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# Multilevel analysis of acoustic variation in a *Scinax fuscomarginatus* population (Anura, Hylidae) of Central Brazil

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The vocalisations of anurans are one of their principal forms of communication and are mainly used for specific recognition involving the attraction of reproductive mates and territorial defense. In this study, we analysed the advertisement calls of 101 individuals from a population of *Scinax fuscomarginatus* sampled in the type locality of *S. pusillus* (currently under the synonymy of *S. fuscomarginatus*). Specifically, we investigated acoustic variation at several levels: intraindividual, interindividual, throughout the night, and across six breeding seasons by analysing temporal and spectral parameters. We identified that all parameters of the advertisement call can be used for individual recognition, with the maximum frequency having the greatest potential. We then observed that all other acoustic parameters were influenced by the predictor variables, with the exception of maximum frequency. The air temperature negatively influenced call duration, number of pulses, dominant frequency and minimum frequency; while it positively influenced pulse rate and call rate during the breeding season. Furthermore, with the exception of call duration and pulse rate, the other acoustic parameters varied significantly across the different nocturnal periods. This study provides data on the variation in *S. fuscomarginatus* acoustic features. Besides, we also discuss the implications of individual recognition. Studies that consider different sources of variation for the same population of a given species are uncommon, but of paramount importance for understanding the behavioural dynamics of the population.

*Keywords:* advertisement call, behaviour, individual recognition, sexual-selection

## INTRODUCTION

The vocalisations of anurans are extremely important as they represent one of their main forms of communication, especially during the breeding season (Gerhardt, 1991; Reichert, 2013; Bee et al., 2016). In anurans, vocalisations are classified based on the context in which they are emitted (Köhler et al., 2017), with the advertisement call being the most frequent (Köhler et al., 2017; Guerra et al., 2018). Calls mediate important social and sexual interactions among individuals, such as specific recognition and attraction of reproductive partners (Pettitt et al., 2013; Arini et al., 2016; Bee et al., 2016). Moreover, calls are also species-specific; therefore, can be useful in behavioural, evolutionary, and taxonomic studies (Blair, 1964; Pombal & Bastos, 2003; Glaw et al., 2010; Bee et al., 2013; Köhler et al., 2017; Tonini et al., 2020).

Several empirical studies have described the influence of environmental, morphological, and social factors on anuran vocalisations over the past few years, which have contributed to a better understanding of the communication process of these animals (see examples in Köhler et al., 2017). For example, amongst environmental factors, it is known that the acoustic parameters of calls can be greatly influenced by precipitation, temperature, relative humidity, and wind (Lemes et al., 2012; Pérez-Granados et al., 2019; Sun et al., 2019). Other factors that also influence call parameters are the characteristics of vocalising individuals, such as morphological variables (e.g. mass and SVL) and physiological conditions (Nevo & Schneider, 1976; Morais et al., 2012; Bee et al., 2013). In anurans, the allometric relationship between the size of individuals and their vocalisations is well known (Tonini et al., 2020), and an inverse relationship between body size and dominant call frequency is expected (Wagner, 1989a; 1989b; Morais et al., 2016; Köhler et al., 2017).

There is also the influence of social interactions on vocalisations (Morais et al., 2015; 2021; Dias et al., 2017). For example, the distance between conspecifics (Morais et al., 2012; Gambale et al., 2014) or the density of the chorus (Bastos et al., 2011) can influence the acoustic parameters of the vocalisations emitted by anurans. In some species it is possible to observe lek

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behaviour, in which several males perform courtship displays to conspecific females through their acoustic signals (Wells, 1977). In these species, the aggregation of individuals engaged in vocalisation activity is common, which can generate intense acoustic competition and consequently, the masking of some acoustic signals due to overlap (Wagner, 1989a; Gall & Wilczynski, 2016; Tanner & Bee, 2019). To minimise these effects, some anuran groups have developed strategies such as altering the dominant frequency and/or duration of their calls (Wagner, 1989b; Lucas et al., 1996; McCauley et al., 2000).

Acoustic parameters can be classified as dynamic (variation greater than 12 %; $CV_{intra} > 12$ %) or static (variation less than 5 %; $CV_{intra} < 5$ %), suggesting that such parameters would be subjected to different types of selection (i.e. directional or stabilising) (Gerhardt, 1991). Although studies addressing acoustic variability at the intra- and interindividual levels are the most common in literature (e.g. Bee et al., 2001; Bee & Gerhardt, 2002; Gasser et al., 2009; Briggs, 2010; Bee et al., 2013; Gambale & Bastos, 2014; Guerra et al., 2017; Röhr et al., 2020). The variation in acoustic signals of anurans at distinct nocturnal periods or between distinct breeding seasons has been barely explored (Gambale et al., 2014; Dias et al., 2017; Andreani et al., 2020).

Studies addressing acoustic variation provide us with important insights into the individual recognition process in anurans, as individuals can potentially be discriminated in a reproductive aggregation based on their calls (Bee & Gerhardt, 2002; Morais et al., 2012). This is a particularly important aspect, given that females choose their reproductive partners based on the acoustic parameters of the signals emitted by them (Welch et al., 1998; Bosch et al., 2000; Schwartz et al., 2002; Byrne, 2008). Thus, changes in acoustic communication patterns in a given species, can lead to changes in reproductive rates (Warren et al., 2006; Costa & Carnaval, 2012; Klaus & Lougheed, 2013; Merrick & Koprowski, 2017). Therefore, changes in population size and structure can occur, and may render populations more susceptible to decline (Laiolo, 2010).

*Scinax fuscomarginatus* (Lutz, 1925) is a small hylid widely distributed in South America, including the Brazilian biomes of Amazonia, Caatinga, Cerrado, Atlantic Forest, and Pantanal (Pupin et al., 2020; Frost, 2023). The vocalisations of this species were formally described in the 1980s and since then several studies have considered its acoustic signals in different contexts (Duellman & Pyles, 1983; De la Riva et al., 1994; Pombal et al., 1995, 2011; Toledo & Haddad, 2005b; Pombal, 2010; Brusquetti et al., 2014; Jansen et al., 2016; Souza et al., 2021). The vocal repertoire of *S. fuscomarginatus* was described as being composed of four call types (Toledo & Haddad, 2005b), with the advertisement call being the most studied. In 2016, Jansen et al. investigated a character shift in the advertisement calls in allopatric and sympatric populations of two related species (*S. fuscomarginatus* and *S. madeirae*) and more recently, Souza et al. (2021) described variation in the advertisement calls emitted by males from ten populations of *S. fuscomarginatus* in Central Brazil.

Here we describe the acoustic behaviour of individuals in a population from the municipality of Rio Verde, state of Goiás, Central Brazil. The population studied was found in the type locality of *Scinax pusillus* Pombal, Bilate, Gambale, Signorelli & Bastos, 2011, currently synonymous with *S. fuscomarginatus* (Brusquetti et al., 2014). Specifically, we investigate the variation in male advertisement calls of this population considering the following levels: intraindividual, interindividual, throughout the night, and over six breeding seasons. Our expectation is to find greater variation in acoustic parameters between than within individuals, enabling acoustic discrimination of these males in a breeding aggregation (Gambale et al., 2014; Guerra et al., 2017). Additionally, we also expect that the acoustic parameters of calls that have a high potential for the discrimination of individuals will maintain this pattern at different times of the night and in different breeding seasons.

## MATERIALS & METHODS

### Study area

Field activities were carried out in a permanent water body located on a rural property in the municipality of Rio Verde, Goiás State, Brazil (17° 48'6.02" S, 51° 05'21 W, ~800 m a.s.l.). The water body is within the Cerrado biome and it is surrounded by different vegetational strata, such as herbs, shrubs and trees. In addition, the study site suffers from anthropogenic activities such as livestock grazing and monoculture plantations (e.g. corn and soybean). The climate in the study region is Aw (tropical wet savanna), according to the Köppen classification, having a well-defined rainy period from October to March, with average annual precipitation of 1,300 mm and average annual temperatures ranging from 20 to 25 °C (Alvares et al., 2014). Besides *S. fuscomarginatus*, several other species of anurans were recorded in the same water body: *Boana albopunctata*, *B. lundii*, *Dendropsophus cruzi*, *D. jimi*, *Scinax* aff. *fuscovarius*, *Elachistocleis cesarii*, *Leptodactylus labyrinthicus*, *Physalaemus cuvieri*, *P. nattereri*, *Pseudopaludicola* sp. and *Rhinella diptycha*.

### Study species

Brusquetti et al. (2014) conducted a taxonomic revision of *S. fuscomarginatus* and related species based on acoustic, molecular, and morphological data, in which they proposed the synonymy of *S. parkeri*, *S. trilineatus*, *S. lutzorum*, and *S. pusillus* with *S. fuscomarginatus*. The population considered in this study is the one found in the type locality of *S. pusillus* (for more information see Pombal et al., 2011). Information on some aspects of the natural history of this population was obtained through a previous study (Pombal et al., 2011) and also through personal observations made in the field. The individuals of this population are active during the rainy season (October to March) and have a lek mating system, as males aggregate to perform courtship displays and consequently, attract reproductive partners. Throughout the night, males emit vocalisations in different periods (from 1800 to 0600) however; their acoustic activity peak occurs around 2100. Pombal et al. (2011) described two types of vocalisations emitted by males of this population; with the advertisement call being the most commonly observed.

### Collection and Data Analysis

We recorded the calls of 101 individuals of *S. fuscomarginatus* between October to March over six breeding seasons: 2014/15 (n = 18); 2015/16 (n = 6); 2016/17 (n = 48); 2017/18 (n = 8); 2018/19 (n = 16) and 2019/2020 (n = 5). Recordings were obtained between 1900 and 0000 with Sennheiser ME-66 (Wedemark-Wennebostel, Germany) microphones coupled to Marantz PMD-660 (Kanagawa, Japan) or Tascan DR-40 (California, USA) recorders, with the following recording settings: 44.1 kHz, 16 bits, WAV format. Each recording session lasted approximately two minutes. We standardised a distance of 50 cm between the microphone and the calling males. Subsequent to the recordings, we collected the males and took the following measurements: snout-vent length (SVL), with a caliper (0.01 mm precision); and total mass, with a digital scale (0.01 g). We also recorded the air temperature following each call with a thermohygrometer (precision 0.1 °C).

Previously, Bastos et al. (2011) suggest that in the first hours of the night, vocalisations are mainly associated with defense and the establishment of vocalisation sites, while in the middle of the night they are mainly associated with the attraction of reproductive partners. This is a relevant topic, because different periods of the night are associated with different contexts and, consequently, can influence differently the acoustic parameters of the calls. To investigate this topic, we considered 13 of the 101 individuals and obtained their vocalisations at different times throughout the night (between 1930 and 2300). Specifically, we made five recordings at 30-minute intervals (e.g. sequences: A, B, C, D, and E) of each individual.

We used the Raven Pro 1.5 software (Bioacoustics Research Program, 2011) to analyze the acoustic parameters of *S. fuscomarginatus* calls. For each recording session, we randomly selected five advertisement calls and measured the following acoustic parameters: call duration (s), number of pulses (pulses/call), dominant frequency (Hz), maximum frequency (Hz), and minimum frequency (Hz). We also measured the pulse repetition rate (pulses/s), which is estimated by dividing the number of pulses per call by the total duration of the call. Finally, we calculated the call repetition rate (calls/min), which is done by dividing the number of calls by the total duration of the recording. The acoustic terminology is according to Köhler et al. (2017) and the figures (spectrogram and oscillogram) were prepared in the R software (R Core Team, 2020) using the Seewave 1.6.4 package (Sueur et al., 2008), with the following settings: window name (Fourier transform window) = Hanning; window length = 256 samples; overlap = 90 %. The collected specimens were deposited in the Coleção de Vertebrados Alípio de Miranda-Ribeiro (CVAMR-An 316-329; 338; 384-390; 400) and the audio recordings were deposited in the Collection of Sound Archives of Neotropical Amphibians (CASAN 025-030; 032-040; 047-049; 147-148; 151-156; 196-198; 200-204; 209-215; 236-302; 360-365; 399-401; 427-443; 479-533) both located in the Rio Verde Campus, Instituto Federal Goiano (IF Goiano), Brazil.

### Intra- and interindividual variation

The influence of temperature on the acoustic parameters of anuran calls is well established in the literature (Köhler et al., 2017). Prior to the analyses of intraindividual and interindividual variation, we controlled the effect of temperature on the acoustic parameters using the equation described by Kaefer & Lima (2012): where $Y$ is the raw value, $Y_{adj}$ is the adjusted value of the parameter, $b$ is the regression coefficient, $T_{local}$ is the temperature at the time of recording, and $T_{average}$ is the average temperature of all recordings.

To describe the intraindividual variation of each acoustic parameter, we obtained its coefficient of variation ($CV_{intra}$), based on a recording session for each individual, where we calculated the $CV_{intra}$ through the individual's standard deviation divided by the mean of the parameter analysed. For the interindividual coefficient of variation ($CV_{inter}$), we used the same formula, but considering the standard deviation and the mean of a given parameter of all individuals analysed, regardless of reproductive season.

We classified the acoustic parameters according to their intraindividual coefficients of variation, following Gerhardt (1991). Thus, the parameters were classified as static ($CV_{intra}$ < 5%); intermediate ($CV_{intra}$ 5 % to 12 %), and dynamic ($CV_{intra}$ > 12 %). To determine whether a given acoustic parameter has a greater variation at the interindividual level than its counterpart at the intraindividual level we calculated the $CV_{inter}/CV_{intra}$ ratio. Acoustic parameters with $CV_{inter}/CV_{intra}$ values above 1.0 determine that the variation between individuals is greater than the variation within individuals, indicating that this acoustic parameter can potentially be used for individual species recognition (Bee et al., 2001).

Finally, in order to identify statistical differences in the acoustic parameters between individuals, we performed a simple Analysis of Variance (ANOVA). However, when the data did not meet the assumptions (i.e. homogeneity of variances and normal distribution) the non-parametric Kruskal-Wallis test was used. We used subjects as predictor variables and acoustic parameters as response variables for these analyses.

### Variation throughout the night

As described above, we calculated the coefficients of variation ($CV_{inter}/CV_{intra}$) and the $CV_{inter}/CV_{intra}$ ratio for the different periods throughout the night (i.e. A, B, C, D, and E). In addition, we performed a repeated-measures Analysis of Variance (ANOVA) to investigate

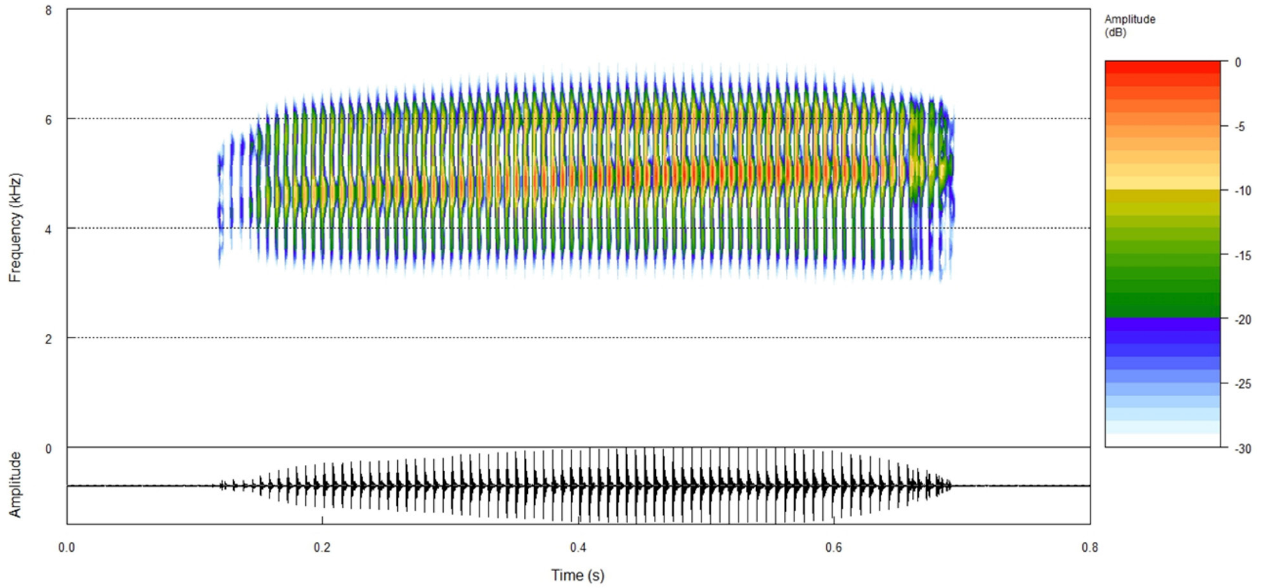

**Figure 1**. Audiospectrogram (above) and oscillogram (below) of the advertisement call of *Scinax fuscomarginatus* from Central Brazil. Air temperature = 21.7 °C; air humidity = 94 %; SVL = 16.53 mm; mass = 0.3 g; CASAN_0479).

the differences in acoustic parameters between the different periods throughout the night, using data corrected for ambient temperature. We used each period of the night as predictor variables, the individual as a repeated measures factor, and the response variables were the acoustic parameters of the individuals. Finally, we applied the Tukey test on the results, which makes pairwise comparisons with the nocturnal periods, making it possible to identify which periods of night differed from each other. The analyses throughout the night were performed using the Jamovi software version 1.8. We adopted a significance level of 0.05 for these analyses and the ones mentioned in the previous topic (Zar, 1996).

### Variation over breeding seasons

To evaluate the variation in the acoustic parameters of advertisement calls across breeding seasons, we followed the approach described by Andreani et al. (2020). First, in order to eliminate the correlation between the SVL and mass body variables, we created a single value by multiplying these variables and named them body condition (Gambale et al., 2014). Subsequently, we also transformed the reproductive season variable into a multistate discrete variable, where the value 0 was assigned to the first reproductive season in our sampling (i.e. our starting point of study observation) and the value of 1 was added to subsequent years. Thus, we have the following values: 2014/2015 = 0; 2015/2016 = 1; 2016/2017 = 2; 2017/2018 = 3; 2018/2019 = 4 and 2019/2020 = 5.

Finally, we applied a Multiple Linear Regression for each acoustic parameter separately to understand how years, environmental temperature and body condition influence acoustic parameters, using the acoustic parameters as response variables and the years,

**Table 1**. Values of acoustic parameters of *S. fuscomarginatus* males including mean, standard deviation, amplitude, intraindividual coefficient of variation (%) (mean, minimum and maximum), interindividual coefficient of variation (%), and $CV_{inter}/CV_{intra}$ ratio

| | **Mean ± SD (Range)** | **Within-male mean CV %** | **Within-male range CV %** | **Between-male mean CV %** | **Ratio $CV_{inter}/CV_{intra}$** |
|---|---|---|---|---|---|
| Call duration (s) | 0.54 ± 0.07<br>(0.25 – 0.82) | 5.21 | 1.01 – 31.1 | 9.76 | 1.87 |
| Number of pulse (pulse/call) | 69.33 ± 7.80<br>(30 – 97) | 5.56 | 0.80 – 29.2 | 9.75 | 1.76 |
| Dominant frequency (Hz) | 5019.74 ± 670.49<br>(656.5 – 6563.5) | 2.32 | 0.00 – 12.6 | 10.17 | 4.39 |
| Maximum frequency (Hz) | 6189.67 ± 295.14<br>(5062.50 – 7125) | 1.03 | 0.00 – 5.59 | 4.66 | 4.52 |
| Minimum frequency (Hz) | 3805.33 ± 1072.22<br>(93.80 – 4875) | 7.6 | 0.00 – 121 | 17.7 | 2.33 |
| Pulse repetition rate (pulses/s) | 129.34 ± 12.30<br>(105.1 – 202.15) | 2.72 | 0.413 – 1.4 | 7.17 | 2.63 |

**Table 2**. Coefficient of variability of advertisement call ($CV_{inter}/CV_{intra}$) for *S. fuscomarginatus* males in each reproductive season sampled. We also present the ANOVA or Kruskal-Wallis results of the interindividual comparisons of the acoustic parameters.

| | **Acoustic parameters** | | | | | |
|---|---|---|---|---|---|---|
| **Breeding seasons** | **Call duration** | **Dominant frequency** | **Maximum frequency** | **Minimum frequency** | **Number of pulses** | **Pulse repetition rate** |
| 2014/2015 | 2.51<br>H = 67.32<br>p = 0.0000 | 2.23<br>H = 68.59<br>p = 0.0000 | 2.84<br>H = 71.51<br>p = 0.0000 | 2.73<br>H = 73.79<br>p = 0.0000 | 1.93<br>H = 65.28<br>p = 0.0000 | 2.81<br>H = 68.02<br>p = 0.0000 |
| 2015/2016 | 1.79<br>H = 15.91<br>p = 0.0031 | 1.03<br>H = 14.37<br>p = 0.0062 | 10.22<br>H = 23.32<br>p = 0.0001 | 0.97<br>H = 18.47<br>p = 0.0010 | 2.55<br>F = 31.29<br>p = 0.0000 | 1.60<br>H = 14.62<br>p = 0.0056 |
| 2016/2017 | 1.55<br>H = 170.88<br>p = 0.0000 | 5.14<br>H = 154.51<br>p = 0.0000 | 3.55<br>H = 202.74<br>p = 0.000 | 3.46<br>H = 193.02<br>p = 0.000 | 1.35<br>H = 155.99<br>p = 0.0000 | 1.74<br>H = 166.02<br>p = 0.0000 |
| 2017/2018 | 1.23<br>F = 6.99<br>p = 0.0097 | 1.24<br>F = 6.23<br>p = 0.0140 | 1.92<br>H = 9.76<br>p = 0.0076 | 1.77<br>H = 8.17<br>p = 0.0168 | 1.45<br>F = 8.48<br>P = 0.0050 | 0.72<br>F = 2.53<br>P = 0.1212 |
| 2018/2019 | 1.61<br>H = 62.57<br>p = 0.0000 | 3.30<br>H = 73.04<br>p = 0.0000 | 4.67<br>H = 70.14<br>p = 0.0000 | 2.01<br>H = 73.68<br>p = 0.0000 | 1.45<br>H = 59.71<br>p = 0.0000 | 3.51<br>H = 60.93<br>p = 0.0000 |
| 2019/2020 | 3.48<br>F = 44.81<br>p = 0.0000 | 3.30<br>H = 19.69<br>p = 0.0006 | 16.13<br>H = 23.08<br>p = 0.0001 | 2.05<br>H = 21.51<br>p = 0.0003 | 4.87<br>F = 103.89<br>p = 0.0000 | 4.98<br>F = 112.92<br>p = 0.0000 |
| Total | 1.87<br>F = 11.6<br>p = 0.001 | 4.39<br>F = 54.0<br>p = 0.001 | 4.52<br>F = 55.7<br>p = 0.001 | 2.33<br>F = 15.7<br>p = 0.001 | 1.75<br>F = 10.9<br>p = 0.001 | 2.63<br>F = 23.1<br>p = 0.001 |

temperature and body condition as predictor variables. We used the multi-model inference framework based on Akaike's selection criteria (AICc) to select the best combinations of variables in each model (Burnham et al., 2011), considering a 0.8 threshold of importance to determine the permanence of the predictor variable in a given model (Calcagno & Mazancourt, 2010). We used the R software (R Core Team, 2020) for all analyses with the Glmuti package for multi-model analyses (Calcagno & Mazancourt, 2010).

## RESULTS

### Call description and intra- and interindividual variation

During field activities, air temperature ranged from 18.6 to 24.4 °C (x = 21.1 ± 1.6 °C), while the SVL and mass of individuals ranged from 16.11 to 20.73 mm (x = 17.9 ± 1.11 mm) and from 0.17 to 0.49 g (x = 0.3 ± 0.06 g), respectively. We analysed 505 advertisement calls emitted by 101 *S. fuscomarginatus* males of the same population (see an example in Figure 1). The mean, minimum, maximum, and standard deviation values for each acoustic parameter analysed are shown in Table 1.

Overall, none of the acoustic parameters were classified as dynamic (Table 1). Call duration ($CV_{intra}$ = 5.21 %), number of pulses ($CV_{intra}$ = 5.55 %), and minimum frequency ($CV_{intra}$ = 7.60 %) were classified as having intermediate acoustic properties, whereas pulse rate ($CV_{intra}$ = 2.72 %), dominant frequency ($CV_{intra}$ = 2.32 %), and maximum frequency ($CV_{intra}$ = 1.03 %) were classified as static (Table 1). Additionally, all acoustic parameters of the advertisement calls had $CV_{inter}/CV_{intra} > 1$ (i.e. they varied more between than within individuals). Overall, the spectral parameters of the advertisement call had the highest values, with the maximum frequency ($CV_{inter}/CV_{intra}$ = 4.52) exhibiting the greatest potential for individual recognition (Tables 1 & 2). However, only call duration, dominant frequency, maximum frequency and number of pulses are the parameters that had $CV_{inter}/CV_{intra} > 1$ across all six breeding seasons (Tables 1 & 2).

### Variation throughout the night

Except for call duration and pulse rate, all other acoustic parameters varied significantly throughout the night ($p < 0.05$ for all cases). We especially noticed the following differences: pulse number (period A ≠ B; $p_{Tukey} < 0.05$); dominant frequency (period B ≠ D; $p_{Tukey} < 0.05$), maximum frequency (period A ≠ C and period A ≠ D; $p_{Tukey} < 0.05$), minimum frequency (period A ≠ E and period B ≠ E; $p_{Tukey} < 0.05$), and call rate (period A ≠ B and period D ≠ E; $p_{Tukey} < 0.05$). Despite the observed differences, we noticed that intraindividual variation remained constant throughout the period analysed. That is, with the exception of minimum frequency, all acoustic parameters were classified as static ($CV_{intra} < 5$ %) or intermediate (5 % < $CV_{intra}$ < 12 %) throughout the night (Table 3).

### Influence of temperature, body condition (allometry) and breeding seasons

Acoustic parameters of the advertisement call varied according to the body condition of individuals, the air

**Table 3**. Means of the intraindividual coefficient of variability (%) of the advertisement call of all *S. fuscomarginatus* males throughout the same night by periods (A, B, C, D, E).

| Different periods throughout the night | Acoustic parameters | | | | | |
|---|---|---|---|---|---|---|
| | Call duration | Number of pulses | Dominant frequency | Maximum frequency | Minimum frequency | Pulse repetition rate |
| A | 4.03 | 4.16 | 2.38 | 0.79 | 6.33 | 1.89 |
| B | 3.42 | 3.39 | 2.67 | 0.69 | 3.29 | 1.91 |
| C | 4.08 | 4.30 | 2.33 | 0.65 | 2.12 | 1.99 |
| D | 3.38 | 3.40 | 3.43 | 0.56 | 2.40 | 1.83 |
| E | 3.81 | 4.65 | 2.59 | 0.50 | 17.43 | 2.52 |

**Table 4**. Results of multiple linear regressions between *S. fuscomarginatus* males and multi-model inference using the threshold of 0.8.

| Acoustic parameters | Variables | Importance | Partial regression coefficient | Unconditional variance | Confidence interval |
|---|---|---|---|---|---|
| Call duration | Body size | 0.9999 | 0.0112 | 6.2257 | 0.0049 |
| | Reproductive season | 0.3760 | -0.0008 | 2.0456 | 0.0028 |
| | Temperature | 1.0000 | -0.0297 | 3.7400 | 0.0038 |
| Number of pulses | Body size | 0.9999 | 1.8645 | 0.1102 | 0.6526 |
| | Reproductive season | 0.3382 | 0.0790 | 0.0256 | 0.3148 |
| | Temperature | 0.9999 | -1.2545 | 0.0662 | 0.5059 |
| Pulse repetition rate | Body size | 0.7166 | 0.6249 | 0.2919 | 1.0621 |
| | Reproductive season | 0.8074 | 0.6640 | 0.2061 | 0.8924 |
| | Temperature | 1.0000 | 4.7617 | 0.1285 | 0.7046 |
| Call repetition rate | Body size | 0.3448 | -0.1151 | 0.0518 | 0.4475 |
| | Reproductive season | 0.8774 | 0.6894 | 0.1436 | 0.7449 |
| | Temperature | 0.9999 | 4.7617 | 0.0808 | 0.5588 |
| Dominant frequency | Body size | 0.4706 | 15.2666 | 494.5974 | 43.7204 |
| | Reproductive season | 0.9040 | -47.0812 | 551.9694 | 46.1866 |
| | Temperature | 0.9522 | -49.1484 | 412.1078 | 39.9084 |
| Maximum frequency | Body size | 0.9998 | -55.8453 | 155.0935 | 24.4825 |
| | Reproductive season | 0.9999 | -64.0891 | 102.6456 | 19.9173 |
| | Temperature | 0.6426 | -10.7501 | 120.3722 | 21.5686 |
| Minimum frequency | Body size | 0.9954 | -115.8327 | 1075.1604 | 64.4607 |
| | Reproductive season | 0.2723 | -2.1464 | 83.8771 | 17.9734 |
| | Temperature | 0.9999 | -149.7444 | 634.9085 | 49.5352 |

temperature, and also throughout the breeding seasons. However, each parameter showed distinct patterns of variation and influence. All acoustic parameters were influenced by ambient temperature, except for maximum frequency (Table 4). We observed an inverse relationship between air temperature and the following acoustic parameters: call duration [Importance = 1.0000; Partial regression coefficient (PRC) -0.0297], number of pulses (Importance = 0.9999; PRC -1.2545), dominant frequency (Importance = 0.9522; PRC -49.1484), and minimum frequency (Importance = 0.9999; PRC -149.7444). On the other hand, we observed a positive relationship between air temperature and pulse rate (Importance = 1.0000; PRC 4.7617), and call rate (Importance = 0.9999; PRC 4.7617) (Table 4).

It was evident that temporal parameters [i.e. pulse rate (Importance = 0.8074; PRC 0.6640) and call rate (Importance = 0.8774; PRC 0.6894)] increased over the years, while spectral parameters [i.e. maximum frequency (Importance = 0.9999; PRC -64.0891) and dominant frequency (Importance = 0.9040; PRC -47.0812)] decreased as the breeding seasons passed. When we took body condition into consideration, call duration (Importance =0.9999; PRC 0.0112) and number of pulses (Importance = 0.9999; PRC 1.8645) were positively related, while maximum frequency (Importance = 0.9998; PRC -55.8453) and minimum frequency (Importance = 0.9954; PRC -115.8327) were negatively influenced by body condition.

# DISCUSSION

Several descriptions of the advertisement call of *S. fuscomarginatus* based on different sample sizes collected from different populations throughout the species' geographic range have been conducted in recent decades (Duellman & Pyles, 1983; De la Riva et al., 1994; Pombal et al., 1995; 2011; Toledo & Haddad, 2005b; Pombal, 2010; Brusquetti et al., 2014; Jansen et al., 2016; Souza et al., 2021). Considering that the advertisement calls of anuran species are important taxonomic tools, bioacoustic studies based on a large sampling effort are important contributors to improving our understanding about the taxonomy of our target species. In this sense, it is important to highlight that the present study characterised the advertisement call of *S. fuscomarginatus* based on an expressive number of individuals that belong to a population that is taxonomically relevant, as it was sampled in the type locality of *S. pusillus* (currently under the synonymy of *S. fuscomarginatus*).

Our results expand the previously known variation of the advertisement call's acoustic parameters for individuals of this population (Pombal et al., 2011). We also observed that some acoustic parameters (e.g. dominant frequency and pulse rate) of the call differ from what was previously described for other populations of *S. fuscomarginatus*, as was reported by Brusquetti et al. (2014). On average, the advertisement calls of individuals considered here have a higher dominant frequency and lower pulse rate than calls recorded for individuals from other localities (Duellman & Pyles, 1983; De la Riva et al., 1994; Pombal et al., 1995; Toledo & Haddad, 2005b; Silva et al., 2008; Brusquetti et al., 2014; Jansen et al., 2016; Souza et al., 2021). Considering that divergences in acoustic parameters between individuals from distinct populations have revealed the existence of a species complex in anurans (Lopes et al., 2020), we suggest that future studies evaluate whether the acoustic differences reported here impact the specific recognition process between individuals from different populations (e.g. through experimental playbacks). This is particularly important considering the recent history of taxonomic change experienced by individuals from the target population of this study (Brusquetti et al., 2014).

Overall, we observed low intraindividual variation in the advertisement calls, as none of the acoustic parameters were classified as having dynamic properties ($CV_{intra}$ < 12 % for all cases). These results are similar to those described by Souza et al. (2021), as these authors also found that none of the parameters of the *S. fuscomarginatus* calls could be classified as dynamic when analysing acoustic variation among populations from Central Brazil. On the other hand, Jansen et al. (2016) reported high intraindividual variability in some acoustic parameters of the species' call. *Scinax fuscomarginatus* is a widely distributed species and consequently, individuals from distinct populations experience different environmental and/or social conditions that may affect their vocalisations in distinct ways. Therefore, this might explain the discrepancies found between different studies on acoustic variation in *S. fuscomarginatus*.

We also observed that all acoustic parameters of *S. fuscomarginatus* calls had $CV_{inter}/CV_{intra}$ ratios above 1. This implies that all parameters analysed have the potential to discriminate individuals in a breeding aggregation. These results are similar to those previously reported for *S. fuscomarginatus* (Souza et al., 2021) as well as for other Neotropical hylids (*Aplastodiscus albosignatus* - Moser et al., 2022; *Dendropsophus minutus* - Morais et al., 2012; and *Boana goiana* - Signorelli et al., 2016). As discussed by Bee & Gerhardt (2001) and Gasser et al. (2009), the pattern observed in the present study reinforces that the individual recognition process in anurans takes place through a set of different acoustic parameters. This is an important issue particularly in regions with high species richness (e.g. Neotropics), because dozens or hundreds of individuals of different species may coexist in the same site and therefore, generate some level of acoustic interference between them (Sugai et al., 2021).

Few studies have considered Neotropical anuran species to assess whether vocalisations vary at different times throughout the night. Two examples are Bastos et al. (2011) and Toledo & Haddad (2005b), who compared the emission rates of different call types of *Scinax centralis* and *S. fuscomarginatus* males throughout the night, respectively. Recently, Dias et al. (2017) included other acoustic parameters (e.g. dominant frequency, note duration, number of pulses, inter-note interval, and repetition rate) in their analysis and found that only the rate of call emission of the advertisement call of *B. goiana* differed over successive night periods. Unlike previous reports by Dias et al. (2017), our results demonstrate that distinct acoustic parameters (e.g. dominant frequency, maximum frequency, minimum frequency, pulse number, and call rate) of the advertisement call of *S. fuscomarginatus* differed throughout the night. Considering that vocal activity is energetically costly (Gerhardt, 1994; Prestwich, 1994), it is expected that individuals will exhibit distinct vocalisation behaviours throughout the night as a way to minimise body mass losses during the course of the breeding season (Robertson, 1986; Mac Nally, 1981). We hypothesise that vocalisation behaviours adopted by *S. fuscomarginatus* males throughout the night can be attempts to optimise female attraction by balancing their energy expenditure. However, future studies are necessary to better evaluate the pattern described here.

There are few studies that address how the acoustic parameters of advertisement calls vary across breeding seasons. In contrast to the lack of variation reported for some species (e.g. *Dryophytes versicolor* – Gerhardt et al., 1996; *Dendrobates pumilio* – Pröhl, 2003; *Scinax constrictus* – Gambale et al., 2014), the temporal (i.e. pulse rate and song rate) and spectral (e.g. maximum and dominant frequency) acoustic parameters of *S. fuscomarginatus* decreased across the breeding seasons. The change in temporal parameters of anuran vocalisations over reproductive seasons has also been reported by other authors (Howard & Young, 1998; Smith & Hunter, 2005; Andreani et al., 2020) and is correlated to the decrease in body mass of *Boana goiana* males over time (Andreani et al., 2020). On the other hand, Smith & Hunter (2005) reported that the variation in spectral parameters in the calls of males of *Litoria booroolongensis* across breeding seasons is caused by changes in body size.

In addition to expanding the known variation of this population, our results indicate that all parameters analysed are potentially important in the process of individual recognition, which may have implications for aggressive interactions and also in the preference of females for reproductive partners.

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