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How the environment shapes animal signals: a test of the acoustic adaptation hypothesis in frogs

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Abstract

Long-distance acoustic signals are widely used in animal communication systems and, in many cases, are essential for reproduction. The acoustic adaptation hypothesis (AAH) implies that acoustic signals should be selected for further transmission and better content integrity under the acoustic constraints of the habitat in which they are produced. In this study, we test predictions derived from the AAH in frogs. Specifically, we focus on the difference between torrent frogs and frogs calling in less noisy habitats. Torrents produce sounds that can mask frog vocalizations and constitute a major acoustic constraint on call evolution. We combine data collected in the field, material from scientific collections and the literature for a total of 79 primarily Asian species, of the families Ranidae, Rhacophoridae, Dicroglossidae and Microhylidae. Using phylogenetic comparative methods and including morphological and environmental potential confounding factors, we investigate putatively adaptive call features in torrent frogs. We use broad habitat categories as well as fine-scale habitat measurements and test their correlation with six call characteristics. We find mixed support for the AAH. Spectral features of torrent frog calls are different from those of frogs calling in other habitats and are related to ambient noise levels, as predicted by the AAH. However, temporal call features do not seem to be shaped by the frogs' calling habitats. Our results underline both the complexity of call evolution and the need to consider multiple factors when investigating this issue.

Introduction

Long-distance acoustic communication is used in many species of insects, birds, mammals and anurans and is of paramount importance for reproductive success in many of these taxa. When travelling from sender to receiver, acoustic signals face environmental constraints

that impede their transmission, depending on the physical properties of the environment (Forrest, 1994). Signals with maximal reach and content integrity in the signalling habitat confer a fitness advantage to the emitter and should thus be selected (Morton, 1975). As a result, the environment shapes acoustic signals through natural selection (e.g. Wilkins *et al.*, 2013). Since the work of Rothstein & Fleischer (1987), this proposition is known as the acoustic adaptation hypothesis (AAH; for a review, see Ey & Fischer, 2009).

Based on the AAH, bioacousticians have predicted which call features should be selected in a given environment, focusing primarily on vegetation structure

(Ey & Fischer, 2009). In forested areas, signals with lower dominant frequency, narrower frequency range, longer duration and low amplitude or frequency modulation are less attenuated or distorted and should therefore be favoured for long-distance communication. In open spaces, short, frequency-modulated signals should be selected (Morton, 1975, 1977; Marten & Marler, 1977; Wiley & Richards, 1978; Richards & Wiley, 1980). In addition, the ground attenuates or reflects sound waves depending on their frequency and on ground porosity. This 'ground effect' favours signals with frequencies above 0.5–1.0 kHz, whereas lower frequencies are attenuated (Morton, 1975; Wiley & Richards, 1978). Finally, ambient noise may partially or totally mask an acoustic signal if the frequency ranges of the two sounds overlap, and would thus favour signals with frequencies outside of the ambient noise frequency range (Klump, 1996; Nemeth & Brumm, 2009; Cunningham & Fahrig, 2010; Goodwin & Podos, 2013). All these call features are thus potentially adaptive to the environment they are produced in.

Studies of the AAH in birds, mammals and anurans have so far yielded inconsistent results with some studies verifying the predictions mentioned above and others finding no impact of the environment on call features or even an opposite relationship to the expected trends (see references in Ey & Fischer, 2009). For example, in Bertelli & Tubaro (2002), the songs of tinamous living in open habitats were higher-pitched and had a wider frequency bandwidth than those of their relatives living in closed habitats, in accordance with the AAH. However, Blumstein & Turner (2005) and Saunders & Slotow (2004) found only weak support of the AAH when examining spectral and temporal characteristics of songs and controlling for phylogenetic effect in 121 and 40 bird species, respectively. Peters & Peters (2010) examined long-distance roars of 27 species of Felidae (taking into account body size and phylogenetic relationships) and found that their dominant frequency was lower in open than in closed habitats, contradicting the AAH prediction. These contradictory results are, at least partially, explained by a very broad categorization of habitats, such as 'open' vs. 'closed', which oversimplifies complex habitat conditions (Bosch & De la Riva, 2004; Goutte *et al.*, 2016). Thus, testing predictions stemming from the AAH requires examination of the acoustic constraints in a microhabitat-specific context (Goutte *et al.*, 2013, 2016) when it is not possible to measure the transmission properties of all the habitats (Penna & Solis, 1998; Penna *et al.*, 2005; Llusia *et al.*, 2013). Using continuous measurements of the habitat, Maddieson & Coupé (2015) showed a correlation between habitat characteristics and the number and clattering of consonants in 663 local human languages, which are comparable to the complexity and the importance of high-frequency components in animal vocalizations.

In torrent habitats, the noise of flowing water masks low-frequency vocalizations (usually below 2 kHz), and most anurans call below 5 kHz (e.g. Hoskin *et al.*, 2009; Gingras *et al.*, 2013a,b; Goutte *et al.*, 2016). Many anuran calls are therefore masked by torrent noise (Dubois, 1977a,b). Based upon the AAH, one would expect vocalizations of torrent-breeding frogs to be adapted to these noisy conditions, and also to the surrounding vegetation structure of these streams. Consequently, all other things being equal, advertisement calls emitted by torrent-breeding frogs should differ from those produced by frogs calling in other habitats because they are subject to different acoustic constraints, particularly high ambient noise level (Goutte *et al.*, 2013).

Torrent-breeding ranids generally produce shorter and higher-pitched advertisement calls than other closely related frogs (Arch *et al.*, 2008; Boonman & Kurniati, 2011; Goutte *et al.*, 2016), although there appears to be no single typical advertisement call type for torrent-breeding frogs. Investigating habitat characteristics at a finer scale, Goutte *et al.* (2016) identified call characteristics in ranids, which could be adaptive to high ambient noise levels in torrent-breeding frogs: high dominant frequency, short note duration and marked frequency modulations. To investigate these call features further, morphological, environmental and phylogenetic information should be integrated into evolution and adaptation analyses because they may include confounding factors (e.g. Martins, 2000; Olson & Arroyo-Santos, 2015). Indeed, factors linked with the anatomy and physiology of the structures involved in call production directly impact call properties, and body size and air temperature are among these factors for anurans. The dominant frequency (DF) of acoustic signals is generally negatively correlated with body size (e.g. Ryan & Brenowitz, 1985; Ryan & Kime, 2003; Gingras *et al.*, 2013a), and body temperature, directly influenced by air temperature in ectotherms, has an effect on some temporal parameters of the calls produced by these organisms (e.g. Walker, 1962; Navas & Bevier, 2001). In addition, closely related species are more likely to share similar traits than more distantly related species, owing to common ancestry (e.g. Felsenstein, 1985). All these factors may affect the evolution of acoustic signals, and they should be considered when investigating correlations between habitat and signal characteristics.

In this study, we investigated potential adaptations in the advertisement calls of torrent frogs using a comparative method that includes potential confounding factors (i.e. body size and air temperature). This method complements the historical approach of ancestral state reconstruction used on the same data set in Goutte *et al.* (2016). Goutte *et al.* (2016) reconstructed the evolutionary history of call characteristics and tested whether it followed models of evolution determined by environmental constraints. Ancestral state reconstructions, as

used in Goutte *et al.* (2016), provide hypotheses on the chronology of habitat and call feature changes. Changes in calls can be inferred as historically concomitant with a change in habitat, but it does not mean that they are necessarily adaptive. Here, to complement the results found in Goutte *et al.* (2016), we statistically test specific predictions derived from the AAH. We examined the correlation between putatively adaptive vocalization characteristics (i.e. dominant frequency, frequency and amplitude modulation, bandwidth, note duration and number of notes per call; Goutte *et al.*, 2016) and (i) ambient noise level, as suggested in Goutte *et al.* (2016), and (ii) in conjunction with vegetation density, as hypothesized under the AAH paradigm (Morton, 1975, 1977; Marten & Marler, 1977; Wiley & Richards, 1978; Richards & Wiley, 1980).

Thus, after reconstructing a molecular phylogeny and identifying the changes in calls that occurred concurrently with habitat changes (Goutte *et al.*, 2016), we now investigate whether frogs calling in habitats with similar constraint profiles produce similar calls as our current understanding of the AAH suggests. In other words, whereas Goutte *et al.* (2016) tested whether changes in calls historically followed changes in calling habitats, here we test predictions derived from the AAH on whether and how calls vary according to environmental conditions. Each approach provides complementary information regarding the adaptive nature of call traits. We conducted these analyses both with broad habitat categories and with a fine-scale habitat description as suggested in Goutte *et al.* (2016).

Materials and methods

Study sites and specimen collection

Sampling efforts were primarily focused on torrent-dwelling species, these being the most time-consuming taxa to record. We targeted species of the family Ranidae because this large clade includes four torrent-dwelling groups: *Amolops* Cope, 1865; *Odorrana* Fei, Ye & Huang, 1990; *Staurois* Cope, 1865; and the clade composed of *Clinotarsus* Mivart, 1869, *Huia* Yang, 1991 and *Meristogenys* Yang, 1991. Fieldwork was conducted in Asia, as most torrent-dwelling ranid species occur in this region. Data were collected at 11 localities within five Asian territories: Preah Vihear Province, Cambodia, from 11 to 20 December 2010; West Kalimantan Province, Indonesia, from 9 June to 3 August 2011; Sichuan, Hunan and Hainan provinces, China, from 7 June to 19 July 2012; and Sabah Province, Malaysia, from 8 to 24 August 2012 (Fig. S1 and Table S1). We collected a total of 112 individuals referred to 37 species of the families Ranidae, Rhacophoridae, Dicroglossidae and Microhylidae for which we recorded vocalizations and fine-scale measurements characterizing their calling

sites (Table S2). In addition, we recorded and collected 18 individuals of 10 other species within these families, but without any precise data about their calling sites (Table S2). We measured snout–vent length (SVL) of each specimen to the nearest 0.1 mm with a SPI dial calliper (Table S3).

Vocalization recording and analysis

Advertisement calls were recorded from a distance between 0.5 and 2 m with a Marantz PMD671 recorder and a Sennheiser ME64 microphone or an Avisoft CM16 microphone. Sampling rate was 44.1 or 96 kHz at 16 bits. The Avisoft CM16 microphone and sampling rate of 96 kHz allowed recording sounds up to 44 kHz (whereas the other setting allowed recording up to 22 kHz); this equipment was used to record species with particularly high call frequencies (up to 23 kHz for *Huia cavitympanum* (Boulenger, 1983)) to ensure we captured all spectral components of the calls.

To supplement our data set, recordings of 38 species were gathered from scientific sound collections or extracted from commercial compact discs (Table S4). In total, the recordings of 225 individuals in 79 species were used in this analysis, representing about 21,500 advertisement call notes. We measured the following acoustic traits with the software *Praat* (Boersma, 2001) and the package *seewave* (Sueur *et al.*, 2008) in the R environment (R Core Team, 2013): dominant frequency (DF), frequency band width (FBW), DF modulation (DFM), amplitude modulation (AM), note duration and number of notes per call (Table S5).

Habitat measurements and categorization

Once an individual had been captured, we measured habitat descriptors shown to be of importance in anuran habitat and calling site choice (Gillespie *et al.*, 2005; Keller *et al.*, 2009; Goutte *et al.*, 2013): depth, width and average slope of the closest water body, air temperature, canopy coverage, ambient noise sound pressure level (SPL) at the exact individual calling location and maximal SPL in a 2 m radius around the frog calling post (Table S2). Ambient noise levels were measured with an American Recorder Technologies SPL meter on A-weighting (precision: 1 dB at 1 kHz) and one-second integration time. Ambient air temperature was measured with a probe-K digital thermometer (Hanna) to the nearest 0.1 °C. The canopy coverage was measured the day following the capture with a convex-A spherical densitometer. We measured maximal depth and mean diameter for ponds and the width of the water body, and the maximum depth across that width at the focal male level for streams.

We produced a broad-type coding for calling sites based on these precise measurements with multifactorial analysis and cluster analysis following Goutte *et al.*

(2013). It resulted in four categories of calling sites: 'torrents', 'ponds', 'rivers/lakes' and 'forest' (Table S2).

Molecular phylogeny

We used the phylogenetic hypothesis reconstructed in Bayesian inference based on five molecular markers and 148 taxa (Goutte *et al.*, 2016; Fig. S2, Table S6). This phylogeny includes the species for which we collected environmental and acoustic data, and it does not differ significantly from previously published phylogenies of the group (e.g. Pyron & Wiens, 2011).

Association of vocalization characteristics with habitats

All statistical analyses were conducted in the R environment (R Core Team, 2013). To test the hypothesis that vegetation density and ambient noise level affected the evolution of vocalization characteristics, we ran phylogenetic generalized least square (PGLS) multiple regression models using the function *pgls* in the R package *caper* (Orme *et al.*, 2013) including noise level (SPL) and canopy coverage (used as a proxy for vegetation density) as predictor variables. Given that temperature and body size influence temporal properties of calls and dominant frequency, we included body size and air temperature as predictors in the corresponding models: body size was incorporated in the PGLS model with dominant frequency as dependent variable, and air temperature was incorporated in the PGLS models with note duration and number of notes as dependent variables. We also tested whether vocalization traits differed among calling site categories (i.e. 'forests', 'ponds', 'rivers/lakes' and 'torrents'). Vocalization characteristics were averaged for each individual and for all individuals in a species.

Multiple regression models require uncorrelated predictor variables. If this condition is not met, estimates become unstable (Quinn & Keough, 2002) and the risk of type II error increases. Therefore, we tested each pair of variables for correlation prior to running the models. All acoustic variables were log-transformed and the square root of body size was used to meet or approach normality of the regression residuals for each model.

Behavioural traits are supposedly more labile than morphological traits (Blomberg *et al.*, 2003), but that does not necessarily mean that they do not retain any trace of their evolutionary history and therefore lack phylogenetic signal (de Queiroz & Wimberger, 1993; Legendre *et al.*, 2014). The strength of the phylogenetic signal (λ) in the residuals of the models was optimized by maximum likelihood when running the models using the function *pgls* as implemented in *caper*.

Species of the genus *Staurois* use visual displays in addition to vocalizations during advertisement (Grafe & Wanger, 2007; Preininger *et al.*, 2009; Grafe *et al.*, 2012), which may alter the selection strength on

vocalizations and thus decrease the potential adaptive signal contained in calls (see Goutte *et al.*, 2016). However, the low incidence of visual communication in the sampled species (visual communication for five species forming a monophyletic group) prevents us from including it as a variable in the analyses (Mundry, 2014).

Results

Associations between habitats and vocalization characteristics

Half of the PGLS models contained significant phylogenetic signal (Tables 1 and 2). Frog vocalization dominant frequency, frequency modulation and frequency bandwidth were significantly different among calling site categories (Fig. 1 and Table 1). All three spectral characteristics had higher values in vocalizations of torrent-dwelling species than in species vocalizing in other categories of calling sites, although call frequency bandwidth was not significantly different between torrent and forest frogs. Call temporal characteristics (note duration, amplitude modulation and number of notes per call) were not significantly different among calling site categories (Fig. 1 and Table 1).

As expected, call dominant frequency was significantly correlated with noise level (Fig. 2 and Table 2). Frequency modulation was also significantly correlated with noise level, which did not correspond to a prediction stemming from the AAH. None of the call characteristics examined was correlated with canopy coverage (Fig. 2 and Table 2), contradicting the AAH.

Discussion

The present study supports several, but not all, predictions inferred from the acoustic adaptation hypothesis as defined by Rothstein & Fleischer (1987). Within our data set, the spectral properties of vocalizations were correlated with habitat categories and ambient noise level, but the temporal properties of calls were not significantly correlated with habitat, noise level or canopy coverage.

Spectral properties of calls as possible adaptations to noise

The impact of noise on communication efficiency and evolution has been increasingly studied lately (Brumm & Slabbekoorn, 2005; Slabbekoorn & Ripmeester, 2008; Barber *et al.*, 2010; Pijanowski *et al.*, 2011). Noise, like that produced by fast-flowing water, constitutes an important constraint for acoustically signalling animals, partially or completely masking the signals of many species. Consequently, animals signalling in noisy environments are expected to produce higher-frequency sounds than animals signalling in quieter habitats.

Table 1 PGLS models for call characteristics and habitat types.

N	Dep. var.	Indep. var.	Variable statistics				Model statistics		
			β	SE	<i>t</i>	<i>P</i> -value	λ	AICc	Loglik
39	DF	Size	-0.25	0.07	-3.79	0.00***	0.73	63.53	-25.88
		Pond	-1.02	0.26	-3.91	0.00***			
		River/lake	-1.11	0.23	-4.80	0.00***			
		Forest	-1.25	0.44	-2.80	0.01**			
39	DFM	Pond	-1.46	0.58	-2.51	0.02*	0.00	154.07	-72.46
		River/lake	-2.17	0.68	-3.21	0.00**			
		Forest	-4.10	0.98	-4.18				
39	FBW	Pond	-0.44	0.19	-2.29	0.03*	0.92	30.07	-10.46
		River/lake	-0.50	0.16	-3.18	0.00**			
		Forest	-0.47	0.33	-1.42	0.16			
39	AM	Pond	0.39	0.62	0.62	0.54	0.00	159.43	-75.14
		River/lake	-0.14	0.72	-0.20	0.85			
		Forest	1.38	1.05	1.32	0.20			
36	Notes per call	Air temp.	0.00	0.06	-0.06	0.95	1.00	85.35	-35.90
		Pond	0.03	1.08	0.02	0.98			
		River/lake	-0.47	0.80	-0.59	0.56			
		Forest	-0.03	2.10	-0.02	0.98			
28	Note duration	Air temp.	0.09	0.06	1.63	0.12	0.00	76.24	-31.75
		Pond	0.16	0.38	0.43	0.67			
		River/lake	-0.15	0.43	-0.35	0.73			
		Forest	0.35	0.88	0.39	0.70			

Spectral characteristics (dominant frequency, frequency modulation and frequency bandwidth) differ significantly between torrent-dwellers' calls and calls of species living in other habitats, whereas temporal characteristics do not vary significantly between habitats. *N* = number of species included in the model; DF = dominant frequency; DFM = dominant frequency modulation; FBW = frequency bandwidth; AM = amplitude modulation. Habitat categories 'pond', 'river/lake' and 'forest' are compared to the habitat category 'torrent'. For each model, the estimated value for the phylogenetic signal (λ), AICc and log-likelihood are reported. For each independent variable, the parameter estimate (β) and its associated standard error (SE), *t*-statistic and *P*-value are given. Significant correlations are indicated by asterisks (*).

Table 2 PGLS models for call characteristics and environmental variables.

N	Dep. var.	Indep. var.	Variable statistics				Model statistics		
			β	SE	<i>t</i>	<i>P</i> -value	λ	AICc	Loglik
28	DF	Size	-0.19	0.12	-1.58	0.13	0.46	46.69	-18.39
		SPL	0.04	0.01	3.49	0.00**			
		Canopy cover	0.02	0.03	0.63	0.54			
28	DFM	SPL	0.07	0.03	2.32	0.03*	0.00	107.93	-50.49
		Canopy cover	-0.04	0.08	-0.43	0.67			
28	FBW	SPL	0.01	0.01	0.61	0.55	0.92	29.33	-11.19
		Canopy cover	0.02	0.02	1.26	0.22			
28	AM	SPL	-0.01	0.03	-0.30	0.77	0.00	110.78	-51.91
		Canopy cover	-0.12	0.09	-1.41	0.17			
27	Notes per call	Air temp.	-0.01	0.06	-0.18	0.86	0.97	93.31	-41.74
		SPL	0.00	0.03	0.03	0.98			
		Canopy cover	-0.02	0.06	-0.41	0.69			
28	Note duration	Air temp.	0.07	0.04	1.61	0.12	0.80	68.66	-29.46
		SPL	-0.01	0.02	-0.45	0.66			
		Canopy cover	-0.04	0.04	-1.03	0.31			

Calls' dominant frequency and frequency modulation are significantly correlated with ambient noise level. The other call characteristics are not correlated with ambient noise level or canopy cover. *N* = number of species included in the model; DF = dominant frequency; DFM = dominant frequency modulation; FBW = frequency bandwidth; AM = amplitude modulation; SPL = ambient noise level. For each model, the estimated value for the phylogenetic signal (λ), AICc and log-likelihood are reported. For each independent variable, the parameter estimate (β) and its associated standard error (SE), *t*-statistic and *P*-value are given. Significant correlations are indicated by asterisks (*).

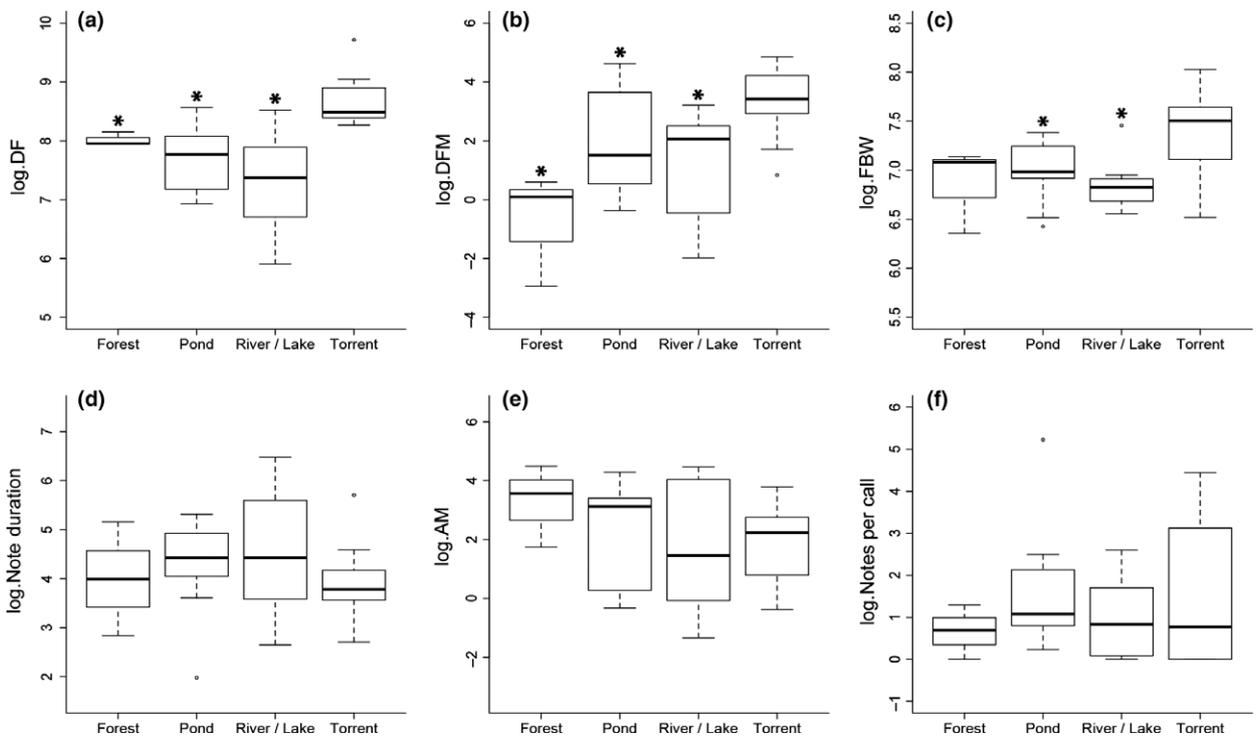


Fig. 1 Vocalization characteristics for each calling site category. (a) Dominant frequency (DF), (b) dominant frequency modulation (DFM), (c) frequency bandwidth (FBW), (d) note duration, (e) amplitude modulation (AM) and (f) number of notes per call. Stars indicate a significant difference to the 'torrent' calling site category in the corresponding PGLS model (see Table 1).

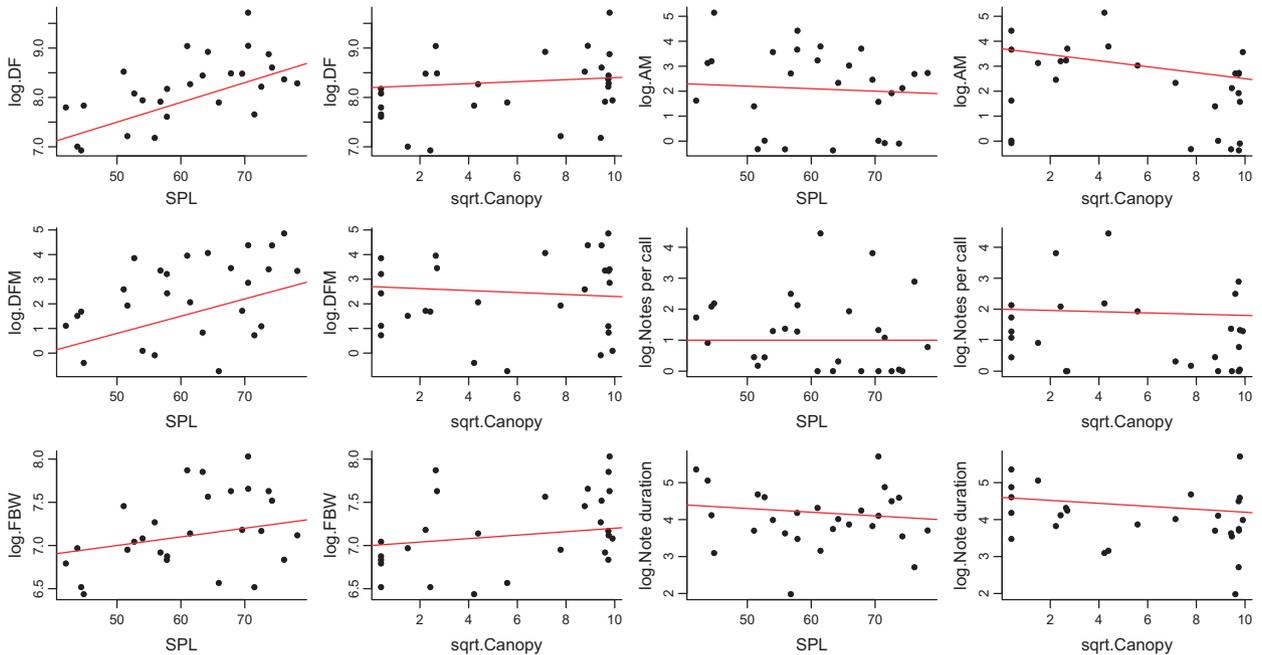


Fig. 2 Relationships between vocalization parameters and calling site characteristics. Regressions from PGLS results are represented by solid red lines.

Unsurprisingly, our results show that spectral properties of frog calls are related to the level of ambient noise at the calling site. Even when considering body size and phylogenetic nonindependence, call dominant frequency was strongly correlated with noise level, with torrent-breeding species calling at higher frequencies than species calling in other habitats. Ranid species advertising in the noisy environment of fast-flowing streams would thus escape noise masking with their higher-pitched calls. Given that high dominant frequencies seem to have evolved when these ranids started to occupy noisy habitats (Goutte *et al.*, 2016), this correlation is congruent with an adaptation hypothesis, even though it does not prove it (Martins, 2000).

The correlation between ambient noise and dominant frequency of animal acoustic signals has been explored in a few studies, yielding heterogeneous results. For example, urban great tits were found to sing at higher frequencies than rural populations (Slabbekoorn & Peet, 2003). In anurans, positive (Hoskin & Goosem, 2010) and negative (Hoskin *et al.*, 2009) correlations were found, but body size and phylogenetic relationships among species, two important factors, were not considered in these studies. Taking into account these two factors, Vargas-Salinas & Amézquita (2014) found no significant difference in call dominant frequency between stream- and non-stream-dwelling species, whereas Röhr *et al.* (2016) found higher dominant frequencies in stream-dwelling frogs. This discrepancy in results may be attributed to the broad categorization of habitats ('stream' vs. 'other'), a limitation we tried to overcome in our study using precise values of ambient noise levels.

Noise was also correlated with calls' frequency modulation: torrent-dwelling species produced calls with more pronounced frequency modulations. This result deviates from predictions derived from the AAH literature (Wiley & Richards, 1978; Richards & Wiley, 1980). Either of the two hypotheses could explain our results: (i) by widening the frequency range, modulation in call frequency reduces the extent to which signals are masked by noise- the signal would thus only be affected for frequencies overlapping with the noise; (ii) a third variable is correlated with both frequency modulation and noise, resulting in a spurious correlation in this particular data set. The third variable could be the amount of air turbulence: Wiley & Richards (1978) predicted more pronounced frequency modulation in vocalizations of species calling in turbulent habitats, and turbulence is linked to noise here because the most important noise source in our data set is fast-flowing water, which creates air turbulence. It would be worth investigating air turbulence further, as it may explain the variability found in frequency modulation within habitat categories (high variability in ponds, rivers and lakes, and low variability in forests and torrents).

The calls of torrent species showed a significantly broader frequency bandwidth than those of species calling in other microhabitats, except for forest species. However, frequency bandwidth was not correlated with noise level. This suggests that a broad frequency bandwidth may be selected for in torrent species, but not only due to the high noise level of torrents, or, conversely, that a narrow frequency bandwidth could be selected in other habitats. For example, in lakes or ponds, the presence of several species signalling simultaneously likely results in acoustic competition, which may drive each species to call within a narrow spectral 'niche' within this *phonocenosis* (Amiet, 2001), that is at a specific frequency range (e.g. Dubois, 1977a; Duellman & Pyles, 1983; Amiet, 1989; Sinsch *et al.*, 2012). This hypothesis has been called 'acoustic niche hypothesis' (Krause, 1987) and should be explored further.

No acoustic adaptation to vegetation structure

Vegetation reflects and absorbs sound waves, creating interference. The density and the height of vegetation modify the amount of air turbulence, which also impact sound waves. Vegetation density is thus supposed to be a factor of prime importance for vocalization adaptations to the environment (Morton, 1975, 1977; Marten & Marler, 1977; Wiley & Richards, 1978; Richards & Wiley, 1980). Here, we used canopy coverage as a proxy for vegetation density because the vegetation profiles of the study sites fell mostly into two categories: either rather dense tropical forests with limited understory vegetation and numerous high trees, or completely open spaces with vegetation limited to patchy grasses and shrubs. In other words, each canopy coverage value corresponded roughly to a single vegetation profile and we thus consider this proxy appropriate for this data set.

Our results show no correlation between canopy coverage and call characteristics in the present data set. We expected species calling in more open microhabitats to produce calls with higher dominant frequency, broader frequency bandwidth and more frequency modulations (Wiley & Richards, 1978), which was not the case. This suggests that other environmental constraints, such as noise level, may constitute stronger selective pressures than vegetation density for vocalization transmission in the habitats we studied. Weir *et al.* (2012) pointed out, for instance, that in addition to excess attenuation in tropical forests (due to dense vegetation), the high-frequency noise produced by insects and acoustic competition were important constraints on song evolution in tropical birds.

The importance of confounding variables and phylogenetic information in the study of acoustic adaptations

As expected from previous studies (e.g. Hoskin *et al.*, 2009; Gillooly & Ophir, 2010), we showed here that

body size and air temperature were significantly correlated with some of the vocalization characteristics we investigated. These correlations may alter the relationships found between environmental conditions and call characteristics, as well as the conclusions drawn for the adaptive nature of vocalizations. These results underline the importance of considering these confounding factors when studying potential adaptations in anuran vocalizations, and likely in other characters and taxa.

In addition, we emphasized the need to incorporate phylogenetic information in the analyses when testing the AAH, regardless of the supposed phylogenetic signal of a trait. The presence of phylogenetic signal within frog calls has been debated in previous studies. Canatella *et al.* (1998) found no phylogenetic signal in vocalizations in nine species of the *Physalaemus pustulosus* (Cope, 1864) group (now *Engystomops pustulosus*; see Nascimento *et al.*, 2005), and Tobias (2011) found very weak signal in two genera of African clawed frogs (*Xenopus* Wagler, 1827). However, Cocroft & Ryan (1995), Wollenberg *et al.* (2007) and Gingras *et al.* (2013b) found a phylogenetic signal within the calls of other anuran groups. Robillard *et al.* (2006) and Goicoechea *et al.* (2010) also demonstrated how choices in acoustic character delimitation may alter the outcome of phylogenetic signal analyses. The detection of a phylogenetic signal in frog vocalization thus appears to be group- or method-dependent.

Towards more integrative tests of the acoustic adaptation hypothesis

The role of environmental constraints on acoustic communication has been widely investigated but yielded mixed results regarding the support of the acoustic adaptation hypothesis. Here, the spectral characteristics of torrent frog advertisement calls were found to be potentially adaptive and noise level appeared to be the major acoustic constraint impacting their evolution. Torrent frogs seem to have evolved higher-frequency vocalizations in response to high ambient noise levels, similarly to urban great tits (Slabbekoorn & Peet, 2003), ecotone little greenbulbs (Slabbekoorn & Smith, 2002) or pygmy marmosets (de la Torre & Snowdon, 2002). However, predictions based on the AAH regarding the topology of habitats were not corroborated by the outcome of our analyses.

This mixed support for the AAH concurs with previous investigations in other groups of frogs (e.g. Vargas-Salinas & Amézquita, 2014), birds (e.g. Saunders & Slotow, 2004; Blumstein & Turner, 2005) and mammals (e.g. Peters & Peters, 2010). A mixed support is unsurprising given the complex nature of acoustic signals and constraints, the number of factors shaping signal evolution, and their intertwined roles. Although a call is perceived as a single signal, decomposing it into spectral and temporal characteristics reveals that these

features may evolve in a decoupled manner. Most acoustic properties of a given habitat are frequency-dependent, so that the environment is expected to constrain mainly call spectral properties. Temporal characteristics, on the other hand, may be more affected by other selection pressure, such as sexual selection.

Our mixed results also demonstrate the need to simultaneously consider factors directly (air temperature) or indirectly (body size, phylogenetic position) affecting signal production when testing the AAH. Other factors, not included here, should be considered in the future such as the roles of (inter- or intra)sexual selection, sensory and physiological limitations (in the signaller and receiver), predation or heterospecific acoustic competition. For example, a limited hearing range or a marked preference for a given call feature in females may overrule environmental constraints on call evolution and need to be considered. Signals evolve as an integrated element of a communication system in a complex environment and in a historical context. More integrative tests of the AAH should also consider factors not directly linked to signal production or environmental acoustic constraints but that may nonetheless impact signal evolution.

In our data set, species of the genus *Staurois* advertise in torrents both acoustically and visually (Grafe & Wanger, 2007; Preininger *et al.*, 2009; Grafe *et al.*, 2012). The use of an additional communication channel offers new possibilities for communication but also presents new constraints (Partan & Marler, 2005). Grafe & Wanger (2007) suggested that vocalizations of *Staurois guttatus* (Günther, 1858) have an alerting function prompting a general orientation towards the caller but mostly lacking informative content, which is delivered visually. These vocalizations may thus be less constrained by the environment than those of species using only acoustic communication. However, the rarity of visual communication in the present data set prevents us from drawing conclusions on its impact on call evolution because of the lack of statistical power. It would be worth investigating call evolution in other frogs using bimodal communication during advertisement, such as *Micrixalus* Boulenger, 1888 or *Hylodes* Fitzinger, 1826 (Preininger *et al.*, 2013; de Sá *et al.*, 2016), and comparing the results with other taxa using bimodal communication to better understand the evolution of multimodal communication in animals (Rosenthal & Ryan, 2000).

The latest tests of the AAH, including ours, have brought mixed outcomes supporting some aspects of the acoustic adaptation hypothesis and refuting others. At this point, the task is not so much to continue testing the AAH, but rather to assess more comprehensively the extent to which the environment has shaped signal evolution. To do so, we suggest that future investigations on the evolution of communication should be as integrative as possible, considering potentially

confounding selection pressure such as sexual selection or sensory biases together with the factors included here. The organisms studied must also be more taxonomically diversified than they are now if one wants to obtain a general understanding on the evolution of animal communication (Rosenthal *et al.*, 2017; Troudet *et al.*, 2017).

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Data archiving

Raw data of body size, calls and phylogenetic inference will be deposited in a Dryad public repository.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article: **Figure S1** Map of sampled localities.

Figure S2 Phylogenetic hypothesis from the Bayesian Inference analysis with two partitions (arithmetic mean of marginal likelihood = -58545.67).

Table S1 Sampled localities.

Table S2 Habitat measurement averaged per species.

Table S3 Average adult male snout-vent length (SVL), number of specimens (N) and source of data for the anuran species investigated in our study.

Table S4 List of species recordings provided by recorders other than [initials of the first author].

Table S5 Call variables average values per species.

Table S6 GenBank accession numbers.