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# Environmental and morphological constraints interact to drive the evolution of communication signals in frogs

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## Abstract

Animals show a rich diversity of signals and displays. Among the many selective forces driving the evolution of communication signals, one widely recognized factor is the structure of the environment where animals communicate. In particular, animals communicating by sounds often emit acoustic signals from specific locations, such as high up in the air, from the ground or in the water. The properties of these different display sites may impose different constraints on sound production, and therefore drive signal evolution. Here, we used comparative phylogenetic analyses to assess the relationship between calling site (aquatic versus nonaquatic), body size and call dominant frequency of 160 frog species from the families Ranidae, Leptodactylidae and Hylidae. We found that the frequency of frogs calling from the water was lower than that of species calling outside of the water, a trend that was consistent across the three families studied. Furthermore, phylogenetic path analysis revealed that call site had both direct and indirect effects on call frequency. Indirect effects were mediated by call site influencing male body size, which in turn was negatively associated with call frequency. Our results suggest that properties of display sites can drive signal evolution, most likely not only through morphological constraints imposed on the sound production mechanism, but also through changes in body size, highlighting the relevance of the interplay between morphological adaptation and signal evolution. Changes in display site may therefore have important evolutionary consequences, as it may influence sexual selection processes and ultimately may even promote speciation.

**KEYWORDS**
constraint, display site, dominant frequency, frog, signal evolution, vocal communication

## 1 | INTRODUCTION

Animals communicate with an extraordinary variety of display behaviours that span most sensory modalities (Bradbury & Vehrencamp, 2011; Stevens, 2013). These chemical, visual or acoustic signals are known to experience strong selection pressures imposed by intended and unintended receivers, in particular in the context of sexual communication. The balance between sexual (e.g. mates) and natural selection pressures (e.g. eavesdropping predators) is, however, not independent from the environment. By

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Muñoz and Goutte joint first authorship.

displaying from sites with particular properties, such as locations with reduced exposure to predators, animals can alter the selection pressures operating on their signals, and thus their evolution.

Irrespective of the sensory modality, one common feature of communication systems is the presence of three interacting components: a sender that produces a signal, a receiver that perceives it and the transmission environment in between them (Bradbury & Vehrencamp, 2011). Selection pressures associated with different environments can operate in any of these three processes, with important consequences for signal evolution. In the case of acoustic signals, several studies have investigated the role of variation in transmission environment as a driving factor of signal evolution (e.g. Derryberry et al., 2018; García-Navas & Blumstein, 2016; Peters & Peters, 2010; Richards & Wiley, 1980). During transmission, sound signals will experience changes in their temporal and spectral properties (Bradbury & Vehrencamp, 2011), which can affect the capacity of receivers to process these signals. Efforts to link acoustic signal features to optimal transmission properties, however, have not yielded consistent results (Ey & Fischer, 2009).

From the receiver's perspective, the presence of noise is another environmental factor relevant for signal evolution. The capacity of receivers to detect and process a signal will be compromised by the presence of background noise. Thus, spectral overlap between noise (e.g. the sounds of other organisms, stream noise or anthropogenic noise) and animal signals is thought to drive changes in the frequency content of sounds produced by senders (e.g. Brumm & Slabbekoorn, 2005; Goutte et al., 2016; Halfwerk et al., 2011; Ryan & Brenowitz, 1985; Slabbekoorn, 2004). Although the transmission environment and background noise can influence signal evolution because they affect the perception of receivers, whether the environment can have more direct effects on the sound production mechanisms is far less understood. These direct effects include, for example, environmental features that affect the mechanical processes involved in the generation of sound signals, such as the inflation or deflation of body structures.

Direct environmental influences on sound production have received less attention, perhaps because the morphology of the vocal structures is generally considered to impose strong constraints on sound production. Still, acoustic signal production can be influenced by external factors. The environment can influence the biomechanics of sound production through changes in a sender's physiology. In ectotherms, the temporal structure of acoustic signals is strongly determined by the environmental temperature (Cusano et al., 2016; Ziegler et al., 2016). Alternatively, the environment immediately surrounding a signaller imposes constraints on the biomechanics of sound-producing organs. The production of vocalizations generally involves changes in body posture and the inflation/deflation of body parts, and environmental constraints on any of these processes will also impact the signal (e.g. Halfwerk et al., 2017). Interestingly, some animals can manipulate their environment to release them from the constraints imposed by their morphology. In tree crickets, the wings are too small relative to the wavelength of the sounds they produce, resulting in poor sound radiation. By modifying leaves to

**Impact statement**

For acoustic signals, the environment is known to influence sound propagation and perception, but potential effects on production are less understood. Here, we studied the relation between calling site (aquatic versus nonaquatic) and call frequency across a wide range of frog species. Frogs that called from water did it at lower pitch, which was partly explained by differences in body size. We argue that the immediate environment can impose limits on traits that are either directly or indirectly involved in signal production. Such a mechanism would be particularly important when species move into new callings sites, as transitions may lead to rapid changes in sexual signalling and attractiveness.

act like acoustic baffles and using them as calling site, these insects overcome the morphological constraint on signal production, greatly improving sound radiation (Mhatre et al., 2017).

Anurans (frogs and toads) represent an excellent group to study the influence of the environment on signal production because of the diversity of calling sites that different species use. Males advertise their readiness to mate to females by calling from the water, while floating, sitting or being submerged, or from land, while sitting on rocks, vegetation or in burrows (Wells, 2007). Furthermore, the acoustic properties of advertisement calls are species-specific and closely linked to the biomechanics of sound production. Frogs produce vocalizations by shuttling air from the lungs, through the larynx and into the vocal sac, and thus, the contraction of trunk muscles is the main power source of phonation. Unlike mammals and birds, anurans are considered to lack extensive neuromuscular control over the larynx (Colafrancesco & Gridi-Papp, 2016). Instead, the spectral content of calls is largely determined by the morphology of the larynx (e.g. Baugh et al., 2018; López et al., 2020) and the pulmonary air pressure (Gridi-Papp, 2014). Experimental studies with excised frog larynxes show that air pressure and call frequency are directly related (e.g. Gridi-Papp, 2014; Martin, 1971; Suthers et al., 2006). These results indicate that frog call frequency is not completely constrained by larynx morphology, and suggest that changes in the pattern of trunk muscle contraction or vocal sac inflation could modify call frequency by altering the internal air pressure. Indeed, observations of calling aquatic and terrestrial frogs show that the pattern of vocal sac inflation is related to the frequency content of calls (e.g. Dudley & Rand, 1991; Zhang et al., 2016). Different calling sites occupied by frogs will impose different constraints on sound production, especially if they affect the shuttle of air between the lungs and vocal sac. For example, túngara frogs calling from shallow water cannot inflate their lungs and vocal sacs to the same extent as freely floating individuals, a biomechanical constraint accompanied by a number of changes in the calls, including the production of higher frequency vocalizations (Goutte et al., 2020). These signal

modifications caused by calling site properties may have important consequences for mate attraction, and thus have the potential to drive signal evolution (Halfwerk et al., 2017).

In the present study, we used comparative phylogenetic methods to study the effect of calling site on the evolution of frog vocalizations. We compared the dominant frequency of species that call from inside and outside of the water, and evaluated how these variables relate to body size. We hypothesized that aquatic calling sites will impose fewer mechanical constraints on the production of calls than nonaquatic sites (i.e. unrestrained inflation of lungs and vocal sac), and therefore, we expect aquatic species to call at lower frequencies than nonaquatic frogs. This prediction is supported by previous intraspecific experiments on frogs calling from deep and shallow water (e.g. Goutte et al., 2020), and natural recordings of frogs calling from the water and from vegetation (e.g. Camurugi et al., 2015; Röhr & Juncá, 2013), but has not been evaluated in a comparative framework.

## 2 | METHODS

### 2.1 | Data collection and categorization

We restricted the data collection to species from the families Ranidae, Leptodactylidae and Hylidae present in the molecular phylogeny published by Pyron (2014). We chose these families because they are species-rich clades relative to other frog families (more than 200 species in each family, Frost, 2020), span wide geographic distributions and are known to occupy both aquatic and nonaquatic calling sites. These families are not closely related to each other (not sister clades) and include species with diverse lifestyles and ecomorphologies. Also, the vocal behaviour of species in these families has been investigated with some detail, and data on call frequency and body size are available from the literature.

For each family, we collected data on the snout–vent length, dominant frequency and calling site. Most of the information was obtained from the literature or other digital sources (see below).
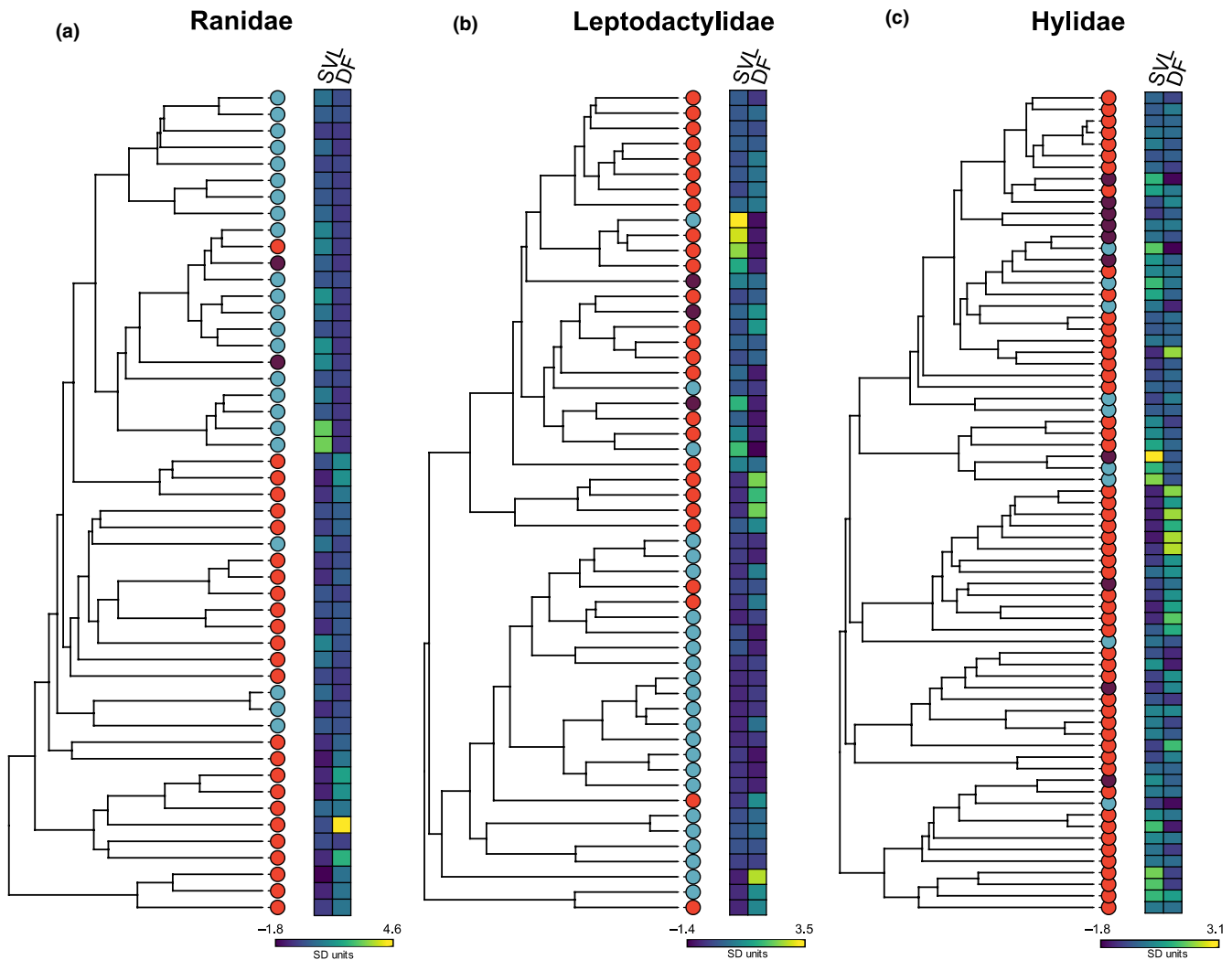


**FIGURE 1** Phylogenetic trees of (a) Ranidae, (b) Leptodactylidae and (c) Hylidae. Coloured circles next to the tips of the trees depict species that call from the water (blue), out of the water (red) or in the mixed category (purple). Body size (SVL) and dominant frequency (DF) data are plotted next to each tree. SVL and DF values were transformed to standardized *SD* units for visualization purposes

Personal measurements made by the authors of the present article were also included. If searched in the literature, body size and call dominant frequency were obtained from other comparatives studies and books. We restricted our search to body size of males and the dominant frequency of advertisement vocalizations. Information on calling sites was obtained mainly from verbal descriptions of frog vocal behaviour present in the literature, the specialized website AmphibiaWeb, and from the personal experience of the authors. Multimedia information available from AmphibiaWeb and YouTube, such as pictures and videos of calling males, was used to confirm ambiguous verbal descriptions. For a few species (19 of 175 species), multimedia information was used as the sole criterion for calling site assignment. Each species was assigned to one of three possible calling site categories: (1) aquatic, (2) nonaquatic and (3) mixed. Aquatic species included frogs that vocalize either standing in water, or floating on the water surface. The nonaquatic category included species that call from the ground, or from perched positions on trees or rocks without direct contact with water. Species calling from cavities dug in the ground or cavity-like structures on vegetation (e.g. the axils of bromeliads) were also included in the nonaquatic category. The few species for which both aquatic and nonaquatic calling was described were assigned to the mixed category. In total, we collected body size, dominant frequency and calling site data for 50 Ranidae, 54 Leptodactylidae and 71 Hylidae species. Phylogenetic trees of each family showing the data for each species are shown in Figure 1.

## 2.2 | Comparative analyses

All the analyses were performed in R (version 3.6.1; R Core Team, 2019). We pruned the phylogenetic tree of Pyron (2014) to exclude all the species that were not present in our data set. Before performing the analyses, we excluded the species in the mixed calling site category (Ranidae $N = 2$, Leptodactylidae $N = 3$, and Hylidae $N = 10$). These corresponded to a small subset of the species and were excluded because one of the analyses allows only binary categorical variables, and because we were mainly interested in the aquatic versus nonaquatic comparison. We used phylogenetic generalized least squares (PGLS) to evaluate the effect of call site and body size on call dominant frequency. For each frog family, we fitted a separate PGLS model, and all the models included the $\log_{10}$-transformed dominant frequency as response variable, and the $\log_{10}$-transformed body size and calling site ('aquatic' versus 'nonaquatic') as explanatory variables. The interaction between calling site and body size was not significant for any family, and we removed it from the models before computing the coefficients reported here. We used the library '*ape*' (version 5.3; Paradis & Schliep, 2019) to create a correlation structure assuming a Brownian motion model of trait evolution, which was then used to fit the PGLS models in R. Plots of residuals versus fitted values and residual quantile–quantile were used to evaluate departures from regression assumptions.
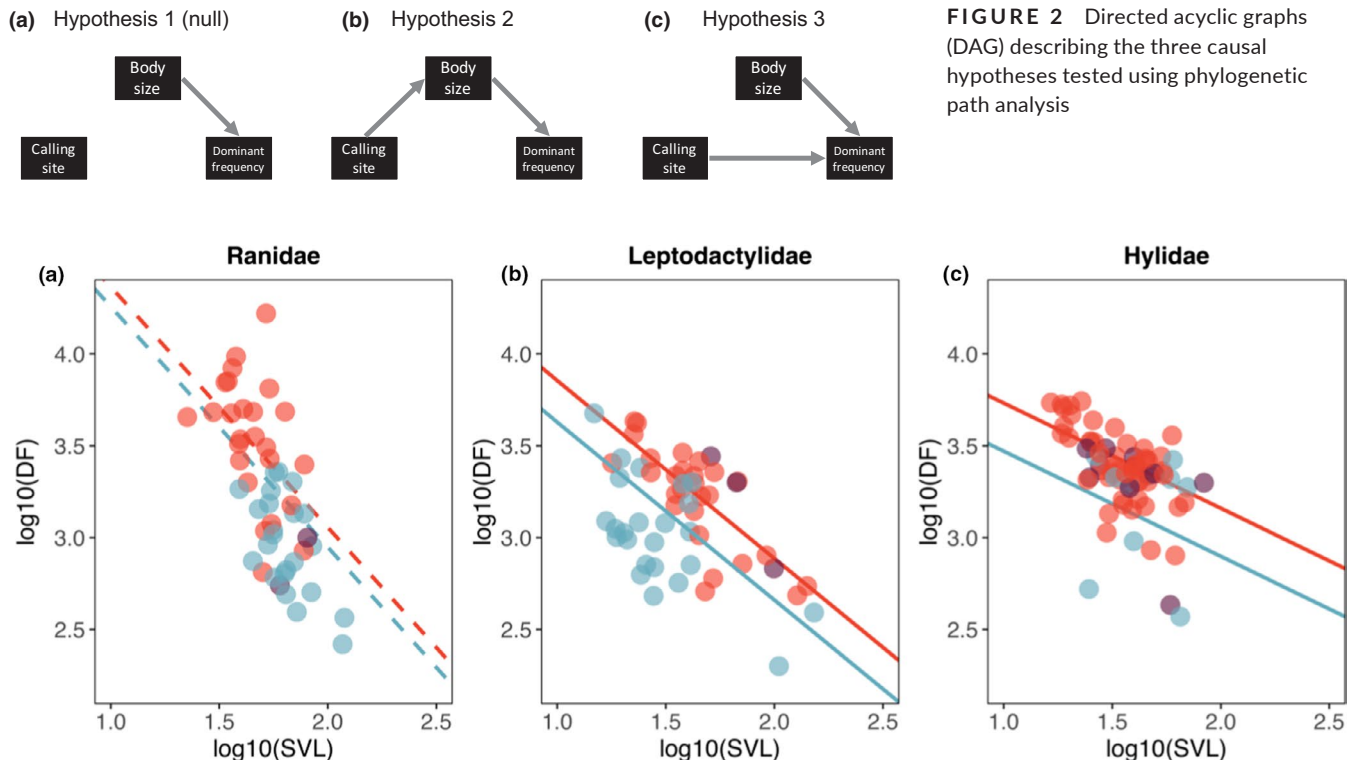
**(a)** Hypothesis 1 (null)  **(b)** Hypothesis 2  **(c)** Hypothesis 3



**FIGURE 2** Directed acyclic graphs (DAG) describing the three causal hypotheses tested using phylogenetic path analysis



**FIGURE 3** Scatterplot showing the association between body size, dominant frequency and the effect of calling site for (a) Ranidae, (b) Leptodactylidae and (c) Hylidae. Colours blue, red and purple correspond to species in the aquatic, nonaquatic and mixed calling site categories. Points represent the raw data, and regression lines represent PGLS model estimates. Species in the mixed calling site category are shown but were not included in the PGLS analyses. The dashed lines in Ranidae depict nonsignificant differences between the intercepts of aquatic and nonaquatic frogs

To further explore the causal relationships between dominant frequency, body size and calling site, we used phylogenetic path analysis (PPA; von Hardenberg & Gonzalez-Voyer, 2013) implemented in the library 'phylopath' (version 1.1.1; van der Bijl, 2018). We a priori defined three hypotheses describing the causal relationships between these variables (Figure 2). The first hypothesis included only a direct path linking body size and call dominant frequency (Figure 2a). We consider this our null model because it excludes any influence of calling site on body size or on dominant frequency. This path was retained in the other alternative models because the negative association between call frequency and body size is a well-described pattern in animal vocal sound production. Hypotheses 2 and 3 included a direct path linking calling site and body size (Figure 2b), and a direct link between calling site and dominant frequency (Figure 2c), respectively. For each family, the three models were compared based on their CICc information criterion value. In case more than one model was best ranked (i.e. more than one model within ΔCICc < 2 from the top ranked model), we used conditional model averaging (i.e. missing paths are not included in the average) to obtain a single average model. Similar to the PGLS analyses, we assumed a Brownian motion model of trait evolution for the linear models underlying the PPAs. Additionally, we also performed the path analysis after pooling together the data collected for the three families into a single data set and phylogenetic tree containing the N = 160 species. For this analysis, we tested the same set of models (Figure 2) and followed the same procedure used for the analyses of the three families by separate.

## 3 | RESULTS

### 3.1 | Phylogenetic generalized least squares analysis (PGLS)

Male body size and call dominant frequency were negatively associated in the three families studied (Table 1). For the families Leptodactylidae and Hylidae, the frogs that called from the water did so at lower dominant frequencies than nonaquatic species (Table 1, Figure 3d, c). A similar trend was followed by Ranidae species, though differences between aquatic and nonaquatic frogs were not significant (Table 1, Figure 3a).

### 3.2 | Phylogenetic path analysis

When families were analysed separately, the causal hypotheses that include a direct effect of calling site on body size (Hypothesis 2), and on dominant frequency (Hypothesis 3) were among the best ranked models (i.e. within ΔCICc < 2) (Table 2). For Ranidae, the null hypothesis where there is no effect of display site on dominant frequency or on body size was also supported (Table 2). Model averaging of the best ranked models showed that the three families followed the same general pattern of causal association between the variables (Figure 4a). That is, calling site had a positive and direct effect on dominant frequency, and a negative direct effect on body size. Nevertheless, the coefficient estimates for these paths did not significantly deviate from zero, as judged by the 95% confidence intervals overlapping with 0 (Figure 4a). As expected, body size had a negative effect on dominant frequency, and was the only significant path for the three families (Figure 4a).

The analysis of the three families together revealed the same trend observed for each family separate. The models that included a causal link between calling site and body size (Hypothesis 2), and between calling site and dominant frequency (Hypothesis 3) outweighed a model where calling site was independent of these variables (Hypothesis 1) (Table 2). The average model included a positive and direct effect of calling site on dominant frequency, and a negative direct effect on body size (Figure 4a, b). It also included a negative effect of calling site on body size, which indicated that calling site can indirectly affect dominant frequency through effects on body size (Figure 4a, b). In the average model, the estimated coefficients of all the paths were of similar magnitude (range: [0.28–0.34]) and significantly different from zero (Figure 4a).

**TABLE 1** Results of PGLS models fitted for the three families. In all the models, the dependent variable was $\log_{10}$-transformed dominant frequency

| Family | Variable | Estimate | SE | t-value | p-value |
|---|---|---|---|---|---|
| Ranidae | Intercept | **5.57** | **0.45** | **12.36** | **<.0001** |
| | $\log_{10}$(SVL) | **−1.31** | **0.25** | **−5.28** | **<.0001** |
| | Display site: nonaquatic | 0.11 | 0.11 | 0.96 | .3418 |
| Leptodactylidae | Intercept | **4.60** | **0.30** | **15.15** | **<.0001** |
| | $\log_{10}$(SVL) | **−0.97** | **0.19** | **−5.02** | **<.0001** |
| | Display site: nonaquatic | **0.23** | **0.07** | **3.37** | **.0015** |
| Hylidae | Intercept | **4.04** | **0.39** | **10.3** | **<.0001** |
| | $\log_{10}$(SVL) | **−0.57** | **0.23** | **−2.45** | **.0175** |
| | Display site: nonaquatic | **0.26** | **0.09** | **2.96** | **.0044** |

Note: Bold numbers depict significant results.

**TABLE 2** Summary of best ranked models tested using phylogenetic path analysis. The set of models evaluated is shown in Figure 2

| Family | Model | k | q | C | p-value | CICc | ΔCICc | Likelihood | CICc weights |
|---|---|---|---|---|---|---|---|---|---|
| Ranidae | **H3** | **1** | **5** | **1.25** | **.535** | **12.7** | **0.00** | **1.00** | **0.474** |
| | **H1** | **2** | **4** | **4.40** | **.355** | **13.3** | **0.65** | **0.724** | **0.343** |
| | **H2** | **1** | **5** | **3.15** | **.207** | **14.6** | **1.89** | **0.388** | **0.184** |
| Leptodactylidae | **H2** | **1** | **5** | **3.17** | **.205** | **14.5** | **0.00** | **1.00** | **0.594** |
| | **H3** | **1** | **5** | **4.99** | **.083** | **16.3** | **1.82** | **0.40** | **0.239** |
| | H1 | 2 | 4 | 8.16 | .086 | 17.0 | 2.53 | 0.28 | 0.168 |
| Hylidae | **H3** | **1** | **5** | **3.99** | **.136** | **15.1** | **0.00** | **1.00** | **0.526** |
| | **H2** | **1** | **5** | **4.94** | **.085** | **16.0** | **0.95** | **0.62** | **0.328** |
| | H1 | 2 | 4 | 8.92 | .063 | 17.6 | 2.56 | 0.28 | 0.146 |
| All families | **H3** | **1** | **5** | **6.90** | **.032** | **17.3** | **0.00** | **1.00** | **0.507** |
| | **H2** | **1** | **5** | **7.14** | **.028** | **17.5** | **0.24** | **0.89** | **0.451** |
| | H1 | 2 | 4 | 14.04 | .007 | 22.3 | 5.01 | 0.08 | 0.042 |

*Note:* Bold numbers depict the best set of causal models (within ΔCICc < 2) that were latter used for model averaging.

Abbreviations: C, Fisher's C statistic; k, number of independence claims; q, number of parameters; ΔCICc, difference in CICc from the top ranked model; CICc weights, model conditional weight.
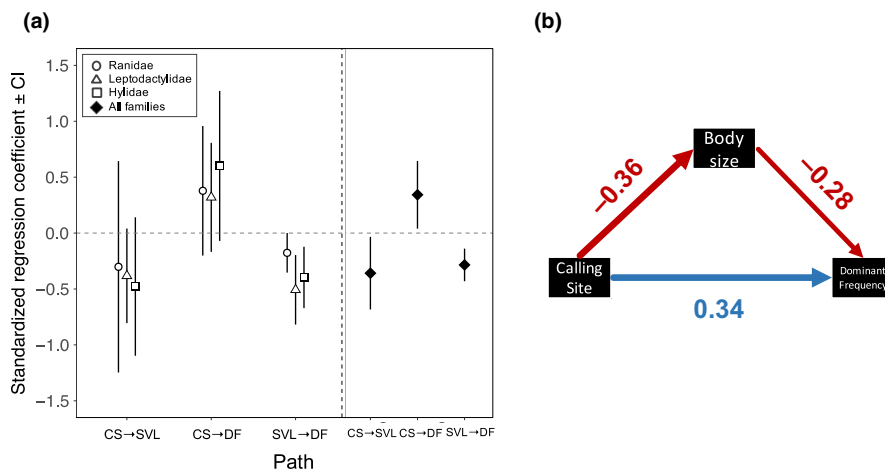


**(a)**

**(b)**

**FIGURE 4** (a) Standardized regression coefficients estimated from the average model for each family (open symbols) and for all the families together (filled symbols). Error bars correspond to 95% confidence intervals obtained after 500 bootstrap replications. (b) Average model for the three families analysed together. Numbers correspond to standardized regression coefficients, and are the same as the filled symbols in Figure 4a. Arrows widths and colours depict the size and the direction of the effect

## 4 | DISCUSSION

Signal evolution is driven by a number of factors, such as the sensory system of receivers, but also the environment where signals are produced and the morphology of the sender. Here, we evaluated the impact of calling site on the evolution of call frequency in three frog families using comparative phylogenetic methods. We found that species vocalizing from the water call at lower dominant frequencies than species calling from nonaquatic locations. Furthermore, our analyses revealed that calling site had both direct and indirect effects on call frequency. Because body size and signal frequency were negatively associated in the three families studied, direct effects of calling site on body size had an indirect impact on signal frequency. These results indicate that environmental constraints interact with morphological constraints to drive the evolution of frog vocalizations.

Our comparison across families revealed a similar pattern of call frequency variation as found within species. In the hylid frogs

*Boana atlantica* and *Hypsiboas crepitans*, the dominant frequency of calls emitted by individuals in the water is, for example, lower than calls produced from vegetation (Camurugi et al., 2015; Röhr & Juncá, 2013). Similarly, floating túngara frogs call at lower dominant frequencies when compared to trials in which individuals are experimentally forced to call while resting on a solid substrate (Goutte et al., 2020). Shallow water conditions prevented males from fully inflating their vocal sac in this study, indicating that call site-induced constraints on sound production have an immediate impact on signal frequency (Goutte et al., 2020). We extend this argument here, and propose that the frequency differences we found in our analyses are mainly caused by different constraints on sound production imposed by aquatic and nonaquatic calling sites. Furthermore, calling sites differ not only in the biomechanical constraints they impose, but also in other factors such as exposure to desiccation or temperature (Camurugi et al., 2015; Cicchino et al., 2020). This suggests that other call variables, such as some temperature-dependent temporal patterns, may also be impacted by calling site choice. Variation in call

sites can therefore influence signal production by altering sender´s physiology or biomechanical constraints.

The size of the sound-producing organ can determine the frequency content of vocalizations, and thus, larger animals produce lower frequency sounds (Fletcher, 2004). The association between size and frequency is a well-described physical consequence of vocal sound production, and it is suggested that ecological factors driving changes in body size also have concomitant effects on signal frequency (Wilkins et al., 2013). A similar case of morphology-driven signal evolution can be found in Darwin finches, where diet-dependent changes in beak morphology are accompanied by modification in song production (Podos, 2001; Podos & Nowicki, 2004). Our analyses show that body size variation in frogs is to some extent explained by the different calling sites they occupy, with consequences for call frequency. Body size evolution in ectotherms has been linked to a number of environmental factors, including temperature, humidity and evapotranspiration potential (e.g. Amado et al., 2019; Velasco et al., 2020) all of which are known to differ between calling sites. Furthermore, morphological adaptations are also expected to differ between calling sites. Arboreal or fossorial habits, for example, are linked to a number of morphological specializations (Moen et al., 2013), including differences in body size (e.g. Dugo-Cota et al., 2019). Many frog species vocalizing out of the water call while sitting on vegetation perched on branches or leaves. Large frogs may be unable of arboreal calling due to the lack of physical support provided by hanging leaves and branches. In contrast, body size may be less constrained in terrestrial or aquatic calling species. In our data, arboreal calling species were included into the nonaquatic calling site category, and were not analysed separately because they were mostly present in the family Hylidae, but scarce in Ranidae and Leptodactylidae. Still, we predict arboreal species to have even higher frequency calls relative to aquatic and terrestrial species due to a combination of body size constraints, and favourable transmission of high frequencies from elevated sites (Cicchino et al., 2020; Mathevon et al., 1996; Schwartz et al., 2016). Variation in body size will not only have a direct impact on call frequency due to allometry, but may also limit the possible calling sites a species can occupy, highlighting the relevance of the interaction between morphology and calling site on signal evolution.

Finally, it is possible that frog calling sites affect not only sound production, but also sound transmission. Calling from the water surface has been shown to minimize sound attenuation relative to sounds broadcast from the ground (Forrest, 1994; Penna & Solís, 1998). Also, frogs calling perched above the ground, from leaves or branches for example, experience lower attenuation rates relative to individuals calling from the ground (Kime et al., 2000; Schwartz et al., 2016). Attenuation phenomena are frequency-dependent, as low-frequency sounds generally propagate further than higher frequencies in a given environment (Wiley & Richards, 1978). It is possible that constraints imposed by the environment on sound transmission (i.e. better propagation of low frequencies) interact with environmental constraints on sound production (i.e. low-frequency vocalization in aquatic display sites) to drive the evolution of frog vocalization. However, studies on frogs have yielded weak evidence of call adaptation to local sound transmission properties (Goutte et al., 2017; Kime et al., 2000). Instead, other environmental factors seem to have a larger influence on frog call evolution, such as the presence of background noise (Goutte et al., 2016, 2017).

Display sites can drive signal evolution through direct impacts on the sound production mechanism, as well as other selection pressures on senders and receivers. Divergent transmission properties between display sites may select for signals with matching properties over evolutionary timescales. Likewise, signal adaptation to noise profiles associated with callings sites may also operate on the long term. Environmental constraints on production mechanisms will however have immediate consequences when senders move to different display sites. For example, a frog that moves from an aquatic to a nonaquatic calling site will likely experience stronger constraints on the inflation of the lungs and vocal sac. This will result in an immediate impact on call frequency, as suggested by experiments on túngara frogs (Goutte et al., 2020) and acoustic measurements of calling male hylids (Camurugi et al., 2015; Röhr & Juncá, 2013). Therefore, the impact of the environment, and in particular of display sites, on vocal production mechanisms has the potential to cause fast signal divergence, and in some cases promote speciation.

## AUTHOR CONTRIBUTIONS

SG, JE and WH conceived and designed the study. MIM, SG and WH collected the data. MIM and SG analysed the data. MIM and WH drafted the initial version of the manuscript. All the authors commented and edited later versions of the manuscript.

## PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/jeb.13713.

## DATA AVAILABILITY STATEMENT

Data will be made available on Dryad upon acceptance https://doi.org/10.5061/dryad.3tx95x6ds.

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