



Eating to the beat of the drum: vibrational parameters of toe tapping behavior in *Dendrobates truncatus* (Anura: Dendrobatidae)

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Abstract

Toe tapping is performed by certain anuran species while foraging for their prey. This behavior has been described in different frog families, with some hypotheses regarding its function, including predator-prey communication, still unverified. To understand the function of toe tapping and its potential relationship with foraging in anurans, the present research focuses on descriptive analysis of vibrational parameters of toe tapping produced during foraging in the poison dart frog *Dendrobates truncatus*. We implemented an experimentally designed arena that allowed us to record toe tapping vibrations using an accelerometer attached to an artificial substrate. Continuous recordings of toe tapping were obtained from 19 individuals, enabling us to identify and define the vibrational parameters, with reference to the time between attacks on prey. The average tap duration was 0.06 ± 0.01 s with an inter-tap interval of 0.15 ± 0.07 s. We also identified a pattern, displayed in 36.5% of the analyzed attacks, of progressive acceleration of toe tapping before an attack. Furthermore, we found that individuals with longer third toes were more likely to accelerate their taps. Lastly, we found no evidence of sexual dimorphism in the toe tapping behavior of *Dendrobates truncatus*. Describing the vibrational parameters of toe tapping in *Dendrobates truncatus* represents a new frontier of research in the field of foraging behavior and paves the way for hypothesis testing regarding its functionality.

Keywords Foraging behavior · Vibrations · Toe twitching · Predator-prey interaction

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Introduction

Vibrational signals can be transmitted and perceived as information traveling through substrates (Endler 2019; Roberts and Wickings 2022), allowing for various communication strategies (Mortimer 2017). In animals, vibrational communication strategies occur in diverse biological contexts, such as the detection of environmental conditions (Márquez et al. 2016), parental care (Hamel and Cocroft 2012), conspecific recognition (Smith and Harper 2003), reproduction (Mazzoni et al. 2013; Lewis et al. 2001), agonistic interactions (Caldwell et al. 2010; Narins et al. 2018), predator-prey interactions (Cividini and Montesanto 2020; Bradbury and Vehrencamp 2011), and foraging (Hill 2008).

The use of vibrational signals during foraging is prevalent among invertebrates (Cokl and Virant-Doberlet 2003; Cocroft and Rodríguez 2005; Roberts and Wickings 2022), with extensive studies conducted on termites (Hager et al. 2019; Evans et al. 2007) and arachnids (Brownell and Farley 1979; Mineo and Del Claro 2006; Cividini and Montesanto 2020). In vertebrates, the use of vibrational signals has been reported in mammals (Randall 2013; Cocroft et al. 2014), birds (Roberts and Wickings 2022), and reptiles (Kaufmann 1986; Hetherington 1989; Young and Morain 2002). For amphibians, despite having heightened vibrational sensitivity (Hill 2008), the use of vibrations has been documented in few behavioral contexts (Narins et al. 2018; De Luca et al. 2023), primarily in anti-predator behaviors of anuran amphibians such as the embryos of *Agalychnis callidryas* (Warkentin 2005; Caldwell et al. 2009; Warkentin et al. 2017), mating (Narins 1990) and potential prey detection during foraging in *Atelopus laetissimus* (Rueda-Solano and Warkentin 2016).

Furthermore, foraging in anuran amphibians often involves rapid movement of one or more toes on the hind feet (Wells 2007; Grafe 2008; Claessens et al. 2020; Sloggett and Zeilstra 2008; Erdmann 2017). Toe movements in anurans are most often observed during foraging (Claessens et al. 2020; Schulte and König 2023) and can occur with the foot raised off the substrate or in contact with the substrate. Toe movements while the foot is raised above the substrate have been described as pedal luring (Murphy 1976; Radcliffe et al. 1986; Bertoluci 2002; Grafe 2008), toe waving (Hagman and Shine 2008) and toe twitching (McFadden et al. 2010) have been proposed to function as a visual stimulus that attracts prey towards the predator's front (Murphy 1976). When the foot is in contact with the substrate, toe tapping will produce substrate vibrations, and Sloggett and Zeilstra (2008) hypothesized that toe-tapping will influence prey primarily through the vibrational rather than the visual modality.

Toe tapping behavior in anuran amphibians has primarily been associated with feeding on invertebrates (Claessens et al. 2020). Several hypotheses have been proposed regarding the function of this behavior. One hypothesis proposes that toe tapping facilitates foraging by keeping the prey in motion (Sloggett and Zeilstra 2008). Another hypothesis proposes that toe tapping serves as a lure, mimicking the vibrations produced by the prey and attracting them towards the anuran (Sloggett and Zeilstra 2008; Hagman and Shine 2008). Erdmann (2017) observed that toe tapping was associated with higher foraging success, along with a reduction in prey movement and an orientation toward the signal source. However, to date, there are no experimental studies that provide conclusive evidence supporting these hypotheses. It is worth noting that toe tapping is not limited to feeding behaviors alone. It has also been documented during reproductive behavior (Starnberger et al. 2018) including courtship (Barquero and Arguedas 2022), amplexus (Landestoy and Ortiz 2015), and call-

ing displays (Claessens et al. 2020). The specific function of toe tapping displays during these behaviors remains unknown. Therefore, understanding the functional significance of toe tapping in specific behavioral contexts is crucial for unraveling its adaptive value in anurans.

Toe tapping occurs in various families of anurans (Claessens et al. 2020). In poison dart frogs of the family Dendrobatidae, such as *Dendrobates auratus* (Erdmann 2017), experimental evidence confirms this behavior occurs in a foraging context (Schulte and König 2023), and field observations demonstrate its use during courtship (Barquero and Arguedas 2022). Observations of toe tapping behavior during feeding have been reported for *Dendrobates tinctorius* (Sloggett and Zeilstra 2008), like other dendrobatid species (Erdmann 2017; Claessens et al. 2020). We studied toe tapping in *Dendrobates truncatus* (Cope 1861), which is closely related to the other toe-tapping species (Grant et al. 2017), and in which the behavior was reported by Claessens et al. (2020). This species has a restricted distribution in Colombia, ranging from the Sierra Nevada de Santa Marta, through the Magdalena River valley, to the northern part of the Choco biogeographic region, with an altitude range between 0 and 1200 m (Cárdenas-Ortega et al. 2019). It inhabits humid, sub-Andean, and dry forests, in microhabitats adjacent to streams (Vargas-Salinas et al. 2019; De la Ossa et al. 2011), exhibiting terrestrial and diurnal activity (Kahn et al. 2016). Its feeding habits have been described, with a diet mainly consisting of ants (Hymenoptera) from the genera *Crematogaster*, *Pheidole*, and *Solenopsis*, as well as mites (Acari) and beetles (Coleoptera) (Erazo-Londoño et al. 2016; Posso-Peláez et al. 2017; Martínez et al. 2019). However, many of the interactions between *Dendrobates truncatus* individuals and their prey, as well as behaviors during foraging, remain unknown, especially those related to the vibrations produced by toe tapping.

Therefore, we directed our research towards conducting the first detailed study of the temporal vibrational parameters produced by toe tapping in an anuran amphibian, using *Dendrobates truncatus* as a model. We designed and standardized a methodology for recording vibrations, identifying, and analyzing the temporal vibrational parameters generated by the toe tapping display during the foraging behavior of *Dendrobates truncatus* individuals. Furthermore, to elucidate potential changes in the expression of the toe tapping display in relation with the morphological traits and sex; we related the snout-vent length and the length of the third toe of the individuals as potential predictors of the vibrational parameters of this behavior. Besides, we conducted a sex comparison of toe tapping to determine if sexual dimorphism exists in the display of this behavior. If changes in the expression of the toe-tapping display are observed, it would suggest that selective pressures may be influencing the toe-tapping behavior during foraging in *Dendrobates truncatus*. This study establishes the foundation for future investigations into the function and significance of toe tapping during foraging in anurans from a vibrational perspective.

Materials and methods

Collection and recording of individuals

We collected 19 individuals of *Dendrobates truncatus* in the villages of Calabazo (11°17'04.7" N 74°00'00.4" W) and Las Tinajas (11°16'15.8" N 74°03'46.2" W), located

within the buffer zone of Tayrona National Natural Park, Magdalena Department, Colombia (Fig. 1A). We searched for individuals during the daytime (9:00 a.m. – 12:00 p.m.) in microhabitats adjacent to streams. The air temperature and relative humidity recorded during sampling were $27.6\text{ }^{\circ}\text{C} \pm 0.35$ and $86.6\% \pm 1.48$, respectively (thermos-hygrometer model RH 101 Extech IR accurate to $2\text{ }^{\circ}\text{C}$ or 2%). *Dendrobates truncatus* exhibits an individually unique ventral pattern (Ferner, 2010), which we identified through photographic records using a Sony Cyber-shot DSC-HX400V digital camera, with an automatic program (P) and the flash level set to maximum (+2.0). Subsequently, each was assigned a unique code in the database (Dt-000) (Fig. 1B). Using the photographs, we digitally measured the snout-vent length (SVL) and the length of the third toe. These measurements were performed using ImageJ software version 1.51 (Schneider et al. 2012). During the experiment, the collected 19 individuals were kept under ex-situ conditions in Laboratory 9 at the Intropic, Universidad del Magdalena, Santa Marta, Colombia, following the animal care guidelines approved by the University's ethics committee. After the experiments, the individuals were released back into their original locality (Fig. 1C).

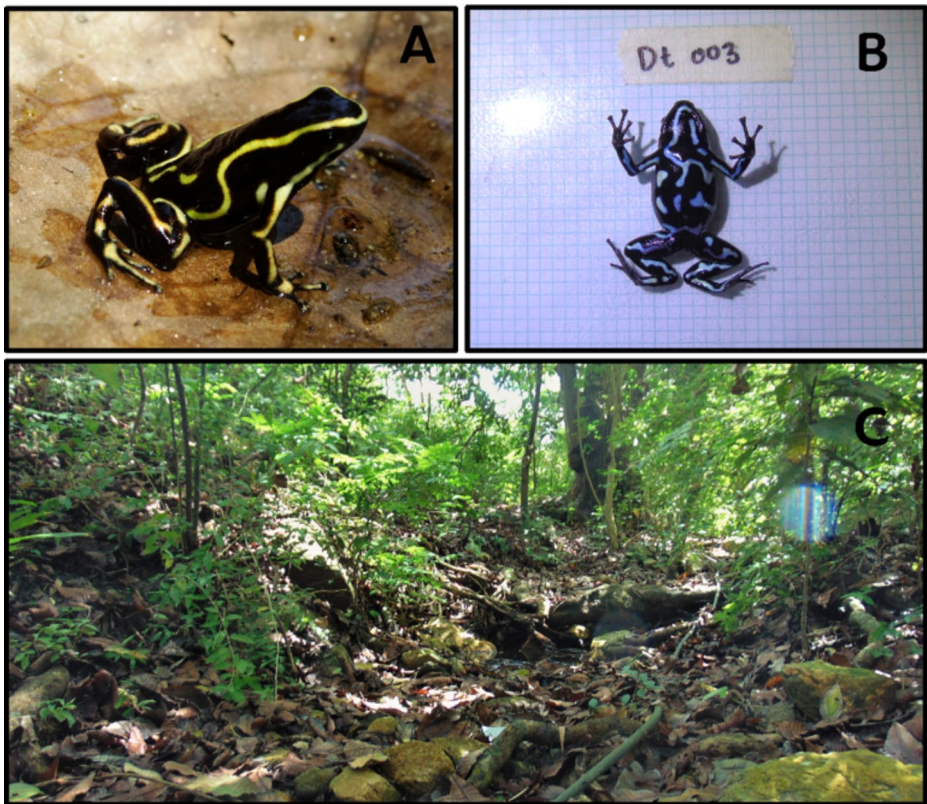


Fig. 1 *Dendrobates truncatus*. (A) Individual found in leaf litter, (B) Collected individual exhibiting a unique ventral pattern, (C) Tropical Dry Forest from Calabazo village within the buffer zone of Tayrona National Natural Park, Magdalena Department, Colombia, where *D. truncatus* individuals were collected and released

Sex identification

To determine the sex of *Dendrobates truncatus* individuals, we inspected the vocal slits, which are responsible for producing vocalizations in males (Duellman and Trueb 1994). Using a rounded-tip sexing probe, we examined the sides of the tongue for the presence of vocal slits. In males, the sex was confirmed when the rounded tip entered the vocal slits. In females, as vocal slits are absent, the rounded tip of the sexing probe remained visible (Rueda-Almonacid et al. 2006).

Experimental arena design

We designed the experimental arena as a recording area with specific conditions, allowing *D. truncatus* individual to forage (see below) and display toe-tapping behavior without any distractions or stress, promoting behavioral habituation (Fig. 2). The design aimed to create an environment with suitable ambient conditions, maintaining the ambient humidity at $90.96\% \pm 4.55$ and the temperature within the arena at $32.44\text{ }^{\circ}\text{C} \pm 0.98$ (measured using a Thermos-hygrometer RH 101 Extech IR).

The design of the experimental arena considered the body size of *Dendrobates truncatus* individuals (snout-vent length=23.5 to 31.0 mm; Gualdrón-Duarte et al. 2016). This arena consisted of a structural part, complemented by recording setup (Fig. 2A-B). The structural assembly had total dimensions of 20 cm in diameter and 30 cm in height. It was composed of three parts: (1) The upper part or dome: It had a hole in the upper area measuring 8 cm, through which the food was initially introduced, followed by the entry of the *D. truncatus* individual, and finally, a Sony Handycam FDR-AX700 video camera, which recorded the events inside the arena from this point and obstructed the top opening. The dome was made of black plastic. (2) The middle part or drum: It had a diameter of 20 cm and a height of 12 cm. In this space, the individual could move freely on an artificial transparent acetate substrate, allowing active foraging of presented prey. The polarized acetate walls of the drum allowed the entry of light while preventing external visual distractions. (3) The lower part or support: It had a height of 18 cm and served as the base for the entire assembly, reducing vibrational noise as it was elevated and adhered to a bed of expanded polystyrene to minimize the influence of environmental vibrations coming from the tabletop. Additionally, the artificial transparent acetate substrate was placed and securely held with clamps between the middle and lower structure (Fig. 2C). The middle and lower parts of the structural assembly of the arena were constructed using materials including white cedar wood, rubber glue, silicone, nails, and frosted polarized acetate.

Standardization of toe-tapping recording methodology

We standardized a recording methodology to capture the toe-tapping behavior of *D. truncatus*. We habituated the individuals to forage within the experimental arena for one week using worker caste ants of *Pheidole indica*. Prior to the recordings, we introduced ants collected from the wild. They were attracted using baits placed inside a petri dish. Subsequently, we selected 19 individuals of *D. truncatus* randomly with the help of a random number table and deprived them of food for 24 h. The fasting frog was then introduced into

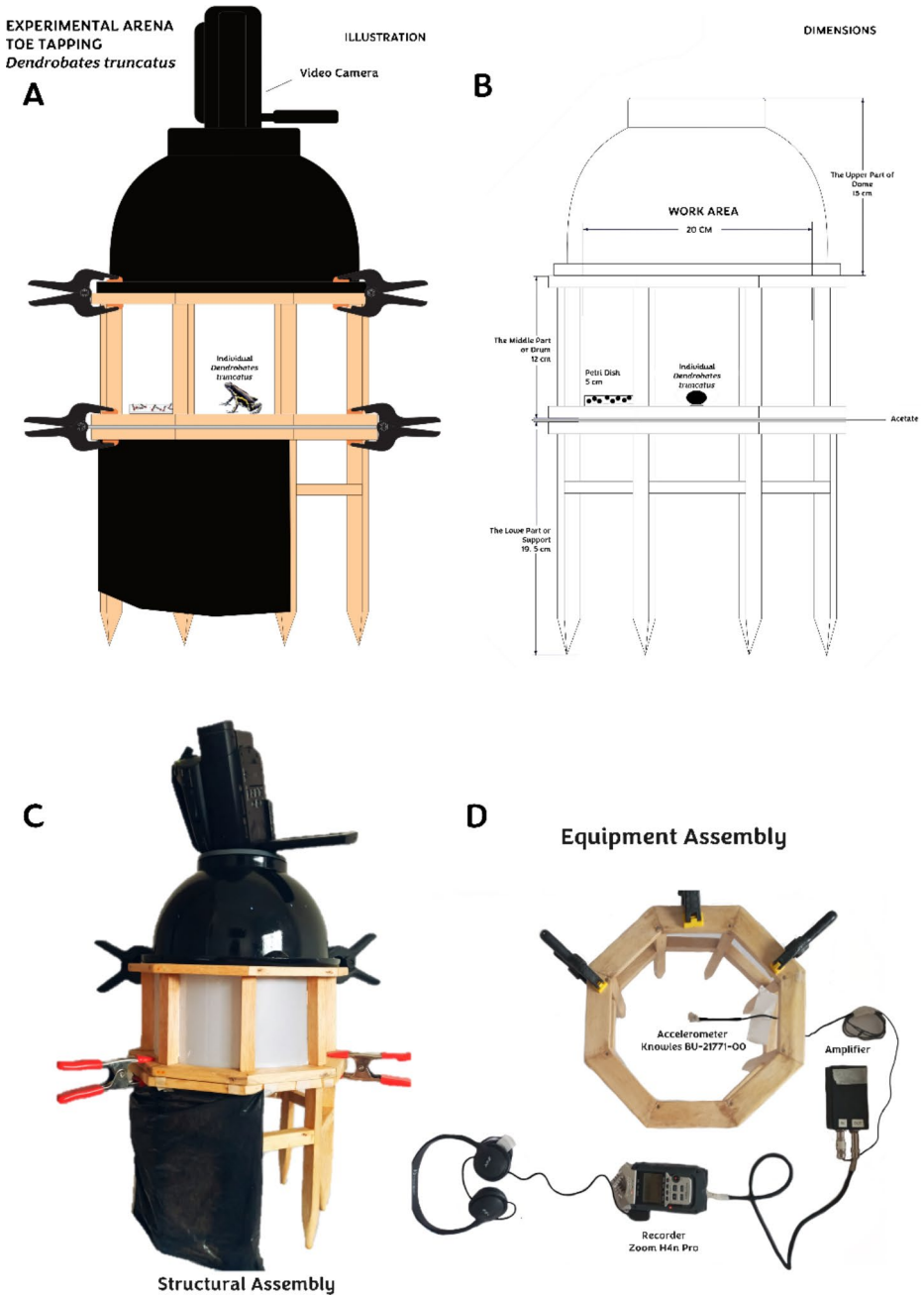


Fig. 2 Experimental arena for recording the toe-tapping behavior of *Dendrobates truncatus*. (A) Illustration of the experimental arena. (B) Plans with measurements of the experimental arena. (C) Structural assembly. (D) Equipment setup

the arena alongside the ants. The arena was moistened with spraying before recording and the temperature and humidity were taken with a Thermos-hygrometer (RH 101 Extech IR).

We conducted a 10-minute recording per individual, allowing it to forage on ants and exhibit toe-tapping behavior. No individual was recorded more than once. To capture the vibrations produced by the individuals during toe-tapping, we used a Knowles BU-21771-00 accelerometer (with a frequency range of 20 Hz to 10 kHz) attached with wax to the underside of the substrate. The vibrations were amplified using a custom-made amplifier, and then, digitally recorded in .wav format with a sampling frequency of 44.1 kHz at 16 bits using a Zoom H4n Pro recorder (Fig. 2D).

Data analysis

The vibration data were analyzed using Raven Pro 1.5 software for Windows, developed by the Lisa Yang Center for Conservation Bioacoustics (2023). We identified and defined the temporal vibrational parameters of toe tapping, considering the reference framework established by the time intervals between prey attacks, which we referred to as “fragments” (Fig. 4). A fragment represents the time unit between one prey attack and the next, where we measured the temporal vibrational parameters produced during the toe tapping behavior. These parameters include tap duration, inter-tap interval, number of taps, and tap rate (see definitions in Table 1). We calculated the individual averages for each temporal vibrational parameter, and then obtained an overall average of those individuals.

To analyze the acceleration of the tap rate observed in certain fragments (see definitions in Table 1), we used 20 fragments per individual and estimated a tap rate for each. The change in tap rate (N° tap/s²) was obtained by dividing each fragment into four equal parts (quartiles). The acceleration for each quartile was calculated as the difference between the final and initial tap rate divided by the total time of the quartile. The tap rates (N° tap/s) were obtained by sampling the number of taps divided by the inter-tap interval at the beginning

Table 1 Definitions of temporal vibrational parameters of toe tapping behavior in *D. truncatus*

Parameter	Definition
Tap	The duration of each individual toe tap, measured as the time elapsed from the start to the end of a tap
Inter-tap interval	The interval between two consecutive toe taps, measured as the time elapsed from the end of one tap to the start of the next
N° tap	The total count of individual toe taps within a fragment, representing the number of taps performed by the individual during that time period
Fragment	Taps recorded during the time interval between one prey attack and the next. The start and end of a fragment are determined by the impact of the tongue flick on the substrate. This tongue flick impact is characterized by a higher amplitude than a regular toe tap but lower amplitude than the movement of the individual's legs
Acceleration	Within the fragment, there is a portion where the toe tap rate increases, resulting in a decrease in inter-tap interval
Tap rate	The speed at which the toe taps occur (N° tap/s), providing an indication of the toe tapping acceleration (N° tap/s ²).

and end of each quartile. For each fragment, the acceleration values of the four quartiles were averaged to determine the overall change in tap rate. To establish the individual's tap rate, the average tap rate obtained from the 20 analyzed fragments was taken. This analysis allowed us to evaluate the changes in acceleration of toe tapping within each fragment and among different individuals. By examining the patterns of acceleration, we were able to gather information about the dynamics and variations of toe tapping behavior and its relationship with the sequence of attack and foraging in *D. truncatus*.

Finally, we used linear regression to examine the relationships between the temporal vibrational parameters and potential predictor variables, such as snout-vent length (SVL) and the length of the third toe of the individuals. Additionally, to evaluate the possibility of sexual dimorphism in the toe tapping behavior of *D. truncatus*, we compared these parameters between sexes. All analyses were conducted by verifying statistical assumptions, followed by implementing the general linear model (lm), where the categorical predictor variable was sex, and the response variables were the vibrational parameters. The function `lm(data$Y ~ data$X)` was used (Bruce and Bruce 2017) in R software version 4.2.2 (R Development Core Team 2023).

Results

We obtained recordings from 10 females and 9 males of *D. truncatus* under controlled experimental conditions. The average time before the feeding with tapping behavior was 8.04 ± 5.06 s. We achieved recording durations on average of 3.04 ± 2.18 min (0.75–8.55 min), which contained vibrations produced by the toe tapping behavior of *D. truncatus* during foraging. Using these recordings, we identified and quantified temporal vibrational parameters between prey attack times (i.e., fragments) (Fig. 3).

Temporal vibrational parameters of *Dendrobates truncatus* toe tapping

A total of 380 fragments were analyzed for the 19 individuals of *Dendrobates truncatus*.

The overall average tap duration was 0.06 ± 0.01 s, while the average inter-tap interval duration was 0.15 ± 0.07 s. The average number of taps obtained from the fragments was 42.96 ± 15.7 (Table 2).

Acceleration occurred in 36.5% of the fragments (139 out of a total of 380 fragments analyzed). For the remaining 63.5% of the fragments, acceleration was absent or even exhibited some deceleration. We estimated the average change in tap rate for the 19 individuals at 0.28 ± 7.03 N° tap/s² (Table 2). The sequence of attacks on prey by individuals of *D. truncatus* tends to follow a pattern of progressive acceleration in the temporal parameters of toe tapping behavior (Fig. 4). This pattern begins after a prey attack in the first quartile of the fragments, where the taps tend to be slowed down (-14.24 ± 20.86 N° tap/s²), predominantly resulting in accelerated and decelerated taps (Fig. 4). Subsequently, in the second (1.83 ± 13.11 N° tap/s²) and third quartile (-4.38 ± 14.41 N° tap/s²), there is an increasing acceleration compared to the initial quartile. This acceleration remains relatively constant during this part of the attack sequence on the prey. The attack sequence concludes with a tendency to further increase the acceleration of the toe tapping behavior in the fourth quar-

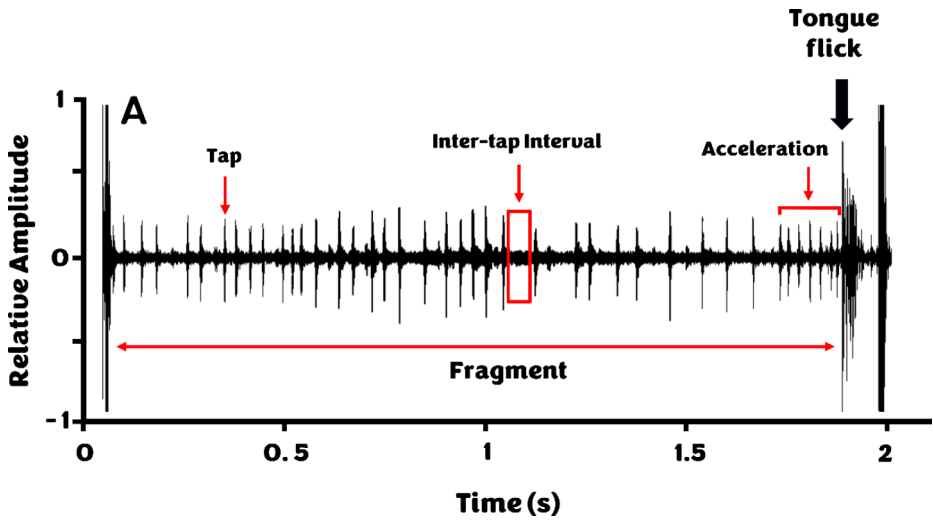


Fig. 3 Oscillogram of the toe tapping recording observed in Raven Pro 1.5 from a fragment of individual Dt-003. (A) Temporal vibrational parameters of toe tapping behavior of *Dendrobates truncatus*: tap duration, inter-tap interval, number of taps and tap rate obtained within the time between prey attacks (= fragment)

Table 2 Temporal vibrational parameters identified in the toe-tapping behavior of *D. truncatus*. Mean \pm SD (Standard Deviation) (Range)

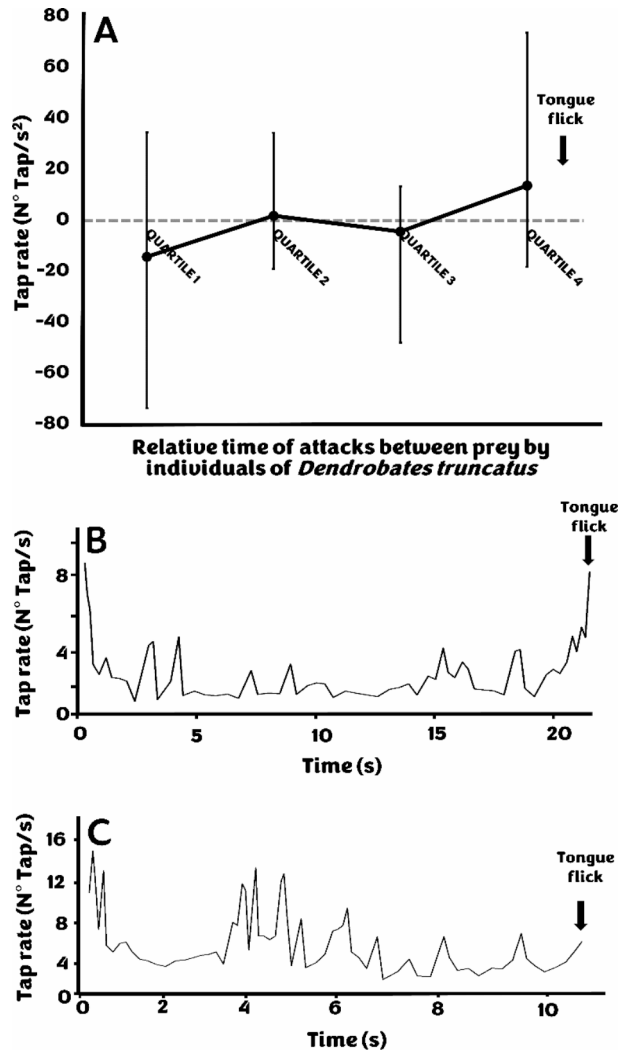
	SLV (mm)	Third toe length (mm)	Tap(s)	Inter-tap interval (s)	N° tap	Tap rate (N° tap/s ²)
Female	28.80 \pm 1.11	6.79 \pm 0.86	0.06 \pm 0.01	0.14 \pm 0.07	41.24 \pm 16.81	0.40 \pm 6.52
n=10	(26.99–30.54)	(0.73–8.50)	(0.04–0.08)	(0.05–0.29)	(19.10–77.10)	(-8.22–10.14)
Male	27.71 \pm 1.46	6.28 \pm 0.73	0.06 \pm 0.01	0.15 \pm 0.07	44.86 \pm 15.29	0.13 \pm 8.09
n=9	(24.60–29.39)	(4.63–7.30)	(0.04–0.07)	(0.07–0.29)	(23.80–76.05)	(-16.27–12.70)
Total	28.28 \pm 1.37	6.55 \pm 0.82	0.06 \pm 0.01	0.15 \pm 0.07	42.96 \pm 15.77	0.28 \pm 7.03
n=19	(24.60–30.54)	(4.63–8.50)	(0.04–0.08)	(0.05–0.29)	(19.10–77.10)	(-16.27–12.70)

tile (13.67 \pm 21.26 N° tap/s²), just before the attack on a new prey (tongue flick), predominantly producing accelerated taps (Fig. 4).

Body measurements, inter-sexual comparison and the toe tapping of *Dendrobates truncatus*

Except for the third toe length (mm) with the change in tap rate (N° tap/s²), where individuals with the longer lengths of the third toe tend to accelerate their taps (Fig. 5), we did not find any relationship between the temporal vibrational parameters of toe tapping and the morphological variables explored (Table 3). Furthermore, there was no sexual dimorphism between males and females of *D. truncatus* (10 females and 9 males), when comparing their temporal vibrational parameters of toe tapping (Table 3; Fig. 6).

Fig. 4 Sequence between attacks on prey with a tendency to progressive acceleration of the temporal vibrational parameters of the toe tapping behavior of *Dendrobates truncatus*. (A) Overall average, minimum and maximum of the tap rate in each of the four parts analyzed (i.e., quartiles) between attacks on prey (i.e., fragments). (B-C) Examples of toe tapping rates between attacks on prey in two individuals *D. truncatus*. Note the variability in rates, including the deceleration immediately after the preceding attack in both examples, and the acceleration toward the time of the next attack in B but not C



Discussion

This research is the first descriptive study of the vibrational temporal parameters of toe tapping associated with foraging behavior in anurans, specifically focusing on the species *Dendrobates truncatus*. Furthermore, the identification and quantification of temporal vibrational parameters has provided us with a more detailed understanding about the structure of toe tapping behavior. Additionally, through the identification of these temporal vibrational parameters, we have established a terminology that describes the composition of toe tapping in a more precise and specific manner.

Our experimental setup relied on the use of an artificial acetate substrate, which played a crucial role in our study. This substrate not only provided a stable structural base but also facilitated effective connections between the equipment setup, the structural elements, and

Fig. 5 Relationship between the third toe length (mm) of *D. truncatus* individuals and the change in their tap rates (N° tap/s²). Black data points representing observations, an orange linear regression line that fits the data distribution more accurately, and the gray shadow indicating the confidence interval (95%). Individuals with the longer third toes tend to accelerate their taps

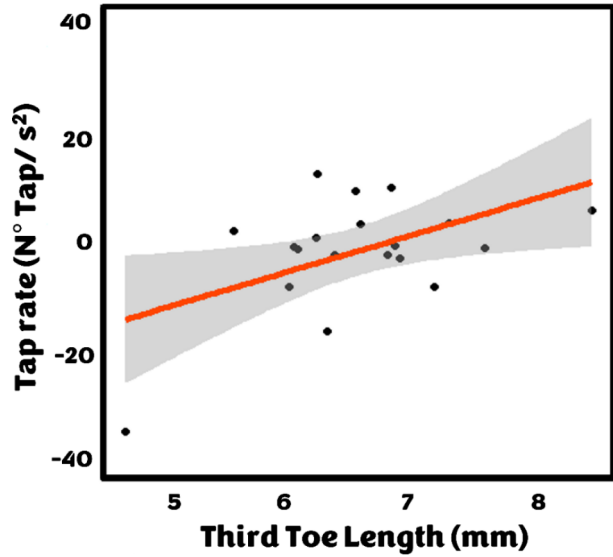


Table 3 Summary of statistical analyses between SVL, third toe length, sex (male/female) and temporal vibrational parameters identified in the toe-tapping behavior of *D. truncatus*

	Estimate	R ²	t-value	P-value
SLV (mm)				
Tap (s)	-0.00	0.02	-1.59	0.13
Inter-tap Interval (s)	-0.00	0.02	-0.58	0.56
N° tap	-0.08	5.90	-0.03	0.97
Tap rate (N° tap/s ²)	-0.07	0.00	-0.04	0.96
Third toe length (mm)				
Tap (s)	-0.00	0.00	-0.38	0.70
Inter-tap Interval (s)	-0.00	0.04	0.88	0.38
N° tap	-4.08	0.04	-0.89	0.38
Tap rate (N° tap/s ²)	6.57	0.26	2.44	0.025*
Sex				
Tap (s)	0.00	0.03	0.75	0.45
Inter-tap Interval (s)	0.00	0.03	-0.83	0.41
N° tap	3.61	0.01	0.48	0.63
Tap rate (N° tap/s ²)	-4.17	0.04	-0.85	0.40

*statistical significance at p<0.05

the substrate itself. This connection was essential for accurately capturing the vibrations generated during toe tapping. Moreover, consistent with the findings presented by Claessens et al. (2020), we observed that the substrate hardness was not related to the occurrence of toe tapping behavior in *D. truncatus*. Because *D. truncatus* is a terrestrial species (Kahn et al. 2016), we did not consider the use of different substrates relevant, nor do we believe

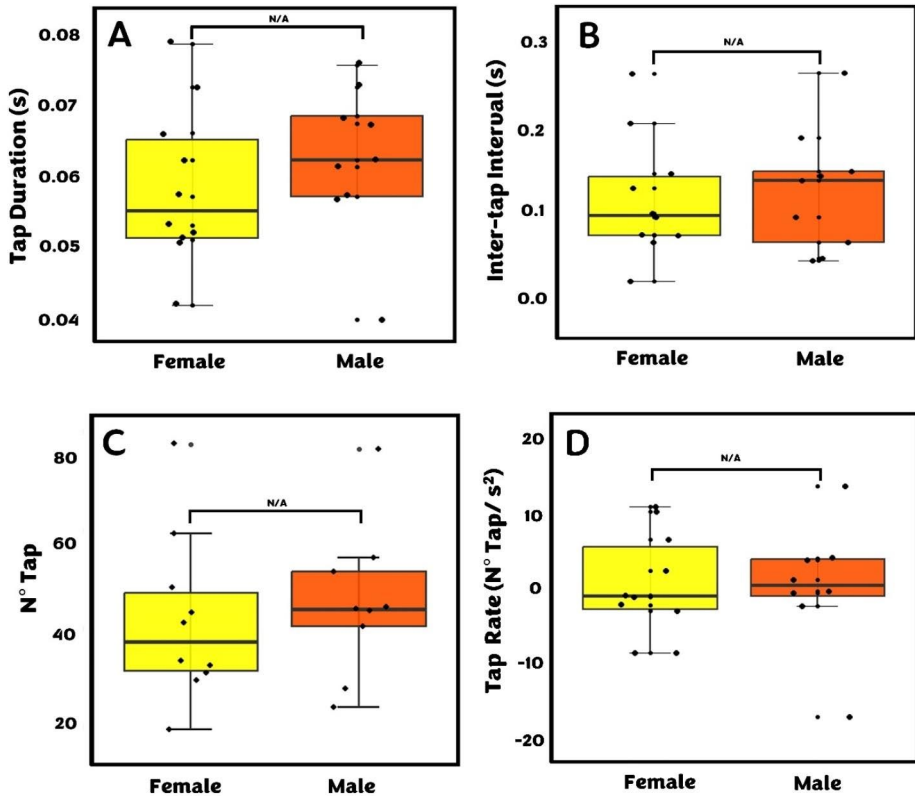


Fig. 6 Inter-sexual comparison of temporal vibrational parameters of toe tapping behavior of *D. truncatus*. (A) Tap duration (s), (B) Inter-tap interval (s), (C) N°. Tap and (D) change in Tap rate

they influenced our results. However, it is important to note that spectral parameters may be influenced by substrate type, whether natural or artificial (Hill 2009; Caldwell et al. 2014). Furthermore, with a percussive signal the frequency spectrum is determined largely by the substrate. Therefore, we focused on characterizing the temporal parameters, allowing us to gain a better understanding of the behavior and vibrational composition of toe tapping in *D. truncatus*.

We obtained an average recording time of 3.04 ± 2.18 min (ranging from 0.75 to 8.55 min), capturing the vibrations generated during *D. truncatus* foraging-related toe tapping behavior. These recordings enabled us to analyze and study the vibrational properties associated with this behavior in detail. A study conducted by Schulte and König (2023) with *D. auratus* recorded video recordings of taps for an average time of 4:52 min. Although the duration of their recordings was slightly longer than ours, both studies provide valuable information on toe tapping behavior in different dendrobatid species. The results obtained from the vibrational temporal parameters reveal characteristics of toe tapping behavior. On average, the duration of taps indicates that they are brief events, while the inter-taps interval suggests the presence of both short and long intervals between taps, and the number of taps

exhibited high variance. It is important to consider that these values represent the average and variability present in the data, which may be related to individual variations.

Some *D. truncatus* individuals exhibit a specific pattern of progressive acceleration in the display of toe tapping behavior in their sequence of attacks on prey during foraging. This increase in the tap rate may be analogous to the foraging behavior observed in bats using echolocation (Griffin 1958; Britton and Jones 1999; Schnitzler and Kalko 2001; Schnitzler et al. 2003). Where search calls are emitted in distinct phases (Griffin 1958; Britton and Jones 1999); in the terminal phase, the repetition rate of pulses or buzzes increases (Griffin 1958; Thomas et al. 2004), and the interval between pulses decreases just before capturing prey (Britton and Jones 1999; Schnitzler et al. 2003). Similarly, analogous foraging behavior has been observed in dolphins (Thomas et al. 2004), beaked whales (Johnson et al. 2006), sperm whales (Miller et al. 2004), and porpoises (DeRuiter et al. 2009). These species produce clicks at a higher frequency than average just before an attack on prey (Madsen et al. 2002). This pattern is considered an indicator of feeding success in toothed whales (DeRuiter et al. 2009; Madsen et al. 2002). All the examples mentioned share the similarity of increasing the frequency of pulses or clicks and decreasing their duration in the terminal phase, such as our results show, accelerated taps were displayed more just before to attack on prey. Hagman and Shine (2008) reported that toe tapping rates vary within individuals but did not indicate whether the rate increased immediately before an attack. Studies for understanding of the ecological implications of tap acceleration display during the *D. truncatus* foraging, would reveal its possible function and how this could be influencing the predator-prey interaction.

Dendrobatas truncatus individuals with larger toes tend to perform more accelerated taps. This relationship between toe morphology and toe tapping behavior suggests the existence of ontogenetic changes in this behavior. According to Schulte and König (2023), this can be attributed to the less pronounced impact of the toe strike on the substrate by juvenile individuals, due to their smaller body size. These findings highlight the importance of considering ontogeny in the study of toe tapping behavior and its relationship with toe morphology in different dendrobatid species. Furthermore, our findings regarding the relationship between vibrational temporal parameters and body size (SVL) do not differ from those presented by Claessens et al. (2020). They postulated that there was no significant correlation between toe tapping probabilities and the body size in dendrobatids species. Therefore, it is necessary to further explore the relationship between morphological variables and toe tapping behavior, which appears to be directly associated with the length of the third toe rather than the body size of the individuals.

Regarding feeding behavior, we found no differences between males and females of *D. truncatus* in relation to the vibrational temporal parameters of toe tapping behavior during foraging. Any changes in the expression of the toe tapping display, particularly in the selected vibrational parameters, could suggest that this behavior functions similarly for both sexes during foraging. Our results are consistent with studies on other dendrobatid species, such as *Epipedobates flavopictus*, where no differences were observed in feeding behavior or diet between sexes, suggesting that males and females hunt in equal proportions for daily energy acquisition (Pesarakloo and Hoseinabad 2023). However, in some cases, feeding behavior differences between sexes can be found in the size and volume of prey consumed (Atencia-Gándara et al. 2021). In *D. truncatus* there is no apparent sexual dimorphism in toe tapping. Nevertheless, the toe tapping behavior of *D. truncatus* could be influenced by

the behavioral context, such as reproduction (Landestoy and Ortiz 2015; Starnberger et al. 2018; Barquero and Arguedas 2022).

In our research, we focused on describing the vibrational temporal parameters of the toe tapping behavior in *D. truncatus*, which was exclusively observed in the presence of prey. These observations lead to the possibility that the vibrations generated by toe tapping could serve as vibrational signals within the context of predator-prey interactions. This aligns with hypotheses proposed by Sloggett and Zeilstra (2008), Hagman and Shine (2008), Erdmann (2017), Claessens et al. (2020), and Schulte and König (2023) regarding the function of this behavior. Future studies exploring this possibility would contribute to a more comprehensive and specific understanding of the adaptive value of toe tapping behavior in anurans.

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Declarations

Competing interests The authors declare no competing interests.

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