Description of the echolocation pulses of insectivorous bats with new records for Southwest Colombia

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Abstract

Despite the high diversity of bats in neotropics, traditional methods such as mist nets, harp traps and roost detection have limitations in capturing that diversity in a landscape, with most detected species restricted to those that forage in the undergrowth or enclosed spaces. Therefore, acoustic records become a tool that complements and enhances the efforts to get more complete bat inventories while avoiding alterations in usual foraging activities and disruption in their life cycles. This study describes the acoustic parameters (spectral and temporal variables) of the echolocation pulses of insectivorous bats to characterise different species of bats in Southwest Colombia acoustically. We recorded echolocation calls between December 2017 and May 2020 in the Andean and Pacific regions of the Department of Nariño. We analysed 81 sequences of echolocation calls from eight bat species belonging to three families: Vespertilionidae, Molossidae and Emballonuridae. We perform recordings on free-flying bats with identity corroboration by capture for recording in flight rooms and examination in the hand. *Myotis riparius* and *Lasiurus blossevillii* were recorded for the first time in the Nariño Department. *M. albescens*, *M. keaysi*, *M. riparius* and *L. blossevillii* (Vespertilionidae) had pulses of frequency modulated (FM) with a quasi-constant frequency (QCF) ending; *Molossus molossus*, *Tadarida brasiliensis* and *Promops centralis* (Molossidae) had pulses with constant frequency (CF) and QCF; and *Saccopteryx bilineata* (Emballonuridae) had pulses with QCF. This study contributes to the efforts to facilitate the identification of insectivorous bats of the Neotropics using the acoustic monitoring approaches, represents a reference to compare the acoustic studies in Southwestern Colombia and contributes to increasing our knowledge of the bat diversity in the region.

Keywords Acoustic monitoring · Bioacoustics · Vocalisations · Nariño

Introduction

Insectivorous bats are among the most diverse mammals in the Neotropical region (Solari and Martínez-Arias 2014). This group shows a broad variation in their diets,

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morphology and ecological adaptations (Baker et al. 2012). Additionally, its echolocation system is based on sounds produced by the larynx (Davies et al. 2013). These adaptations allow insectivorous bats to cover a range of habitats from the lowlands to high mountain forests (Patterson et al. 2003; Meyer and Kalko 2008). However, there is an overall lack of natural history information on Neotropical insectivorous bats as well as difficulties in their appropriate taxonomic identification due to acoustic similarities among species with phenotypic plasticity (Obrist 1995), hybridisation processes and cryptic groups (Walters et al. 2013) or with species showing a large amount of intra and interspecific variation (Kalko and Schnitzler 1993; Jung et al. 2014).

The specialised echolocation system allows bats to move, orient and obtain food in different habitats (Schnitzler and Kalko 2001). Ecological studies have traditionally employed conventional capture methods such as mist nets or harp traps (Kunz 1988; O'Farrell and Miller 1997). The feeding habits of bats may bias the records with traditional methodologies. For instance, phyllostomid bats make better use of lower vegetation strata, increasing the capture rates in mist nets (Simmons and Voss 1998). Meanwhile, since some insectivorous species use the upper strata of the vegetation to catch their prey in flight, the rates of mist net captures are reduced in the understory. However, these insectivorous bats are efficiently recorded using ultrasonic detectors (Kalko et al. 2008). Therefore, the analysis of echolocation calls by the measuring of its acoustic spectro-temporal parameters has supported the insectivorous bat species identification in several studies (Fullard et al. 1994; Rautenbach et al. 1996; McCracken et al. 1997; O'Farrell and Gannon 1999; Ochoa et al. 2000; Russo and Jones 2002; Gillam and McCracken 2007). More specifically, these identifications can be carried out by analysing of the echolocation pulses in the search phase (set of pulses emitted by the bat when it moves or looks for food). It is characterised by presenting parameters with stereotypical values, which means that variables such as initial and final frequencies, pulse duration and interpulse interval, among others, remain little variable. For this reason, the pulses emitted during the search phase are used to describe and identify different species (Fenton and Bell 1981).

More than 50% of the world's bat families are represented in Colombia (Solari et al. 2013), which includes 72 genera and 205 species (Ramírez-Chaves et al. 2016). The Department of Nariño is an area of high bat species richness (Ramírez-Chaves and Noguera-Urbano 2010), with 23 species of insectivorous bats reported (Calderón-Leytón et al. 2020). To date, field studies in Nariño have focused on the analysis of plant-bat interactions (Cabrera-Pantoja 2007), species inventories (Ramírez-Chaves and Noguera-Urbano 2010), activity patterns and species abundance (Martínez 2007). Our study provides the first description of insectivorous bat echolocation calls for this region and contributes to building a bat sound library of the region, which may serve

as a reference to identify, validate and compare recordings from different species and localities.

Materials and methods

Study area

This study was conducted in eight localities of the Nariño Department in Colombia through an altitudinal gradient of 8 to 2668 m a.s.l. covering the Pacific region in the municipalities of Tumaco (Maragrícola farm), Barbacoas (Rio Ñambí Natural Reserve and Altaquer settlement) and Ricaurte (Pilispi settlement); and the Andean region in the municipalities of Puerres (Palos Verdes settlement), Pasto (Briceño settlement), El Peñol (San Antonio settlement) and Taminango (Remolino settlement) (Fig. 1; Table 1). Rainfall in the Pacific region is abundant throughout the year, varying from 2500 to about 7000 mm, with temperatures ranging from 24 to 28 °C. Meanwhile, the Andean region's rainfall varies from 1000 to 6000 mm annually and temperatures from 6 to 24 °C (Solarte et al. 2007).

Capture methods and species identification

Fieldwork was carried out between December 2017 and May 2020. We captured bats using ten mist nets (8 or 12 m long by about 2 m high) placed in the understory, the canopy and where bats shelter. We sampled 3 days per locality between 18:00 and 06:00 h for a total sampling effort of 3925 net-h. To increase detectability, we include different habitat types (open areas near water bodies and pathways). The captured individuals were identified up to the species level using taxonomic keys and bibliographic reference materials (e.g., Gardner 2007; Díaz et al. 2016) and original descriptions of species groups. Specimens of each species were deposited in the Mammal Collection of the Museum of Vertebrate Zoology at the Universidad de Nariño (hereafter PSO-CZ): *Myotis albescens* (5), *Myotis keaysi* (1), *Lasiurus blossevillii* (1), *Myotis riparius* (2), *Molossus molossus* (10), *Tadarida brasiliensis* (2), *Promops centralis* (1) and *Saccopteryx bilineata* (3).

Recording echolocation pulses

In order to get a first approach to the bat diversity in the area, we identified all the captured individuals at the species level as follows (number of individuals per species in brackets): *M. albescens* (5), *M. keaysi* (1), *L. blossevillii* (1), *M. riparius* (5), *M. molossus* (10), *T. brasiliensis* (5) and *S. bilineata* (4). Later, each individual was placed inside a closed flight room (2 m long × 2 m wide × 2 m high). We set up a room with thin material (insect awning cloth) to avoid
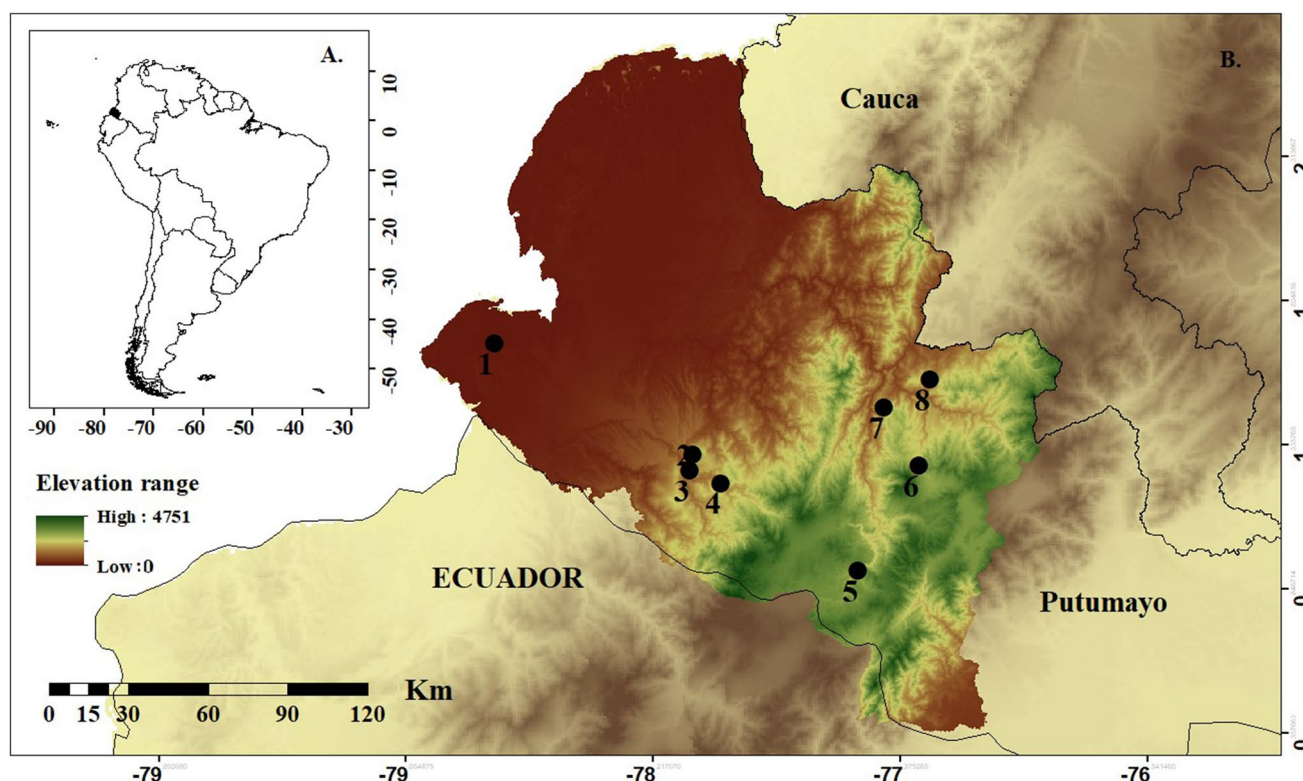
Fig. 1 Map of the study area. The Department of Nariño representing the Pacific and the Andean regions and sampled localities (shown as black dots; see details in Table 1) in an elevational gradient. (A) Department of Nariño in southwest Colombia in South America

Table 1 Localities where bats were captured to record echolocation pulses

N°	Locality	Municipality	Latitude	Longitude	Elevation	Land-cover/land-use
1	Mar Agrícola station	Tumaco	1.6733333	−78.7525	8	Tropical wet forests with secondary forests, anthropic intervention, open areas, mangroves, estuaries and artificial water bodies (Delgado-Chaves et al., 2014)
2	Rio Ñambi Natural Reserve	Barbacoas	1.3332778	−78.08329972	1654	Subtropical rainforests with primary and secondary forests with a high density of epiphytes (Gutiérrez-Zamora et al., 2004)
3	Altaquer	Barbacoas	1.24725	−78.09130556	1016	Subtropical rainforest with secondary forests and cultivated landscapes (Alcaldía Municipal Barbacoas, 2005)
4	Pilispi	Ricaurte	1.2047	−77.98539972	1492	Subtropical wet forest with cultivated areas (Canticús et al., 2006)
5	Palos Verdes	Puerres	0.9072778	−77.52208333	2668	Warm temperate wet forests with anthropic intervention and cultivated areas containing commercial timber species (Alveiro and Fundación Patia, 2000)
6	Briceño	Pasto	1.2651	−77.31499972	2442	Warm temperate moist forest with highly urbanised areas
7	San Antonio	El Peñol	1.4601	−77.43259972	1395	Tropical dry forests with anthropic intervention and cultivated areas
8	Remolino	Taminango	1.5565	−77.2772	1560	Tropical dry forests with anthropic intervention and open areas

The locations are numbered sequentially, coordinates are given in decimal degrees and elevation above sea level is presented in meters

sound bouncing and large amounts of echo in recordings since more porous and shiny fabrics may reduce the reflection of several frequencies (Estrada-Villegas et al. 2012). Once the individual was quiet, it was left alone in the flight room, and its vocalisations were recorded continuously for around 30 min. This allowed to generate several files per individual when flying inside the flight room. Additionally, we get recordings of free-flying bats under natural conditions (Zamora et al. 2020) from 6:00 p.m. to 6:00 a.m. Individuals were recorded in real-time with the Echo Meter EM3 recorder (Wildlife Acoustics, Inc, Maynard, MA, USA), configured with a sampling frequency of 250 kHz in WAV format at a 16-bit resolution.

Finally, for the acoustic analysis and the descriptions of the calls, we only selected recordings of echolocation pulses emitted by individuals in free flight only in the study area selected. We used flight room recordings to determine distinguishable traits and patterns as a reference to confirm species identification of free-flying individuals, but they were not used in the analysis. For example, in the case of *M. molossus*, this species is characterised by exhibiting alternating and frequency-modulated (FM) pulses that can promote longer sounds to allow for changes in FM (Marín 2009). This property allowed the verification that each species emitted characteristic pulses that were distinguishable from other species.

To deal with pseudo-replication problems that would have arisen from including several pulses from the same individual in the analysis in a non-controlled manner, we choose sequences from individuals recorded in different sampling points in each type of vegetation, recorded on separate days and times, following Orozco-Lugo et al. (2013). We ensure no pseudo-replication in echolocation call sequences since the bat species recorded show differences in their activity patterns between individuals, demonstrating periods of bimodal activity, unimodal activity or some peaks in activity during the night (Rivero-Monteagudo and Mena 2023). Additionally, this activity can vary according to sex, reproductive condition, energy requirements and time of the year (O'Donnel 2002). We identify free-flying species through comparisons with publications and the library of echolocation calls of bats from Ecuador (Rivera-Parra and Burneo 2013).

Acoustic analyses

We selected a minimum of ten sequences for each species for the analyses. Each sequence represents a vocalisation emitted by an individual. We followed the call classification by Estrada-Villegas et al. (2012). We assumed a sequence to be a regular succession of calls, the latter being a discrete sound emission equivalent to a series of echolocation pulses. Therefore, we selected five pulses in the search phase of

each sequence. These pulses were selected because they had the highest energy in decibels (generally the fundamental frequency, where the bat concentrates the greatest amount of energy during the emission of the echolocation pulses). Pulses were determined using a zero-crossing analysis in the Kaleidoscope Pro v.4.5.0 software (Wildlife Acoustics, Inc, Maynard, MA, USA). We generated spectrograms using a Hamming window, a 256 FFT window size and a 50% overlap.

We quantified nine structural features of echolocation pulses (Rivera-Parra 2011; Martinez-Medina et al. 2021): (1) F_{start} (starting frequency of the selection being analysed for each of the five pulses), (2) F_{end} (the final frequency of the selection being analysed for each of the five pulses; it was selected from the point of the oscillogram where the amplitude increased or decreased in a monotonic way), (3) F_{min} (minimum full spectrum frequency, which is an estimate of the minimum signal frequency), (4) F_{max} (maximum full spectrum frequency, which is an estimate of the maximum signal frequency), (5) F_{mean} (average full spectrum frequency, which is the mean spectrum power frequency weighted by amplitude), (6) F_{peak} (full spectrum peak frequency, which is the maximum spectrum frequency), (7) bandwidth (difference between F_{max} and F_{min}). These frequencies were measured in kilohertz (kHz) (Fig. 2). We measured variables 1 through 6 using the "spectral analysis" function in Kaleidoscope. In addition, we measured two time-related parameters (milliseconds, ms): (8) duration (time between the start point and the pulse endpoint) and (9) interval (difference between the initial time of the first and second pulses).

Statistical analysis

We obtained descriptive statistics such as the mean and standard deviation for each spectral and temporal variable from free-flying bat recordings (five pulses of each of the ten sequences per species). Subsequently, we performed a discriminant function analysis (DFA) based on the different species of bats belonging to Vespertilionidae, Molossidae and Emballonuridae. This multivariate statistical technique, using Bayes' theorem, allows us to analyse whether there are significant differences between groups of objects with respect to a set of variables measured on them. In the case of the prior probability, it indicates the probability that any observation belongs to a class, in this case, the eight recorded species of bats. The variables used were F_{start}, F_{end}, F_{min}, F_{max}, F_{mean}, F_{peak}, bandwidth, duration and interval. The standardised discriminant function coefficients were used to determine the contribution each variable made to the ability of discriminant function analysis to classify calls (Rivera-Parra and Burneo 2013; Borcard et al. 2014).
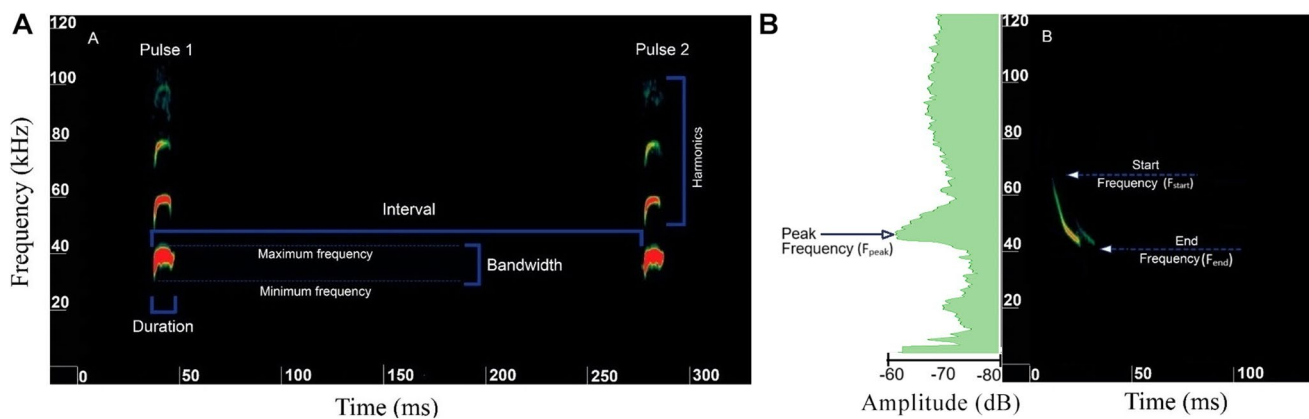
Fig. 2 Spectrogram of echolocation calls from **A** *S. bilineata* and **B** spectrogram with power spectra of echolocation calls from *L. blossevillii*, showing the acoustic parameters measured and analysed in this study. The colour intensity corresponds to the signal's amplitude at a given frequency and at a given point in time

Results

We obtained a total of 81 sequences of echolocation calls coming from 81 free-flying individuals from the family Vespertilionidae (*Myotis albescens* (10), *M. keaysi* (10), *M. riparius* (10) and *Lasiurus blossevillii* (10)), Molossidae (*Molossus molossus* (10), *Tadarida brasiliensis* (10) and *Promops centralis* (11)) and Emballonuridae (*Saccopteryx bilineata* (10)). For the flight room recordings, we obtained a total of 80 sequences coming from 31 individuals from all species except *P. centralis* since it was not recorded in the flight room considering the evidence of the flight room consequences on high variation in their pulses and recommendations to avoid using these methods in species adapted to open areas (see Mora et al. 2004; Martinez-Medina et al. 2021; Table 2). However, the identity of this species was determined by the detection of its shelter and the manual identification under the skin and skull of each species recorded in this study.

Vespertilionidae

The species belonging to this family presented FM echolocation pulses. The species *L. blossevillii* recorded in San Antonio (El Peñol) (F_{start} 63.77 ± 4.77, F_{end} 37.45 ± 1.05, duration 4.52 ± 0.31 and interval 52.4 ± 2.83) presented the lowest frequency range in its pulses. In contrast, *M. keaysi* (F_{start} 109.05 ± 2.35, F_{end} 57.35 ± 0.66, duration 3.48 ± 0.33 and interval 55.15 ± 9.47) of the subfamily Myotinae, (Río Ñambí Natural Reserve, Barbacoas) presented the highest F_{start} followed by *M. albescens* (F_{start} 103.29 ± 6.44, F_{end} 38.05 ± 2.56, duration 2.51 ± 0.28 and interval 72.1 ± 4.99) recorded in Palos Verdes (Puerres) and *M. riparius* (F_{start} 99.94 ± 5.97, F_{end} 46.93 ± 0.61, duration 4.46 ± 0.27 and interval 65.75 ± 1.89) (Ricaurte) which had the lowest F_{start} and F_{end} values of this subfamily (Table 2; Fig. 3).

Molossidae

We identified echolocation calls of three species (Fig. 4). *M. molossus* (F_{start} 32.51 ± 0.69, F_{end} 24.35 ± 0.92, duration 9.90 ± 2.04 and interval 234.8 ± 1.17) recorded in El Remolino (Taminango) exhibited pulses of FM. Additionally, this species presented alternated pulses (i.e., low-frequency pulses followed by high-frequency pulses). *T. brasiliensis* (F_{start} 30.3 ± 1.96, F_{end} 22.24 ± 1.64, duration 15.04 ± 2.05 and interval 319.5 ± 8.17) recorded in Pilispi (Ricaurte) presented constant frequency (CF) pulses with the lowest slope that is exhibited at the end of the pulse. *P. centralis* (F_{start} 19.04 ± 1.31, F_{end} 28.07 ± 1.13, duration 7.34 ± 1.52 and interval 261.1 ± 8.08) (Briceño, Pasto) presented low quasi-constant frequency (QCF) calls. The start frequency was lower than the end frequency, with the highest energy in the first harmonic (Table 2).

Emballonuridae

We recorded *Saccopteryx bilineata* (F_{start} 31.21 ± 0.21, F_{end} 43.45 ± 0.24, duration 8.11 ± 0.0004 and interval 128.1 ± 0.003) at the Maragrícola farm (Tumaco). We also detected its refuges and captured and collected three specimens deposited in the PSO-CZ. Echolocation calls were narrowband and multi-harmonic pulses with QCF (Fig. 5). F_{max} was present in the second harmonic (Table 2). None of the pulses of the ten sequences showed alternation, even when feeding buzzes were recorded.

Table 2 Characteristics of calls of bat species by two methods: free-flying and flight room

Species	Type	Inds	Seq	np	F_{start}	F_{end}	F_{min}	F_{max}	F_{mean}	F_{peak}	DUR	INT	BW
Recording method: free flight													
M. albescens	P1	10	10	50	103.29±6.44	38.05±2.56	37.96±1.86	63.22±3.67	54.64±3.91	50.45±1.35	2.51±0.28	72.1±4.99	25.26±4.45
M. keaysi	P1	10	10	50	109.05±2.35	57.35±0.66	58.06±2.24	72.68±9.92	69.13±4.88	62.92±3.04	3.48±0.33	55.15±9.47	14.58±8.90
M. riparius	P1	10	10	50	99.94±5.97	46.93±0.61	46.29±0.48	61.04±2.87	58.64±3.71	52.28±1.33	4.46±0.27	65.75±1.89	14.74±2.73
L. blossevillii	P1	10	10	50	63.77±4.77	37.45±1.05	38.04±0.61	52.4±2.83	46.16±1.45	42.79±0.94	4.52±0.31	52.4±2.83	14.36±2.45
M. molossus	P1	10	10	50	32.51±0.69	24.35±0.92	24.046±0.72	34.10±0.99	28.98±0.55	29.51±0.37	9.90±2.04	234.8±1.17	10.06±1.23
	P2			50	37.77±1.09	29.65±0.38	29.33±0.53	37.00±0.34	33.69±0.23	34.22±0.21	12.77±0.001	239.21±5.48	7.67±1.61
T. brasiliensis	P1	10	10	50	30.3±1.96	22.24±1.64	22.10±1.21	29.76±1.98	25.21±2.41	25.21±2.28	15.04±2.05	319.5±8.17	7.74±2.01
P. centralis	P1	11	11	55	19.04±1.31	28.07±1.13	19.18±1.87	28.23±0.93	23.57±1.21	23.59±1.21	7.34±1.52	261.1±8.08	9.05±2.13
S. bilineata	H2	10	10	50	31.21±0.21	43.45±0.24	30.30±0.14	43.80±0.11	38.92±0.03	39.09±0.03	8.11±0.0004	128.1±0.003	12.24±0.44
	H3			50	35.01±2.42	58.1±1.31	39±1.29	53.66±0.96	47.83±0.474	47.95±0.37	7.81±1.30	129.6±3.78	14.64±1.39
Recording method: flight-rooms													
M. albescens	P1	5	20	100	113.92±4.10	37.50±2.073	45.70±1.26	66.12±6.57	60.63±6.07	54.73±6.71	2.16±5.168	65.47±2.88	20.42±3.17
M. riparius	P1	5	10	50	112.46±1.97	47.94±1.16	47.3±1.35	80.14±1.45	63.92±2.73	56.75±3.33	2.32±1.54	57.75±1.90	24.±2.69
M. keaysi	P1	1	10	50	127.47±0.59	59.46±1.54	64.92±7.07	78.98±7.21	76.18±4.37	69.66±5.28	1.03±0.26	81.67±1.60	14.06±1.34
L. blossevillii	P1	1	10	50	70.87±3.45	35.15±2.23	37.99±2.81	60.9±3.79	56.76±3.55	46.97±2.87	2.72±0.49	59.93±3.43	24.36±1.55
M. molossus	P1	10	10	50	50.98±6.532	24.28±6.532	37.50±7.130	46.98±1.00	43.09±6.314	44.05±9.618	8.20±6.476	280.90±2.69	13.48±9.92
T. brasiliensis	P1	5	10	50	118.33±6.96	20.316±1.13	41.90±7.26	64.35±6.91	53.68±3.91	53.77±6.31	11.21±6.12	463.85±3.60	22.45±7.47
S. bilineata	P2	4	10	50	48.98±1.31	68.77±1.04	52.87±0.88	63.89±0.65	59.85±0.41	60.10±0.42	12.88±1.65	133.44±3.81	11.01±1.08

Type of pulse: P, pulse; H, harmonic. Inds, number of individuals; Seq, number of sequences; np, number of pulses. F_{start}, initial frequency; F_{end}, final frequency; F_{min}, minimum frequency; F_{max}, maximum frequency; F_{mean}, medium frequency; F_{peak}, peak frequency; DUR, duration of each pulse; INT, interval between pulses; BW, bandwidth. Values are shown as mean and standard deviation
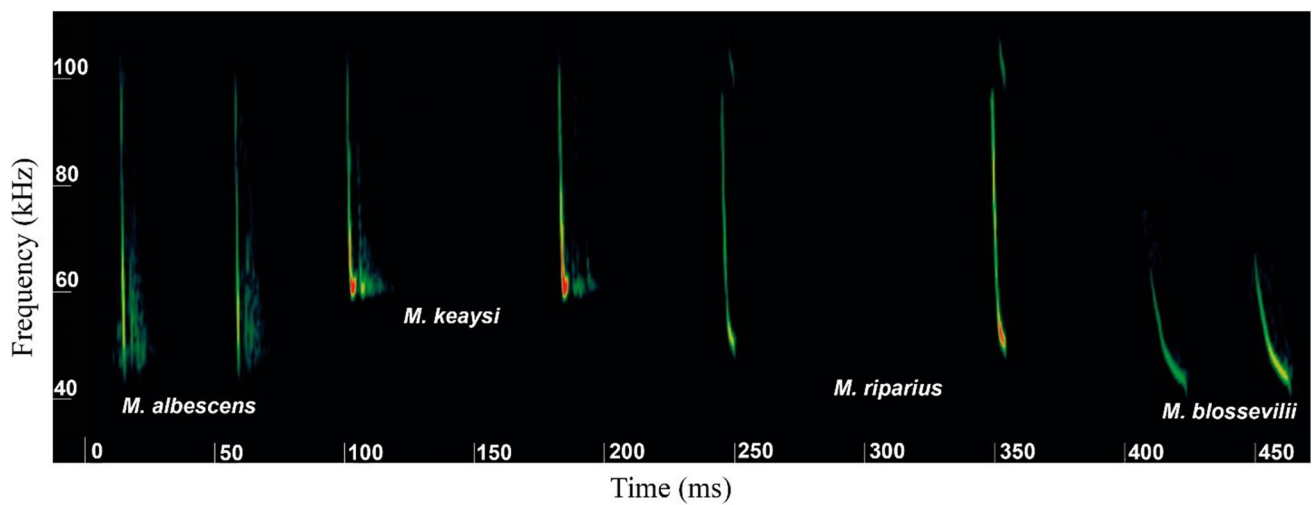
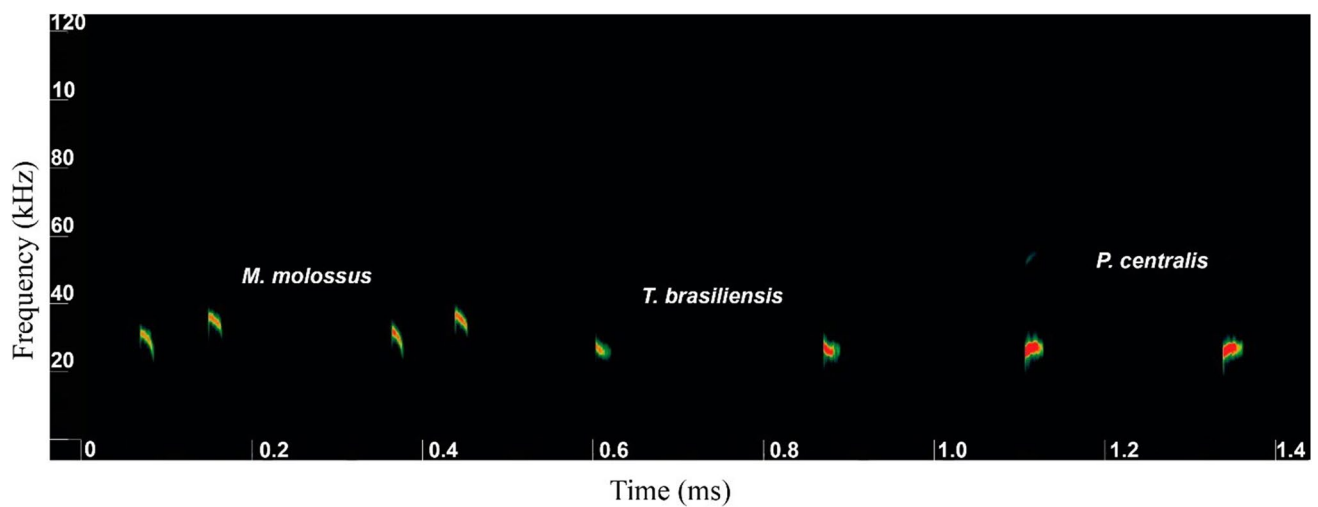**Fig. 3** Spectrogram of the search phase calls of free-flying species, family Vespertilionidae

Fig. 4 Spectrogram of the search phase calls of free-flying species, family Molossidae
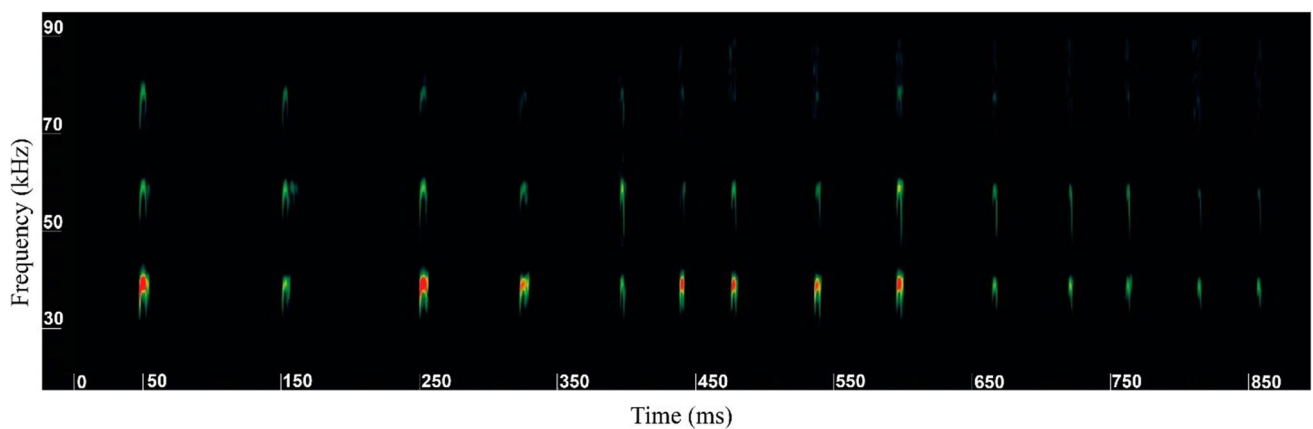

Fig. 5 Spectrogram of the search phase calls of free-flying *Saccopteryx bilineata*

Differences between temporal and spectral variables

Our results show that the level of accuracy of the DFA performed with four species of the Vespertilionidae family, three species of the Molossidae family and one *Emballonurid* species was high (93.25%, $P < 0.05$). The first discriminant function accounted for 68.67% of the variation in the data, while the second function accounted for 24.58% of the variation (Fig. 6; Table S.1). Temporal and spectral features (F_{start}, F_{max} and bandwidth) were the most important features to differentiate the eight insectivorous bat species recorded in our study (Table S.2).

Discussion

In this study, we characterised the echolocation calls of eight species of insectivorous bats of the Vespertilionidae, Molossidae and Emballonuridae families from Southwest Colombia. *M. riparius* and *L. blossevillii* are recorded for the first time in the Department of Nariño. Even though both species have been recorded in other locations in Colombia, we described in detail the spectro-temporal parameters of their pulses. Considering the results derived from the statistical analyses of the spectral and temporal variables in this study, it is crucial to highlight the challenge of making direct comparisons with existing literature. This difficulty arises from the fact that, up to this point, not all authors have comprehensively examined spectral and temporal variables. Instead, a partial focus has been common, with some
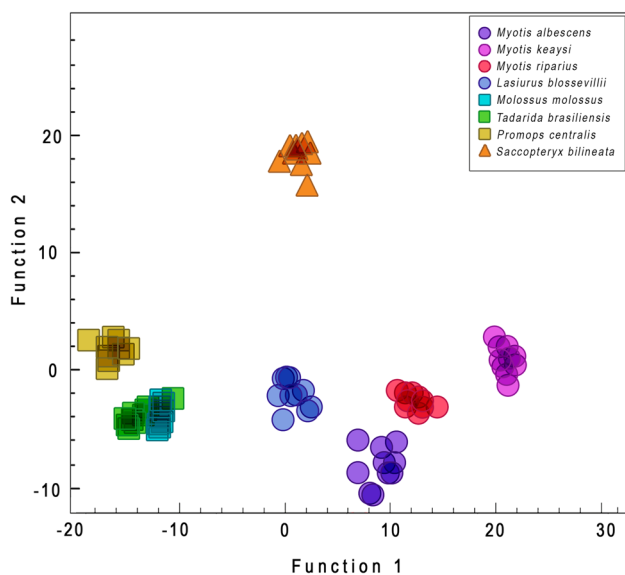

Fig. 6 Discriminant function analysis carried out with eight species of bats belonging to the Vespertilionidae, Molossidae and Emballonuridae families

emphasising specific variables such as F_{start}, F_{end}, F_{max}, duration and interval in their analyses.

Vespertilionidae

It should be noted that although the general structure of the echolocation pulses in the search phase recorded in free-flight is like that reported in the literature, it is necessary to understand that the spectral and temporal parameters may or may not be like others found in works carried out in other countries. This may be due to the following: (1) the correlation between foraging areas and the structure of the acoustic signal (Neuweiler 1984; 1989); (2) the relationship between the type of habitat, the search strategy and the type of food (Kalko 1995); or (3) the body size of the coexisting species (Aldridge and Rautenbach 1987; Norberg and Rayner 1987). In general, the structure of the echolocation pulses for the Vespertilionidae family could be distinguished by the frequency modulated (FM) with an ending quasi-constant frequency (QCF), similar to what was recorded by O'Farrell and Miller (1999). According to Hase et al. (2018), the final variations in the pulses contain information on each individual's identity, allowing individuals to discriminate their pulses from both conspecific and heterospecific pulses.

The measurements of the spectral and temporal variables for the species *M. albescens* were different from those reported by other studies, indicating that this species has terminal frequencies ranging from 43 to 46 kHz (Surlykke and Kalko 2008; Estrada-Villegas et al. 2012; Arias Aguilar 2017). This variation of pulses within populations of the same species may be because they are located in different geographic regions, as well as the type of habitat and environmental conditions (Heller and Helversen 1989; Barclay and Brigham 2004; Ratcliffe et al. 2004, Jung et al. 2007). In previous studies, *Myotis keaysi* was reported to have short pulses (approximately 2.5 ms; Rydell et al. 2002). Contrastingly, we found that this species' pulses presented a duration between 3.15 and 3.8 ms. The difference in duration results from the challenges the bat faces in its natural environment. If these bats forage in open areas, they not only use longer pulses than individuals that fly in the understory but also have longer intervals between pulses, presumably to ensure that all echoes from the previous call are received before the next call is issued (Jones and Holderied 2007). Moreover, it is important to consider that variations in duration may be attributed to differences among the following: (1) individual bats; (2) recording conditions, including factors such as the distance between the bat and the microphone; and (3) adaptive adjustments associated with foraging habitats, such as proximity to obstacles and levels of acoustic noise (e.g., Kalko and Schnitzler 1993; Obrist 1995).

However, there were similarities in the F_{start} and the F_{end} and the structure of the echolocation pulses. These

similarities in the spectral variables may be explained by the fact that this species usually emits its most typical pulses when it flies in open areas (Rydell et al. 2002).

Regarding the echolocation pulses of *M. riparius*, we describe the presence of harmonics (not previously reported) and lower F_{max} values in contrast with those reported by Fenton et al. (1999; F_{max} values of 121.9 ± 3.1). These differences can be attributed mainly to the methodology used by the authors since they recorded this species in a permanent greenhouse made of mesh. Although this is a good option for recording vocalisations, it may not represent of the bat's vocalisations in their natural habitat. Our records of the *L. blossevillii* calls showed lower F_{max} and F_{min} values than those reported by other studies (see Kraker-Castañeda et al. 2013). The differences in these frequencies correspond to variations in the emission of echolocation signals due to the structural complexity of the areas where they fly (e.g., whether individuals forage at the understory or canopy). Kraker-Castañeda et al. (2013) recorded *L. blossevillii* in grassland and forest while we recorded the species over a body of water. *M. riparius* and *L. blossevillii* are new records for the Department of Nariño (Ricaurte and El Peñol, respectively). Although the echolocation pulses emitted by these species have already been described to differing degrees of detail (Fenton et al. 1999; Kraker-Castañeda et al. 2013), more studies are needed to help clarify taxonomic difficulties associated with the similarity of their vocalisations.

In Colombia, *M. riparius* has been recorded in Valle del Cauca and Boyacá departments (Gardner 2007), covering an altitudinal range of 50–150 and 100–1100 m, respectively (Moratelli et al. 2013). This species prefers wooded areas and forages along streams, rivers, trails and open areas (Simmons and Voss 1998). However, we recorded this species at 1492 m a.s.l. in an urbanised area. On the other hand, *L. blossevillii* is reported in humid and dry forests of the departments of Cundinamarca and Cauca (Gardner 2007) from 200 to 2600 m a.s.l. (Gonzalez et al. 2016). We recorded the species at 1395 m a.s.l. in San Antonio (El Peñol), but recent explorations throughout the Andean region in the Department of Nariño indicate that this species is also distributed in other localities such as the municipalities of Sotomayor, Guaitarilla and Samaniego (Arévalo-Cortés et al. unpublished data).

Molossidae

The family Molossidae exhibits excellent plasticity in the structure of its echolocation pulses in the search phase, which implies frequency changes and frequency alternations (Mora et al. 2004; Gillam and McCracken 2007). According to Jung et al. (2014), the species *M. molossus* can present two pulses, a low frequency pulse followed by a higher frequency pulse, which is in line with our results (Fig. 4).

Alternating their frequencies will allow a bat to distinguish between echoes from different pulses emitted. Pairing may allow the bat to process the echoes of the first pulse while emitting the second. This pattern could also present an advantage in prey capture (Jung et al. 2014).

In several studies carried out on the species *T. brasiliensis*, values of F_{start} (Jung et al. 2014; Krauel et al. 2018), F_{max} (Ratcliffe et al. 2004; Briones-Salas et al. 2013) and duration (Gillam and Montero 2016) are similar to those we report here, supporting the idea of the differences between the variables for this species not related to habitat structure (Ratcliffe et al. 2004). Even though Molossidae species exhibit high plasticity in their echolocation calls, the spectral and temporal variables of *P. centralis* presented distinctive pulses, as has been reported in other studies (Jung et al. 2014; Froidevaux et al. 2020). Regardless that *P. centralis* may present a flexible adjustment of the echolocation system to face sensory challenges in the environment, the identity of each echolocation call was preserved.

Emballonuridae

The family Emballonuridae includes species of insectivorous bats that generally feed in open areas, on water surfaces or at the edges of vegetation (Jung et al. 2007). This foraging pattern suggests that the echolocation pulses of the species belonging to this family cover a small bandwidth and generally contain a QCF with certain species adding an FM component (Kalko and Schnitzler 1998; Jung et al. 2007; MacSwiney et al. 2008). In the case of *S. bilineata* echolocation pulses, the second harmonic contains higher energy than the first one.

S. bilineata also presented slightly lower frequencies, which differs from the results obtained by Biscardi et al. (2004; F_{max} values of 43.8 ± 0.3 kHz; F_{min} values 39.2 ± 2.1 kHz). Ratcliffe et al. (2011) reported that this species uses two different pulse sequences, a first pulse at 45 kHz followed by a second pulse at 48 kHz (Barclay 1983; Jung et al. 2007). This information differs from our findings. Although we recorded the echolocation calls of this species through methods such as flight rooms and free flight, we did not observe the vocal behaviour of different sequences of pulses since the frequencies were maintained uniformly over time in a sequence and did not show doubling alternation in the pulses (Fig. 5). It should be noted that we corroborate the identification of this species with the collected individuals (Table 3) and its external and cranial morphology.

According to Aldridge and Rautenbach (1987), the fact that this species does not present two different pulse sequences may be due to the correlation between the foraging areas and the structure of the acoustic signal. For instance, environmental selection pressures such as local microclimate and vegetation structure can influence the

Table 3 List of specimens of the families Vespertilionidae, Molossidae and Emballonuridae collected in the Department of Nariño and deposited in the Mammal collection of the Museum of Vertebrate Zoology at the Universidad de Nariño (National Register Number: PSO CZ-041)

Catalogue number	Event date	Scientific name	Municipality	Locality
MAST0928	19/12/2017	*Molossus molossus*	Barbacoas	Altaquer
MAST0929	19/12/2017	*Molossus molossus*	Barbacoas	Altaquer
MAST0930	19/12/2017	*Molossus molossus*	Barbacoas	Altaquer
MAST0931	19/12/2017	*Molossus molossus*	Barbacoas	Altaquer
MAST0932	19/12/2017	*Molossus molossus*	Barbacoas	Altaquer
MAST0933	19/12/2017	*Molossus molossus*	Barbacoas	Altaquer
MAST0934	22/02/2018	*Myotis albescens*	Puerres	Palos Verdes
MAST0935	22/02/2018	*Myotis albescens*	Puerres	Palos Verdes
MAST0936	22/02/2018	*Myotis albescens*	Puerres	Palos Verdes
MAST0937	22/02/2018	*Myotis albescens*	Puerres	Palos Verdes
MAST0938	22/02/2018	*Myotis albescens*	Puerres	Palos Verdes
MAST0939	16/04/2018	*Molossus molossus*	El Peñol	San Antonio
MAST0940	16/04/2018	*Molossus molossus*	El Peñol	San Antonio
MAST0941	16/04/2018	*Molossus molossus*	El Peñol	San Antonio
MAST0942	16/04/2018	*Lasiurus blossevillii*	El Peñol	San Antonio
MAST0943	16/03/2018	*Saccopteryx bilineata*	Tumaco	Mar Agrícola station
MAST0944	16/03/2018	*Saccopteryx bilineata*	Tumaco	Mar Agrícola station
MAST0945	16/03/2018	*Saccopteryx bilineata*	Tumaco	Mar Agrícola station
MAST0946	17/03/2018	*Tadarida brasiliensis*	Ricaurte	Pilispi
MAST0947	17/03/2018	*Tadarida brasiliensis*	Ricaurte	Pilispi
MAST0948	17/03/2018	*Molossus molossus*	Ricaurte	Pilispi
MAST0949	17/03/2018	*Myotis riparius*	Ricaurte	Pilispi
MAST0950	17/03/2018	*Myotis riparius*	Ricaurte	Pilispi
MAST0951	18/03/2020	*Promops centralis*	Pasto	Briceño
MAST0952	06/04/2018	*Myotis keaysi*	Barbacoas	Río Ñambí Natural Reserve

spectro-temporal structure of echolocation calls. Ratcliffe et al. (2011) found that *S. bilineata* produces sequences of pulses at a single frequency when it is close to its perching site while it emits pulses of alternating frequency at the feeding site. However, we found the species to emit pulses at the same frequency, regardless of whether prey was detected or captured, suggesting that this species emits pulses of the same frequency when it is in open areas as we recorded it in the Maragrícola farm, Tumaco, which contains open areas with artificial water bodies.

Differences between temporal and spectral variables

The results of the DFA are consistent with the results of Rivera-Parra (2011), in which the species are separated by the variables F_{start}, F_{max} and bandwidth (Table S.2). While these differences represent diverse foraging strategies, habitat preferences and phylogenetic relations between the families, they are consistent with an adaptation of signal design to foraging habitat (Surlykke and Kalko 2008). For instance, low frequencies, short bandwidths, long durations and extended intervals commonly occur in bats that forage in open spaces (Siemers et al. 2001). Meanwhile, high

frequencies, long bandwidths, short durations and narrow intervals widely occur in bats that forage in cluttered spaces (Jones and Holderied 2007).

It is essential to note that the sampling areas in this study exhibit diverse natural and environmental conditions. Consequently, the analysis of certain spectral and temporal variables of echolocation pulses (F_{max}, F_{mean} and duration) in low-lying areas tends to yield higher values. This is attributed to the predominantly open nature of these spaces, where both the inherent echoes and background noise are diminished. As a result, there is an enhanced specificity in the detection and capture of prey (Schnitzler and Kalko 2001; Estrada-Villegas et al. 2012). In contrast, Schnitzler and Kalko (2001) and Estrada-Villegas et al. (2012) assert that species often emit pulses at lower frequencies with longer wavelength ranges in areas characterised by obstacles. This adaptation is employed to facilitate the detection of sounds from the environment with greater amplitude, particularly in environments where capturing prey involves dealing with various obstacles.

Although surveys have been carried out in Southwestern Colombia, studies on the chiropteran fauna still need to be included in this region. Traditional methods such as mist nets or harp traps have limitations in the diversity

estimation of insectivorous bats due to their low detection of species that forage in open areas and canopy. For this reason, it is necessary to complement existing survey methods with bioacoustics tools and analyse echolocation calls as a basis for the taxonomic identification of insectivorous bats (Pech-Canche et al. 2010; Martinez-Medina et al. 2021). Additionally, we suggest identifying bat roosts with the help of local communities to obtain more complete species inventories.

To date, only seven insectivorous species have been reported in the Department of Nariño: *Eptesicus brasiliensis* (Barbacoas), *E. andinus* (Barbacoas), *M. albescens* (Barbacoas and Tumaco), *M. keaysi* (Barbacoas and Ricaurte), *M. nigricans* (Barbacoas and Tumaco), *M. oxyotus* (Mallama) and *Rhogeessa io* (Leiva and Taminango) (Ramírez-Chaves and Noguera-Urbano 2010). Until 2018, only 29 specimens corresponding to the Vespertilionidae family had been deposited in the PSO-CZ museum (Calderón-Leytón 2017; Calderón-Leytón et al. 2020). With this work, we contribute new information about the diversity of bats of the family Vespertilionidae that inhabit the ecosystems in the southwestern region of Colombia. Here, we report the first observations in Nariño of the species *M. riparius* (Ricaurte) and *L. blossevillii* (El Peñol) supported with audio recordings and skin vouchers with contributions to the acoustic libraries (regional and national) and an increase of 42 the number of Vespertilionidae specimens for the PSO-CZ. The lack of systematic sampling may explain why these species were not previously recorded in the region.

The information provided for the combination of several survey methodologies is essential to know the real biodiversity in our territories and understand their vulnerabilities. For instance, bats have been highly affected due inappropriate management by the local community to attend public health and agricultural issues, where the common solution is the indiscriminate extermination. This entails the loss of bat populations that fulfil functions for the maintenance of various processes that ensure the persistence of natural ecosystems; therefore, this project impacts and expands the conservation or research of wildlife because (i) it generates an expansion of the knowledge of the diversity of bats in the Andean region of the department of Nariño, (ii) proposes a baseline on the biological diversity of bats in the department, which may help compare with other biological groups and conducting vulnerability analysis due to climate change or the valuation of environmental services, (iii) is aware of local communities, considering the different ecosystem services bats provide and (iv) generates valuable knowledge for the conservation, management and manipulation of bats in Colombia.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13364-023-00734-x.

Data availability Acoustic files generated during this study were deposited in the regional library of sounds at the Universidad de Nariño -SONAR (see Table S3). A copy of these files is available in the acoustic public repository Xeno-Canto accessing to the following URL: https://xeno-canto.org/set/8577.

Declarations

Ethics approval This study followed the guidelines for the use of wild mammal species in research (Sikes and Bryan 2016) and was carried out under the permit for collecting wildlife species of biological diversity for non-commercial scientific research purposes provided by the regional environmental authority (CORPONARIÑO; Resolution No., 126—19/02/2015).

Competing interests The authors declare no competing interests.

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