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Background noise as a selective pressure: stream-breeding anurans call at higher frequencies

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Abstract Acoustic signals are an important part in the behaviour of many species and may play a key role in speciation. However, little is known about the importance of natural selection on the evolution of such signals. Acoustics signals are the main communication channel for most anuran species, and background noise from streams is a constant source of masking interference for species reproducing in these environments. Herein, we test if the noise of flowing water habitats has favoured advertisement calls with higher dominant frequencies in frogs. Phylogenetic generalized least square model analysis revealed a significant influence of reproductive environment and body size on dominant frequency, with no significant interaction between habitat and body size. While stream breeders call at higher dominant frequencies, this acoustic parameter is inversely correlated with body size in both environments. We discuss the biological consequences of

long-term adaptive shift in this acoustic parameter and possible trade-offs with other evolutionary forces.

Keywords Acoustic communication · Advertisement call · Comparative methods · Evolution · Masking interference

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Introduction

Acoustic signals are a fundamental part in the communication system of many species, having evolved independently several times in different clades (Gerhardt and Huber 2002). Stochastic processes, pleiotropic effects, and sexual and natural selection may drive the evolution of sound communication in animals (Wilkins et al. 2013). The role of stochastic evolution has been quantified contrasting molecular and acoustic variation with the aid of recent phylogenetic hypotheses (Goicoechea et al. 2010). Morphological and physiological constrains affect signal characteristics, and selective pressures on these may lead to pleiotropic signal divergence (Podos 2001). Sexual selection is the best-studied evolutionary force shaping acoustic signal evolution. Females may show strong preference for specific acoustic parameters, resulting in differential mating success (Ritchie 1996) and ultimately leading to species divergence. In contrast, much less is known about the role of natural selection on acoustic signal evolution (Wilkins et al. 2013).

Background noise is one of the main constraints on acoustic communication, limiting the active space of every natural communication system (Brumm 2013). Short duration noise is circumvented by plastic responses, whereas more predictable and constant noise should result in long-term adaptive processes (Brumm 2013). While short-term plastic responses to background noise have been fairly well studied, less is known about long-term adaptive processes in constantly noisy environments (Brumm and Slabbekoorn 2005).

Stream noise is characterized by constancy, often high intensities, and emphasized energy in low frequency bands (Goutte et al. 2013) that potentially overlap with low frequency anuran vocalizations (Wells 2010). Hence, higher frequencies should be favoured in stream breeders by reducing the energy expenditure needed to diminish interference by increasing intensity. Indeed, flowing water noise pressure level is one of the best predictors of anuran community composition in the vicinity of streams (Goutte et al. 2013) and communicating in high frequencies near streams improves signal detection and discrimination (Boonman and Kurniati 2011). Still, the role of flowing water noise as a selective pressure on anuran advertisement calls is contentious (Boeckle et al. 2009; Hoskin et al. 2009). One analysis using 110 species in five families found that stream species use slightly higher dominant frequencies, but this trend vanished in analyses controlling for body size and phylogeny (Vargas-Salinas and Amézquita 2014).

Herein, we test if masking interference from low frequency noise of streams has favoured advertisement calls with higher dominant frequencies in frogs reproducing near these environments. To do so, we gathered information on calls of 509 species from 31 frog families in all biogeographic realms. We test this hypothesis using phylogenetic comparative methods controlling for adult male body sizes.

Materials and methods

We constructed a database composed of mean advertisement call dominant frequencies (the frequency band with the greatest amount of energy) and maximum male body sizes (snout-vent length (SVL)) reported for each species from data available in the literature. We searched for species reproducing exclusively in flowing or still waters (leaving out species that use both habitats and species which reproduce independently from water bodies) and included in the phylogeny proposed by Pyron and Wiens (2011). In order to achieve a large data set, we used practical and pre-established criteria for data inclusion. For multiple literature hits on the same species, we included the most recently reported mean dominant frequency and the overall largest male body size. However, to ensure that these criteria do not include a bias in the analyses, we tested a random subset of the data demonstrating that there is no significant difference in dominant frequency between older and recent publications and that maximum and mean SVL are highly correlated (more than 98 %) (Supporting Information Sects. 2.4 and 2.5). For a few species where authors reported a dominant frequency range, we used the average between maximum and minimum values. In rare cases where the publication did not report values for dominant frequency but included a spectrogram with a straight and clearly identifiable emphasized spectrum, we included a visual estimation of this parameter.

We evaluated the phylogenetic signal of our data set using Blomberg's K, which varies from zero to infinity and indicates the strength of phylogenetic signal under Brownian motion model of evolution (Blomberg et al. 2003). Next, we used a phylogenetic generalized least square model (PGLS), which takes into account the nonindependence of observations due to phylogeny and assumes a Brownian motion model of evolution (Freckleton et al. 2002). We used the dominant frequency as the response variable and reproduction habitat (still/flowing) and SVL as the explanatory variables to test if dominant frequency was affected by reproduction environment. Dominant frequencies and body sizes were log transformed (natural logarithm) before the analysis. To optimize branch length transformation, the lambda value was set by maximum likelihood (Orme et al. 2012). All statistical analyses were performed in R 3.1.2 using the packages Caper (Orme et al. 2012) and Picante (Kembel et al. 2010).

Results

We complied a dataset of 509 species representing 31 of the 54 currently recognized anuran families (see Supporting Information Sect. 2 for phylogenetic tree and dataset; see Appendix 1 for complete table with references). Stream-reproducing species ($N = 177$) have a mean dominant frequency of 3.37 ± 2.04 kHz (range 0.42–15.97) and a mean SVL of 41.7 ± 20 mm (range 20–138), while still water reproducing species ($N = 332$) average dominant frequency and SVL were 2.18 ± 1.26 kHz (range 0.18–9.17) and 51.2 ± 29.3 mm (range 15–245), respectively.

Dominant frequency ($K = 0.37$, Z variance $= -4.16$, $p < 0.001$) and SVL ($K = 0.44$, Z variance $= -4.45$, $p < 0.001$; Table 1) presented a significant phylogenetic signal. PGLS analysis revealed a strong influence of reproductive environment and body size on dominant frequency ($R^2 = 0.38$), with no significant interaction between habitat and body size (Table 2; Fig. 1; see Sect. 4.5 in Supporting Information for model diagnostic). While stream breeders call with higher frequencies than still water species, dominant frequency decreases with increasing body size in both environments ($\beta = -0.874$, standard error $= 0.052$). Model residuals

Table 1 Phylogenetic signal for dominant frequency (DF) and body size (SVL) calculated through Blomberg's K

Source	K	PIC.mean	PIC.rdn.mean	p value
logDF	0.3660	0.00754	0.02918	0.001
logSVL	0.4387	0.00321	0.01501	0.001
Residuals	0.1002	0.00013	0.00016	0.173

From Blomberg et al. 2003

Table 2 ANOVA table for the phylogenetic generalized least square model {log(DF) − habitat × log(SLV)} evaluating the effects of body size (SVL) and habitat on advertisement call dominant frequencies

Source	df	SQ	MSQ	F	p value
Habitat	1	0.0764	0.0764	33.0	<0.001
SVL	1	0.6461	0.6461	279.4	<0.001
Habitat × SVL	1	0.0008	0.0008	0.3	0.5674
Residuals	505	1.1675	0.0023	–	–

showed a nonsignificant phylogenetic signal ($K = 0.055$, Z variance = 1.301, $p = 0.888$).

Discussion

Frogs reproducing in streams use higher dominant frequencies, suggesting that advertisement calls have evolved to diminish masking interference from flowing waters background noise by reducing spectral overlap. This hypothesis was previously corroborated in studies on a single community (Preininger et al. 2007) and one specific genus (Boeckle et al. 2009) but contradicted in another analysis (Hoskin et al. 2009). Nevertheless, all these studies used a limited taxonomic sampling and did not account for phylogeny. Conversely, an analysis including a wider taxonomic sampling found that, although stream breeders call with higher average dominant frequencies, this difference is not significant when controlling for phylogeny and body size (Vargas-Salinas and Amézquita 2014). The authors found that stream breeders were significantly smaller and attributed this difference to habitat filtering (size selected for higher dominant frequency), natural selection favouring small size in those habitats (reduced pressure from evaporative loss), or both (Vargas-Salinas and Amézquita 2014). The dataset used by

the authors was one fifth of the one used in our present analysis (110 species), included only five anuran families (and hence a significantly smaller number of phylogenetic contrasts), and was restricted to New World frogs, mostly from the Amazon region. Indeed, while few species reproduce in flowing waters in the Amazon region, about half of the species in southeast Asia, for example, are riparian and develop in streams (Zimmerman and Simberloff 1996), a biogeographic bias that is likely to influence the results. The current study encompasses a much larger interspecific variation in body size (230 mm vs 123 mm in their study) and a larger overlap in body size between the two categories of reproductive environment (118 mm vs 47 mm). Therefore, the families and species chosen in Vargas-Salinas and Amézquita (2014) survey do not adequately represent size differences among reproductive habitats for all anurans, making it difficult to disentangle the effects of body size and environment.

Although environmental influence on dominant frequency is highly significant in our analysis, its effect is small when compared to body size (Table 2). This is expected considering the inverse relationship between vocal apparatus mass and call frequency, which makes the variation in this acoustic parameter limited by morphological constraints. Indeed, our complete PGLS model accounts for about 40 % of the variation in this parameter, and other selective forces might be important (see below). Moreover, the importance of environmental noise as a selective pressure can vary among different anuran clades, and future studies should focus on more restrictive groups (such as a single family) with better representation of its species and accurate measures of sound pressure levels. Even though the environment is not the main driver of dominant frequency variation, there is a mean difference of nearly 1200 Hz between environments. Thus, considering the importance of this parameter for anuran reproduction (Gerhardt and Huber 2002), its biological relevance should not be overlooked.

Fig. 1 Relationship between dominant frequency and body size (SVL) for species calling in still and flowing waters ($n = 509$). *Lines* represent PGLS regressions

$Y = -0.87x + C$
Flowing water (C = 11.05)
Still water (C = 10.86)
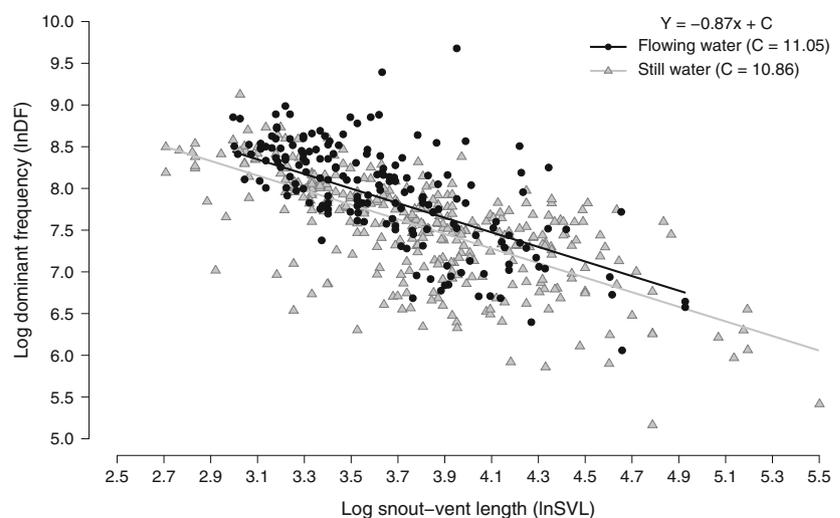
In large species, even an evolutionary increase in dominant frequency, within physical constraints on sound production mechanisms, may still not overcome the emphasized spectrum from background stream noise to obtain release from masking interference. Furthermore, because advertisement calls are crucial for anuran reproductive behaviour, other evolutionary forces besides pleiotropic effects of body size and noise interference might be involved in the establishment of dominant frequency differences. For instance, some species/clades may evolve different strategies to cope with such interference, such as visual communication (Starnberger et al. 2014; Hödl and Amézquita 2001).

Several complex trade-offs among selective pressures may be involved in shaping anuran vocalization. Call attractiveness to females and detectability may be selected by opposing forces in streams. Females may show increased phonotaxis for low or median values of dominant frequency, leading to directional or stabilizing selection (Gerhardt (1991), but see Gerhardt and Schwartz (2001) for further discussion on female preference for dominant frequency). During aggressive acoustic encounters, dominant frequency might be determinant for the outcome (Davies and Halliday 1978), and territorial males may lower call frequency in the presence of intruders (Wagner 1989; Bee and Bowling 2002). Hence, males near streams may face a trade-off between the need to increase call frequency to enhance signal detection at the expense of reducing attractiveness and overall recognition.

Additionally, a trade-off between sound propagation and detectability in forested stream environments is also expected. Low-frequency calls are more efficient in habitats with many physical barriers compared to higher frequencies (Ey and Fischer 2009). Thus, species reproducing in forest streams should face opposite selective pressures, where low dominant frequencies suffer less attenuation and degradation, but high dominant frequencies experience less masking interference. Furthermore, community composition may promote additional limits and selective pressures by driving the evolution of anuran advertisement call dominant frequencies in two distinct manners. First, the presence of sympatric phylogenetically related taxa with similar vocalizations may lead to sexual character displacement to decrease hybridization probability (Lemmon 2009). Second, in highly diverse acoustic habitats, calls may evolve to fill different acoustic niches and spectral silent windows should be favoured (Chek et al. 2003). In either case, dominant frequency changes favoured by these scenarios could reinforce or counterbalance the selective forces of flowing water masking interference.

Although background noise is probably the main difference in the acoustic scenario between still and flowing water habitats, these environments also vary in a myriad of other factors that might affect its acoustic community and should be considered in future studies, such as (1) community of sound-guided predators (Ryan and Tuttle 1983), (2)

vegetation coverage which might act as propagation barriers (Ey and Fischer 2009), (3) sympatric species with prominent acoustic signals (Chek et al. 2003), and (4) tadpole development environment leading to differences in adult body size and steroid hormones (Wells 2010).

Considering all the different evolutionary processes acting upon anuran advertisement calls, the importance of stream background noise as a selective pressure is expected to vary between clades, especially considering that stream colonization took place many times independently and the evolutionary time under this condition varies. For example, when only the three most representative families with species from both habitats were tested separately, the habitat effect was not significant for one family, while the effect of size was very different between the two others (Supporting Information Sect. 4.7.2). Therefore, our study reveals a general pattern for anurans (broad phylogenetic scale), while selection by background noise might vary between clades with contrasting evolutionary histories.

Finally, even with this complex evolutionary scenario, we found a significant trend for anuran species calling near streams to use higher dominant frequencies. Other advertisement call characteristics may respond similarly. For example, sound intensity and call rate are expected to be higher in frogs reproducing in stream habitats and using calls with dominant frequencies similar to surrounding noise. Patterns for other variables, such as call duration and complexity, are less clear. Testing predictions for these variables, however, is much harder because of the lack of appropriate descriptions in the literature. Background noise from streams is clearly determinant for the evolution of anuran advertisement calls, and future work should explore the generality of these results for other groups of animals.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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