increase is called excess attenuation (Forrest 1994; Gerhardt & Huber 2002).

Sound scattering and reflection also play a role in call degradation, defined as the decreasing of call integrity by losing definition in temporal traits and amplitude patterns (Forrest 1994). Local vegetation structure can increase the signal attenuation and degradation, decreasing the acoustic transmission distance and the signal accuracy. Temporal and spectral components of acoustic signals are differentially affected by environmental conditions; for example, higher frequencies attenuate more rapidly than lower frequencies in any environment (Morton 1975; Gerhardt & Huber 2002; Ellinger & Hödl 2003). In the Acoustic Adaptation Hypothesis (AAH), selection in the local environment would drive the selection for call design (Morton 1975). Commonly, AAH is tested by field playback experiments in order to quantify the signal attenuation and degradation, comparing the habitat where the species lives with a contrasting habitat, usually forest vs open area. AAH predicts that, in comparison with densely vegetated areas (e.g., a forest), calls in open areas will (1) be shorter in length, (2) have a higher repetition rate, (3) have frequency modulation, (4) have a higher minimum frequency, (5) have a higher maximum frequency, (6) have a higher dominant frequency, and (7) have a wider frequency bandwidth (Morton 1975). However, the results concerning AAH are, in general, ambiguous, and the response to environmental pressure may be varying on a fine scale that is usually not tested (Boncoraglio & Saino 2007; Ey & Fisher 2009; Ziegler et al. 2011).

Anuran advertisement calls have the primary functions of attracting females and announcing territory possession to other males (Duellman & Trueb 1994). The advertisement call transmits information about the calling male, and females might base their mate-choice on that information. Male body size can be presented in the advertisement call, because in anurans, the dominant frequency is often inversely related to the body size, with larger males producing lower-frequency calls than smaller males (e.g., Zimmerman 1983; Ryan 1988; Gerhardt 1991). Thus, anuran calls could be under different evolutionary pressures, e.g., sexual selection, species recognition, morphology, and phylogeny (Ryan 1986). Advertisement call production is costly (for a review see Wells 2007), as is a heterospecific mating (Panhuis et al. 2001). Because of its importance to the mating system, it is expected that (1) the transmission distance of advertisement calls would be maximised, facilitating call detection and recognition by conspecific females, thus avoiding energy wasting; and (2) that the transmission distance would vary according to the surrounding environmental characteristics. Ey & Fisher (2009) reviewed only three articles on AAH in anurans, that indicated some environmental effect on advertisement call traits, but the general findings about AAH in anurans were inconclusive.

Here we will review a larger number of studies of AAH and environmental influences on anuran calls, to attempt to identify generalisations that are well supported, and to indicate how studies may be improved to allow better evaluations of AAH.

MATERIALS AND METHODS

We systematically searched in the Web of Knowledge database (http://apps.isiknowledge.com) with combinations in triads with the words "habitat", "environment*", "adaptation", "acoustic*", "call", "acoustic communication" and "anura*". Some articles that were not found by the systematic search were included, in order to complete the list of publications about acoustic adaptation in anurans and environmental effects on advertisement calls. These articles were found by checking references in related articles, theses, and occasional searches in Google (www.google.com) and ScienceDirect (www.sciencedirect.com). Articles consulted are summarised in Table 1. The main temporal and spectral call traits evaluated are described in Table 2. Call traits specific to one or a few species were not included. Because phylogenetic history and body size can affect the call structure, we recorded whether the studies included phylogeny and body size in their analyses. Sample size, i.e., number of sampled sites and sampled species, as a methodologically important trait, was also noted.

RESULTS

We found 12 articles dealing with environmental effects on anuran advertisement call traits and the acoustic adaptation hypothesis in anurans (Table 1).

Environmental effects on specific temporal and spectral traits (for a description of call traits, see Table 2) were tested in six studies. Sometimes, one article analysed more than one temporal and spectral trait, and therefore the number of studies investigating temporal and spectral traits and the number of call traits considered were not the same. For temporal traits, environmental effects were found 9 times (in four studies): 4 times for call duration, 2 times for pulse rate, 1 time for call rate, 1 time for inter-call interval, and 1 time for inter-note interval. In three tests (in two studies), temporal traits were not consistent with AAH predictions. These studies investigated: pulse rate (n = 1), call rate (n = 1), and call duration (n = 1).

For spectral traits, support for the AAH predictions was found 3 times (three studies) for dominant frequency (higher frequencies in open areas), 2 times for frequency modulation, and 1 time for frequency bandwidth. In one study, frequency modulation was inversely related to microhabitat characteristics (more complex environments showing higher-frequency modulation). In three tests (in two studies) there was no response related to AAH predictions for dominant frequency (n = 1) or frequency bandwidth (n = 2). No relationship was found between environment and number of notes per call (n = 1), and the number of different notes added to the advertisement call (n = 1). Also, environment influenced call intensity (n = 1), and the number of different notes added to the advertisement call (n = 1).

Table 1.

Environmental effects on advertisement call traits of anurans. The response to environment is shown by: (–) no environmental influence reported, (+) environmental influence reported. Accordance with the Acoustic Adaptation Hypothesis (AAH) follows the authors' conclusion: (–) results do not support AAH or any environmental effect, (+) some support for AAH conditions or environmental effect.

Taxa	Intra/interspecific dataset	Body size	Phylogenetic inference	Habitat description	Call duration	Call rate	Pulse rate	Intercall interval	Internote interval	Dominant frequency	Frequency bandwidth	Frequency modulation	Call intensity	Number of notes	Number of different notes	Accordance with AAH	Reference
56 Amazonian species	inter	yes	yes	Open, Forest			–			+	+	+				–	ZIMMERMAN 1983
Ranidella riparia; R. signifera	inter	no	no	Rock, Mud and reeds	+		+				–					+	ODENDAAL et al. 1986
Bufo woodhousii; B. valliceps	inter	yes	no	Two sites												–	RYAN & SULLIVAN 1989
Acris crepitans	intra	no	no	Open, Forest												+	RYAN et al. 1990
5 Chilean species	inter	yes	no	Brush, Water												–	PENNA & SOLÍS 1998
22 Panamanian species	inter	no	no	Open, Forest												–	KIME et al. 2000
Metaphrynella sundana	intra	no	no	Air depth inside a hole	+			+		+			+			+	LARDNER & LAKIM 2002
Pseudacris crucifer crucifer	intra	no	no	Models of trees, shrubs and ponds cover												+	PARRIS 2002

3 taxa *Bufo viridis* complex	inter	no	no	% covering 1 m^2 quadrats and background noise										–	CASTELLANO et al. 2003
95 Bolivian species	inter	no	yes	Ecoregion, Macrohabitat, Microhabitat	–	–			–	–	+	–	–	–	BOSCH & DE LA RIVA 2004
8 *Scinax* species	inter	no*	yes	Open, Forest	+	+	+		+				+	+	BEVIER et al. 2008
Hypsiboas pulchellus	intra	yes	no	Vegetation cover, used in a path analysis										+	ZIEGLER et al. 2011
	intra	yes	no	% covering 25 × 25 cm quadrats	+			+						+	ZIEGLER et al. 2011

*BEVIER et al. (2008) presented body mass measurements.

Table 2.

Description of temporal and spectral call traits considered in the revised articles. Most of them were presented in Bosch & De La Riva (2004).

Call trait		Description
Temporal	Call duration	The call length from its onset until the end.
	Number of notes	Number of notes within a call.
	Call rate	Number of calls emitted per minute.
	Pulse rate	Number of pulses emitted per second.
	Intercall interval	Interval between two consecutive calls.
	Internote interval	Interval between two consecutive notes.
Spectral	Dominant frequency	The call frequency value with the highest energy in the call.
	Frequency bandwidth	The difference between the upper and lower call frequency.
	Frequency modulation	The changing of call frequency.
	Call intensity	The intensity of call, measured in decibels (dB).
	Number of different notes	Number of different notes composing an advertisement call.

The remaining studies (n = 6) analysed environmental effects on call degradation by field playback experiments of call propagation, and calculated cross-correlation coefficients to quantify the effects of attenuation and degradation (n = 5), or by model testing (n = 1); they did not report their results on specific call traits. Four of these studies did not find a relationship between environment and call degradation, and in one study, the environment apparently influenced the call propagation pattern (Ryan et al. 1990). The negative results (i.e., the environment was not affecting the call propagation pattern) in Ryan & Sullivan (1989) were attributed to the high similarity between the studied areas.

The power of extrapolation of results depends on project design. We list four characteristics that deserve special attention: environment representation, body size, sample size, and phylogenetic inference.

Environment representation

The environment was represented as a qualitative variable in eight studies. Only two studies quantified the vegetation structure around the calling site (Castellano et al. 2003; Ziegler et al. 2011), and one quantified the proportions of water and air in the holes used as calling sites (Lardner & Lakim 2002). In one case, the environment was also represented as the background noise (Castellano et al. 2003). Although background noise can be a source of selection for call traits, it is not the focus of this review, and additional studies on this theme were not analysed (e.g., Hödl & Amézquita 2001; Penna et al. 2005; Preininger et al. 2007).

Body size

The body-size information was included in four studies, and in one study (Bevier et al. 2008) morphology was represented by body mass. In these studies, the inverse relationship between the call-dominant frequency and body size or body mass was evident.

Sample size

Usually, the experimental design consisted in testing call propagation or comparing call traits between one open area and one forested area. The appropriate number of studied species should vary according to the study question. In the studies evaluated it varied from 1 to 95, and from 1 to 51 species per area.

Phylogenetic inference

Interspecific datasets were analysed in eight studies, and four studies analysed intraspecific datasets. Only three studies considered the phylogenetic influence on signal structure through species relationships (genus and family), but the authors did not use comparative phylogenetic methods to incorporate the species' phylogenetic relationships within or exclude them from the statistical analysis. In summary, six articles found results compatible with AAH or at least showed the existence of an acoustical response flexibility related to environmental characteristics. No evidence supporting AAH or environmental influence was reported in six studies. The only interspecific study showing an environmental effect on call trait analysed three environmental types (ecoregion, macrohabitat, and microhabitat), and found a weak relationship that was contrary to that expected for AAH for frequency modulation with microhabitat (Bosch & De La Riva 2004). Like Bosch & De La Riva (2004), who found an environmental effect on call trait contrary to AAH, Zimmerman (1983) explained the relationship of spectral traits with the environment as a confounding effect with body size and phylogenetic effects.

DISCUSSION

The results of the articles that we reviewed showed that there is no general consensus about the importance of the environment as an evolutionary pressure affecting the evolution of advertisement calls in anurans. However, it is not possible to be sure whether this reflects different biology or different project designs. Advertisement calls were well represented in the studies, where spectral and temporal traits were tested for a similar number of times. Nevertheless, call intensity and structural traits (e.g., the addition of different notes to the call) were used less often.

Biological concerns

Because the advertisement call is composed of temporal and spectral traits, its response to evolutionary pressures may vary within call traits. As a consequence, the acoustic signal design will be a result of the trade-off between the evolutionary pressures on call traits. Anuran advertisement call traits may exercise different roles in species recognition and sexual selection, and they may be classified as static or dynamic according to their coefficient of variation within and between males (GERHARDT 1991). Static traits are those with low variability within and between males, such as spectral traits, and dynamic traits are those with high variability within and between males, such as temporal traits (GERHARDT 1991). GERHARDT (1991) suggested that static traits should be used in species recognition, whereas dynamic traits would be more important for sexual selection. Therefore, call traits may vary according to evolutionary pressures, and sexual selection can be stronger than environmental pressures when the call trait plays a role in mate-choice.

The relationship between dominant frequency and body size is well documented in anurans (e.g., ZIMMERMAN 1983; RYAN 1988; GERHARDT 1991). The reviewed studies that included body size in their statistical analyses found the expected inverse relationship between the body size and dominant frequency. However, they failed to find a relationship between dominant frequency and environment. Possibly, in these cases, morphology represented by body size is a greater evolutionary pressure on call frequencies than is the environment itself. BEVIER et al. (2008) found environmental effects on dominant frequency and included body mass in their statistical analyses, but the results were contrary to those expected according to the AAH: species occurring in open areas had higher body mass and produced lower-frequency calls. On the other hand, in studies where a dominant frequency was related to environmental type or condition, the body size was not evaluated.

Background noise is a source of selection and can favour higher frequencies than the frequency bandwidth occupied by noise, even higher than those expected based on body size (PREININGER et al. 2007). It might also favour the appearance of other communication systems, such as the use of visual signals (for a review, see HÖDL & AMÉZQUITA 2001), or ultrasonic sounds (FENG et al. 2006). Background noise along with signal reverberations produced by the local vegetation may contribute to the degradation of temporal structure of *Hyla chrysoscelis* advertisement calls by "filling" the intervals between pulses, but despite the loss in pulse structure, degraded calls still elicited female phonotaxis (KUCZYNSKI et al. 2010).

Methodological concerns

This review found contrasting results concerning the effects of the local environment and the AAH on anuran advertisement calls. Thus, we are not able to predict the call adjustment to the environment in anurans as a whole. Nevertheless, the evidence is very limited, and project designs may explain many of the discrepancies. The best environment-fitted acoustic signal (i.e., with high performance in the species' own habitat), as suggested by MORTON (1975) and ENDLER (1992), is rarely found to be inclusive for a well-studied species group such as birds (for a review on AAH in birds, see BONCORAGLIO & SAINO 2007; EY & FISHER 2009). The AAH was based solely on call-propagation performance in very discrepant environments: a densely vegetated habitat, such as a forest, and an open area, such as grasslands. This was a very important and fundamental step for our understanding of bioacoustics and animal acoustic communication, but why has the experimental design not improved since then? Below, we list and discuss the four main points that we believe need to be taken into account for a successful test of AAH.

Study argument 1. Environment representation. The way that the environment is represented is extremely important for the interpretation of results. Usually, the vegetation structure is summarised as a broad qualitative trait. The need for more detailed vegetation information has been pointed out previously by BOSCH & DE LA RIVA (2004), WELLS (2007), and EY & FISHER (2009). The broad qualitative representation of habitat types could be masking the effective environment that a small frog uses to communicate. The major problem is the scale on which the environment is usually represented. Broad categories of environment may not be adequate to represent the vegetation structure that affects the call propagation, particularly in the case of small taxa. Thus, a key concept is the definition of local environment, which must be measured on an appropriate scale in relation to the focus taxa. Also, to investigate the environmental effects on call propagation, more precise measurements of vegetation structure are required, i.e., to characterise the vegetation microstructure. A more precise environment representation will allow better hypothesis testing. Environment representations may be done in a variety of ways: ZIEGLER et al. (2011) measured the cover percentage inside sampling quadrats distributed in a 2 m radius around a male calling site; CASTELLANO et al. (2003) represented the environment, consisting of open grasslands, by the percentage of vegetation cover and the vegetation height, both measured in quadrats distributed along the propagation paths – transects 32 m long. The study site and, mainly, study question will determine the best representation for the local environment conditions. In a forested area, for example, to combine techniques to measure herbs, grass, and shrubs and techniques to measure trees would be desirable. But the study question will dictate how the measurements should be done. Numerous field techniques to measure vegetation are found in botanical literature. For large interspecific datasets, where habitat representation in categories is used, the statistical analysis must include information on phylogeny.

Study argument 2. The study should explicitly examine body-size effects. The perfect scenario would be to use individuals of the same species occurring in forested and open areas. However, as this scenario is difficult to find, pairs of species with similar body sizes should be used, as well as inclusion of body size as a covariate in analyses, which also helps to minimise unwanted effects of body size on the analysis.

Study argument 3. The number of sample units. Avoiding pseudoreplication and, consequently, misinterpretation of collected data (for a review see HURLBERT 1984) is the principal challenge in all project designs. Further research must take into consideration increasing the number of sample units, i.e., the number of sampled areas. For example, call propagation playback experiments might be performed in several forested and open areas, rather than pseudoreplicates in one location. There is no magic number for how many sample units must be used. However, it is imperative to increase the number of sites above the numbers that were used in previous studies (usually the comparison of one forest with one open area).

Study argument 4. The study should take into account phylogenetic effects. Depending upon the theoretical or field design, different approaches may be adopted to incorporate or exclude phylogenetic effects. Comparative phylogenetic methods (e.g., phylogenetic independent contrasts, Hansen's adaptation test) are preferable in theoretical studies. In field playback experiments, phylogenetic differences can be controlled by selecting species that occur in both forested and open areas. The ideal scenario would be to use individuals of the same species that live in both types of area. Such a scenario is not easy to find and, alternatively, pairs of sister-species or the closest phylogenetically-related species could be used. The inclusion of different species-pairs is enough to achieve species replication.

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