

REDESCRIPTION OF THE ADVERTISEMENT CALL OF *DENDROPSOPHUS SENICULUS* (COPE, 1868) AND THE CONSEQUENCES FOR THE ACOUSTIC TRAITS OF THE *DENDROPSOPHUS MARMORATUS* SPECIES GROUP (AMPHIBIA: ANURA: DENDROPSOPHINI)

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ABSTRACT. Intraspecific morphological variation has been cited as the main difficulty in species delimitation in the *Dendropsophus marmoratus* species group. However, acoustic characters of the advertisement calls seem to be helpful to establish limits between species of the group. When the advertisement call of *D. nahdereri* was described, questions were raised as to some traits that might be shared with other members of the *D. marmoratus* group. Although six of the eight species recognized for the group have had their advertisement calls described, some of these require revisions due to certain inconsistencies in the original descriptions. Herein the advertisement call of *D. seniculus* is redescribed on the basis of analysis of 143 calls recorded from seven individuals in the Municipality of Silva Jardim, Rio de Janeiro state, Brazil. A physiologically based note definition is used owing to its advantages in recognizing primary homology. Among the novelties reported for the group are: a change in the dominant frequency within the call, the presence of more than two harmonics, and a long, frequency modulated, final pulse. The original description of the call was based on an audiospectrogram with side-bands that was mistakenly interpreted as having too many harmonics and no pulses. Acoustic differences and similarities among the species reinforce the use of this character source in the taxonomy and phylogeny of the group. Because *D. seniculus* is acoustically more similar to *D. soaresi* than to the other species in the group, the phylogenetic relevance of this similarity should be tested.

KEYWORDS. Bioacoustics; Acoustic characters; Taxonomy; Systematics; *Dendropsophus marmoratus* species group.

INTRODUCTION

The *Dendropsophus marmoratus* group is composed of eight species characterized by the presence of a marbled dorsal pattern that mimics bark or lichens, crenulated limb margins, well-developed interdigital membranes, and a large vocal sac (Bokermann, 1964; Faivovich *et al.*, 2005). Several authors have commented on the difficulty of delimiting species in the group (Bokermann, 1964; Heyer, 1977; Caramaschi and Jim, 1983; Gomes and Peixoto, 1996), the primary source of confusion being intraspecific morphological variation in adults and tadpoles (Gomes and Peixoto, 1996). However, acoustic characters of the advertisement calls seem to be helpful to establish limits between members of the group (Orrico *et al.*, 2009).

The advertisement calls of six species of the *D. marmoratus* group (Table 1) have been described as being composed of a single, multipulsed note, in which the call of *D. seniculus*, as described by Bokermann (1967), would differ from those of the remaining species of the group. Given that Bokermann's description is simplistic for today's standards and that his interpretation of the audiospectrogram presented in his paper was flawed (discussed herein and by Orrico *et al.*, 2009), the advertisement call of *D. seniculus* should be reanalyzed. In addition, Márquez *et al.*

(1993) and Orrico *et al.* (2009) reported that in some members of the *D. marmoratus* group, there are two visible harmonics and a final pulse cluster (Orrico *et al.*, 2009). These findings lead us to reanalyze, and re-describe, the call of *D. seniculus* as part of an interpretation of the call characteristics of the *D. marmoratus* group as a whole.

MATERIALS AND METHODS

Calls of *Dendropsophus seniculus* were recorded in an open pasture (22°27'10.20"S; 42°18'6.28"W) in the Municipality of Silva Jardim, Rio de Janeiro state, between 23:15 h and 3:00 h on 28-29 November 2009. Sound recordings were obtained at sample rate of 44.1 kHz and sample size of 16 bits with a Tascam DR-100 digital recorder, coupled to a Sennheiser ME-67 microphone at an air temperature of 22°C. Sound analyses were made with Raven Pro Ver. 1.3 from the Cornell Laboratory of Ornithology (Bioacoustics Research Program). Call parameters measured were: note duration, number of pulses per note, pulse rate, dominant frequency, pulse number in which the change in the dominant frequency occurs, fundamental frequency, and call rate. Numerical call parameters are given as range, followed by mode

TABLE 1. Species of the *Dendropsophus marmoratus* group and the authority for the description of the advertisement call.

| Species | Advertisement call description(s) |
|--|--|
| <i>Dendropsophus acreanus</i> (Bokermann, 1964) | Marquez <i>et al.</i> (1993) |
| <i>Dendropsophus dutrai</i> (Gomes and Peixoto, 1996) | Not described |
| <i>Dendropsophus marmoratus</i> (Laurenti, 1768) | Duellman (1978); Duellman and Pyles (1983); Zimmerman and Bogart (1984); Rodriguez and Duellman (1994) |
| <i>Dendropsophus melanargyreus</i> (Cope, 1887) | Duellman and Pyles (1983); Marquez <i>et al.</i> (1993) |
| <i>Dendropsophus nahdereri</i> (B. Lutz and Bokermann, 1963) | Orrico <i>et al.</i> (2009); Conte <i>et al.</i> (2010) |
| <i>Dendropsophus novaisi</i> (Bokermann, 1968) | Not described |
| <i>Dendropsophus seniculus</i> (Cope, 1868) | Bokermann (1967) |
| <i>Dendropsophus soaresi</i> (Caramaschi and Jim, 1983) | Guimarães <i>et al.</i> (2001) |

(M), mean (\bar{x}), and standard deviation (SD). Temporal parameters were measured from the oscillogram and frequency parameters were measured from the audiospectrogram. We also counted the number of harmonically related frequencies observed in the audiospectrogram and power spectrum. Although these may vary with recording distance and quality, it is important to note their presence when possible (Angulo and Reichle, 2008). Technical terms used follow those of Littlejohn (2001). A note is defined in the sense of McLister *et al.* (1995) on the same basis as did Orrico *et al.* (2009) because this confers advantages in recognizing the primary homology (Robillard *et al.*, 2006; Orrico *et al.*, 2009), thereby facilitating comparisons of the acoustic structures.

We analyzed 18-21 calls in detail for each of seven *Dendropsophus seniculus* voucher specimens; this represents a total of 143 calls in 7 recordings. Sound recordings were deposited in the Arquivo Sonoro Professor Elias Pacheco Coelho (ASEC) of the Laboratório de Bioacústica, Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Brazil. Specimens were killed, fixed, and preserved following the techniques of Calleffo (2002), and deposited at the Coleção de Anfíbios do Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro (ZUF RJ), Brazil. Catalog numbers of specimens and respective sound recordings are: ZUF RJ 11733 (ASEC 16385), ZUF RJ 11736 (ASEC 16386), ZUF RJ 11743 (ASEC 16387), ZUF RJ 11744 (ASEC 16388), ZUF RJ 11745 (ASEC 16389), ZUF RJ 11746 (ASEC 16390), ZUF RJ 11747 (ASEC 16391). Data for other species (not *D. seniculus*) were taken from literature.

RESULTS

Large choruses of *Dendropsophus seniculus* called from the ground and from perches on small shrubs

after heavy rain in open pasture with ponds. The advertisement call is a single, multipulsed note with 35-55 pulses (M = 48; \bar{x} = 47.7; SD = 3.7). The note duration (equivalent to call duration in this case) ranged from 0.257-0.365 s (M = 0.330; \bar{x} = 0.315; SD = 0.029). The amplitude gradually increased until three quarters of the note and sharply decreased until the end, producing a fan-shaped note (Figs. 1A, B oscillograms). This amplitude modulation was accompanied by a slight ascending-descending frequency modulation (Fig. 1A, audiospectrogram). Up to eight harmonics were observed, from the first to ninth, except the seventh, which showed no detectable energy (Fig. 1C). The fundamental frequency ranged from 1,875-2,438 Hz (M = 2,250; \bar{x} = 2,079.5; SD = 166.4). The dominant frequency ranged from 1,875-4,500 Hz (M = 4,125; \bar{x} = 3,968.7; SD = 688.2). Initially, the dominant frequency was the first (fundamental) harmonic which then switched to the second harmonic along the call. This change occurred between the fourth and the twenty-fourth pulse (M = 18; \bar{x} = 13.6; SD = 5.9), corresponding to 7.6-52.0% of the total time of the call (M = 9.1; \bar{x} = 26.3; SD = 12.6). The pulse repetition rate ranged from 127.7-162.8 pulses per second (M = 157.9; \bar{x} = 151.8; SD = 5.9). Frequently (91.6%; 131 calls), the final pulse was longer and had a cyclic amplitude modulation, a short cyclic frequency modulation, and a descending frequency modulation at the end (Fig. 1B). The call repetition rate of the seven specimens ranged from 0.944-1.105 calls per second (M = no value; \bar{x} = 1.013; SD = 0.048).

The general acoustic structure is similar among the calls and individuals. However, the final pulse was highly variable (Fig. 2). Some calls lacked the longer final pulse and its peculiarities (*e.g.*, sudden descending frequency modulation at the end, see Fig. 2, ZUF RJ 11744-45). Others had a longer final pulse but with more (ZUF RJ 11743) or less (ZUF RJ 11746) relative energy (*i.e.*, amplitude, see Fig. 2) and/or more (ZUF RJ 11746) or less (ZUF RJ 11733) frequency modulation (Fig. 2).

DISCUSSION

The call of *Dendropsophus seniculus* described here differs in several aspects from that described by Bokermann (1967), with only the note durations being the same. However, Bokermann's report of 32 visible harmonics and no pulses is certainly a mistake that can be explained by inspection of the audiospectrogram presented in his paper (Bokermann, 1967:

fig. 8), which shows structures that seem to be side-bands (*sensu* Vielliard, 1993), and which Bokermann interpreted as harmonics (see Orrico *et al.*, 2009). The presence of these side-bands results from the reduction of the time-discriminating power of the audiospectrograms, which may even prevent the display of pulses in some cases (Vielliard, 1993; Jackson, 1996).

The variation we found in the longer final pulse seems to be a kind of individual signature, because

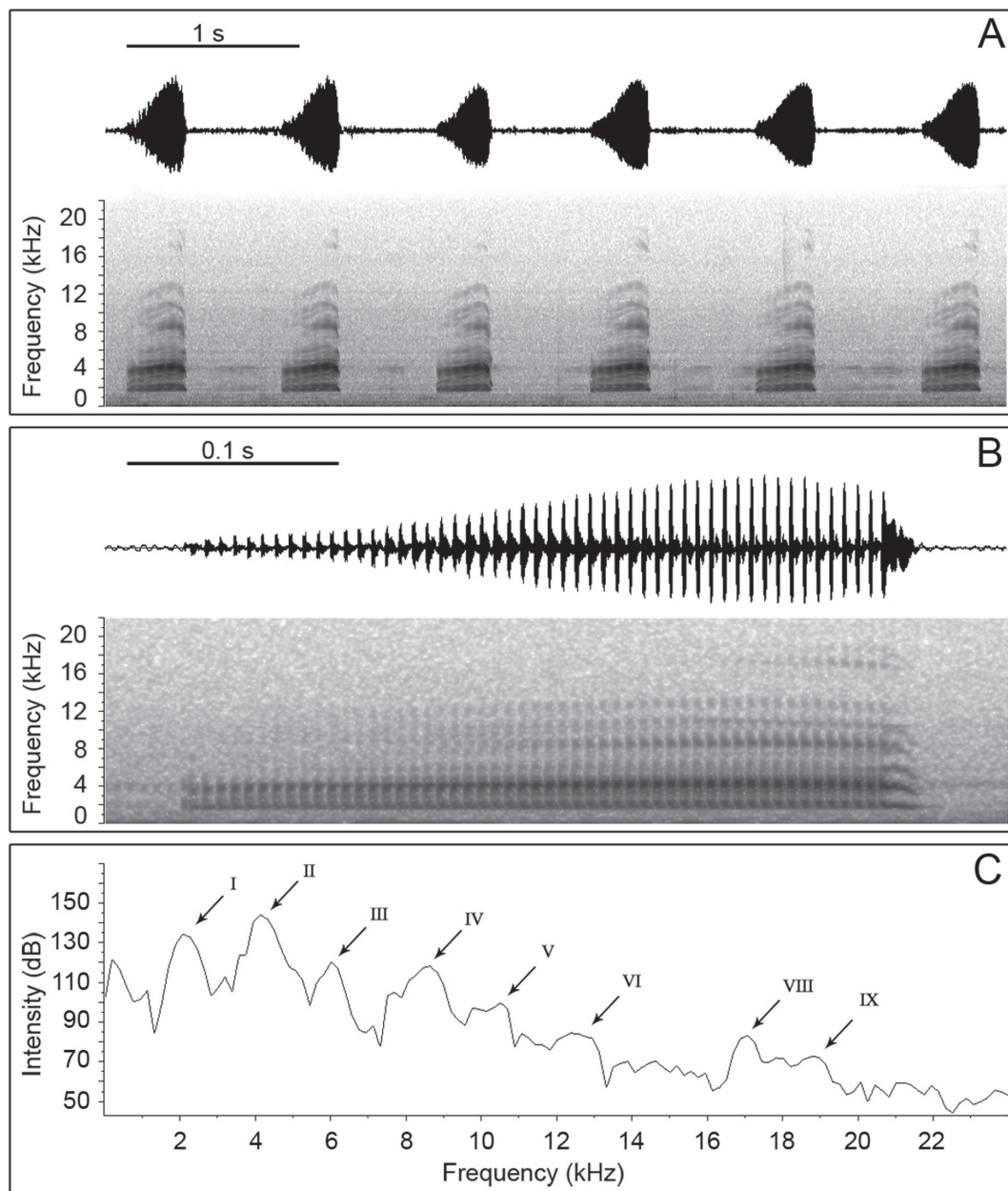


FIGURE 1. Advertisement call of *Dendropsophus seniculus* (ZUF RJ 11747). (A) Six calls, oscillogram above and audiospectrogram below (window function Hann, amplitude logarithmic, window size 512 samples, overlap 99%). (B) One call in detail, oscillogram above and audiospectrogram below (window function Hann, amplitude logarithmic, window size 256 samples, overlap 99%). (C) Power spectrum of a last pulse with harmonics indicated by Roman-numbered arrows (window function Hann, amplitude logarithmic, window size 256 samples, overlap 99%)

individuals with a particular type of final pulse tended to repeat the same structure in other calls. Moreover, some of these particular final pulses, such as a very long final pulse with a pronounced frequency modulation, were present only in one individual (Fig. 2, ZUFRJ 11746). However, we cannot reject the possibility that this variation results from momentary differences in chorus excitement between the calling males.

Call duration, about 0.3 s, is about the same as that of *Dendropsophus acreanus*, *D. melanargyreus*, and *D. soaresi*. It is longer than the notes of *D. marmoratus* and shorter ($\sim 50\%$) than those of *D. nahdereri*.

The fundamental frequencies reported for *Dendropsophus marmoratus* and *D. melanargyreus* apparently are an analytical artifact (Orrico *et al.*, 2009) and are not considered here. The value of the fundamental frequency given by Duellman (1978) might refer to a side-band in his unpublished spectrogram, as in Bokermann (1967). If so, then it is possible that the value of the dominant frequency, in fact, corresponds also to that of the fundamental frequency. The fundamental frequency of the call in the *D. marmoratus* group varies from approximately 1500 to 2500 Hz. and the call of *D. seniculus* has the highest fundamental frequency of the group so far.

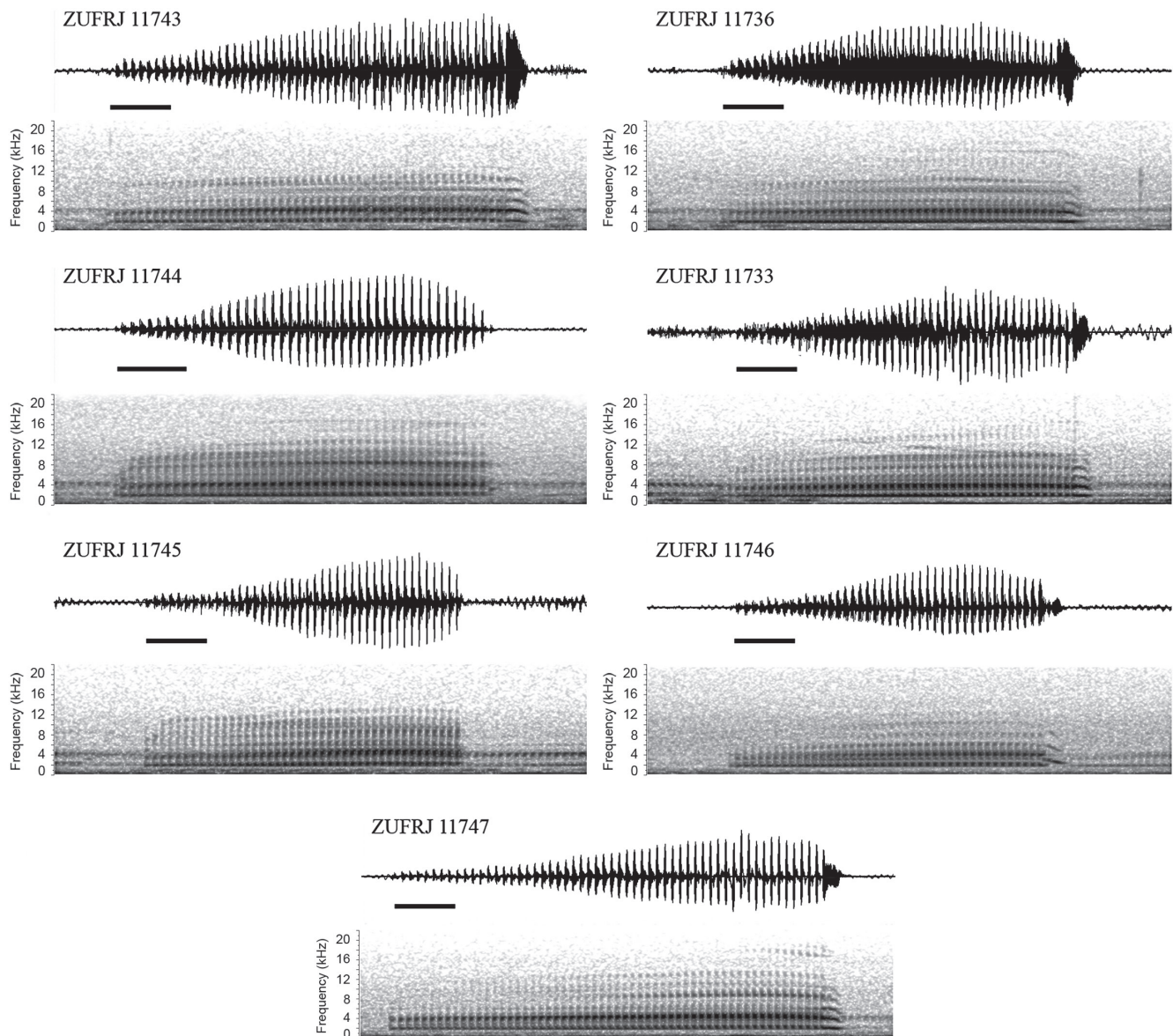


FIGURE 2. Unique calls of the seven individuals of *Dendropsophus seniculus*; oscillograms above and audiospectrograms below (window function Hann, amplitude logarithmic, window size 256 samples, overlap 99%). Scale bars equal 0.05 s. Note the spectral and amplitude variation between the last pulses.

The dominant frequency of *Dendropsophus seniculus* is the highest of the group, and shifts from the first to the second harmonic in the beginning of the call. Although this last feature is difficult to discern from the printed audiospectrogram, it is evidenced by gradual adjustment of brightness and contrast through the sliding controls of the program used for the analysis. This shift seems to occur also in the advertisement call of *D. soaresi* described by Guimarães *et al.* (2001); their audiospectrogram shows an apparent increase in energy in the second harmonic throughout the note and the authors indicate values corresponding to the first two harmonics as the dominant frequency (Guimarães *et al.*, 2001: fig. 8, Table 1). The other species keep more relative energy in only one harmonic; the first harmonic in *D. nahdereri* and possibly *D. marmoratus* (but see problems with description of advertisement call of *D. marmoratus* above) and the second harmonic in *D. acreanus* and *D. melanargyreus*. However, some of the reported differences between species or populations might be mistakes, that arise when the amount of energy in two harmonics is very similar, making it difficult to discern which one represents the dominant frequency (Lingnau *et al.*, 2008; Conte *et al.*, 2010).

The number of pulses is known for *Dendropsophus acreanus*, *D. melanargyreus*, *D. nahdereri*, *D. seniculus*, and *D. soaresi*. All the calls have more than 30 pulses per note as a mean; calls with more than 40 pulses are found in *D. seniculus* and *D. nahdereri*.

Márquez *et al.* (1993), Orrico *et al.* (2009) and Conte *et al.* (2010) pointed out the presence of two harmonics for *Dendropsophus acreanus*, *D. melanargyreus*, and *D. nahdereri*; this is an obvious divergence from the eight harmonics we found for *D. seniculus*. Visible harmonics may vary according to recording distance and quality (Angulo and Reichle, 2008). The fewer harmonics observed by those authors might result from a greater recording distance from the calling males and/or from higher noise intensity relative to our recordings of *D. seniculus*. However, from inspection of the lower contrast audiospectrogram in figure 3 of Orrico *et al.* (2009) it seems that other harmonics, with much lower intensity, might be present above the first two, which concentrate most of the call energy. The same might also apply to the results of Conte *et al.* (2010), in which the high-contrast audiospectrogram and power spectrum with a clipping level set too high, presented in figures 9a and 9c respectively, might be failing to show other but the first two, most emphasized, frequencies. Interestingly, the seventh harmonic was not

observed for *D. seniculus* (Fig. 1C). If it is possible to visualize harmonics above the second in the other species of the group, then the patterns of energy distribution between the highest harmonics should be examined, described, and compared, as well as the other acoustic characters.

The wide variation in the repetition rate of pulses and notes (or calls in this case) in the same species (e.g., *Dendropsophus marmoratus* and *D. melanargyreus*), and the absence of such data in some descriptions, prevent reliable interspecific comparisons. Moreover, the repetition rates are known to vary according to environmental and social factors such as temperature and density of the chorus (Wells, 2007). Thus, the repetition rates can only be compared when these factors are controlled.

Two short notes often appearing at the end of the advertisement call were reported for *Dendropsophus acreanus* (Márquez *et al.*, 1993), as well as final pulse clusters for *D. nahdereri* (Orrico *et al.*, 2009). Orrico *et al.* (2009) suggested that Márquez *et al.* (1993) might be referring to the same structures they termed pulse clusters, and that these might be present in other species of the *D. marmoratus* group. However, isolated final pulse clusters were not found in the call of *D. seniculus*. Instead, there is a longer pulse with cyclic amplitude modulation and frequency modulation at the end of the call. This pulse seems similar to that found in the low-resolution audiospectrogram of Guimarães *et al.* (2001) for the advertisement call of *D. soaresi*, although there is no mention of it in their description.

Orrico *et al.* (2009) proposed that the combination of multipulsed single notes with two harmonics, a low dominant frequency, and a final pulse cluster might be diagnostic for the *D. marmoratus* group within *Dendropsophus*. The absence of pulse clusters and the presence of more than two harmonics in *D. seniculus* preclude this diagnosis. However, all the advertisement calls of the species in the *D. marmoratus* group described are multipulsed single notes with the first two harmonics being those with most energy. *Dendropsophus seniculus* and *D. soaresi* are unique in the group in sharing the following call characters: the longer last pulse with downward frequency modulation, and a shift of dominant frequency from the first to second harmonic. These traits can be acoustic synapomorphies of a clade composed by these species contradicting the “Northeastern semiarid clade” hypothesis of Gomes & Peixoto (1996). However, a complete acoustic revision and a phylogenetic study with acoustic characters of the group is necessary in order to determine the character states in all species

and to test which of these characteristics are indeed synapomorphies for the group.

Acoustic data have been shown to be useful taxonomic characters in many anuran groups (e.g., Angulo and Reichle, 2008; Hepp and Carvalho-e-Silva, 2011). The interspecific acoustic differences in members of the *Dendropsophus marmoratus* group suggest that this data source might be a powerful taxonomic tool in this group. Moreover, acoustic traits are considered as phylogenetically informative as morphological and molecular characters when the primary homologies are well established (e.g., Robillard *et al.*, 2006). The presence of patterns of acoustic similarity among members of the *D. marmoratus* group suggests that acoustic characters may be informative in phylogenetic studies.

RESUMO

A variação morfológica intraespecífica tem sido citada como a principal dificuldade na delimitação das espécies do grupo *Dendropsophus marmoratus*. Contudo, caracteres acústicos dos cantos de anúncio parecem ser úteis para ajudar a estabelecer limites entre as espécies desse grupo. A descrição do canto de anúncio de *D. nahdereri* levantou questões quanto a algumas características que podem ser compartilhadas com outros membros do grupo *D. marmoratus*. Embora seis espécies das oito reconhecidas para o grupo tenham seu canto de anúncio já descrito, algumas necessitam de reanálise devido a certas inconsistências nas descrições originais. Aqui o canto de anúncio de *D. seniculus* é redescrito com base na análise de 143 cantos de sete indivíduos gravados no município de Silva Jardim, Rio de Janeiro, Brasil. Uma definição da nota com base fisiológica é utilizada devido às suas vantagens no reconhecimento de homologia primária. Entre as novidades encontradas para o grupo estão: mudança na frequência dominante ao longo do canto; presença de mais de dois harmônicos; e um último pulso longo e com frequência modulada. A descrição original do canto baseou-se em um audio-espectrograma com bandas-laterais (*side-bands*) que foi enganosamente interpretado como apresentando um número excessivo de harmônicos e ausência de pulsos. Diferenças acústicas e semelhanças entre as espécies reforçam o uso desta fonte de caracteres na taxonomia e filogenia do grupo. *Dendropsophus seniculus* é acusticamente mais parecida com *D. soaresi* do que com as outras espécies do grupo e a relevância filogenética dessa semelhança deve ser testada.

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