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ORIGINAL ARTICLE

Female preferences for dominant frequency in frogs: constraints and impact on sexual size dimorphism

José Vinícius Bernardy[1] · Isabella Melo[1] · Diego Llusia[3] · José Alexandre Felizola Diniz-Filho[2] · Rogério Pereira Bastos[2]

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Abstract

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Favoring males' specific sexual signals, female preferences play a major role in frogs' evolutionary process by selecting traits linked to those signals. However, the factors constraining and determining those preferences are scarcely explored in an evolutionary background. Here, through a phylogenetic comparative approach we check whether anuran species phylogenetic proximity and calling site predicts female preferences for dominant frequency and whether those preferences influence species sexual size dimorphism. Our hypotheses are as follows: 1) closer species have similar females' preferences related to the dominant frequency of the partners' calls; 2) the calling site influences sound propagation and consequently the preference of females for the dominant frequency of the males' calls; and 3) the preference for calls with low dominant frequency influences the size of the males and consequent reduction of the biSased dimorphism for females. We did not find support for our hypotheses, neither for the influence of phylogenetic proximity nor for calling site determining these preferences. Moreover, female preferences did not impact on species sexual size dimorphism. Besides shedding light into our hypotheses, this study represents a considerable advance on evolutionary studies of female preferences in anura, which still lacks broad species comparative approaches. Furthermore, we suggest future studies to expand knowledge regarding frogs' female preferences.

Significance statement

This study advances our comprehension of female preferences in frogs by investigating the factors that shape these preferences and their implications for species sexual size dimorphism. Utilizing phylogenetic comparative methods, an approach rarely used in the context of anuran female preferences, this study represents a significant step in applying broad comparative approaches in this field. Highlighting the complex nature of mate choice and its relationship to morphology, soundscape, and phylogeny, we present important insights into evolutionary hypotheses related to female preferences. Lastly, we provide advice on how future studies could further explore this topic in a broader comparative framework while also discussing the limitations of available data on anuran mating preferences.

Keywords Intersexual selection · Female preferences · Sexual size dimorphism · Phylogenetic signal · Anura

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✉ José Vinícius Bernardy
jvbernardy@gmail.com

[1] Programa de Pós-Graduação em Ecologia e Evolução, Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Campus Samambaia, Goiânia, Goiás, CEP 74001-970, Brazil

[2] Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Campus Samambaia, Goiânia, Goiás, CEP 74001-970, Brazil

[3] Terrestrial Ecology Group (TEG), Departamento de Ecología, Universidad Autónoma de Madrid, 28049 Madrid, Spain

Introduction

Female preferences play a major role on animal's sexual selection by determining mate choices based on sexual signals (Andersson and Simmons 2006). Favoring a specific trait variant, mating preferences might result in important evolutionary changes in male morphology, behavior, and on species extinction or adaptation in contexts of environmental change (Houde and Endler 1990; Ptacek 2000). Many studies have focused on hypotheses to explain evolution of specific mating preferences (e.g., good genes (Zahavi 1975), direct benefits (Williams 1966), and Fisher's process (Fisher 1930)). However, more efforts are needed to understand how female choice acts on sexual selection to understand its role in species adaptation (Candolin and Heuschele 2008).

Anura is one of the most well-studied taxa in female preference research (Gerhardt and Huber 2002). Anuran females choose their mates based on several characteristics, such as territory quality (Wells 1977; Howard 1978), parental ability (Márquez 1993), morphology (Robertson 1986; Zhu et al. 2016), and specially by their acoustic features (Gerhardt and Huber 2002). Experimental playback approaches have already shown that females from several species might choose their mates based on call properties like dominant frequency, calling rate, and call duration (Gerhardt and Huber 2002; Bee 2008; Moreno-Gómez et al. 2015; Yu et al. 2020). Specifically, the dominant frequency (i.e., the frequency in the call where most energy is concentrated (Köhler et al. 2017)) is widely used by anuran females to choose their mates (Wollerman et al. 1998; Lardner and Lakim 2004; Zhu et al. 2016). Directly determined by males' body size (Gingras et al. 2013a), this characteristic is used by several animals in their mate choice process, including anura (Fitch and Hauser 2003; Reby and McComb 2003).

As in other animal groups (Colleye et al. 2011; Arato and Fitch 2021), closely related anurans are known to have similar call characteristics, especially those related to morphological characters, such as dominant frequency (Hepp et al. 2017). Compliant with that, using phylogenetic comparative tools, studies have shown that phylogenetic close anurans share many of their call's characteristics (Goicoechea et al. 2010; Gingras et al. 2013b). Furthermore, considering the idea that species have pre-existent preferences inherent to signal perception neurological aspects (Ryan and Rand 1993), this acoustic resemblance could also reflect on similar preferences between related species. Yet, this topic is still a gap in the evolutionary knowledge of anura.

Choosing a mate represents a cost in terms of predation risk, time, and energy (Milinski and Bakker 1992; Godin and Briggs 1996). Therefore, the capacity of females to correctly evaluate a mate plays a major role in the cost–benefit balance of mating decision processes (Wiley 1994). Acoustic signals in nature are subject to the influence of environmental factors (e.g., topography, air temperature, wind speed, or vegetation cover) that constrain the efficiency of signal transmission, affecting its quality and range (Wiley and Richards 1978). Accordingly, studies have explored how frog species microhabitat and calling site affect sound propagation (Goutte et al. 2016, 2018; Tonini et al. 2020). Calling from herbaceous vegetation or trees represents an advantage in terms of signal propagation, as those sites provide longer signal propagation distance due to their height while also facing few physical barriers and therefore, diminished excess attenuation (Marten and Marler 1977; Wiley and Richards 1978; Römer 1992). In contrast, acoustic signals emitted from the ground are more susceptible to signal attenuation, since part of the reflected signal energy is absorbed by the soil (Marten and Marler 1977; Forrest 1994). While signal reflection is better in water than in ground, attenuation is still dependent on water depth and on the interaction between water and water-surface, which increases signal attenuation for specific frequency windows (Forrest 1994). Moreover, sound production in water might be problematic as depth also affects species ability to float, limiting their vocal sac inflation, which impacts calls attractiveness (Halfwerk et al 2017). These constraints on sound production and propagation imply that frog females are subject to errors while interpretating signals coming from calling males (Forrest 1994; Bee and Micheyl 2008). Thus, females from species in which males typically call from disadvantageous sites in terms of signal transmission properties and production would receive a less reliable signal, not being able to correctly evaluate mates and exert their mating preferences.

Sexual selection can strongly influence sexual size dimorphism, by both increasing and decreasing differences in the size of the sexes (Andersson and Iwasa 1996). However, the relationships between sexual selection and sexual size dimorphism in anurans were only explored considering competition between males as a proxy for sexual selection (Shine 1979; Han and Fu 2013; Pincheira-Donoso et al. 2020). On the other hand, female choice is an alternative to explore the relationship between sexual selection and sexual size dimorphism, as a previous meta-analysis on call frequency and male body size preferences in anurans as observed that females, in general, prefer males that vocalize with a low dominant frequency, that indicate larger males (McLean et al. 2012). In this sense, as female choice can indirectly affect male size through the selection of specific call frequencies, this preference could affect sexual size dimorphism.

Despite the well-established knowledge on female preferences for call frequencies in anurans (Marquez 1995; Rosso et al. 2006; Schrode et al. 2012), large-scale approaches on their evolutionary determinants are still scarce. Therefore, assessing those relationships turns out to be a relevant matter in terms of ecological and evolutionary knowledge for anura. Thus, using phylogenetic comparative tools (Felsenstein 1985) we test the following hypotheses: (1) preference for call frequency is a phylogenetically conservative trait, and thus females of closely related species share similar preferences for dominant frequency; (2) male calling site influences sexual preferences, and thus females do not exhibit preferences for dominant frequency in species with males calling from poor sound propagation sites (i.e., water and ground in comparison to perched, see methodology); and (3) species in which females exhibit preferences for lower dominant frequency have sexual size dimorphism less skewed or skewed toward males.

Methods

Female frequency preference data

We retrieved female frequency preference (FFP) through a systematic literature search using Scopus and Web of Science database. The search included articles in English containing the following terms combination in their abstract, keywords or title: (Anura* OR frog* OR treefrog* OR toad* OR (all anuran families)) AND ("sexual select*" OR "mat* choic*" OR "mat* preference*" OR "female choic*" OR "female preference*" OR "assortative mat*" OR "mat* success" OR "reproductive success"). Our survey includes records published until January, 2022, starting from 1970 for Scopus and from 1945 for Web of Science. We identified three types of FFP in 30 species: preference for lower dominant frequencies, preference for average dominant frequencies, and absence of preference. In a few species (3 cases), three or more studies had divergent results regarding FFP (species), in those cases we considered the most consensual result between them.

Calling site data

We determined calling site using a previous classification by Tonini et al. (2020), that divides anuran species into three groups according to their preferred calling site: water (6), ground (16), and perched (8). For a few species of our FFP dataset which were not included in that classification (3), we searched scientific literature using Google Scholar and AmphibiaWeb platforms to classify their calling site.

Sexual size dimorphism data

To calculate sexual size dimorphism (SSD), we retrieved maximum body size (snout-vent length, SVL) for males and females from the Pincheira-Donoso et al. (2020) and additional literature search. Maximum SVL was used because it is indicative of the potential size of taxon with indeterminate growth, due to allometric limitations (Levy and Heald 2015). For duplicate species in the database, we used the highest SVL found. The SSD calculation was done as follows: *ln* (male maximum SVL/female maximum SVL). This proportion is common in literature, allowing a simple interpretation of values (Smith 1999). Thus, SSD is equal to zero in species with males and females of the same size, and takes negative values in species with larger females and positive values in species with larger males.

Comparative analyses

All our analytical procedures were based on 1000 phylogenetic trees for the amphibians and all 30 species in our data were matched on the Jetz and Pyron (2018) phylogeny. Species names of our data sources (above) were paired with those defined in the available phylogenies and nomenclature standardized accordingly.

To test phylogenetic patterns in FFP shape, we use the *fit Discrete* function, which is suitable for fitting models that involve discrete traits and phylogenetic trees. We tested all available evolutionary tree transformation models (Brownian, ACDC, lambda, kappa, delta, and white noise) and selected the one with the lowest average AICc (considering the 1000 phylogenetic trees) as the best evolutionary model for our data.

To test the relationship between FFP and calling site, we used phylogenetic GLM models, with the phyloGLM function, computing 100 bootstraps and using maximum penalized likelihood estimation. Here, we only used the presence or absence of FFP. This model was performed 1000 times (once for each phylogenetic tree) and we used the average coefficients to account for the phylogenetic uncertainty.

To test the relationship between SSD and FFP, we performed a phylogenetic linear model, with the "phylolm" function. FFP are categorized as lower dominant frequencies, preference for average dominant frequencies, and absence of preference. Here, we also use the average coefficients obtained from the 1000 trees. All analytic and phylogenetic procedures were performed in the software R v4.3.0 (R Core Team 2022), using the packages *phytools* (Revell 2012), *phylolm* (Tung Ho and Ané 2014), and *geiger* (Harmon et al. 2008).

Results

We obtained data for FFP for 30 species from 12 different families (see Supplementary Data). While almost half our species show preferences for lower values of dominant frequency (~53%), a considerable number prefer average values (20%) or do not show any preferences for call frequency (~27%). No species show preferences for higher values of dominant frequency. Figures 1, 2, and 3 present the distribution of studied traits (FFP, calling site, and SSD) mapped onto the phylogeny.

Following the AICc criteria, the white-noise model had the best fit to the evolution of FFP in all our phylogenies (99.9% of trees; mean of AICc = 67.746; Table 1), coherent with Pagel's lambda close to 0. As this model converts the tree into a star phylogeny, losing all traces of shared ancestry, we do not support the relation between phylogenetic proximity and FFP.

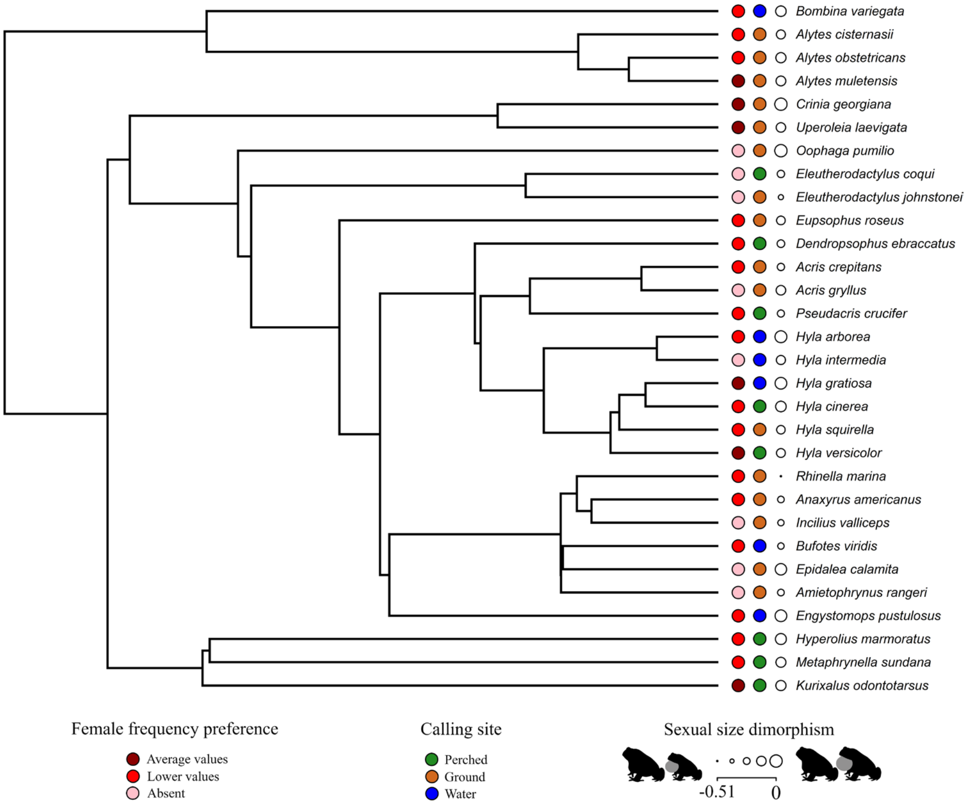

Fig. 1 Species phylogenetic relationships and studied traits: female frequency preference (FFP), calling site and sexual size dimorphism (SSD), following one of the 1000 simulated trees by Jetz and Pyron (2018). Absence of dots represents data absence

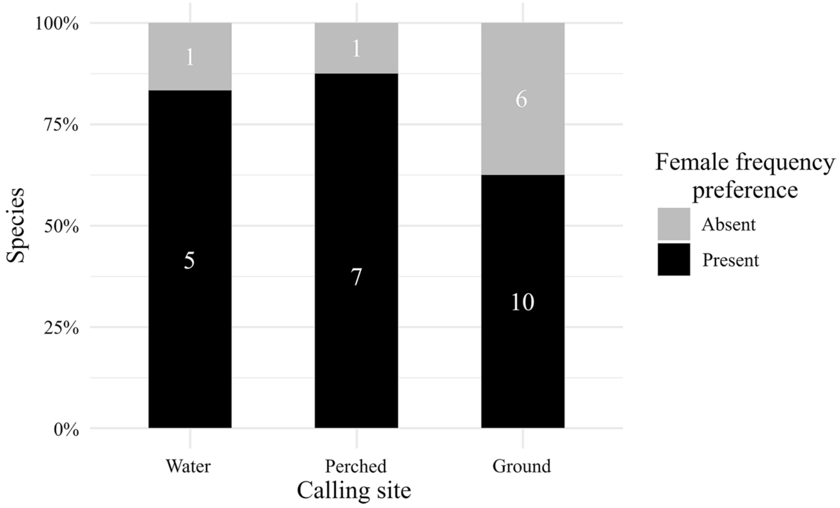

Fig. 2 Number of anuran species according to presence of FFP (female frequency preference) and their calling sites (aquatic, arboreal, or terrestrial)

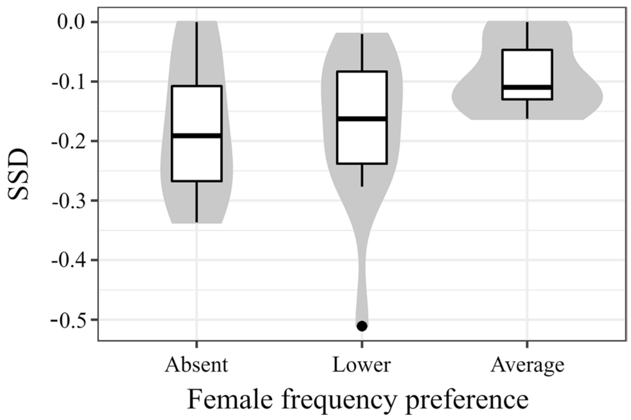

Fig. 3 Relationship between female frequency preference (FFP) and sexual size dimorphism (SSD) in anuran species. The box horizontal lines represent the interval between 25, 50 (median), and 75% percentiles. The vertical line represents the highest and lowest values excluding outliers (observations which fall outside by 1.5 times the interquartile range). Violin plots represent data distribution

We do not find support for calling site influence on female frogs' preference for dominant frequency (Table 2). Also, we find no effect of the FFP on species SSD (Table 2).

Discussion

Overview

Using phylogenetic comparative methods, we did not find support for our hypothesis that females from close related species share similar preferences for dominant frequency. Furthermore, we did not find support for the influence of calling site on determining these preferences. Finally, according to the data available, female preference did not seem to influence sexual size dimorphism. Besides shedding light into our hypotheses, this study also raises relevant questions regarding data availability, usage, and future research topics.

Phylogenetic signal

Contrary to our expectations, FFP is not a phylogenetically conserved trait across frogs' evolutionary history according to the data available for female preferences in the study group. Female preference is probably a trait with high levels of phenotypic plasticity and might be affected by several factors, such as temperature, social aggregations size, and species interaction (Gerhardt 1978; Höbel and Gerhardt 2003; Tanner and Bee 2019). Thermal coupling, for example, occurs when in face of a temperature change, both the signals emitted by conspecifics and the preference are changed in the same direction (Gerhardt 1978). However, there are cases, as seen in *Hyla cinerea* (Schneider 1799), where only the signal or the preference is altered by temperature, which impairs the identification and evaluation of the signals emitted by conspecifics (Gerhardt and Mudry 1980). Considering background noise from chorus, females of *Dendropsophus ebraccatus* (Cope, 1874) do not exhibit preferences for dominant frequency when there is a high level of chorus noise

Table 2 Mean coefficients with respective standard deviations and confidence intervals (95%) for the 1000 PHYLOglm (FFP–calling site) and Phylolm (SSD–FFP) performed considering the 1000 phylogenetic trees. The intercept represents water site and absence of preference, respectively. *Metaphrynella sundana* (Peters, 1867) was not considered for SSD–FFP analysis as it is known that males' dominant frequency is not related to their body size in this species (Lardner and Lakim 2004)

FFP–calling site				
	Estimate	Lower limit	Upper limit	*Z*
Intercept	1.36	−0.74	3.43	1.33
Ground	−0.88	−3.23	1.46	0.78
Perched	0.25	−2.61	3.11	0.18
SSD–FFP				
	Estimate	Lower limit	Upper limit	*t*
Intercept	−0.17	−0.26	−0.09	−4.41
Low frequency	0.004	−0.10	0.10	0.07
Average frequency	0.09	−0.04	0.22	1.42

Table 1 Mean, minimum, and maximum AICc values obtained for different evolutionary tree transformation models (ACDC, lambda, kappa, delta, white noise, and Brownian). Each transformation was made for 1000 phylogenetic trees. Some models were discarded due to fit errors (710 ACDC models and 68 delta). The % of trees in which each model has the lowest AICc among others is presented and indicates the most plausible evolutionary tree transformation model

Model	Lambda	ACDC	Kappa	Delta	White	Brownian
Mean AICc	65.31	69.10	69.80	70.33	65.02	68.060
Min AICc	65.31	61.68	69.80	68.99	65.02	68.060
Max AICc	65.31	70.36	69.80	70.36	65.02	68.060
% Lowest AICc	0	0.1	0	0	99.9	0

(Wollerman and Wiley 2002). Furthermore, in sympatry, species interactions might modify female frequency preference to avoid hybridation (Márquez and Bosch 1997).

Males' call frequencies are not the only characteristic driving females' mating decisions. For example, female preferences for temporal characteristics like call rate and call duration have been documented for several anuran species (Bosch and Márquez 2005; Dawson and Ryan 2009; Richardson et al. 2010; Laird et al. 2016). Mate choice may also be related to characteristics that involve direct benefits for the female, such as males' territories or nests (Wells 1977; Höbel 2000; da Rocha et al. 2018). It might also be related to the good gene model of female preference so that attributes such as color can indicate males that have higher genetic quality (Maan and Cummings 2009). Studies have shown that females of some frog species from our dataset also express preferences for male characteristics other than call frequency (Backwell and Passmore 1990; Bosch and Márquez 2001; Baugh and Ryan 2011; Richards-Zawacki et al. 2012). For instance, *Oophaga pumilio* (Schmidt, 1857) females choose their mates based on visual cues related to males' colors (Summers et al. 1999; Maan and Cummings 2009). Furthermore, studies with *Engystomops pustulosus* (Cope, 1864) suggest that male attractiveness should be a multidimensional characteristic, in which females choose their mates based on the evaluation of several characteristics simultaneously and not exclusively through their dominant frequency (Ryan and Rand 2003; Baugh et al. 2008). The phenotypic plasticity of female preferences as well as the preference for other characteristics might explain why according to our results, closely related taxa do not share female frequency preferences. However, it is important to highlight that despite being a considerable effort in comparison to other studies in the area while embracing 30 species with described FFP, this represents only a very small sample of all anura diversity (i.e., approximately 7500 species (Frost 2020)).

Calling site

Females' signal perception and interpretation might not be such a limiting and costly factor for mating choice as we expected. As predicted by sound propagation properties, specific calling sites might represent real challenges to signal transmission (Wiley and Richards 1978; Richards and Wiley 1980; Hardt and Benedict 2020). However, the acoustic adaptation hypothesis (Morton 1975; Wiley and Richards 1978) predicts that species' acoustic signals should evolve to optimize their transmission in their habitats. For instance, while comparing species calling from water and non-floating ones, Muñoz et al. (2020) found that water species had lower dominant frequencies, an advantage in terms of signal propagation distance. Moreover, animals might develop behavioral strategies to minimize signal degradation like increasing their call amplitude and duration (Brumm and Slater 2006; Ey et al. 2009). Finally, receivers are also expected to evolve their cognitive systems in order to interpret those degraded signals (Naguib and Wiley 2001). Thus, if both senders and receivers are adapted to minimize the impact of acoustic signal degradation, females should be still able to exert and maintain their preferences regardless of environment signal propagation constraints.

In contrast with FFP, species calling site data is a lot more representative (i.e., Tonini et al. (2020) database classifies 2176 species according to their calling sites). However, we should consider that using different scales on habitat classification may represent different aspects of signal propagation. For instance, Zimmerman (1983) tests the effect of habitat on frogs' acoustic signal evolution using a binary classification (open and closed habitats), while Goutte et al. (2018) uses a continuous measure of canopy cover to represent habitat propagation properties. While the calling site classification we use embrace several species, it is not necessarily the best representation of the environmental constraints on signal propagation and therefore female choosiness.

Female preferences and SSD

We found no evidence that female preference for call frequency influences SSD in anurans. Probably, other factors, such as parental care, fecundity selection, and different life history traits between sexes, act more intensely in the direction of SSD. For instance, it is known that the presence of parental care might decrease SSD in anurans (Han and Fu 2013) and larger female size is favored by fecundity selection, since larger females have greater fecundity (Han and Fu 2013; Nali et al. 2014). Considering that anurans have indeterminate growth, female anurans have greater longevity, age, and size compared to males, and much of the SSD variation in anurans can be explained by the age difference between the sexes (Monnet and Cherry 2002). Furthermore, even if female frequency preferences do not appear to play a role in SSD, other aspects related to sexual selection might play a role.

Concluding remarks

In this study we explored some of the evolutionary relationships determining and constraining female preferences for call frequency in anura. Moreover, we also explore the influence of those preferences on sexual size dimorphism. Through phylogenetic comparative methods we showed that, contrary to our expectations, related species do not share dominant frequency preferences and these preferences are not determined by species calling sites. Additionally, we found no effect of female preferences on SSD, which might indicate that other factors play a more important role than sexual selection in determining SSD.

Despite of the large dataset gathered for this study, which represent a considerable advance on evolutionary studies of female preferences in anura, data availability is still scarce and might be a limitation to identify robust patterns. Perhaps expanding the data on FFP to more species and using different scales of species calling habitat could lead to different results. In addition, other aspects of sexual selection must be explored to understand its role on SSD. Lastly, we recommend future studies to also explore other possibly relevant variables, such as species mating systems, operational sex ratio, and reproductive pattern.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-023-03418-3.

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Author contribution Conceptualization: JVB, IM, DL, and RPB; methodology: JVB, IM, and JAFD-F; formal analysis and investigation: JVB and IM; writing—original draft preparation: JVB and IM; writing—review and editing: JVB, IM, DL, JAFD-F, and RPB.

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Data availability Data generated or analyzed during this study comes from a literature survey; therefore, in addition to the data used, we provide complete references for the studies from which they are derived in the supplementary data.

Declarations

Ethics approval This study uses data from a literature survey and, therefore, does not involve any direct observation or manipulation of animals by the authors.

Conflict of interest The authors declare no competing interests.

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