

RESEARCH ARTICLE

Individual variation in the advertisement call of *Aplastodiscus albosignatus* (Anura: Hylidae) is correlated with body size and environmental temperature

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ABSTRACT. The importance of amphibian bioacoustics is widely documented in ecological, taxonomical and evolutionary studies, as calls might act as a primary mechanism of reproductive isolation. The influence of air temperature and male size on the variation of the advertisement calls in anurans is widely recognized but still insufficiently analyzed in Brazilian species. Our goals were to (1) describe the advertisement call of *Aplastodiscus albosignatus* (Lutz & Lutz, 1938), (2) test the influence of temperature and body size on its acoustic signals and (3) evaluate the variation of within and between-male acoustic signals. Advertisement calls of *A. albosignatus* consist of an unpulsed note with four harmonics. In most cases, the dominant frequency is the third harmonic but, in some calls, it was the minimum frequency (first harmonic). The average duration of calls was 0.191 s, the interval between calls was 2.08 s and the repetition rate was 33 calls per minute. On average, the minimum frequency was 550.15 Hz, the maximum frequency was 3531.70 Hz and the third harmonic was 2498.9 Hz. To evaluate the effect of air temperature, and body size on the variation of call parameters, we performed generalized linear models. The most explanatory model for spectral parameters was temperature plus body size. Concerning temporal variables, the best model that explains the variation in call duration was body size, while for the interval between calls was air temperature. The maximum frequency and the frequency of the third harmonic had little variation in the calls of both the same male and different males. Thus, these parameters were considered important in species recognition.

KEY WORDS. *Albosignatus* group, Atlantic Forest, coefficient of variation, dominant frequency, harmonics.

INTRODUCTION

Acoustic signals represent the main form of intra- and inter-specific communication in anurans. These signals are a fundamental characteristic of the natural history of this group and are mainly associated with sexual selection, reproduction, rival assessment and recognition (Wells 2010, Toledo et al. 2014, Bee et al. 2016). The most common vocalizations emitted by males are the advertisement calls, which are species-specific and function as a mechanism of pre-zygotic reproductive isolation (Wells 2010, Gambale and Bastos 2014, Guerra et al. 2018). These

acoustic signals contain important information for females and possible competitors, indicating, for example, the individual's position, body size, body temperature and energetic condition (Wells 2010, Toledo et al. 2014).

Since anurans are ectothermic animals, their acoustic signals can be influenced by abiotic factors such as temperature, resulting in differences between individuals (Robertson 1984, Giacoma et al. 1997, Navas and Bevier 2001, Lingnau and Bastos 2007). Some species reduce the duration of the call at higher temperatures, which may be related to an attempt to avoid increased metabolism and energy expenditure (Lingnau and

Bastos 2007, Boschetti et al. 2019). For example, the temperature can influence the rate of call emissions and pulse repetition, while spectral parameters (e.g., minimum frequency), which are not related to muscular contraction, can be less affected by temperature (Wong et al. 2004).

Body size is also a factor that can influence a species' acoustic signals (Castellano et al. 2002, Bernal et al. 2005, Wells 2010). In general, spectral signals such as the dominant frequency are more influenced by the size of the individual, while temporal parameters tend to be more influenced by air temperature (e.g., Lemes et al. 2012, Morais et al. 2012, Bee et al. 2013). This occurs due to the influence of the size of the vocal cords and other components of the larynx (Wong et al. 2004). Understanding how these variations occur in the advertisement calls of species contributes to a better taxonomic delimitation and can generate an ecological basis for hypotheses about the change in acoustic traits over time (Castellano et al. 2002).

The calls formed by a single type of note are called simple calls, while those formed by different notes are called complex calls (Köhler et al. 2017). Simple calls are common in many species, such as those of the genera *Physalaemus* (e.g., Baêta et al. 2007, Gambale and Bastos 2014, Hepp et al. 2020) and *Aplastodiscus* (e.g., Abruñhosa et al. 2005, Zina and Haddad 2006). Complex calls, with a larger number of notes, and greater variation of these notes, are found in other Neotropical species such as *Dendropsophus minutus* (Peters, 1872) and *Bokermannohyla ibitiguara* (Cardoso, 1983) (Nali and Prado 2014, Turin et al. 2018).

Among the species that present simple calls, *Aplastodiscus* Lutz, 1950 (Hylidae) currently comprises 16 described species (Berneck et al. 2016, Frost 2021, Pinheiro et al. 2021) all with simple advertising calls (Abruñhosa et al. 2005, Zina and Haddad 2006, Berneck et al. 2016, Bezerra et al. 2020). *Aplastodiscus albosignatus* (Lutz & Lutz, 1938) is endemic to the Atlantic Forest and associated with streams in mountainous regions (< 850 m). The species' distribution was originally considered to extend from the state of Minas Gerais to Santa Catarina. A recent taxonomic study (Berneck et al. 2016), however, suggests that the populations previously recognized as *A. albosignatus* that occur in southern São Paulo, as well as in Paraná and Santa Catarina, consist of an undescribed species (*Aplastodiscus* sp. 5). The advertisement call of *A. albosignatus* was described by Abruñhosa et al. (2005) based on 10 calls of only one individual. To date, there are no other analyzed recordings of the vocalization of this species (Guerra et al. 2018). In the present study, we extend previous knowledge on the calls of *A. albosignatus* by: 1) providing a more robust description of the advertisement call; 2) examining the influence of abiotic (temperature) and biotic (body size) factors on the acoustic signals and (3) evaluating the intra-individual and inter-individual variation of the calls. To fulfill these goals, we expect that, as already described for other Neotropical species, 1) air temperature will be negatively associated with variation of temporal parameters of the advertisement calls (Lingnau and Bastos 2007, Köhler et al. 2017), 2) body size will be negatively

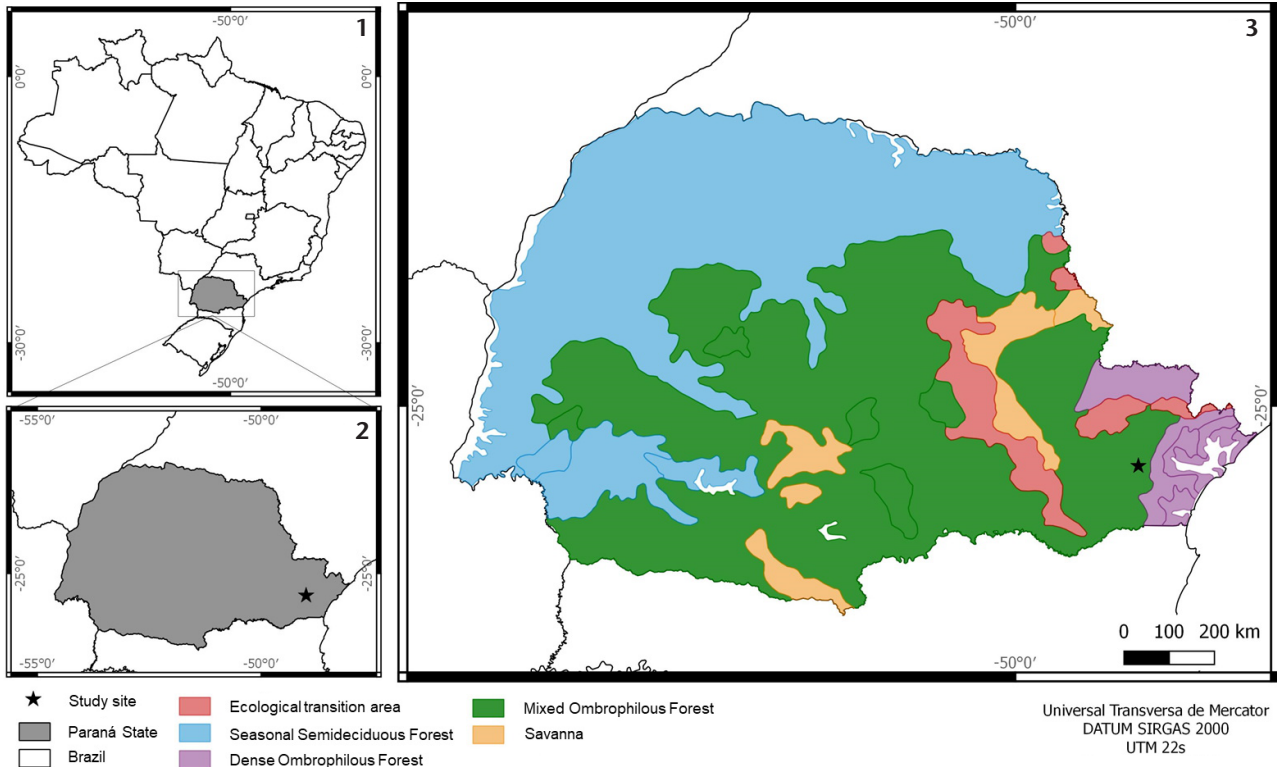
associated with spectral parameters (Lingnau and Bastos 2007, Köhler et al. 2017) and 3) the variation of acoustic signals will be greater between males (inter-individual) than the individual variation itself (intra-individual).

MATERIAL AND METHODS

The study was carried out in lotic environments of a subtropical forest (25°29'46"S 48°58'58"W, 1000 a.s.l.) of the Atlantic Forest, municipality of Piraquara, state of Paraná, southern Brazil (Figs 1–3). The collections of individuals occurred at Mananciais da Serra, more specifically on the Ipiranga Trail, which is about seven kilometers long. The sampled region is located in a transition zone between the phytophysiognomies Mixed Ombrophilous Forest, dominated by *Araucaria angustifolia* (Araucaria Forest) and Dense Ombrophilous Forest (Reginato and Goldenberg 2007). Annual rainfall ranges from 1400 to 1700 mm, with rainfall concentrated from October to March (Paraná 1987). The average temperature is 22 °C in the hottest months and 18 °C in the coldest months (Ferreira 1996).

We recorded 22 males of *A. albosignatus* between January 2019 and February 2020. When vocalizing males were located, at first their vocalization was recorded. The distance between the microphone and the individual was approximately 50 cm. After recording, we captured and individualized the amphibian and recorded air temperature with a thermometer (0.1 °C precision). We recorded the vocalizations with a CSR HT81 – YOGA unidirectional microphone coupled to a Tascam DR-40 recorder. After the collections, we weighed and measured the snout-vent length (SVL) of the recorded males with a scale (0.01 g precision) and digital caliper (0.05 mm precision). Afterward, we euthanized individuals with xylocaine, fixed them in 10% formalin and conserved them in 70% ethanol. The collections were carried out with the competent Federal Organ authorization, SISBIO (authorization #66853-2) and also with authorization of the Ethics Committee for Animal Use from the Biological Sciences Section of the Federal University of Paraná (CEUA/BIO, UFPR, process number 23075.043325/2019-27). The collected individuals were stored in the Herpetological Collection of the Universidade Tecnológica Federal do Paraná, Francisco Beltrão Campus (RLUTF 251, 252, 341, 343, 467, 468, 469, 489, 715, 716, 718, 732, 733, 734, 735, 736, 737, 749, 1218, 1219, 1220 and 1221). Call recordings were deposited at the Fonoteca Neotropical Jacques Vielliard, where they can be accessed under the codes FNVJ 45561 - 45582.

We analyzed 220 calls from 22 males with Raven pro 1.6 software for Windows (Cornell Lab of Ornithology, Bioacoustics Research Program 2011), using FFT (Fast Fourier Transformation) = 256. There was no need to use filters. The following acoustic parameters were analyzed: minimum frequency (Hz), maximum frequency (Hz), frequency of the third harmonic (Hz), call duration (s), interval between calls (s) and repetition rate (calls/min). Spectral measurements were obtained by selecting three variables in the "choose measurements" option in Raven 1.6: (1) low frequency, (2)



Figures 1–3. Location of the study area: (1) map of Brazil highlighting the state of Paraná; (2) map of Paraná indicating the study area; (3) map of Paraná highlighting the physiognomy of the vegetation.

high frequency and (3) peak frequency. The bioacoustic terms were used according to definitions proposed by Köhler et al. (2017), with an adaptation for calculating the dominant frequency. The dominant frequency values in *A. albosignatus* can be in the first or third harmonic (see data below), and therefore an average of the dominant frequency values could not be provided, which would be an uninformative value. Thus, we inform the values of minimum frequency (first harmonic) and third harmonic that better illustrate the location of the dominant frequency.

We generated oscillograms and spectrograms using R software (R Development Core Team 2016), with a window width of 512 samples, 90% overlap and FFT of 512 samples. We used the packages TuneR version 1.0 (Ligges et al. 2013) and Seewave version 1.7.3 (Sueur et al. 2008).

To evaluate the effect of air temperature and body size on call duration, the interval between calls, fundamental frequency, maximum frequency and peak frequency of the third harmonic, we performed generalized linear models using Gauss distribution in R software (version 4.1.0) and the following packages: corrplot (Wei et al. 2017) fBasics (Wuertz et al. 2007), DescTools (Signorell et al. 2016). We multiplied mass by snout-vent length (mass * SVL) to obtain a 'body size' variable that was used for hypothesis testing. We checked the normality of the variables using the Shapiro Wilk test. We found that the interval between calls and

peak frequency of the third harmonic did not have a normal distribution. Thus, all variables were transformed by square root. We tested five hypotheses, where the dependent variables (call duration, interval between calls, minimum frequency, maximum frequency and peak frequency of the third harmonic) are influenced by body size plus temperature (e.g. call duration ~ body size + temperature). To choose the best model, we used Akaike's Information Criterion (AIC, Arnold 2010).

The variability of the acoustic parameters of the calls of each male (intra-individual) and between males (inter-individual) was analyzed from the variation coefficient for each parameter, as proposed by Gerhardt (1991), where $CV = (DP/x) \times 100$. The intra-individual variation coefficient (CV_{intra}) considers the mean and standard deviation of the calls of each individual. The inter-individual coefficient of variation (CV_{inter}) is considered the mean and standard deviation of the parameters of all individuals. When the variation coefficient is equal to or less than 5%, the evaluated parameter is considered to be static, and when it is greater than or equal to 12%, it is considered to be dynamic (Gerhardt 1991).

To assess whether there is variability between male vocalizations, the ratio of the two variation coefficients was calculated (CV_{inter}/CV_{intra}). When the value obtained is $CV_{inter}/CV_{intra} > 1$, the evaluated acoustic signal assists in individual recognition (Márquez and Eekhout 2006).

RESULTS

The individuals had an average size of $42.6 \text{ mm} \pm 1.8 \text{ mm}$ ($39.4\text{--}45.8 \text{ mm}$) and an average mass of $4.66 \pm 0.5 \text{ g}$ ($3.8\text{--}5.7 \text{ g}$). The average temperature recorded during the samplings was $16.5 \pm 1.7 \text{ }^\circ\text{C}$ ($13\text{--}19 \text{ }^\circ\text{C}$). Individuals were found vocalizing on tree branches, usually more than two meters high.

The advertisement call of *A. albosignatus* is formed by a single note and a single pulse, with four visible harmonics. In general, the dominant frequency occurs in the third harmonic but, in some calls, the dominant frequency was recorded at the minimum frequency (first harmonic) (Table 1, Figs 4, 5). In a total of 220 analyzed calls, the dominant frequency was in the third harmonic in 145 calls (66%), and in the first harmonic in 75 calls (34%). The same male could present calls with the dominant frequency in the first or third harmonic. The mean duration of the calls was $0.191 \pm 0.028 \text{ s}$ ($0.12\text{--}0.25$), the interval between calls was $2.08 \pm 1.20 \text{ s}$ ($0.56\text{--}9.61$) and the repetition rate was 33 ± 14.73 calls per minute ($15\text{--}66$) (Table 1). On average, the minimum frequency was $550.15 \pm 42 \text{ Hz}$ ($421.09\text{--}689.06$), the maximum frequency was $3531.70 \pm 144.20 \text{ Hz}$ ($3253.9\text{--}3828.12$) and the third harmonic $2498.9 \pm 100.3 \text{ Hz}$ ($2239.45\text{--}2670.12$) (Table 1).

Table 1. Main acoustic parameters of the advertisement call of *Aplastodiscus albosignatus* in Mananciais da Serra, Paraná, Brazil. Legend: X = average; \pm SD = standard deviation; Min = minimum recorded value; Max = maximum recorded value. All data refer to 10 analyzed calls of 22 males, totaling 220 analyzed calls.

Acoustic signal	X \pm SD	(Min – Max)
Minimum frequency (Hz)	550.15 ± 42	421.09 – 689.06
Maximum frequency (Hz)	3531.7 ± 144.2	3253.9 – 3828.1
Third harmonic frequency (Hz)	2498.9 ± 100.3	2239.4 – 2670.1
Call duration (s)	0.191 ± 0.028	0.12 – 0.25
Interval between calls (s)	2.08 ± 1.20	0.56 – 9.61
Repetition rate (call/min)	33 ± 14.73	15 – 66

According to the AIC criterion, the most explanatory model for the three spectral parameters (minimum frequency, maximum frequency and third harmonic frequency) was temperature plus body size, conditioning jointly these variables (Table 2). Concerning temporal variables, the best model that explains the variation in call duration was body size, while for the interval between calls the best model was the air temperature (Table 2).

The variation coefficient indicated that the minimum frequency has an intermediate variation. The maximum frequency and the frequency of the third harmonic were considered static parameters (Table 3). Regarding temporal parameters, the call duration was considered as a static intra-individual and dynamic inter-individual parameter, while the interval between calls was dynamic in both comparisons. The ratio between CV_{inter} and

CV_{intra} of all the analyzed acoustic signals was greater than 1, indicating that there is greater variation between males than at the individual level (Table 3).

Table 2. Most supported models ($\Delta\text{AIC} < 4$) for each dependent variable considering two independent variables: temperature and body size. The values highlighted in bold represent the best model for the variable in question.

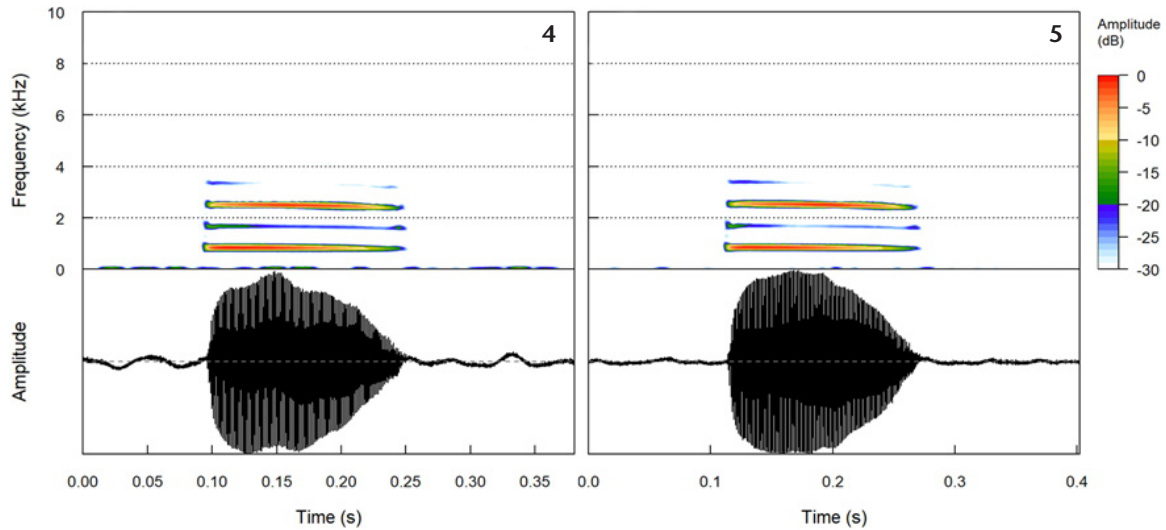
Acoustic signal	Model	AIC	ΔAIC	Weight
Call duration	Body size	88.218	0.00	0.00
	Temperature + body size	91.09	2.872	0.00
	Temperature	99.927	11.709	0.02
Interval between calls	Temperature	19.133	0.00	0.00
	Body size	23.016	3.883	0.01
	Temperature + body size	24.856	5.723	0.01
Minimum frequency	Temperature + body size	104.86	0.00	0.00
	Body size	207.15	102.29	0.16
	Temperature	213.13	108.27	0.17
Maximum frequency	Temperature + body size	91.09	0.00	0.00
	Body size	244.33	153.24	0.23
	Temperature	258.71	167.62	0.26
Third harmonic frequency	Temperature + body size	19.063	0.00	0.00
	Body size	67.56	48.497	0.07
	Temperature	67.908	48.845	0.07

Table 3. Variation of the main acoustic signals of the vocalizations of *Aplastodiscus albosignatus* in Mananciais da Serra, Paraná, Brazil. Legend: CV_{intra} = intra-individual variation coefficient; CV_{inter} = interindividual variation coefficient.

Acoustic signals	CV_{intra}	CV_{inter}	$CV_{\text{inter}}/CV_{\text{intra}}$	Static/Dynamic
Minimum frequency (Hz)	6.74	9.93	1.47	Intermediate
Maximum frequency (Hz)	1.26	4.18	3.31	Static
Third harmonic frequency (Hz)	0.96	4.11	4.28	Static
Call duration (s)	3.94	15.28	3.87	Dynamic
Interval between calls (s)	33.75	70.97	2.10	Dynamic

DISCUSSION

The species belonging to the *A. albosignatus* group have non-pulsed calls consisting of a single note (Abrunhosa et al. 2005). A difference observed between the previous description of *A. albosignatus* and the present description is the dominant frequency since Abrunhosa et al. (2005) proposed that the frequency with the highest peak energy always occurs in the third harmonic, between 2.61 and 2.66 kHz. In the recordings analyzed for the population of Piraquara (PR), we observed that the dominant frequency can occur in either the third or first harmonic, between 0.4 and 0.6 kHz. This difference is likely to be related to the fact that Abrunhosa et al. (2005) analyzed only 10 calls of a single male, while we analyzed the calls of a larger number of males. Most of the analyzed calls had a dominant



Figures 4–5. Spectrogram and oscillogram of two advertisement calls of the same male of *Aplastodiscus albosignatus*: (4) call with the dominant frequency in the first harmonic (= minimum frequency); (5) call with the dominant frequency in the third harmonic. Male recorded on January 14, 2020, voucher of specimen RLUTF 1220, voucher of recording FNJV 45563, 4.7 g, 44.8 mm, 18.1 °C.

frequency in the third harmonic (66%) but, in some cases, the dominant frequency was in the first harmonic (34%). Sometimes, the same male had dominant frequencies in the third harmonic and, in another call, in the first harmonic. This pattern can also be seen in *Aplastodiscus callipygius* (Cruz & Peixoto, 1985) (Abrunhosa et al. 2005) and *A. leucopygius* (Zina and Haddad 2006).

Aplastodiscus leucopygius has calls with three harmonics and the dominant frequency can be present in the first, second and third harmonics (Zina and Haddad 2006). The authors observed on two occasions that, when the same male was recorded alone, he emitted the dominant frequency in the third harmonic, but, when recorded in antiphony with another male, he emitted the dominant frequency in the first harmonic (Zina and Haddad 2006). The dominant frequency can transmit information about the male body size and, in most species, this acoustic signal is inversely proportional to the size of the calling male (Wagner 1989, Bee et al 1999, Vilaça et al 2011, Morais et al. 2012). Studies show that larger males vocalize at lower dominant frequencies (Guimarães and Bastos 2003, Toledo and Haddad 2009, Morais et al. 2012) due to the morphological structure of the components of the larynx (Martin 1971). The vibration of the vocal cords, which depends on the size of the individuals, mainly influences the minimum frequency of the calls (Giacoma et al. 1997). This correlation can provide information about the body size of the calling male to other competing males, which avoids physical combat (Bastos et al. 2011). Small males of *Acris crepitans* Baird, 1854, during an experiment with playback, decreased the dominant frequency of their calls (Wagner 1989). Wagner (1992) proposed the hypothesis that males can change the frequency of their calls so their opponents receive wrong information about the emitting male's fighting ability.

Subsequently, Bee et al. (2000) performed playback experiments with *Rana clamitans* Latreille in Sonnini de Manoncourt and Latreille, 1801 and their results support the theory of emission of dishonest signals by the frogs. Thus, the variation in the dominant frequency in the call of *A. albosignatus* may be socially dependent. However, experiments with playback are necessary to evaluate this interaction more precisely.

In general, the size of the males is considered a factor that influences mainly the spectral parameters of the call, such as dominant and minimum frequency (Toledo and Haddad 2009, Vilaça et al. 2011, Turin et al. 2018). It is possible to observe a pattern in which smaller individuals present higher frequencies. Our result may indicate that heavier males invest more energy to emit the advertisement call since the energy costs also depend on the size of the individuals (Gerhardt 1994, Turin et al. 2018). However, in the present study, the variation in spectral parameters was better explained by the body size plus temperature model. This is an interesting result, as air temperature tends to influence the temporal acoustic parameters, while spectral parameters are considered mostly thermally independent among frogs (Navas and Bevier 2001). Nevertheless, there are reports of some contrasting results, of temperature influencing spectral parameters (Ziegler et al. 2016 and references therein), indicating that these patterns are still not fully understood.

Regarding temporal acoustic parameters, the interval between calls was influenced mainly by temperature, as expected according to the literature. The influence of temperature on temporal parameters has been recorded in many anuran species (Lingnau and Bastos 2007, Morais et al. 2012, Boschetti et al. 2019). Temperature has a great influence on the metabolism of amphibians, mainly in acoustic signals affected by active muscle

contraction, which reflects in the amount of energy spent in the emission of the calls (Navas and Bevier 2001, Wells 2010). Regarding call duration, the model that best explained the variation was body size. We can interpret this result as meaning that investing in longer calls can increase male reproductive success through sexual selection. Another possible explanation is that larger males can store larger volumes of air in their lungs, producing positive correlations with temporal parameters (Bernal et al. 2005).

The maximum frequency and the peak frequency of the third harmonic were acoustic signals considered static, that is, they have little variability and mainly affect the quality of the call (Gerhardt 1991). Static acoustic signals are important for species recognition since they tend to remain constant among males (Gerhardt 1991, Márquez and Eekhout 2006). Temporal parameters are usually dynamic factors in relation to intra-individual variation (Tárano 2001). In this study, the call duration and the interval between calls were considered dynamic parameters. Characteristics of the call with wide variation, which are considered dynamic, are important in sexual selection (Gerhardt 1991). Temporal parameters, in general, are more variable than spectral parameters because they tend to be more influenced by changes in ambient temperature and social conditions (Gerhardt and Huber 2002, Wong et al. 2004).

The ratio between CV_{inter} and CV_{intra} indicated that there is greater variation between males than the individual variation itself, as found in other species (Morais et al. 2012, Forti et al. 2017). There are several possible explanations for the variation between males, such as genetic variation, variation in morphology and physiology, and directed sexual selection (Morais et al. 2012). The frequency of the third harmonic and call duration were the acoustic signals with the highest value of the CV_{inter}/CV_{intra} ratio among the analyzed parameters. This may suggest a potential for male identification by females and competing males (Morais et al. 2012, Turin et al. 2018). Temporal parameters, such as call duration, have already been considered important in individual recognition (Gambale et al. 2014, Gasser et al. 2009). Since both parameters are correlated with male size, it is plausible to consider that females can identify larger males from these call features (Turin et al. 2018).

With this work, we have extended the description of the advertisement call of *A. albosignatus*, providing information based on a larger number of males and calls than previously reported in the literature. For *Aplastodiscus*, a similar number of call analyses is available only for *A. arildae* and *A. leucopygius* (Zina and Haddad 2006). Increased knowledge about the variation in advertisement calls contributes to a finer taxonomic delimitation and can provide a basis for hypotheses about the change in acoustic features over time (Castellano et al. 2002). Future efforts should try to obtain recordings of *A. albosignatus* near its type locality, in Paranapiacaba (=Alto da Serra), São Paulo (Werner C. Bokermann, unpublished data), for a better definition of the species' advertisement calls due to the discussions of

Berneck et al. (2016) of a possible new species under this name. Since we notice that both temperature and body size are factors that influence the calls of this species, this should also be taken into strong consideration when comparing the calls of species in the genus *Aplastodiscus*.

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