



# Are good fighters also good singers? The relationship between acoustic traits and fight success in the treefrog *Pithecopus nordestinus* (Phyllomedusidae)

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## Abstract

Morphological characteristics are known to be important predictors of victory in aggressive disputes in the animal world. Among anurans, however, acoustic communication also plays an important role in intraspecific conflicts. Although there is evidence for the influence of spectral parameters of calls (e.g., fundamental and dominant frequencies) in anuran disputes, the role that temporal parameters (e.g., duration and repetition rate) play in success during physical conflicts is still poorly understood. We describe the behavior of male frogs in agonistic interactions and investigate the functions of the different types of calls emitted in different social contexts. We also evaluate how body characteristics (mass and body size) and bioacoustic characteristics (repetition rate of the calls) influence success in physical conflicts of *Pithecopus nordestinus* (Anura: Phyllomedusidae). Agonistic disputes involved gradation in the emission of calls, visual displays, and physical clashes. The fighting call increased in proportion during clashes, indicating a function associated with aggression/intimidation. The uneasiness call (new subcategory herein defined) was only performed by losers during physical clashes, suggesting a meaning of submission or restlessness. No differences were found in any of the morphological parameters between winners and losers of physical disputes. On the other hand, the repetition rate of the aggressive call was positively related to success in fights and proved to be a good predictor of success in fights between males of *P. nordestinus*. Our results contribute to understanding the influence of temporal parameters of calls on success in physical disputes of this Neotropical treefrog.

**Keywords** Anura · Caatinga · Aggressive call · Agonistic dispute · Physical clashes · Acoustic interactions

## Introduction

Agonistic interactions are behaviors related to confrontations between individuals involving not only physical clashes but also threatening and submissive attitudes among rivals (Scott and Fredericson 1951; Briffa and Hardy 2013). Confrontations can be gradual in intensity, usually having physical clashes as a last resort (Arnott and Elwood 2009;

Reichert and Gerhardt 2011). The resolution of confrontations is usually accompanied by direct or indirect benefits to the winners, such as the possession of breeding sites and females for mating (e.g., birds, amphibians and wasps; Webster and Robinson 1999; Martins et al. 1998; Dunn et al. 2014). Agonistic disputes, however, also entail costs, such as high-energy expenditure and greater vulnerability to predators and parasites (Hamilton and Zuk 1982). Thus, performance in these disputes can positively or negatively affect individual aptitude (*fitness*) (Hosken and House 2011).

An important predictor of victory in agonistic disputes is asymmetry between competitors (Parker 1974). Such differences are mainly based on the ability to fight (resource holding potential (RHP)) and on the value of disputed resources (e.g., Bergman et al. 2010; Lopes and Peixoto 2013). In disputes involving physical contact, morphological characteristics that confer strength or ability to cause and sustain injuries, such as mass, body size, and size of ornaments used in fights, are among the main predictors of success (Marden and Waage

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1990; Vieira and Peixoto 2013). However, even with physical contact, it is possible that success in agonistic interactions is not associated with morphological characteristics (Wogel et al. 2002; Jones et al. 2011), but in asymmetries in the motivation or resistance of competitors (e.g., amount of energy reserves) (Krebs 1982; Marden and Waage 1990; Vieira and Peixoto 2013).

Even though the calling activity of anurans involves high energy expenditure (Taigen and Wells 1985; Grafe 2005), it plays a relevant role in several social contexts, sometimes incorporating different types of calls (Wells 1977; Hödl and Amézquita 2001; Grafe 2005). In intersex interactions, the advertisement call is an important tool for mating, acoustic emissions of high-energy expenditure being potentially related to a greater capacity to attract females (Taigen and Wells 1985; Ryan 1998; Tárano and Herrera 2003). In intrasex interactions, calls can act in the defense and maintenance of territories and in providing information about the quality and aggressiveness of rivals (Wells 1988; Reichert and Gerhardt 2011; Osiejuk and Jakubowska 2017). In the case of changes in the social context, such as the proximity of rivals (Wells 1988; Reichert and Gerhardt 2011), males can respond acoustically with the emission of aggressive calls and by increasing their repetition rate, duration, and intensity (Márquez et al. 2001; Bastos et al. 2011). Although the emission of calls is widely known to be an intermediary of agonistic interactions between anurans (reviews in Wells 1988; Wells and Schwartz 2006; Dyson et al. 2013), there remain many gaps in the knowledge of the subject. For example, it is known that spectral parameters (e.g., dominant frequency) of calls can influence success in agonistic disputes between males (e.g., Reichert and Gerhardt 2013), as well as the attitude of moving forward or backward in response to playbacks (Arak 1983). However, the influence of temporal parameters of calls (e.g., call duration and number of pulses; Burmeister et al. 2002) on success in disputes involving physical contact is little known (Wells 2007; Dyson et al. 2013). Acoustic parameters of calls can be closely associated with morphological attributes (e.g., Guimarães and Bastos 2003), thus constituting honest signals of the fighting ability of individuals (Bee et al. 2016). For example, the dominant frequency of calls is commonly related to male body attributes (e.g., Giasson and Haddad 2006) and is therefore considered an important predictor of quality for rival males (Arnott and Elwood 2009).

In this work, we evaluated in situ the influence of morphological and bioacoustic characteristics on success in physical disputes between males of the Neotropical treefrog *Pithecopus nordestinus* (Anura: Phyllomedusidae). Our specific objectives were to: (1) describe the behavior of males during agonistic interactions; (2) investigate the functions of the different types of calls of the species in different social contexts; (3) evaluate the effects that morphological characteristics have on success in physical clashes, with the

prediction that males with greater body size (mass and body length) will be more successful; and (4) evaluate the influence of acoustic parameters on success in physical clashes, expecting that victory would be positively related to the emission of acoustic signals (call repetition rate).

## Material and methods

### Model and study area

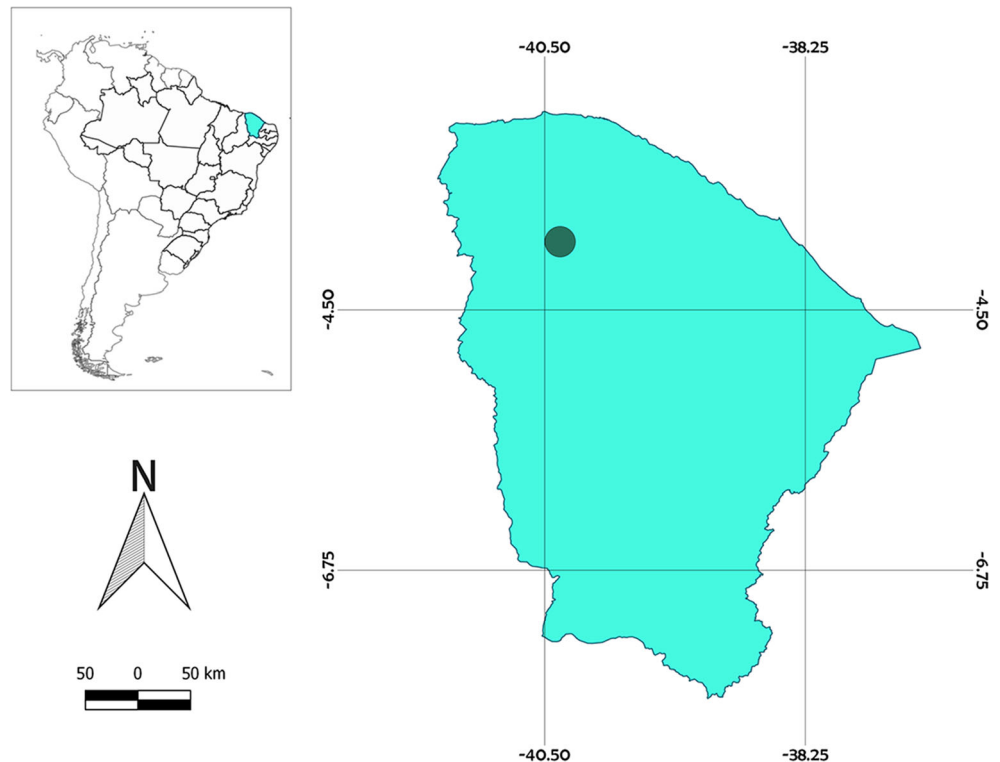
*Pithecopus nordestinus* (Caramaschi 2006) is an anuran of the family Phyllomedusidae that is widely distributed in Northeast Brazil (Caramaschi 2006; Borges-Leite et al. 2014; Santana et al. 2015; Ferreira-Silva et al. 2016). The species is arboreal and uses herbs and shrubs for vocalization (Caldas et al. 2016). Males of *P. nordestinus* vocalize in reproductive aggregations and engage in agonistic interactions using calls and physical attacks (Vilaça et al. 2011; Caldas et al. 2012). The species exhibits a vocal repertoire composed of at least three types of calls: an advertisement call and two “territorial” calls (the adequacy of this concept is discussed later). “Territorial call I” is generally issued in aggressive contexts (Vilaça et al. 2011), but when issued during physical clashes, it has been suggested that it be called a fighting call (see Toledo et al. 2014). “Territorial call II” is usually performed in aggressive circumstances (suggested as a release call by Mângia et al. 2019), but as it is also emitted during handling by researchers, it can be considered a type of distress call (Vilaça et al. 2011).

The study was carried out in the municipality of Groaíras (Fig. 1) in the state of Ceará in Northeast Brazil. The mean temperature of the region varies between 26 and 28 °C, the climate is tropical hot semi-arid, and the mean annual rainfall is 904.5 mm, with rains concentrated from January to April (IPECE 2016). Data were collected at four bodies of water: two dams (reservoirs) and two temporary ponds at the localities of Itamaracá (3° 52' 04.2" S, 40° 22' 11.9" W and 3° 51' 49.7" S, 40° 22' 16.5" W) and Lagoa do Peixe (3° 56' 19.5" S, 40° 23' 39.2" W and 3° 56' 18.2" S, 40° 23' 17.3" W), separated from each other by a distance of at least 500 m. The banks of the bodies of water had predominantly herbaceous and shrubby vegetation with some individual plants of arboreal size.

### Data collection

Sampling was carried out between February and May 2017, during the rainy season, when the species reproduces and vocally active males are easily found. Most of the sampling was performed between 18:00 and 00:00 hours (70% of the observations), a period of time that encompasses most of the

**Fig. 1** Location of the municipality of Groaíras (point), in the state of Ceará (colored), Northeast Brazil



vocal activity of the species (Ferreira-Silva et al. 2016). The rest of the sampling occurred during the early hours of dawn (between 05:25 and 07:30 hours), when agonistic disputes were also recorded. In all, the sampling effort totaled 218 h-person of activity in the field. Observations of target individuals were made from about 1 m away, and their behaviors were recorded audio-visually (Sony DSC HX200v and Canon SX50) for a total of 10 h of video-sampling. This audiovisual database was housed in the Coleção Audiovisual do Semiárido (CASA) (voucher numbers CASA 055–CASA 110) at the Universidade Federal Rural do Semi-Árido (UFERSA). A time of habituation was taken prior to the beginning of recording observations to ensure that the individuals were not changing their behavior due to the presence of observers (the time was around 5 min, except for disputes in progress). At the end of agonistic disputes, the target individuals were manually captured and measured for mass with a scale (0.01 g resolution) and snout-vent length (SVL) with a caliper (0.1 mm resolution). After the measurements, the flank region of each individual was photographed to allow identification of individual specimens so as to avoid pseudoreplication (Lima-Araújo et al. in prep; Oliveira et al. 2012; Oliveira 2017). The individuals were then released at the site of capture.

To evaluate visual exhibitions associated with agonistic behaviors, we identified visual signals, taking into account redundant, conspicuous and stereotyped movements (limb movements and different body postures), and classified them

based on descriptions available in the literature (Hödl and Amézquita 2001; Hartmann et al. 2005; Sá et al. 2016). We counted the frequency of visual displays performed by individuals in each social context based on the distance between individuals (< 50 or > 50 cm) and the stage of dispute (before or during physical contact). In order to evaluate the function of *P. nordestinus* calls, we recorded the proportion in which each type of call (advertisement call, “territorial call II”, and “territorial call I”) was emitted in different social contexts (before or during physical contact). We also calculated the repetition rate of each call type (number of calls per minute) emitted during fights.

For purposes of definition, we considered physical clashes as agonistic interactions involving direct physical contact between rivals (Reichert and Gerhardt 2011). We considered losers of a physical clash to be individuals that exhibited at least two of the following behaviors: (1) flee from the area of the clash; (2) adopt a submissive (see Body lowering in Table 2; Fig. 3d) posture inside or outside the place of the clash; (3) do not vocalize after the physical clash (advertisement call or “territorial call I”). We considered winners individuals who exhibited at least two of the following behaviors: (1) remain in the area of combat immediately after the clash; (2) do not maintain a submissive posture after the clash and (3) vocalize after the clash (advertisement call or “territorial call I”). When both combatants had two characteristics associated with victory, a third characteristic was considered to be the tiebreaker.

## Statistical analyses

We compared morphological (mass and SVL) and acoustic (repetition rates of advertisement call, “territorial call I”, and “territorial call II”) between winning and losing males of physical clashes by logistic regression. We also performed Spearman correlations to evaluate the association between the repetition rate of calls (in calls per minute for advertisement call, “territorial call I”, and “territorial call II”) and the morphological variables (mass and SVL). We used chi-square tests with Yates correction to compare the proportions of the different types of vocalizations (advertisement call, “territorial call I”, and “territorial call II”) of winning and losing males between the contexts of prior to and during fights. We conducted all statistical analyses in R software v.3.4.3 (R Core Team 2017), with a significance level of  $\alpha = 0.05$  and provide descriptive statistics as mean  $\pm$  standard deviation (minimum–maximum).

## Results

### Behaviors of winners and losers

We analyzed a total of 30 agonistic disputes between males. The duration of the physical clashes ranged from 5 s to 20 min ( $3.67 \pm 5.4$  min,  $N = 30$ ). Of the total number of clashes sampled, observations of 53% ( $N = 16$ ) began before the start of the physical dispute and 47% ( $N = 14$ ) began during the course of fights. Of the physical disputes observed prior to the start, five (31.3%) involved two vocalizing males and eight (50%) involved one vocal and one silent male (Fig. 2). It was not possible to determine if males were vocalizing prior

to the beginning of the fights in the other three (18.7%) disputes.

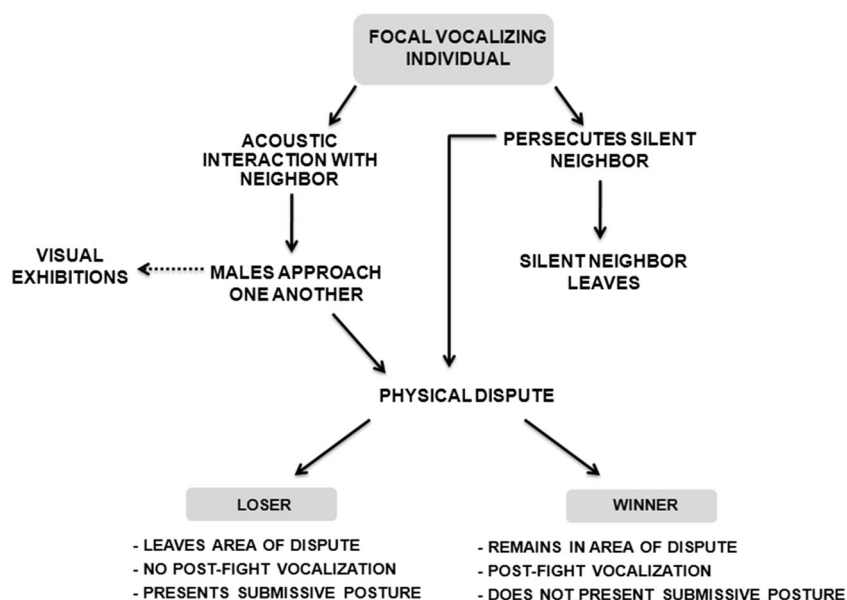
It was possible to define winning and losing males in 28 of the 30 clashes analyzed. All males that won agonistic disputes called and posed erect after physical clashes. The majority (82.1%,  $N = 23$ ) of the winning males remained at the scene of the dispute after the fighting ended. On the other hand, the majority (75%,  $N = 21$ ) of losing males withdrew from the place where the combat took place after the dispute with the rival. Among the losers that remained at the scene of the fight (25%,  $N = 7$ ), all exhibited a submissive posture at the end of the dispute. Only 14.3% ( $N = 4$ ) of the losing males called after the fight, but in these cases, the vocalizations occurred after leaving the site of the clash (Table 1).

Four different types of visual displays were recorded in the presence of rivals ( $N = 24$  individuals). In body raising, the body was raised with the extension of the four limbs, raising the belly from the ground (Fig. 3a). Leg kicking consisted of stretching and rapidly replacing the hind leg in a similar movement to a kick (Fig. 3b). Body jerking consisted of an abrupt forward movement of the body, without removing the front legs from the ground, and then returning to the initial posture (Fig. 3c). The movements body raising, leg kicking, and body jerking were always carried out at a distance of less than 50 cm from the rival. Body lowering consisted of lowering the abdomen completely onto the substrate, with head and limbs usually close to the body (Fig. 3d). These visual displays were often accompanied by acoustic signals (Table 2).

### Different types of calls and their social contexts

The proportion of different calls emitted by males in the contexts of prior to and during physical clashes was obtained from

**Fig. 2** Sequence of events that encompassed the formation and conclusion of physical disputes between males of *Pithecopus nordestinus*. Dashed arrows indicate that the visual displays may have occurred prior to the physical disputes



**Table 1** Combinations of behaviors associated with victory or defeat in physical clashes between males of *Pithecopus nordestinus* and the frequency at which they were observed ( $N=28$  physical clashes)

Combination of criteria	Status	Percentage	Number
Stay+call+erect	Winner	0.41	23
Exit+call+erect	Winner	0.09	5
Stay+no call+submission	Loser	0.13	7
Exit+call+erect <sup>a</sup>	Loser	0.07	4
Exit+no call+erect	Loser	0.05	3
Exit+no call+submission	Loser	0.09	5
Exit+no call	Loser	0.16	9

*Stay*, remain in the place of the fight after the clash; *Exit*, withdraw from the place where the clash occurred; *call*, vocalize after the fight; *no call*, keep silent after the fight; *submission*, abdomen near the substrate, limbs usually close to the body; *erect*, abdomen away from the substrate, limbs never arranged close to the body

<sup>a</sup> Although with two criteria of victory, these males were considered losers because their rivals remained in the area of the fight, while these left the area

the analysis of the emission of calls prior to agonistic disputes ( $N=15$  males) and of the calls emitted during physical disputes ( $N=39$  males). The samples of contexts preceding physical disputes had a duration of  $3.4 \pm 1.75$  min, while the samples of contexts during physical clashes lasted  $4.7 \pm 4.4$  min. The proportion of different types of emitted calls varied between the different social contexts (Fig. 4). The emission of advertisement calls diminished between before (winners, 48%,  $N=8$ ; losers, 53.6%,  $N=7$ ) and during (winners, 16.3%,  $N=19$ ; losers, 0%,  $N=20$ ) physical contact in fights, both for male winners ( $X^2=16$ ,  $df=1$ ,  $P<0.001$ ) and losers ( $X^2=54$ ,  $df=1$ ,  $P<0.001$ ). On the other hand, the emission of “territorial call I” by winning males increased from 52% ( $N=$

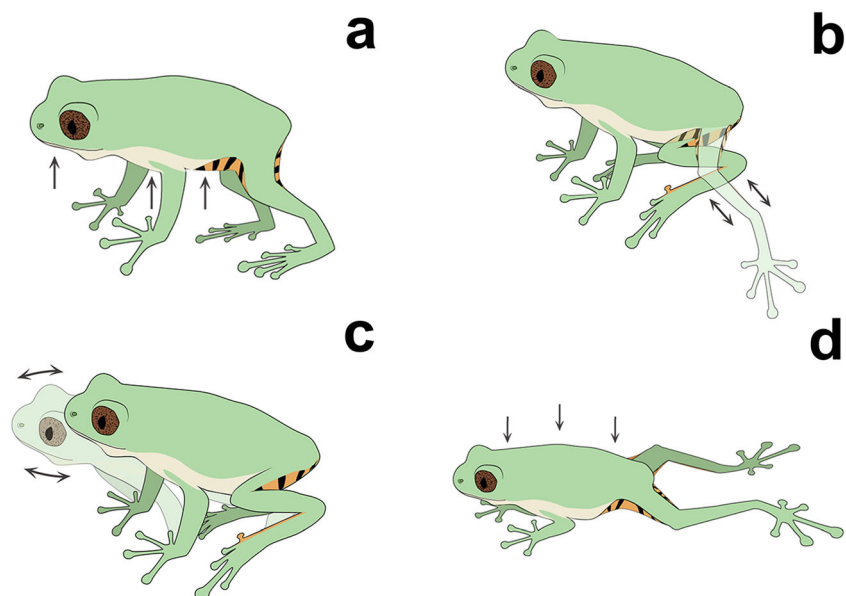
8) before the disputes to 83.7% ( $N=19$ ) during fights ( $X^2=321.23$ ,  $df=2$ ,  $P<0.001$ ) but decreased from 46.4% ( $N=7$ ) to 22.1% ( $N=20$ ) among loser males ( $X^2=8.47$ ,  $df=1$ ,  $P=0.004$ ). “territorial call II” was only emitted by male losers during physical clashes (83.3% of the events) and was not issued by male winners in any context. There was no significant difference in the proportions of emission of the advertisement call and “territorial call I” between winning and losing males prior to fights ( $X^2=0.32$ ,  $df=1$ ,  $P=0.6$ ). During fights, the advertisement call was not emitted by loser males but accounted for 16.3% of the calls emitted by winners. “territorial call I” corresponded to 83.7% of the calls emitted by winners and 22.1% of the calls emitted by losers during fights ( $X^2=36.3$ ,  $df=1$ ,  $P<0.001$ ; Fig. 4).

### Predictors of winners of fights

Mass and SVL of winning ( $N=27$ ) and losing ( $N=25$ ) males were obtained from the analysis of 28 physical fights. The mass of winners averaged  $1.64 \pm 0.2$  g ( $1.29-2.05$ ,  $N=27$ ) and that of losers  $1.63 \pm 0.2$  g ( $1.24-2.05$ ,  $N=25$ ). There was no influence of mass (Coef=0.11, SE=1.4,  $P=0.94$ ,  $N=52$  individuals) on success in physical disputes. The SVL for winners averaged  $3.17 \pm 0.1$  cm ( $2.9-3.46$ ,  $N=27$ ) and of losers  $3.18 \pm 0.1$  cm ( $2.9-3.4$ ,  $N=25$ ). There was also no influence of SVL (Coef=0.75, SE=2.22,  $P=0.73$ ,  $N=52$  individuals) on success in agonistic disputes.

The repetition rate of calls of winning ( $N=19$ ) and losing ( $N=20$ ) males were obtained from the analysis of 20 physical disputes. The repetition rate of the advertisement call during physical disputes averaged  $1.31 \pm 1.65$  calls  $\text{min}^{-1}$  ( $0-4.5$  calls  $\text{min}^{-1}$ ) for winners. This call was not issued by losing males. The repetition rate for “territorial call I” emitted during physical

**Fig. 3** Visual exhibitions performed by males of *Pithecopus nordestinus*. Arrows pointed in a single direction indicate unique, non-repeated movements (**a**, **d**). Arrows in opposite directions indicate fast and repeated movements (**b**, **c**). **a** body raising; **b** leg kicking, **c** body jerking, **d** body lowering





**Table 2** Context of visual exhibitions performed by males of *Pithecopus nordestinus*, mean number of exhibitions per individual, and association of exhibitions with the different types of calls

Exhibition		Number	Calls	N
Body stationary				
Body raising	During vocal interaction or at the end of physical clashes, over male in lowered posture (body lowering).	Single movement	Ter I, An	2
Body lowering	At the end of physical clashes, under the male in erect posture (body raising), or after escaping physical disputes.	Single movement	–	11
Body moving				
Body jerking	Before physical clashes or over male in lowered posture (body lowering).	4 ± 1.94 (1–8)	Ter I	9
Leg kicking	During vocal interaction or at the end of physical clashes over male in lowered posture (body lowering).	4.3 ± 4.04 (2–9)	Ter I, An	3

Ter I, “territorial call I”; An, advertisement call; N, number of individuals that performed the movement

disputes averaged  $7.87 \pm 7.32$  calls  $\text{min}^{-1}$  (0–22.5 calls  $\text{min}^{-1}$ ) for winners and  $1.12 \pm 2.93$  calls  $\text{min}^{-1}$  (0–10.7 calls  $\text{min}^{-1}$ ) for losers. There was a positive influence of the repetition rate of “territorial call I” on success in agonistic interactions (Coef = 0.27, SE = 0.09,  $P < 0.01$ , Fig. 5). The repetition rate of “territorial call II” during agonistic disputes averaged  $15.69 \pm 20.7$  calls  $\text{min}^{-1}$  (0–66 calls  $\text{min}^{-1}$ ) for losers. This call was not emitted by winning males. There was no correlation between the repetition rate of calls emitted during fights and mass (advertisement call  $\rho = 0.04$ ,  $P = 0.81$ ; “territorial call I”  $\rho = 0.09$ ,  $P = 0.59$ ; “territorial call II”  $\rho = -0.05$ ,  $P = 0.78$ ) or SVL (advertisement call  $\rho = -0.11$ ;  $P = 0.51$ , “territorial call I”  $\rho = -0.1$ ,  $P = 0.55$ ; “territorial call II”  $\rho = 0.19$ ,  $P = 0.26$ ).

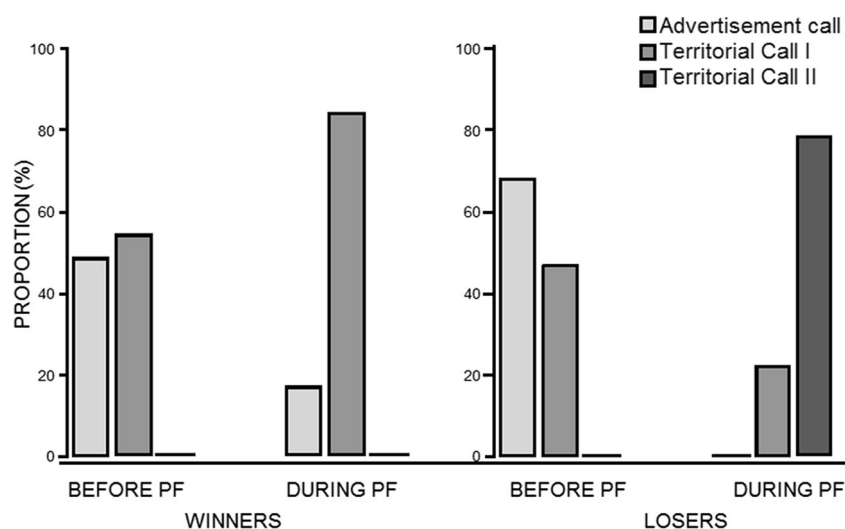
## Discussion

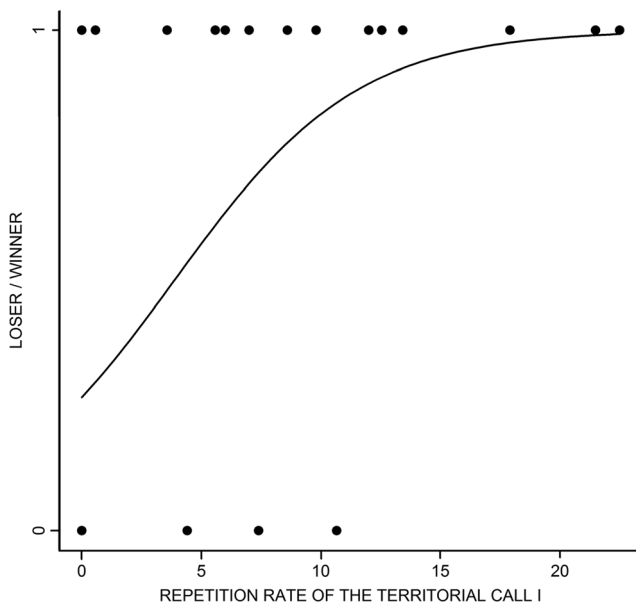
### Visual displays in agonistic disputes

Agonistic disputes between males of *P. nordestinus* included acoustic interactions, visual displays and physical fights.

Anuran fights can progress through levels of aggression and advance from advertisement calls emitted in antiphony between neighbors, to the emission of aggressive calls, the display of visual signals (in species that perform this behavior) and even culminate in physical fights (Wogel et al. 2004; Reichert and Gerhardt 2011). The results presented here record for the first time the occurrence of the visual signals body raising, body jerking, and leg kicking for a Phyllomedusidae species, thus indicating that their occurrences may be more extensive in the evolutionary history of anurans. Those displays were recorded predominantly in short-distance interactions between rivals and prior to physical fights and have previously been linked to aggressive contexts for other anurans (e.g., *Hylodes asper*, *Boana albomarginata*, *H. dactylocinus*, *H. pyllodes*, *Dendropsophus werneri*, and *Crossodactylus schmidtii*—Hödl and Amézquita 2001; Hartmann et al. 2005; Narvaes and Rodrigues 2005; Toledo et al. 2007; Miranda et al. 2008; Caldart et al. 2014). Leg stretching is the most commonly recorded visual display in an aggressive context for species of the family Phyllomedusidae (e.g., *Phyllomedusa sauvagii*, *P. boliviana*,

**Fig. 4** Proportion of calls emitted (advertisement call, “territorial call I,” and “territorial call II”) by males (winner and losers) of *Pithecopus nordestinus* before and during physical fights. BEFORE PF, before physical fighting; DURING PF, during physical fighting





**Fig. 5** Relationship between success in physical fights and repetition rate (calls  $\text{min}^{-1}$ ) of “territorial call I” in males of *Pithecopus nordestinus*. Value 1 was assigned to winners and 0 to losers. Six winners and seventeen losers did not emit this kind of call (points overlaid on the graph). The line represents the trend based on expected values by a logistic regression model

and *P. iheringii*—Halloy and Espinoza 2000; Jansen and Köhler 2008; Dias et al. 2017) but was not performed by *P. nordestinus*.

In particular, the behavior of lowering the body, similar to the posture described for body lowering, has been previously recorded for *P. nordestinus* and is performed by males that are physically attacked by conspecifics (Vilaça et al. 2011). This posture may indicate submission to the rival (Hartmann et al. 2005), and the association with other behaviors observed in the present study (e.g., not singing and leaving the site of the fight) reinforces this interpretation, demonstrating that this behavior may be indicative of defeat in physical fights, being exhibited by 43% of the losing males. The description of visual displays for *P. nordestinus* generates a more integrated knowledge of the elements that compose agonistic disputes, and support for investigations focused on the importance of visual signaling in social interactions of this species.

### Functions of the different types of calls

The “territorial call I” was emitted most often by winning *P. nordestinus* males during fights (composing 83.7% of all calls emitted by winning males and 22.1% of calls by losing males). Field observations suggest that the issuance of “territorial call I” is influenced by the distance between rivals. In contexts in which target males were more than 0.5 m away from a rival, “territorial call I” constituted only 10% of the emissions (90% were the advertisement call). These data reinforce the aggressive function suggested for this call.

Gradations in aggressive calls occur by modifying, usually increasing, temporal parameters of the call, such as the number of notes and repetition rate, and less frequently, by spectral parameters, such as dominant frequency (Morais et al. 2012; Reichert and Gerhardt 2013). In fact, investment in altering these temporal parameters of calls usually increased with reduced distance between rival males or in response to the emission of calls by conspecifics (Osiejuk and Jakubowska 2017). If the advertisement call has the primary function of attracting females for mating in *P. nordestinus*, and if aggressive calls are less attractive to females (Wells and Schwartz 2006), then there must be a *trade-off* between attracting females and repelling males in the vocal activity of males *P. nordestinus*. The findings of the present study support this idea since the proportion of aggressive call emission (“territorial call I”) increases during fights and decreases with increasing distance between rival males.

Considering that the function of the so-called “territorial call I” was demonstrated to be independent of the establishment of territories between rival males, and that the use of the term “territorial” should be applied only in situations of clear defense of territories and not in any aggressive context, especially for species where there is no evidence of the establishment of territories (Wells 2007; Toledo et al. 2014), we strongly recommend changing the nomenclature of “territorial call I” of *P. nordestinus* to only aggressive call or, specifically, fighting call when emitted during fights and encounter call when preceding fights, in the context of a small distance between males. Inconsistencies in the use of names can lead to great problems with interpretation (Toledo et al. 2014), especially when applied by non-specialists of the study model, such as in behavioral research, for example. These results contribute to understanding the functions of the aggressive calls of *P. nordestinus*, as the present study broadened information about the contexts of use of each type of call.

“Territorial call II” of *P. nordestinus* in the studied area was also associated with aggressive interactions among males, as previously reported for another population (Vilaça et al. 2011). However, we observed that this vocalization was emitted predominantly by disadvantaged males during physical disputes. The literature reports that this call can be emitted during handling by researchers, and thus can be considered a type of distress call (Vilaça et al. 2011); however, it can also be emitted when a male is inappropriately clasped by another male, and thus can be considered a release call (Mângia et al. 2019). These contrasting findings suggest that the term “territorial call II” is not the most adequate since there is no evidence that it is directly associated with territorial defense. Moreover, since the previous studies did not evaluate the entire behavioral context of emissions, as done in the present study, we suggest a new subcategory for this call. We recommend the term uneasiness call (when the individual is in discomfort or in an unpleasant context) as a substitute for

“territorial call II”, since it was exclusively emitted by loser males in contexts of submission. Therefore, the evidence of the present study reinforces the need to evaluate the specific contexts in which calls not directly associated with reproduction are emitted (aggressive and defensive calls sensu Toledo et al. 2014) for a better understanding of the specific signals transmitted by them.

### Predictors of success in agonistic interactions

There was no influence of mass or body size on success in agonistic disputes between males of *P. nordestinus*, similar to what had been observed by Vilaça et al. (2011) for another population of *P. nordestinus* in the Atlantic Forest. In disputes involving physical contact, body traits associated with strength or ability to cause damage are more commonly related to success in fights (e.g., Vieira and Peixoto 2013). However, Vilaça et al. (2011) suggested that *P. nordestinus* prioritized vocalization in detriment of physical attacks in agonistic disputes, justifying the low number of physical confrontations recorded by them ( $N=4$  physical disputes). The results of the present study are based on a much more representative sampling ( $N=30$  physical disputes) and reinforce the idea that the emission of acoustic signals was more closely associated with success in agonistic interactions than body characteristics of males. In this sense, it is known that when damage inherent to agonistic disputes is not associated with the capacity to cause injury (e.g., aggressive disputes without physical contact), the combat decision may be related to resistance asymmetry (e.g., quantity of energy reserves) or motivation of competitors, due to, for example, the value of disputed resources (Krebs 1982; Marden and Waage 1990; Vieira and Peixoto 2013). For anurans, an interesting perspective would be to evaluate whether differences in resistance (e.g., due to the amount of energy reserves) are associated with calling activity and, consequently, how the relationship between acoustic signal emission, energy expenditure and motivation help explain victory or defeat in fights.

The present study reports a positive relationship between repetition rate of the fighting call and success in physical disputes. The relationship between temporal parameters of calls and success in physical attacks is still little investigated compared with similar studies with spectral parameters of calls (Giasson and Haddad 2006; Bastos et al. 2011; Reichert and Gerhardt 2013). Regarding the influence of temporal parameters on success in fights, Burmeister et al. (2002) did not find a relationship between temporal parameters (e.g., call length and number of pulses) and the attitude of attacking an intruder or abandoning an agonistic dispute. The literature reveals, however, that males in acoustic interactions without physical contact can change acoustic parameters of their calls, such as increasing the duration and number of notes, as a sign of increased aggressiveness or of presenting attributes of the

ability to fight against rivals (review in Bee et al. 2016). A greater effort in these attributes, however, can generate a higher-energy expenditure (Wells 2007). Some hypotheses suggest that maintaining costly features may be a sure sign of the quality of individuals (Zahavi 1975; Hamilton and Zuk 1982). Thus, if the emission of certain acoustic signals is considerably onerous, it may be an important signal of the quality of the individual. In animal disputes, however, it is possible that other characteristics, independent of body attributes or onerous signals (e.g., hierarchy, residence; Senar et al. 1989; Wogel et al. 2002; Wogel et al. 2004), are related to success in fights (Krebs 1982; Carvalho et al. 2016). The present research revealed that most of the interactions analyzed (83.7%) were between vocal and silent males (or males that only emitted uneasiness calls, indicative of submission), with vocal males as winners. In this way, investigating asymmetries in fighting ability and motivation contributes to a more solid understanding of the reasons for success in physical fights. Thus, we corroborate the hypothesis that success in physical fights of *P. nordestinus* is positively related to the emission of acoustic signals (fighting call), thus contributing to fill an important knowledge gap regarding the influence of temporal parameters of calls on the success of physical disputes in anurans.

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### Compliance with ethical standards

**Ethical approval** All national guidelines applicable to the care and use of animals were followed.

**Conflict of interest** The authors declare that they have no conflict of interest.

### References

- Arak A (1983) Sexual selection by male–male competition in Natterjack toad choruses. *Nature* 306:261–262. <https://doi.org/10.1038/306261a0>
- Amott G, Elwood RW (2009) Assessment of fighting ability in animal contests. *Anim Behav* 77:991–1004. <https://doi.org/10.1016/j.anbehav.2009.02.010>
- Bastos PR, Alcantara MB, Morais AR, Lingnau R, Signorelli L (2011) Vocal behaviour and conspecific call response in *Scinax centralis*. *Herpetol J* 21:43–50
- Bee MA, Reichert MS, Tumulty J (2016) Assessment and recognition of competitive rivals in anurans. *Adv Stud Behav* 48:161–249



- Bergman M, Olofsson M, Wiklund MO (2010) Contest outcome in a territorial butterfly: the role of motivation. *Proc R Soc B* 277: 3027–3033 <https://doi.org/10.1098/rspb.2010.0646>
- Borges-Leite MJ, Rodrigues JFM, Borges-Nojosa DM (2014) Herpetofauna of a coastal region of northeastern Brazil. *Herpetol Notes* 7:405–413. <https://doi.org/10.1590/1676-06032015001715>
- Briffa M, Hardy ICW (2013) Introduction to animal contests. In: Hardy ICW, Briffa M (eds) *Animal contests*. Cambridge University Press, Cambridge
- Burmeister SJ, Ophir AG, Ryan MJ, Wilczynski W (2002) information transfer during cricket frog contests. *Anim Behav* 64:715–725. <https://doi.org/10.1006/anbe.2002.4012>
- Caldart VM, Iop S, Cechin SZ (2014) Social interactions in a neotropical stream frog reveal a complex repertoire of visual signals and the use of multimodal communication. *Behaviour* 151:719–739. <https://doi.org/10.1163/1568539X-00003165>
- Caldas FLS, Silva BD, De-Carvalho CB, Santos RAD, Santana DA, Gomes FFA, Faria RG (2012) *Phyllomedusa nordestina* (Northeast Orange-legged leaf frog). Physical attack. *Herpetol Rev* 43:635
- Caldas FLS, Silva BD, Santos RAD, Santana DA, Gomes FFA, Faria RG (2016) Autoecology of *Phyllomedusa nordestina* (Anura: Hylidae) in areas of the Caatinga and Atlantic Forest in the State of Sergipe, Brazil. *North-West J Zool* 12:271–285
- Caramaschi U (2006) Redefinição do Grupo de *Phyllomedusa hypochondrialis*, com redescritção de *P. megacephala* (Miranda-Ribeiro, 1926), revalidação de *P. azurea* Cope, 1862 e descrição de uma nova espécie (Amphibia, Anura, Hylidae). *Arquivos do Museu Nacional* 64:159–179
- Carvalho RMR, Peixoto PEC, Benson WW (2016) Territorial clashes in the Neotropical butterfly *Actinote pellenae* (Acraeinae): do disputes differ when contests get physical? *Behav Ecol Sociobiol* 70:199–207. <https://doi.org/10.1007/s00265-015-2042-6>
- Dias MT, Santos TG, Maragno FP, Oliveira VF, Lima C, Cechin SZ (2017) Breeding biology, territoriality, and reproductive site use by *Phyllomedusa iheringii* (Anura: Phyllomedusidae) from the South American Pampa in Brazil. *Salamandra* 53:257–266
- Dunn DW, Charlotte JK, Anayra G, Lamas C, Pereira RAS (2014) Mortal combat and competition for oviposition sites in female pollinating fig wasps. *Behav Ecol* 26:1–7. <https://doi.org/10.1093/beheco/aru191>
- Dyson ML, Reichert MS, Halliday TR (2013) Contests in amphibians. In: Hardy ICW, Briffa M (eds) *Animal contests*. Cambridge University Press, pp 228–257
- Ferreira-Silva C, Oliveira DB, Oliveira HF, Ávila RW (2016) Spatial and temporal distribution in two anuran communities in the Chapada do Araripe, Northeastern Brazil. *Biota Neotrop* 16:e0166
- Giasson LOM, Haddad CFB (2006) Social interactions in *Hypsiboas albomarginatus* (Anura: Hylidae) and the significance of acoustic and visual signals. *J Herpetol* 40:171–180
- Grafe TU (2005) Anuran choruses as communication networks. In: McGregor PK (ed) *Animal communication networks*. Cambridge University Press
- Guimarães LD, Bastos RP (2003) Vocalizações e interações acústicas em *Hyla raniceps* (Anura, Hylidae) durante a atividade reprodutiva. *Iheringia Ser Zool* 93:149–158
- Halloy M, Espinoza RE (2000) Territorial encounters and threat displays in the Neotropical frog *Phyllomedusa sauvagii* (Anura: Hylidae). *Herpetological Natural History* 7:175–180
- Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–387
- Hartmann MT, Giasson LOM, Hartmann PA, Haddad CFB (2005) Visual communication in Brazilian species of anurans from the Atlantic forest. *J Nat Hist* 39:1675–1685
- Hödl W, Amézquita A (2001) Visual signaling in anuran amphibians. In: Ryan MJ (ed) *Anuran communication*. Smithsonian Institution Press, Washington, pp 121–141
- Hosken DJ, House CM (2011) Sexual selection. *Curr Biol* 21:62–65 <https://doi.org/10.1016/j.cub.2010.11.053>
- Instituto de Pesquisa e Estratégia Econômica do Ceará (IPECE) (2016) Perfil Básico Municipal—Groaíras (2016). [http://www.ipece.ce.gov.br/perfil\\_basico\\_municipal/2016/Groairas.pdf](http://www.ipece.ce.gov.br/perfil_basico_municipal/2016/Groairas.pdf). Accessed 29 Sept 2017
- Jansen M, Köhler J (2008) Intraspecific combat behavior of *Phyllomedusa boliviana* (Anura: Hylidae) and the possible origin of visual signaling in nocturnal treefrogs. *Herpetol Rev* 39:290–293
- Jones MC, Dixon JR, Forstner MRJ (2011) Is bigger always better? Mate selection in the Houston toad (*Bufo houstonensis*). *J Herpetol* 45: 455–456
- Krebs JR (1982) Territorial defence in the great tit (*Parus major*): do residents always win? *Behav Ecol Sociobiol* 11:185–194
- Lopes RS, Peixoto PEC (2013) Males of the dragonfly *Diastatops obscura* fight according to predictions from game theory models. *Anim Behav* 85:663e669
- Mângia S, Camurugi F, Pereira EA, Carvalho P, Röhr DL, Folly H, Santana DJ (2019) Release calls of four species of Phyllomedusidae (Amphibia, Anura). *Herpetozoa* 32:77–81
- Marden JH, Waage JK (1990) Escalated damselfly territorial contests are energetic wars of attrition. *Anim Behav* 39:954–959
- Márquez R, Pargana JM, Crespo EG (2001) Acoustic competition in male *Pelodytes ibericus* (Anura: Pelodytidae): interactive playback tests. *Copeia* 4:1142–1150
- Martins M, Pombal J Jr, Haddad CFB (1998) Escalated aggressive behaviour and facultative parental care in the nest building gladiator frog, *Hyla faber*. *Amphibia-Reptilia* 19:65–73
- Miranda DB, Garey MV, Monteiro-Filho ELA, Hartmann MT (2008) Sinalização visual e biologia reprodutiva de *Dendropsophus werneri* (Anura: Hylidae) em área de Mata Atlântica no estado do Paraná, Brasil. *Papéis Avulsos de Zoologia* 48:335–343
- Morais AR, Batista VG, Gambale PG, Signorelli L, Bastos RP (2012) Acoustic communication in a neotropical frog (*Dendropsophus minutus*): vocal repertoire, variability and individual discrimination. *Herpetol J* 22:249–257
- Narvaes P, Rodrigues MT (2005) Visual communication, reproductive behavior, and home range of *Hylodes dactylocinus* (Anura, Leptodactylidae). *Phyllomedusa* 4:147–158
- Oliveira FFR (2017) Mating behaviour, territoriality and natural history notes of *Phyllomedusa ayeaye* Lutz, 1966 (Hylidae: Phyllomedusinae) in southeastern Brazil. *J Nat Hist* 51:657–675. <https://doi.org/10.1080/00222933.2017.1296196>
- Oliveira FFR, Nogueira PAG, Eterovick PC (2012) Natural history of *Phyllomedusa megacephala* (Miranda-Ribeiro, 1926) (Anura: Hylidae) in southeastern Brazil, with descriptions of its breeding biology and male territorial behavior. *J Nat Hist* 46:117–129. <https://doi.org/10.1080/00222933.2011.626127?journalCode=tnah20>
- Osiejuk ST, Jakubowska A (2017) Song duration mediates responses of territory owner in a songbird species with a small song repertoire. *Acta ethol* 20:137–145
- Parker GA (1974) Assessment strategy and evolution of fighting behaviour. *Anim Behav* 29:223–243
- Reichert MS, Gerhardt HC (2011) The role of body size on the outcome, escalation and duration of contests in the gray treefrog, *Hyla versicolor*. *Anim Behav* 82:1357e1366
- Reichert MS, Gerhardt HC (2013) Gray tree frogs, *Hyla versicolor*, give lower-frequency aggressive calls in more escalated contests. *Behav Ecol Sociobiol* 67:795–804
- Ryan MJ (1998) Energy, calling and selection. *Integr Comp Biol* 28:885–898

- Sá FP, Zina J, Haddad CBF (2016) Sophisticated communication in the Brazilian torrent frog *Hylodes japi*. PLoS One 11:1–24
- Santana DJ, Mângia S, Silveira-Filho RR, Barros LCS, Andrade I, Napoli MF, Juncá F, Garda AA (2015) Anurans from the Middle Jaguaribe river region, Ceará State, Northeastern Brazil. Biota Neotrop 15: e20150017
- Scott JP, Fredericson E (1951) The causes of fighting in mice and rats. Physiol Zool 24:273–309
- Senar JC, Camerino M, Metcalfe NB (1989) Agonistic interactions in siskin flocks: why are dominants sometimes subordinate? Behav Ecol Sociobiol 25:141–145
- Taigen TL, Wells KD (1985) Energetics of vocalization by an anuran amphibian (*Hyla versicolor*). J Comp Physiol 155:163–170. <https://doi.org/10.1007/BF00685209>
- Tárano Z, Herrera EA (2003) Female preferences for call traits and male mating success in the Neotropical frog *Physalaemus enesefae*. Ethology 109:121–134. <https://doi.org/10.1046/j.1439-0310.2003.00848.x/abstract>
- Toledo LF, Araújo OGS, Guimarães LD, Lingnau R, Haddad CBF (2007) Visual and acoustic signaling in three species of Brazilian nocturnal tree frogs (Anura, Hylidae). Phyllomedusa 6:61–68
- Toledo LF, Martins IA, Bruschi DP, Passos MI, Alexandre C, Haddad CBF (2014) The anuran calling repertoire in the light of social context. Acta Ethol 18:87–99. <https://doi.org/10.1007/s10211-014-0194-4>
- Vieira MC, Peixoto PEC (2013) Winners and losers: a meta-analysis of functional determinants of fighting ability in arthropod contests. Funct Ecol 27:305–313
- Vilaça TRA, Silva RSS, Solé M (2011) Vocalization and territorial behaviour of *Phyllomedusa nordestina* Caramaschi, 2006 (Anura: Hylidae) from southern Bahia, Brazil. J Nat Hist 45:1823–1834. <https://doi.org/10.1080/00222933.2011.561018?journalCode=tmah20>
- Webster MS, Robinson SK (1999) Courtship disruptions and male mating strategies: examples from female-defense mating systems. Am Nat 154:717–729
- Wells KD (1977) The social behaviour of anuran amphibians. Anim Behav 25:666–693
- Wells KD (1988) The effect of social interactions on anuran vocal behaviour. In: Fritzsche B, Ryan MJ, Wilezynski W, Hetherington TE, Walkowiak W (eds) The evolution of amphibian auditory system. John Wiley and Sons, New York, pp 433–454
- Wells KD (2007) The ecology and behaviour of amphibians. The University of Chicago Press, Chicago, 1148p
- Wells KD, Schwartz JJ (2006) The behavioral ecology of anuran communication. In: Narins PM, Feng AS, Fay RR, Popper AN (eds) (orgs.) Hearing and sound communication in amphibians, vol 28. Springer Handbook of Auditory Research, pp 44–86
- Wogel H, Abrunhosa PA, Pombal JP Jr (2002) Atividade reprodutiva de *Physalaemus signifer* (Anura, Leptodactylidae) em ambiente temporário. Iheringia Ser Zool 92:57–70
- Wogel H, Abrunhosa PA, Pombal JP Jr (2004) Vocalization and aggressive behavior of *Phyllomedusa rohdei* (Anura: Hyllidae). Herpetol Rev 35:239–243
- Zahavi A (1975) A selection for a handicap. J Theor Biol 53:205–214

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