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FREDERICO SIMÃO HINTZE DE OLIVEIRA

USO INTEGRADO DE MÉTODOS BIOACÚSTICOS E DE MODELAGEM ESPACIAL NA DISTRIBUIÇÃO DE QUIRÓPTEROS INSETÍVOROS NO NORDESTE DO BRASIL

Recife
2020

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Tese apresentada ao Programa de Pós-graduação em Biologia Animal, da Universidade Federal de Pernambuco, como parte dos requisitos parciais para obtenção do título de Doutor em Biologia Animal.

Área de concentração: Zoologia

Orientador: Prof. Dr. Enrico Bernard

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Aprovada em: 11/09/2020

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"- Bumblebee bat, how do you see at night?
- I make a squeaky sound that bounces back from whatever it hits. I see by hearing."

(Darrin Lunde)

"In conclusion, it appears that nothing can be more improving to a young naturalist, than a journey in distant countries."

(Charles Darwin)

RESUMO

Os quirópteros representam a segunda ordem mais diversa de mamíferos, com mais de 1400 espécies descritas, e no Brasil é conhecida a ocorrência de 181 destas espécies. Todas desempenham um papel crucial na prestação de serviços dos ecossistemas, e utilizam ecolocalização para navegar e capturar as suas presas. A maioria exibe padrões de ultrassons diferenciados, permitindo o uso de metodologias acústicas para sua identificação e fazer estudos ecológicos, de distribuição e comportamento. Recentemente, também os modelos de distribuição de espécies (SDMs) têm tido grande importância no desenvolvimento de estudos de distribuição espacial e na conservação de espécies animais em todo o mundo. Porém, estes modelos podem não traduzir exatamente a distribuição das espécies, implicando uma urgente necessidade de validação em campo (validação *in situ*). Nesta tese, numa abordagem pioneira para o Brasil, procurou-se catalogar vocalizações de morcegos e utilizar o registro destes sinais para a validação *in situ* e refinamento de SDM's de morcegos insetívoros no nordeste brasileiro. Assim, este estudo objetivou utilizar métodos bioacústicos: (a) para inventariar e descrever vocalizações; (b) aumentar o conhecimento da distribuição; (c) como método de validação em campo de mapas de distribuição potencial; e (d) investigar a potencial cripticidade em espécies de morcegos no Brasil. Usando gravações previamente identificadas, testou-se primeiro a acurácia de softwares automatizados para a identificação acústica de morcegos brasileiros. Verificou-se que a acurácia dos softwares, assim como nível de concordância entre os softwares, são bastante baixas e impraticáveis no momento. Após um esforço de compilação de todas vocalizações conhecidas de espécies brasileiras, propus-me avaliar o uso da bioacústica em três possíveis aplicações práticas. Na primeira, avaliei-a como método adequado e não-invasivo para identificar quatro espécies cavernícolas, facilmente graváveis e identificáveis à saída de caverna. Concluindo que a bioacústica tem o potencial de reduzir consideravelmente os distúrbios causados pela pesquisa em colônias de morcegos. Na segunda, usando novos registros acústicos e técnicas de SDM, revisou-se a distribuição de *Promops centralis* na América do Sul (uma das espécies brasileiras menos capturadas em redes-de-neblina), expandindo-a em mais de 3,8 milhões de km^2. Nesse estudo foi também possível descrever um padrão incomum de vocalizações da espécie, com indivíduos emitindo pelo menos três tipos de vocalização distintas e altamente variáveis. Numa última aplicação, pretendi utilizar a bioacústica para validar *in situ* mapas de distribuição potencial gerados através de SDM de seis morcegos neotropicais. Concluiu-se que, sem uma escolha adequada de parâmetros de modelagem e uma validação *in situ* independente, aumentaremos o risco de modelos imprecisos

impactarem a implementação de melhores políticas de conservação e planos de manejo das espécies. Nesta tese demonstrou-se a eficácia da bioacústica como meio não-invasivo para identificar e estender a distribuição, e validar mapas preditivos de espécies de difícil captura em regiões mal amostradas. Embora exija treinamento específico, criação de bibliotecas de vocalizações e de protocolos mínimos adaptados regionalmente, os resultados deste estudo demonstram inequivocamente que a bioacústica não pode mais ser negligenciada no estudo de morcegos no Brasil.

Palavras-chave: Bioacústica. Modelos de distribuição de espécies. Vocalizações. Diversidade críptica.

ABSTRACT

Bats represent the second most diverse mammals order, with more than 1400 described species, where 181 are known to occur in Brazil. These species play a crucial role in providing ecosystem services and use echolocation to navigate and capture their prey at night. Most species exhibit differentiated ultrasound patterns, allowing the bioacoustics application for identification and ecological, distribution, and behavioral bat studies. Recently, species distribution models (SDM's) have also played an essential role in developing spatial distribution studies and animal species conservation worldwide. However, even these models may not translate precisely the species distribution, which implies an urgent need to carry out their validation in the field (*in situ* validation). As a pioneering approach for Brazil, in this thesis, I sought to catalog bat vocalizations and use recordings in northeastern Brazil for the *in situ* validation and refinement of insectivorous bats' SDMs. Thus, this study aimed to use bioacoustics methods: (a) to inventory and describe vocalizations; (b) increase knowledge of distribution; (c) as a field validation method for potential distribution maps; and (d) investigate the occurrence of cryptic species; for Brazilian bats. I tested the accuracy of automated software for the acoustic identification of Brazilian bats using previously identified recordings. I found that the software's accuracy, and its agreement level, are very low and impractical at the moment. After an effort to compile all known vocalizations of Brazilian species, I set out to evaluate the use of bioacoustics in three possible practical applications. In the first application, I evaluated bioacoustics as a suitable and non-invasive method for four cave-dwelling species identification. I found those species are clearly recorded and identifiable clearly during cave emergence. Therefore, bioacoustics has the potential to reduce disturbances caused by bat colonies research. In the second application, we reviewed the distribution of Promops centralis in South America (one of the least mist-net captured Brazilian species) using new acoustic records and SDM techniques, expanding it by more than 3.8 million km^2. In this study, it was also possible to describe an unusual pattern of the species' vocalizations, with individuals emitting at least three distinct and highly variable call types. In the last application, I intended to use bioacoustics to in situ validate potential distribution maps of six neotropical bats generated through SDM. Without adequate modeling parameters and independent in situ validation, there are increased threats that inaccurate models impact conservation policies and species management plans. In this thesis, I showed the bioacoustics effectiveness as a non-invasive method to identify and extend species distribution and validate difficult-to-capture species predictive maps in poorly sampled regions. Although requiring specific training and

need regionally adapted vocalization libraries and the development of minimum protocols, bioacoustics can no longer be neglected in bat studies in Brazil.

Keywords: Bat calls. Bioacoustics. Cryptic diversity species. Species distribution models.

SUMÁRIO

1 INTRODUÇÃO

A presente tese está dividida em três seções. A primeira secção contém esta introdução, os objetivos e hipóteses do trabalho, e o referencial teórico onde são abordados os princípios e o estado de arte sobre morcegos e a ecolocalização, a bioacústica, sobre modelagem espacial e a necessidade de validação dos mapas de distribuição potencial.

A Seção II é formada por capítulos no formato de artigos: O primeiro capítulo é composto pelo artigo "*Uma nota de precaução sobre a identificação automática de chamados de ecolocalização de morcegos no Brasil*", publicado no Boletim da Sociedade Brasileira de Mastozoologia (volume 77, páginas 163-171), em 2016. Este trabalho abordou o problema do uso indiscriminado e acrítico de softwares automatizados para a identificação de morcegos e finalizou com a proposta de algumas boas práticas para o uso e para a boa implementação deste método no Brasil. O segundo capítulo é composto pelo manuscrito "*Bioacoustics as a non-invasive method for the study of cave-dwelling bat species in Brazil´s drylands*", que será submetido para publicação em breve. Neste estudo foi avaliado se monitoramentos acústicos poderão ser um método não invasivo adequado para identificar morcegos insetívoros comumente encontrados em cavernas do Brasil. O terceiro capítulo é composto pelo artigo "*Molossid unlimited: outstanding extension of range and unusual vocalization patterns of the bat, Promops centralis"*, publicado na revista Journal of Mammalogy (volume 101, edição 2, páginas 417-432), em 2020. Este trabalho tratou do uso conjunto de técnicas de bioacústica e modelagem de distribuição de espécies (SDM) para o aumento do conhecimento ecológico e de distribuição de uma espécie raramente capturada no Brasil e a descrição de um tipo de vocalização incomum. O quarto e último capítulo é composto pelo manuscrito "*Using bioacoustics for the validation of species distribution modelling: an example with bats in Brazil*", que será submetido para publicação em breve. Neste capítulo trato do uso da bioacústica, como método de registro de dados independentes coletados no terreno, para validar mapas de distribuição potencial de seis espécies de morcegos insetívoros neotropicais gerados através de modelagem espacial.

Finalmente, a secção III encerra esta tese com conclusões gerais e perspectivas futuras, onde é feita uma síntese da abordagem adotada neste trabalho e as suas implicações para o futuro.

1.1 OBJETIVOS

1.1.1 Objetivos gerais

Analisar e avaliar o uso das metodologias acústicas no aumento do conhecimento sobre vocalizações, ecologia e a distribuição de espécies de morcegos insetívoros no nordeste do Brasil, além de propor e avaliar o uso da bioacústica como método de validação de mapas preditivos para distribuição espacial de espécies de morcegos no Brasil gerados a partir de modelagem espacial.

1.1.2 Objetivos específicos

1. **Inventariar e descrever vocalizações de quirópteros:**

   1.1. Avaliar o uso de identificadores automatizados para a identificação acústica de morcegos na metodologia acústica no Brasil;

   1.2. Integrar e compilar informações sobre chamadas de ecolocalização de morcegos insetívoros no Brasil, apontar quais espécies são acusticamente reconhecíveis de maneira confiável e quais as lacunas de conhecimento;

   1.3. Criação de uma chave de identificação e uma biblioteca de vocalizações de morcegos do Brasil;

2. **Avaliar o uso da bioacústica como método de validação no terreno de mapas de distribuição potencial de espécies de morcegos:**

   2.1. Criação de mapas de distribuição potencial de algumas espécies de morcegos usando MaxEnt como meio de modelagem espacial de espécies (MDE);

   2.2. Validar *in situ* dos mapas de distribuição potencial usando a amostragem bioacústica e refinamento das áreas de distribuição potencial de espécies detetadas;

3. **Com base na ecolocalização, investigar a potencial ocorrência de espécies crípticas de morcegos no nordeste brasileiro.**

2 REFERENCIAL TEÓRICO

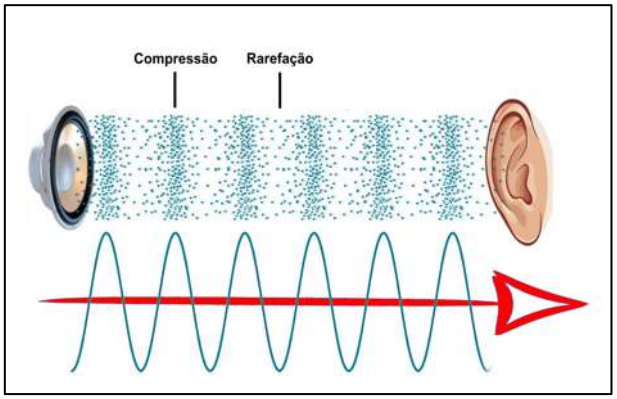
2.1 O SOM

2.1.1 Características do som

O som é a energia produzida por um objeto vibratório que, através de um movimento ondulatório, se propaga ao longo do tempo e do espaço num determinado meio (i.e. essa energia é transmitida através de compressão e descompressão ou rarefacção da matéria) (Figura 1) (OPENSTAX, 2018). Para poder ser mensurado, o som terá que ser convertido para uma representação digital e visual (ver secção "Representação do som"). Assim, o som possui estas características ondulatórias mensuráveis (Figura 2) (OPENSTAX, 2018):

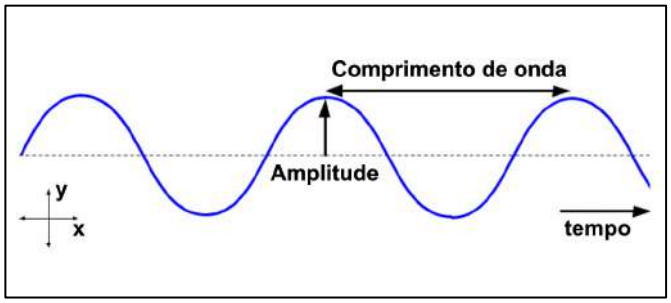
- **Comprimento de onda (λ)**, definido pela distância linear entre dois ciclos. Basicamente, é a distância entre dois valores repetidos consecutivos de uma onda;
- **Amplitude**, é a quantidade de energia gerada durante máxima perturbação do meio durante um ciclo da onda. Esta medida está diretamente relacionada com a

Figura 1 – Esquema representativo da propagação do som através da matéria.



Fonte: adaptada de "Science ABC" (https://www.scienceabc.com/pure-sciences/movement-of-sound-waves-through-different-media.html).

Figura 2 – Características de uma onda sonora.



Fonte: Adaptada de "Khan Academy" (https://www.khanacademy.org/science/ap-physics-1/ap-mechanical-waves-and-sound/wave-characteristics-ap/a/wave-characteristics-review-ap-physics-1).

intensidade ou volume do som. A **intensidade do som** é expressa em decibéis (dB) e é proporcional ao quadrado da amplitude.

- **Frequência (f)**, é o número de ciclos completos de uma onda por unidade de tempo. Basicamente, pode dizer-se que a frequência se refere à quantidade de vezes que as partículas vibram por unidade de tempo. A frequência é medida em Hertz (Hz, 1 Hz = 1 ciclo por segundo);

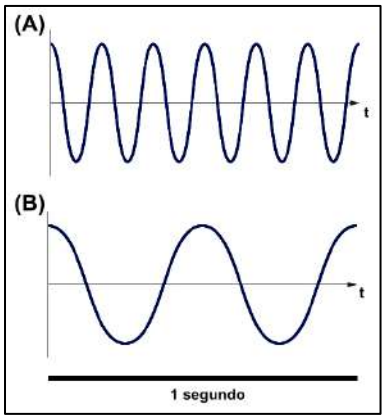
Dada a equação abaixo, verificamos que o comprimento de onda **(λ)** e a frequência **(f)** estão intrinsecamente ligados numa relação proporcionalmente inversa:

$$f = \frac{c}{\lambda}$$

c (velocidade de propagação do som no ar) = 343 m/s, a 20ºC.

Isto quer dizer que se diminuirmos o comprimento de uma onda, a frequência dessa onda aumentará na mesma proporção. Assim, uma onda que realize 6 ciclos por segundo (frequência igual a 6 Hz; Figura 3-A) possuirá um comprimento de onda três vezes menor do que uma onda que realize 2 ciclos por segundo (frequência igual a 2 Hz; Figura 3-B). O ouvido humano pode

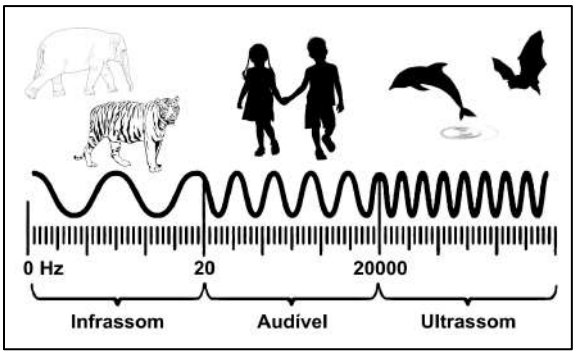
Figura 3 – Esquema representando duas ondas com frequências diferentes: (A) Onda com frequência maior (6 Hz); (B) Onda com frequência menor (2 Hz).



Fonte: Adaptada de "Physics Classroom" (https://afsharphysics.wordpress.com/optics/optics-part-1-introduction-to-waves/sound/).

detectar sons entre 16 (20) Hz e 20 kHz (20.000 Hz) e todos os sons dentro deste intervalo de frequências são considerados "audíveis", enquanto sons com frequências abaixo são denominados de "infrassons" e os acima de "ultrassons" (Figura 4) (OPENSTAX, 2018).

Figura 4 – Esquema representando os intervalos das frequências de infrassons, sons audíveis e ultrassons.

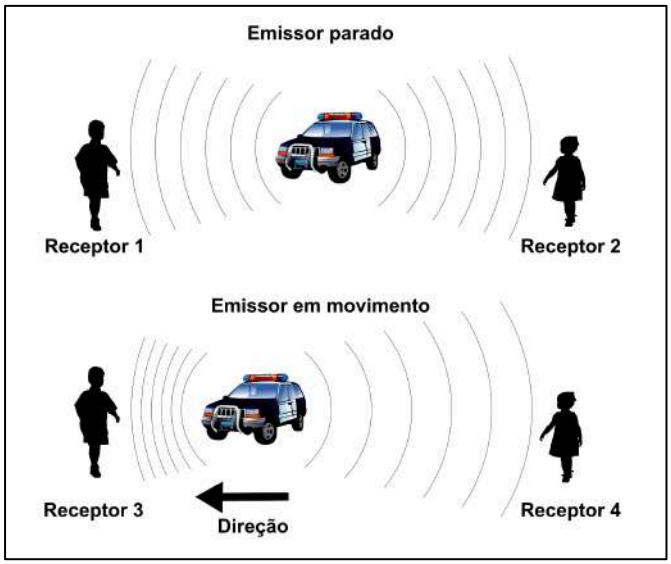


Fonte: Adaptada de "Neuroscience News" (https://neurosciencenews.com/sonogenetics-brain-control-14689/).

Qualquer som gerado propaga-se em todas as direções (como um campo esférico), e como a energia (amplitude) das ondas não é infinita, esta perder-se-á ao longo do espaço – a **atenuação** (OPENSTAX, 2018). Esta perda de energia deve-se ao cada vez maior número de partículas que terão que oscilar para que a transmissão desse som ocorra, assim para que um som percorra grandes distâncias, este necessita que a sua amplitude seja elevada na origem (OPENSTAX, 2018). A distância percorrida por um som está também dependente do seu comprimento de onda, i.e. dois sons com a mesma amplitude, emitidos no mesmo meio, mas com frequências distintas percorrerão distâncias distintas. Quanto menor for o comprimento de onda (↑ frequência), menor será a distância percorrida por esse som, já que "ondas curtas" (frequências altas) necessitarão de oscilar mais moléculas no espaço (encontrarão mais obstáculos) do que ondas de baixa frequência (OPENSTAX, 2018).

Outro dos efeitos do som a ter em conta é o **efeito de Doppler**, fenómeno que explica as mudanças na percepção do som pelo receptor em relação ao som original produzido por um emissor em movimento. O efeito de Doppler ocorre quando a percepção do som pelo receptor é alterada pelas mudanças de velocidade e de distância da sua fonte (OPENSTAX, 2018). Quando o emissor se encontra estacionário, não existe alteração na percepção das frequências dos receptores (Figura 5, receptores 1 e 2); porém, quando a fonte do som se move e se aproxima do receptor existe a percepção de um aumento da frequência (Figura 5, receptor 3) e quando a fonte se afasta, existe uma percepção de diminuição da frequência (Figura 5, receptor 4).

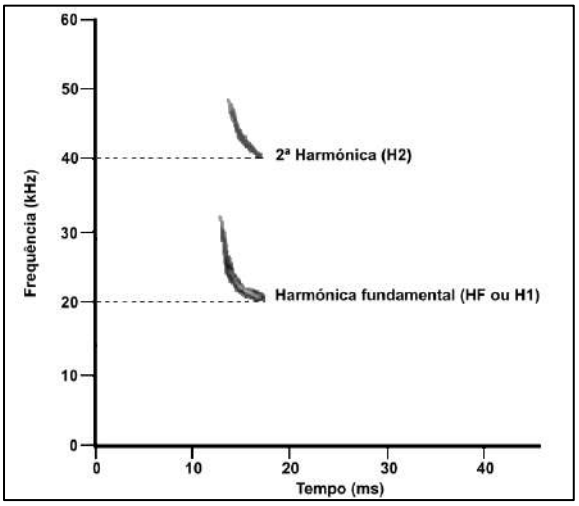
Figura 5 – Representação esquemática do efeito de Doppler.



Fonte: Adaptada de "How do we know it?" (https://www.howdoweknowit.com/2013/04/08/how-do-we-know-that-there-are-planets-orbiting-other-stars/combined_doppler/).

Por vezes, a mesma fonte emite simultaneamente frequências diferentes a partir do mesmo som – **harmônicas** (BRIGHAM et al., 2004; OPENSTAX, 2018). As harmônicas são frequências componentes daquela com frequência mais baixa (**harmônica fundamental)**, e são sempre múltiplas desta (Figura 6). Todas as harmônicas com frequência superior à fundamental são chamadas de **harmônicas secundárias** (Figura 6). Por exemplo, se a frequência fundamental for 20 Hz será esperado que a frequência da segunda harmónica seja de 40 Hz e a terceira 60 Hz. A interação destas harmônicas produz tipos de onda mais complexos, conferindo características tonais ao som, que permitem que o ouvido as distinga facilmente. Na verdade, todo o som é constituído por harmônicas, podendo ser uni-harmônico, se composto apenas por

Figura 6 – Espectrograma de uma vocalização de um morcego com representação de duas harmônicas.

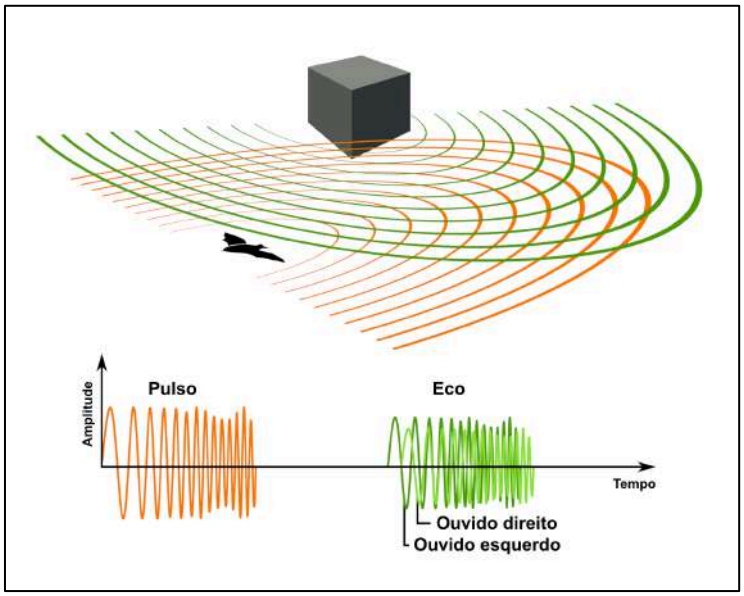


Fonte: Adaptado de RUSS (1999).

uma única harmônica, ou multi-harmônico, quando composto por mais do que uma harmónica (OPENSTAX, 2018).

Quando uma onda encontra um alvo ou obstáculo, além de poder ocorrer atenuação, ocorre a reflexão dessa onda – o **eco –** resultando uma onda de menor intensidade e invertida em relação à original (Figura 7) (OPENSTAX, 2018). Se o alvo estiver parado, a frequência do eco será a mesma da onda original, enquanto se estiver em movimento, a frequência será diferente à frequência original (OPENSTAX, 2018). A ecolocalização surge a partir da descodificação destas características do eco, e dependendo das frequências utilizadas no som original, os morcegos poderão ser capazes de detectar a posição, o tamanho, a forma e até a velocidade do seu alvo (ver secção "os morcegos, o som e a ecolocalização").

Figura 7 – Esquema representativo do eco gerado a partir da reflexão de um pulso de ecolocalização de um morcego.



Fonte: Adaptada de "Medium" (https://medium.com/@aamustaf/deep-sonar-how-neural-networks-can-make-your-phone-a-sonar-b79741eafaf7).

2.1.2 Representação do som

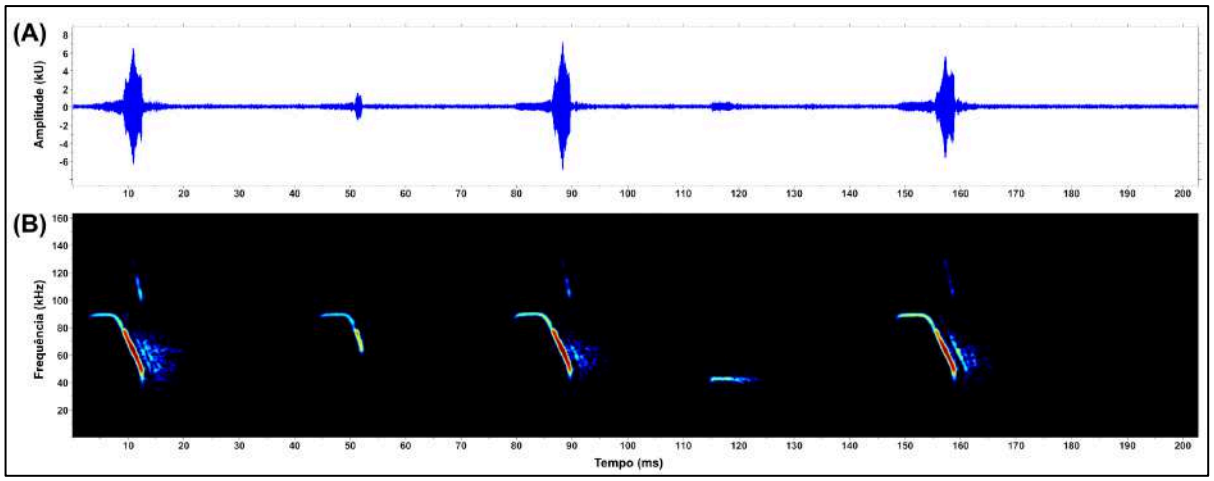
Para podermos representar e medir qualquer som necessitamos de converter o sinal sonoro em código binário para que os nossos computadores o consigam processar. Esse som é amostrado através de um microfone e depois convertido num sinal digital. No entanto, para que essa conversão seja possível e completa, é indispensável que o *teorema de Nyquist-Shannon* seja respeitado, i.e. a **taxa de amostragem** (*sampling rate*, medida em Hz) mínima do equipamento deve ser, pelo menos, o dobro da frequência mais alta do sinal a gravar (BRIGHAM et al., 2004; BRUDZYNSKI, 2018). Por exemplo, um sinal emitido a 50 kHz deverá ser gravado com uma taxa de amostragem de, no mínimo, 100 kHz. O **tamanho de**

amostragem (*sampling size* ou *bit depth*, em bits) também tem um papel importante na qualidade dessa conversão, já que fará a amostragem da amplitude do sinal. Normalmente, para estudos bioacústicos, gravações a 16 bit (ou, no máximo 24 bit) são suficientes (BRIGHAM et al., 2004; BRUDZYNSKI, 2018).

Após a conversão, o som pode ser representado visualmente através de oscilogramas, espectrogramas e espectros de potência (BRIGHAM et al., 2004; FENTON et al., 2016; BRUDZYNSKI, 2018):

- O **oscilograma** é a representação mais simplificada do som, que aparece em forma de ondas (Figura 8-A). É uma representação gráfica da pressão do som (por vezes, representada pela amplitude) sobre o tempo. A escala da pressão é relativa, variando entre -1 e 1, e o tempo é representado em segundos (ou milissegundos).

Figura 8 – Representação de uma sequência de ecolocalização de um morcego num (A) oscilograma e num (B) espectrograma.



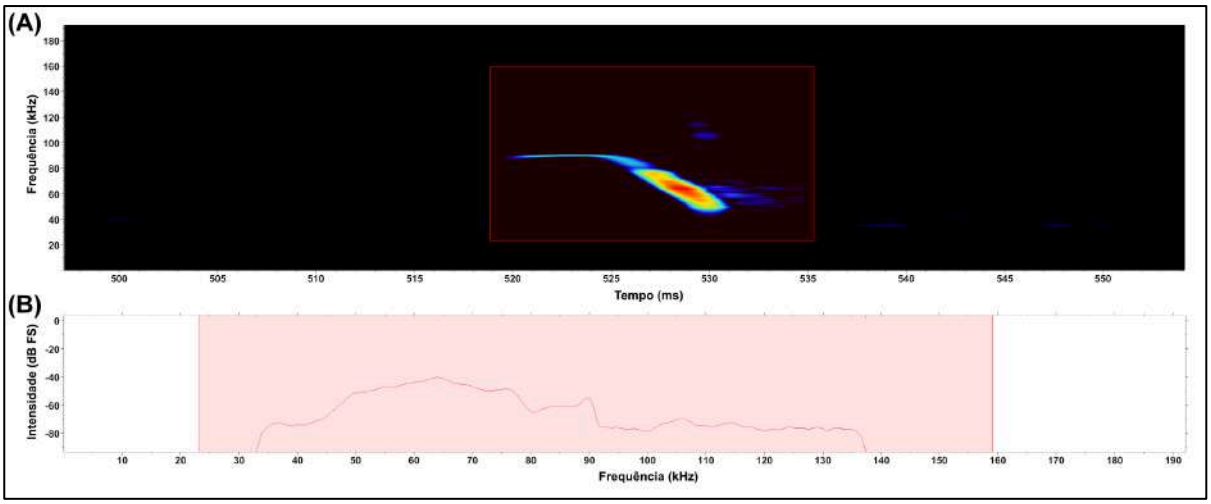
Fonte: Frederico Hintze (autor).

- O **espectrograma** é uma representação gráfica pseudo-3D de frequência, tempo e amplitude (Figura 8-B; Figura 9-A), esta última representada por uma escala de cores. Permite visualizar a estrutura dos pulsos, assim como verificar como as frequências (e a amplitude) variam ao longo do tempo. Para a criação de espectrogramas, o software utiliza o método de **Fast Fourier Transformation (FFT)** que permite a transformação da informação dos oscilogramas (amplitude, tempo e frequência). Usando este método, a taxa de FFT é diretamente proporcional à resolução de frequência e amplitude do pulso, i.e. quanto maior a taxa de FFT escolhida, maior será a resolução de frequência e amplitude dos sons no espectrograma. No entanto, a resolução do tempo é

indiretamente proporcional à taxa de FFT, pelo que não convém utilizar taxas de FFT demasiado altas. Quando é necessário usar taxas de FFT altas, pode-se diminuir a **taxa de sobreposição** (*overlap*) para se obter uma maior resolução aparente do tempo. Para a criação destes espectrogramas, é importante a definição do tipo de janela a usar: Hanning, Hamming, Blackman, rectangular, etc. Normalmente, as duas primeiras são as mais usadas nos estudos bioacústicos já que produzem ótimas resoluções na frequência e são menos propensas a *spectral leakage* (BRUDZYNSKI, 2018), resultante de vazamento de energia do pico para outras amostras próximas. Quando o som possui amplitude próxima à do ruído de fundo, a janela Blackman poderá ser a mais indicada (BRUDZYNSKI, 2018).

- O **espectro de potência** (*power spectrum*) é uma representação simples da intensidade do sinal (ou amplitude) pela frequência (Figura 9-B). Permite quantificar a intensidade de uma dada frequência num determinado intervalo de tempo selecionado. Este tipo de representações também é gerado através de FFT.

Figura 9 – Representação de um pulso de ecolocalização de um morcego num (A) espectrograma e num (B) espectro de potência.



Fonte: Frederico Hintze (autor).

É importante ter em conta que a medição de cada variável, deve ser feita na representação gráfica que possui a melhor resolução para o efeito. Assim, em estudos bioacústicos, a estrutura do sinal deve ser obrigatoriamente analisada através do espectrograma, assim como as variáveis de tempo (duração de pulso e intervalo entre sinais) devem sem ser analisadas pelo oscilograma (BRIGHAM et al., 2004; KUNZ; PARSONS, 2009). Já as análises de variáveis de frequência do sinal devem ser efetuadas no espectrograma ou no espectro de potência.

2.2 OS MORCEGOS, O SOM E A ECOLOCALIZAÇÃO

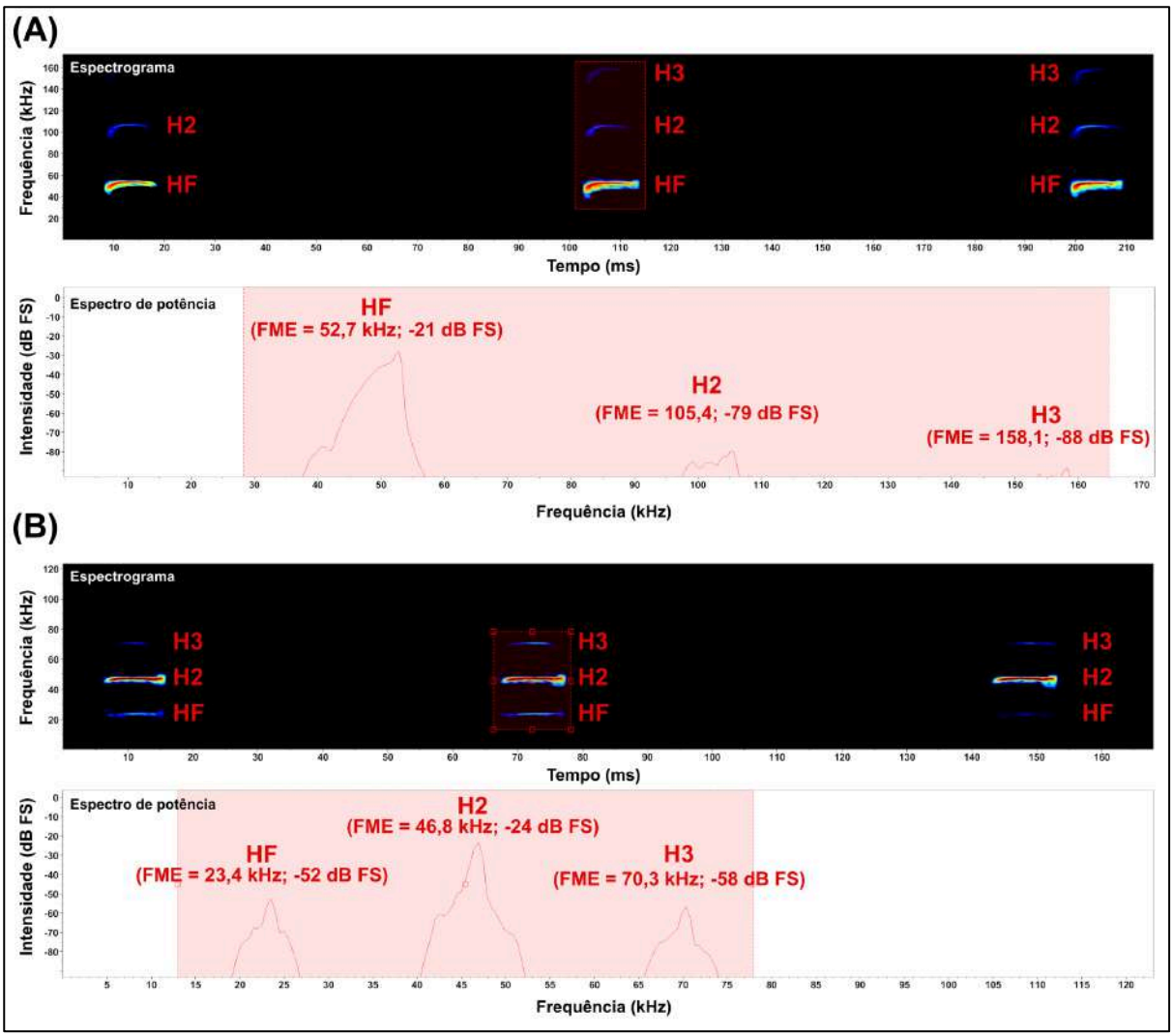
Uma boa parte dos animais terrestres, incluindo a nossa espécie, depende bastante da sua visão para a percepção do meio envolvente ou para forragear (LAZAREVA; SHIMIZU; WASSERMAN, 2012), utilizando o som para comunicar e socializar, normalmente associado a eventos de reprodução ou a manifestações de territorialidade (LAIOLO, 2010). No entanto, no caso de animais noturnos, a baixa luminosidade do meio e a reduzida dimensão das suas presas impõem dificuldades adicionais para a sua sobrevivência e subsistência (NEUWEILER, 2000; KUNZ; FENTON, 2006). A maioria das espécies de morcegos tem que lidar com estes problemas, porém devido às suas ótimas capacidades de audição no espectro ultrassônico, a evolução conduziu-as a uma otimização das suas capacidades de produção e recepção desses ultrassons (NEUWEILER, 2000; KUNZ; FENTON, 2006; FENTON et al., 2016). Assim se desenvolveu a **ecolocalização**, a capacidade de utilizar o som para percepção do meio envolvente e orientação no espaço.

A ecolocalização é considerada um sistema ativo de orientação, já que o sinal transportador da informação (eco) é resultante de um sinal produzido pelo próprio animal (NEUWEILER, 2000; KUNZ; FENTON, 2006; FENTON et al., 2016). Basicamente, a ecolocalização consiste na emissão de um som e a recepção do seu eco (NEUWEILER, 2000; KUNZ; FENTON, 2006; FENTON et al., 2016) (veja Figura 7, acima). Através deste sistema, os morcegos tornaram-se independentes da luz solar como meio de percepção do meio envolvente, já que lhes fornece informações como a localização espacial, dimensão e distância aos obstáculos ou presas e até a forma destes; permitindo aos morcegos ocupar um nicho ecológico muito específico, evitando a competição com outros grupos (e.g. aves) (NEUWEILER, 2000; KUNZ; FENTON, 2006). A produção do som faz-se a partir da laringe e a recepção do eco é feita através das orelhas e a sua associação ao sistema nervoso, que o interpreta. Biologicamente, a ecolocalização processa-se em três etapas principais:

1) **Produção e emissão:** O som é produzido na laringe, e a maioria dos morcegos emite-o a partir da boca. Porém, alguns morcegos emitem o som através das narinas (NEUWEILER, 2000; FENTON et al., 2016). No caso destes últimos, a epiglote adequa-se de forma a isolar a cavidade oral criando uma passagem diretamente desde a laringe até à cavidade nasal – o tracto naso-laringeal (NEUWEILER, 2000; FENTON et al., 2016). Esta passagem contém câmaras-de-ar adicionais que podem funcionar como órgãos ressonantes, atenuando assim a primeira harmónica e aumentando a intensidade das harmônicas secundárias do

sinal de ecolocalização (NEUWEILER, 2000; FENTON et al., 2016). Curiosamente, caso estes sejam obrigados a vocalizar através da boca, a harmónica mais intensa será a primeira, e não nenhuma das secundárias, tal como acontece com a maioria das espécies de morcegos (NEUWEILER, 2000; FENTON et al., 2016). Basicamente, as famílias de morcegos podem apresentar frequência de maior energia na harmónica fundamental (1ª harmônica, Figura 10-A) ou numa das harmônicas secundárias (Figura 10-B) (sobre harmônicas, ver secção "O som e as suas características").

Figura 10 – Espectrograma e espectro de potência de duas sequências de morcegos: em (A) a harmónica fundamental (HF) apresenta-se mais intensa do que as harmónicas secundárias (H2 e H3); em (B) a segunda harmónica (H2) apresenta-se mais intensa do que a harmónica fundamental e a terceira harmónica (H3).



Fonte: Frederico Hintze (autor).

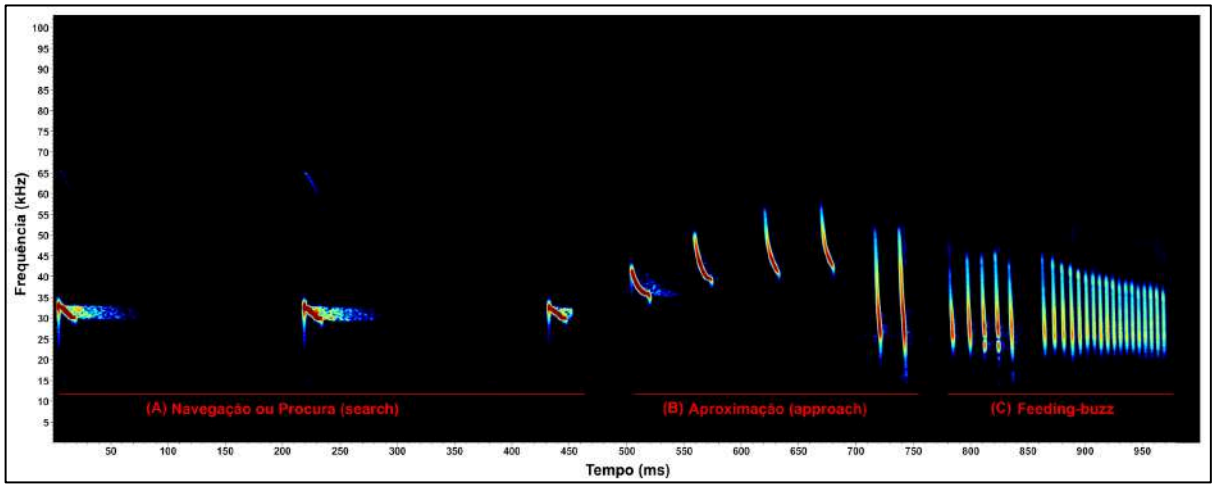
2) **Recepção do eco:** Após o som ser refletido numa superfície, as orelhas irão atuar como **receptores** dos ecos gerados. Isto é feito pelo ouvido

externo e médio, que transmitirão o som para o ouvido interno - o órgão final recetor do som (NEUWEILER, 2000; FENTON et al., 2016).

3) **Interpretação:** Após a recepção, ocorre uma excitação nervosa que é transmitida via nervo auditório para o centro de audição localizado no cérebro. É aí que o eco será interpretado e comparado com o sinal original nos domínios de frequência e tempo (NEUWEILER, 2000; FENTON et al., 2016). Essa interpretação permite-lhes criar uma imagem do que os rodeia, onde o nível de detalhe estará associado às frequências associadas e ao número de sons emitidos num intervalo de tempo.

Dependendo da situação, uma sequência de ecolocalização de um morcego poderá conter até três fases (Figura 11): navegação ou procura (*search*), aproximação (*approach*) e de alimentação (*feeding-buzz*) (NEUWEILER, 2000; FENTON et al., 2016). Diferentemente das vocalizações de comunicação (mais longas e complexas), um morcego usando ecolocalização emite uma média de quatro a doze pulsos por segundo, separados por intervalos de tempo irregulares, e "pulsos de navegação" têm, por vezes, mais de 10 milissegundos de duração (NEUWEILER, 2000; FENTON et al., 2016).

Figura 11 – Sequência de ecolocalização de um morcego, exibindo três fases (A) navegação ou procura (search), (B) aproximação (approach) e (C) feeding-buzz.

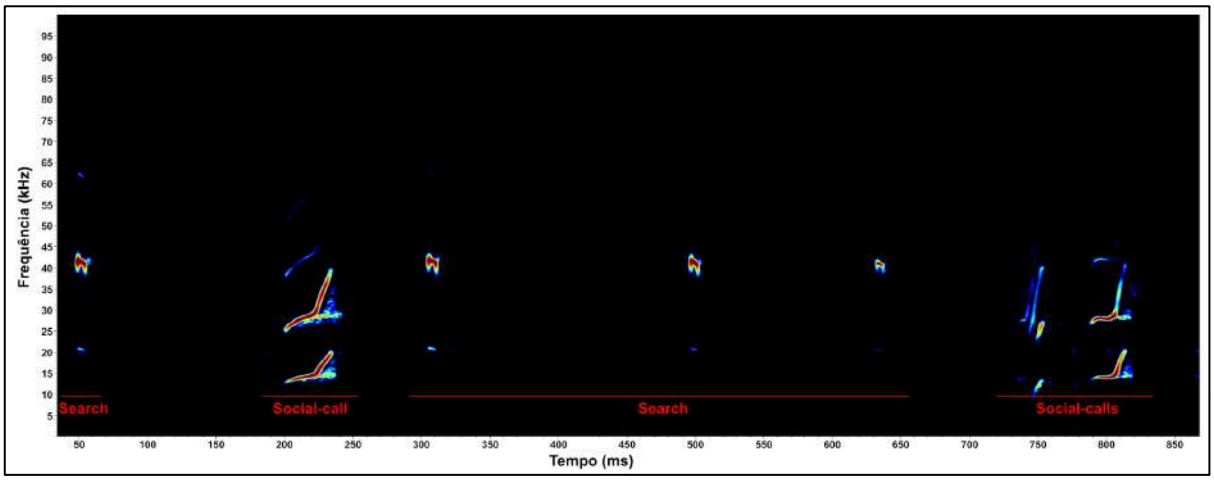


Fonte: Frederico Hintze (autor).

Os pulsos de navegação são emitidos quando o morcego está à procura de alimento ou quando estão a comutar de um determinado local para o outro, sem se aproximar de um obstáculo ou presa (SCHNITZLER; KALKO, 2001; SCHNITZLER; MOSS; DENZINGER, 2003; FENTON et al., 2016). Normalmente, durante esta fase, a duração e o intervalo entre pulsos é constante, podendo ocorrer ou não alternância de frequências entre os pulsos (Figura

11-A). Quando o morcego detecta um alvo, começará a fase de aproximação (Figura 11-B), os pulsos possuem uma maior taxa de repetição (o intervalo entre pulsos decresce sucessivamente). Quando o morcego está em perseguição da presa, a repetição de pulsos pode aumentar até cerca de quarenta e cinquenta vezes por segundo (SCHNITZLER; KALKO, 1998; NEUWEILER, 2000; SCHNITZLER; KALKO, 2001; FENTON et al., 2016). Imediatamente antes de capturar o inseto, o morcego emite uma sequência de dez a vinte e cinco pulsos separados por intervalos mínimos – o "*feeding buzz*" (Figura 11-C) – aumentando a taxa de repetição em cerca de 90% (NEUWEILER, 2000; SCHNITZLER; KALKO, 2001; FENTON et al., 2016). Esta sequência de detecção, perseguição e captura da presa, dura usualmente entre um a dois segundos. Durante o vôo em fase de procura, ou mesmo quando em repouso, os morcegos podem emitir pulsos mais longos e complexos (**social-calls**, Figura 12). Os *social-calls* não são pulsos de ecolocalização, e como o nome indica, são usados em contexto social e comunicação com outros morcegos.

Figura 12 - Sequência de ecolocalização de um morcego contendo social-calls.



Fonte: Frederico Hintze (autor).

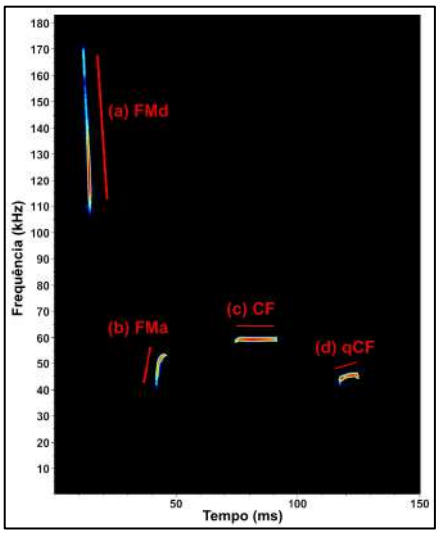
Como dito acima, este fato está intimamente ligado na forma como os morcegos fazem a emissão dos seus pulsos, se pela boca ou pelas narinas. Os pulsos de ecolocalização exibem também vários padrões na estrutura tempo-frequência predominante, que poderão estar presentes individualmente, ou em combinação entre si, que poderão ser categorizados em dois tipos básicos (SCHNITZLER; KALKO, 2001; PARSONS; SZEWCZAK, 2009; FENTON et al., 2016):

(1) O mais frequente é o de **frequência modulada** (FM). Basicamente, a frequência deste sinal varia (modula) ao longo do tempo, podendo ser descendente (a frequência diminui – FM descendente; Figura 13-A) ou

ascendente (a frequência aumenta ao longo do tempo – FM ascendente (FMa); Figura 13-B);

(2) **Frequência constante** (CF, do inglês "Constant Frequency") é um sinal que não modula (Figura 13-C); ou modula muito levemente a sua frequência ao longo do tempo, **frequência *quasi*-constante** (qCF) (Figura 13-D).

Figura 13 – Espectrograma com 4 pulsos apresentando estruturas tempo-frequência distintas: (a) Frequência modulada descendente (FMd); (b) Frequência modulada ascendente (FMa); (c) Frequência constante (CF); e (d) Frequência quase-constante (qCF).



Fonte: Frederico Hintze (autor).

Um pulso de ecolocalização pode ser composto por mais do que um destes tipos básicos de estrutura, e podem ser classificados também como pulsos *broadband* ou *narrowband* (SCHNITZLER; KALKO, 2001; SCHNITZLER; MOSS; DENZINGER, 2003; FENTON et al., 2016). Um pulso *broadband* possui componente(s) FM mais evidentes, possuindo um aspecto 'alongado' e 'vertical' (Figura 13-A e B), enquanto no segundo as componentes CF ou qCF têm maior destaque, possuindo um aspecto 'achatado' e 'horizontal' (Figura 13-C e D). Geralmente, os morcegos de áreas abertas ou de borda florestal possuem estrutura mais *narrowband*, enquanto morcegos de áreas fechadas possuem estruturas mais *broadband* (SCHNITZLER; KALKO, 2001; KUNZ; FENTON, 2006; FENTON et al., 2016; DENZINGER; TSCHAPKA; SCHNITZLER, 2017). Como usam um grande número de frequências, os ecos de pulsos *broadband* transmitirão assim uma maior quantidade de informação distinta ao morcego. A única exceção a esta 'regra' é o caso dos morcegos *high duty-cycle* (ver abaixo), cujos pulsos são *narrowband*. No entanto, estes morcegos utilizam o efeito de doppler em seu benefício, que lhes permite obter informações muito detalhadas em habitats mais fechados (ver abaixo, SCHNITZLER; KALKO, 2001; LAZURE; FENTON, 2011; FENTON; FAURE; RATCLIFFE, 2012; FENTON et al., 2016; DENZINGER;

TSCHAPKA; SCHNITZLER, 2017). *Duty-cycle* (DC) é uma medida que avalia o período de tempo que o morcego vocaliza em comparação com o tempo em que não está a vocalizar (LAZURE; FENTON, 2011):

$$DC\ (\%) = \frac{Dur}{IPI + Dur} \times\ 100$$

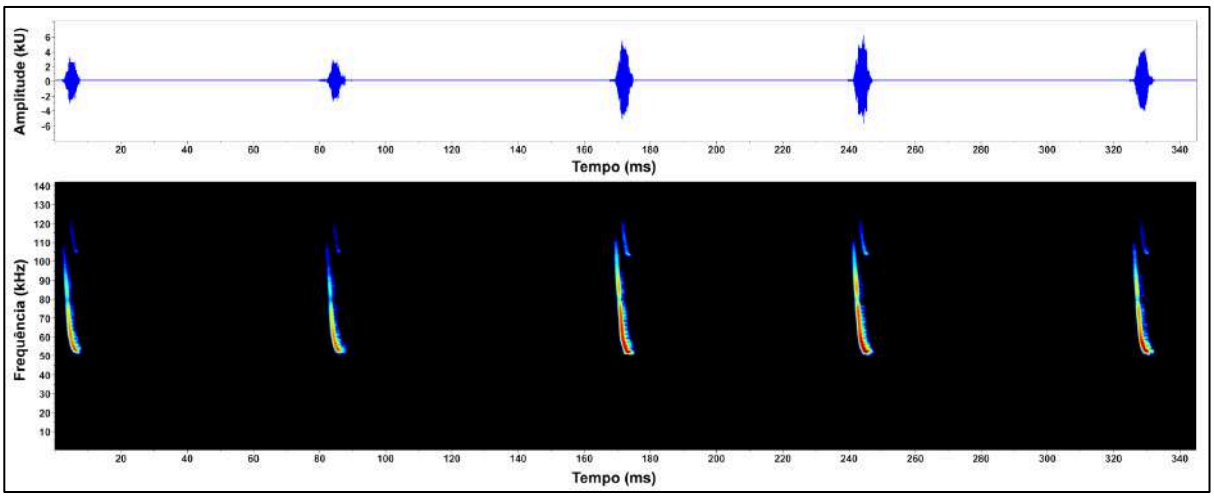
Dur = Duração do pulso

IPI = Intervalo entre pulsos

Quanto ao tipo de ecolocalização, podemos dividir os morcegos em dois tipos:

(1) **Low duty-cycle** (LDC): Este tipo de ecolocalização caracteriza-se por sequências de pulsos com intervalos entre si consideravelmente maiores do que a duração dos pulsos (Figura 14). Assim, estima-se que estes morcegos não possuem informação disponível do que lhes rodeia durante cerca 4/5 do tempo de voo (NEUWEILER, 2000; SCHNITZLER; KALKO, 2001; FENTON et al., 2016). Simplificadamente, o morcego emite o som e espera ouvir o eco desse som antes de emitir um novo som. Quantitativamente, as sequências de ecolocalização destes morcegos possuem *duty-cycle* médio inferior a 25%. A esmagadora maioria das espécies de morcegos é LDC;

Figura 14 – Oscilograma e espectrograma de uma sequência de ecolocalização *low duty-cycle,* da espécie *Myotis lavali.*

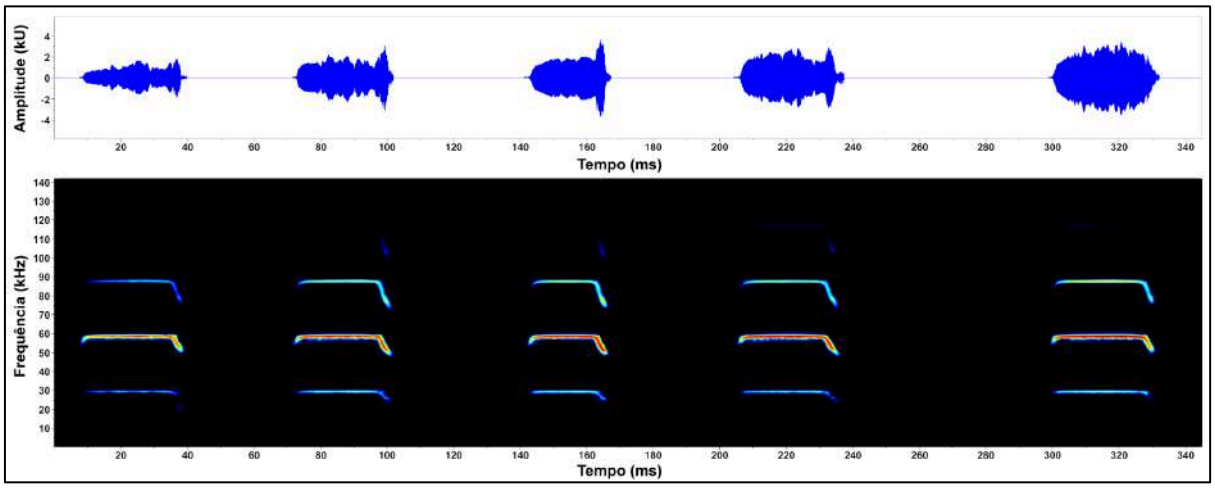


Fonte: Frederico Hintze (autor).

(2) **High duty-cycle** (HDC): Este tipo de ecolocalização caracteriza-se por sequências de pulsos com intervalos entre os pulsos muito semelhantes à duração (Figura 15). Simplificadamente, os morcegos recebem os ecos dos pulsos

enquanto vocalizam novos pulsos (não tendo períodos ‘cegos’) e é graças a uma cóclea especializada no seu ouvido interno que estes morcegos conseguem discernir os ecos (mais fracos) das suas vocalizações, utilizando o efeito de doppler em seu benefício (NEUWEILER, 2000; SCHNITZLER; KALKO, 2001; LAZURE; FENTON, 2011; SCHNITZLER; DENZINGER, 2011; FENTON et al., 2016). Os pulsos são muito longos (duração superior a 20 ms) e possuem uma componente CF bastante expressiva. O *duty-cycle* médio das sequências é 25% (LAZURE; FENTON, 2011). Nas Américas, é conhecido apenas um complexo de espécies HDC – o complexo *Pteronotus cf. parnellii,* da família Moormopidae. Outros exemplos são os morcegos pertencentes às famílias Rhinolophidae e Hipposideridae, que ocorrem no ‘velho mundo’.

Figura 15 – Oscilograma e espectrograma de uma sequência de ecolocalização *high duty-cycle*, da espécie *Pteronotus rubiginosus*.

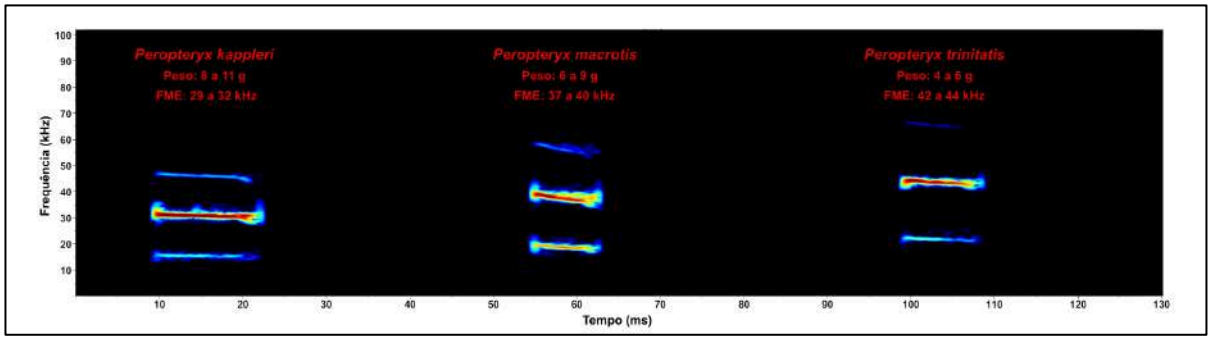


Fonte: Frederico Hintze (autor).

A delimitação do intervalo de frequências a que cada grupo ou espécie pode emitir, ou é sensível, é das maiores evidências de que o sistema de ecolocalização dos morcegos sofreu alterações através de processos de seleção natural (SIMMONS; STEIN, 1980; SCHNITZLER; KALKO, 2001; JONES; TEELING, 2006; FENTON et al., 2016; JACOBS; BASTIAN, 2017). O pressuposto anatómico é um dos que mais determinam o som produzido, uma vez que a frequência do som está intrinsicamente associada às características físicas do emissor do som. Isto é, um animal de pequeno porte geralmente emite sons com frequências mais elevadas do que outro animal de grande porte, devido ao tamanho e forma da laringe (SIMMONS; STEIN, 1980; NEUWEILER, 2000; SCHNITZLER; KALKO, 2001; JONES; TEELING, 2006; JUNG; MOLINARI; KALKO, 2014; FENTON et al., 2016; JACOBS; BASTIAN, 2017). Uma forma

bem simples de se entender este pressuposto são as diferenças entre a voz de um homem adulto e de uma criança. A voz de homem adulto é mais 'grave' (frequências mais baixas) enquanto a voz de uma criança é mais 'aguda' (frequências mais altas). Normalmente, nos morcegos de uma mesma família ocorre uma relação inversamente proporcional entre o tamanho e as frequências a que vocalizam (JUNG; MOLINARI; KALKO, 2014) (Figura 16).

Figura 16 – Espectrograma de pulsos de três espécies do género *Peropteryx* (fam. Emballonuridae) ilustrando a relação inversamente proporcional entre o peso corporal e a frequência de máxima energia de cada espécie.



Fonte: Frederico Hintze (autor).

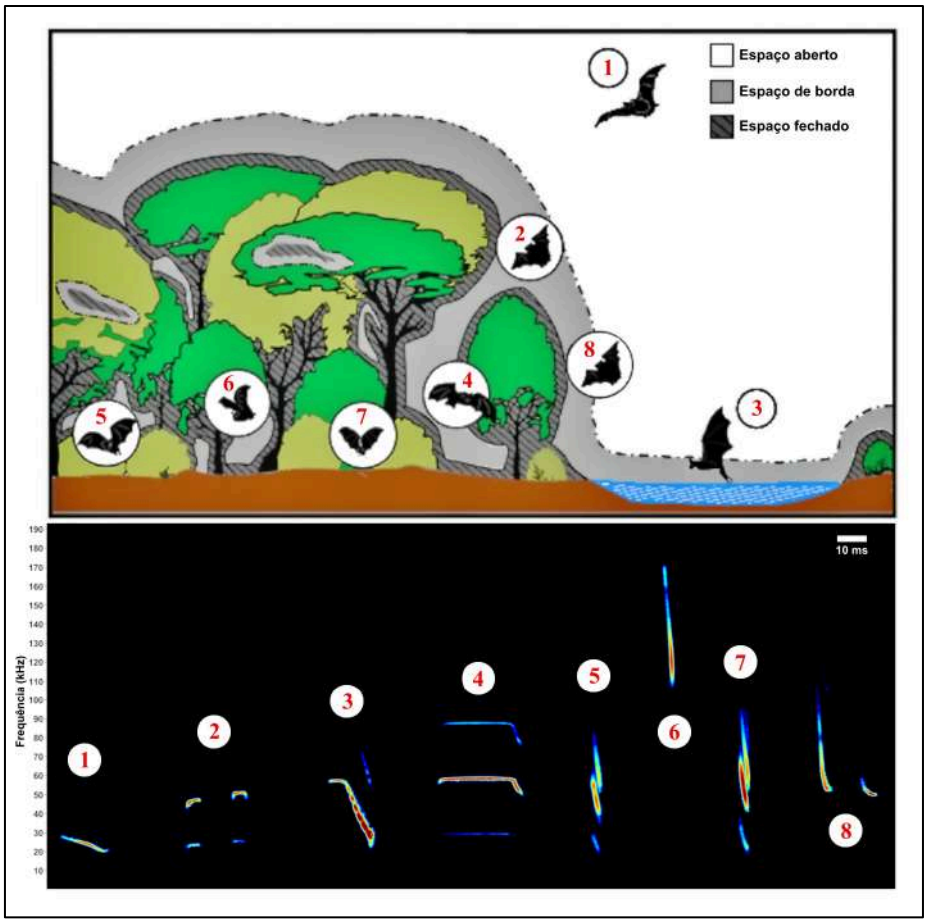
Já o pressuposto ecológico, menos restrito a uma regra 'geral', é determinado por diversos fatores, tais como a estrutura das asas e tipo de vôo, o tipo de ambiente envolvente, ou tipo e dimensão de presa e guilda trófica (Figura 17) (e.g. SCHNITZLER; KALKO, 2001; JONES; TEELING, 2006; KUNZ; FENTON, 2006; DENZINGER; SCHNITZLER, 2013; FENTON et al., 2016; DENZINGER; TSCHAPKA; SCHNITZLER, 2017; ROEMER et al., 2019). Como frequências altas possuem comprimentos de onda curtos, logo pulsos com frequência alta permitirão detectar objetos menores e obter mais detalhes do meio envolvente. Assim, é de se esperar que espécies de morcegos florestais, ou se alimentem de insetos de dimensão reduzida, tenham evoluído para vocalizar utilizando pulsos *broadband* e com frequências muito altas (Figura 17-6) (e.g. SCHNITZLER; KALKO, 2001; DENZINGER; SCHNITZLER, 2013; DENZINGER; TSCHAPKA; SCHNITZLER, 2017; ROEMER et al., 2019).

Em contraponto, como as frequências mais altas dissipam mais rapidamente, estes morcegos apenas conseguirão detectar objetos muito perto de si, ficando bastante expostos em ambiente aberto, já que a maioria destes apresenta asas que lhes permitem muita manobrabilidade mas não voos muito rápidos (NORBERG; RAYNER, 1987; SCHNITZLER; KALKO, 1998; SCHNITZLER; MOSS; DENZINGER, 2003; DENZINGER; SCHNITZLER, 2013; FENTON et al., 2016; DENZINGER; TSCHAPKA; SCHNITZLER, 2017). Além dos morcegos catadores, uma das exceções a essa regra são os morcegos florestais high duty-cycle, que apresentam pulsos *narrowband* bastante longos, mas usam a sua capacidade de utilizar e interpretar o efeito de Doppler em seu benefício (Figura 17-4) (e.g. LAZURE; FENTON, 2011;

SCHNITZLER; DENZINGER, 2011; FENTON; FAURE; RATCLIFFE, 2012; DENZINGER; SCHNITZLER, 2013; DENZINGER; TSCHAPKA; SCHNITZLER, 2017).

Já morcegos de áreas abertas, ou que voem acima da copa das árvores, apresentam pulsos *narrowband* com frequência baixa e duração alta (Figura 17-1) o que, além de permitir um gasto energético menor na produção das vocalizações, possibilita também detectar objetos mais distantes e, consequentemente, poderão efetuar vôos mais rápidos (NORBERG; RAYNER, 1987; SCHNITZLER; KALKO, 1998; SCHNITZLER; MOSS; DENZINGER, 2003; DENZINGER; SCHNITZLER, 2013; FENTON et al., 2016; DENZINGER; TSCHAPKA;

Figura 17 – Estrutura das vocalizações de morcegos de acordo com o tipo de ambiente: (1) *Cynomops planirostris*, morcego de espaço aberto insetívoro; (2) *Saccopteryx leptura*, morcego de borda insetívoro; (3) *Noctilio leporinus*, morcego catador aquático (*trawling*) piscívoro; (4) *Pteronotus rubiginosus*, morcego florestal insetívoro (*high duty-cycle*); (5) *Phyllostomus discolor*, morcego catador florestal omnívoro (*gleaning*); (6) *Furipterus horrens*, morcego florestal insetívoro; (7) *Artibeus planirostris*, morcego florestal catador frugívoro; (8) *Myotis lavali*, morcego de borda insetívoro.



Fonte: Adaptado de Denzinger e Schnitzler (2013) e Fenton et al. (2016).

SCHNITZLER, 2017). Porém, essas características impossibilitam a esses morcegos uma exploração eficiente de áreas florestais fechadas ou mesmo de borda. Já a maioria dos morcegos de borda possui uma grande plasticidade vocal, utilizando pulsos com frequências

intermediárias comparando com os de áreas florestais e os de borda, e normalmente compostos por uma componente FM e uma componente CF (ou qCF), que variam na expressão consoante o tipo de ambiente que os rodeia (SCHNITZLER; KALKO, 1998; SCHNITZLER; MOSS; DENZINGER, 2003; DENZINGER; SCHNITZLER, 2013; FENTON et al., 2016; DENZINGER; TSCHAPKA; SCHNITZLER, 2017).

Se o morcego estiver voando num local com muitos obstáculos, a componente FM terá maior expressão e o pulso terá menor duração; se estiver voando num ambiente aberto, a componente CF (ou qCF) terá maior expressão e o pulso terá maior duração (Figura 17-8). Porém, certos morcegos de borda florestal apenas produzem sequências compostas por pulsos *narrowband*, mas possuem a peculiaridade de emitirem sequências com dois ou três pulsos de frequências diferentes que, dependendo da família, vão alternando regular ou irregularmente entre si (Figura 17-2). A explicação deste tipo de comportamento de ecolocalização é ainda alvo de debate e as diferentes teorias não são excludentes (RATCLIFFE et al., 2011). Estes morcegos utilizarão esta estratégia porque lhes permitirá: contornar a dissipação e detectar objetos mais longe (BEHR; KNÖRNSCHILD; VON HELVERSEN, 2009), detectar objetos em segundo plano enquanto se alimentam (aumentando a profundidade do "campo de visão") e aumentam a taxa de emissão (obtendo mais informação) (e.g. DENZINGER et al., 2001; JUNG; KALKO; HELVERSEN, 2007; HIRYU et al., 2010; RATCLIFFE et al., 2011), ou aumentar a eficiência de captura em áreas de borda e aberturas da floresta (DENZINGER et al., 2001).

Finalmente, os *gleaning bats* (morcegos catadores que caçam sobre superfícies) também apresentam ecolocalização diferenciadas (SCHNITZLER; KALKO, 1998; SCHNITZLER; MOSS; DENZINGER, 2003; DENZINGER; SCHNITZLER, 2013; FENTON et al., 2016; DENZINGER; TSCHAPKA; SCHNITZLER, 2017) e podem ser divididos em dois grupos: *gleaning bats* ("*stricto sensu*") e *trawling bats*. Os *gleaning bats* "stricto sensu" são morcegos que caçam sobre o solo ou outras superfícies sólidas como folhas ou troncos de árvore, e apresentam pulsos *broadband* multi-harmônicos e de frequência variável (Figura 17-5; Figura 17-7). A criação destas harmônicas múltiplas permite-lhes obter uma grande profundidade do "campo de visão", distinguindo facilmente os seus alvos das superfícies onde estes estão, assim estes morcegos conseguem navegar e forragear facilmente em espaços muito fechados. Já os *trawling bats* são morcegos catadores que caçam sobre a água, e normalmente apresentam pulsos com pontos de inflexão bastante evidentes (Figura 17-3). Isto permite-lhes detectar e alimentar-se de insetos e pequenos peixes que se encontram junto à superfície de corpos-de-

água calmos (SCHNITZLER; KALKO, 1998; SCHNITZLER; MOSS; DENZINGER, 2003; DENZINGER; SCHNITZLER, 2013; FENTON et al., 2016; DENZINGER; TSCHAPKA; SCHNITZLER, 2017).

2.3 A DETECÇÃO E IDENTIFICAÇÃO ACÚSTICA DE MORCEGOS

No final do século XVIII, Lazaro Spallanzani observou que os morcegos conseguiam orientar e alimentar-se em locais com total ausência de luz e que, ao contrário das suas corujas de estimação, obtinham a mesma taxa de sucesso quando lhes tapava os olhos (GALAMBOS, 1942a; FENTON et al., 2016). Após várias experiências subsequentes, Spallanzani e Louis Jurine verificaram que, quando se tamponavam os seus ouvidos, os morcegos não conseguiam orientar-se na escuridão, concluindo que os morcegos dependiam da audição para se orientar no espaço (GALAMBOS, 1942a; FENTON et al., 2016).

A primeira proposta do uso de ecolocalização surge apenas em 1920 por Hartridge, que sugere que apenas o uso de sons de alta frequência permitiria a detecção dos pequenos objetos que os morcegos necessitam evitar durante o vôo (HARTRIDGE, 1920; GALAMBOS, 1942a; FENTON et al., 2016). Esta proposta só seria experimentalmente comprovada por Donald Griffin e George Pierce em 1938, quando gravaram os primeiros sinais de ecolocalização de morcegos (PIERCE; GRIFFIN, 1938; FENTON et al., 2016). Após vários estudos entre 1940 e 1942, Griffin e Robert Galambos demonstraram que os morcegos emitiam sons de alta frequência pela boca e usavam os respectivos ecos para se orientar no espaço (GRIFFIN; GALAMBOS, 1940; GRIFFIN; GALAMBOS, 1941; GALAMBOS, 1942b; FENTON et al., 2016). Donald Griffin dedicou grande parte da sua vida acadêmica ao estudo do desempenho da ecolocalização dos morcegos e é, possivelmente, o pesquisador mais preponderante nos primeiros estudos bioacústicos de morcegos. Vários outros pesquisadores e estudos posteriores foram essenciais para conhecimento da ecolocalização dos morcegos e no desenvolvimento de nova tecnologia, métodos e técnicas de estudo da bioacústica de morcegos.

O uso da acústica para o estudo de morcegos é dividido em dois momentos: (1) a aquisição (gravação) dos sons, onde são utilizados aparelhos especialmente desenhados para o efeito – os detectores de ultrassons – que permitem a gravação dos morcegos em vôo livre no campo ou em ambiente controlado; e a (2) análise acústica, onde através de software próprio se faz uma análise acústica das gravações obtidas. Para gravar o som de morcegos necessitamos de um sistema de gravação (ou conversão) que permitam a gravação de ultrassons ou com a capacidade de converter esses sons em sons audíveis – os detectores de ultrassons (AHLÉN;

BAAGOE, 1999; LIMPENS; MCCRACKEN, 2004; MACSWINEY; CLARKE; RACEY, 2008; PARSONS; SZEWCZAK, 2009; ADAMS et al., 2012; FENTON et al., 2016).

Ultimamente os detectores de ultrassons tiveram uma grande evolução, não apenas tecnológica, mas também no custo de produção. Há alguns (poucos) anos atrás, os únicos detectores RT disponíveis eram dispositivos muito caros (> 5000 dólares) e, portanto, inacessíveis à grande maioria dos pesquisadores. Hoje temos disponíveis no mercado opções cada vez mais baratas (< U$ 1500.00), que tenderão a ficar cada vez mais acessíveis como é exemplo o Audiomoth (Open Acoustics Devices) que custa cerca de U$ 60.00 a unidade. Na verdade, são o desempenho, capacidade de configuração e a qualidade dos materiais que definem o valor de um detector RT. Assim, atualmente, os detectores de tempo real passaram a ser os mais comumente usados, já que usando uma configuração correta permitem desempenhar praticamente todo o tipo de estudos.

A escolha de um detector ou mais detectores deve ter sempre em conta a tarefa ou estudo a ser executado, porque embora à partida o preço ou tipo de sistema possam parecer os fatores mais importantes, não serão apenas esses que mais influenciarão (AHLÉN; BAAGOE, 1999; LIMPENS; MCCRACKEN, 2004; MACSWINEY; CLARKE; RACEY, 2008; ADAMS et al., 2012). Existem outras características que se deve sempre ter em conta, tais como: o tipo, direcionalidade, sensibilidade, frequências e *signal to noise ratio* do microfone, a taxa de amostragem, presença de filtro de *anti-aliasing* e o tipo de armazenamento digital do sistema de gravação, ou mesmo o consumo energético, a forma, dimensão e peso do detector (LIMPENS; MCCRACKEN, 2004; MACSWINEY; CLARKE; RACEY, 2008; PARSONS; SZEWCZAK, 2009; ADAMS et al., 2012).

O monitoramento acústico de morcegos poderá ser efetuado de acordo com um vasto número de finalidades, desde simples inventários e distribuição de espécies até estudos ecológicos e comportamentais mais complexos (SCHNITZLER et al., 1994; BRIGHAM et al., 2004; PARSONS; SZEWCZAK, 2009; JUNG; KALKO, 2010). Durante esse monitoramento, podem ser utilizados dois tipos básicos de amostragem:

a) **Amostragem ativa:** este tipo de amostragem implica que o pesquisador esteja presente. O pesquisador selecionará quais são os seus sinais de interesse e os escolherá ativamente. Para isso, necessitará de ouvir os morcegos em campo com a ajuda de um sistema de conversão (HET ou FD) ou ter um *tablet* para a visualização dos sonogramas em tempo real.

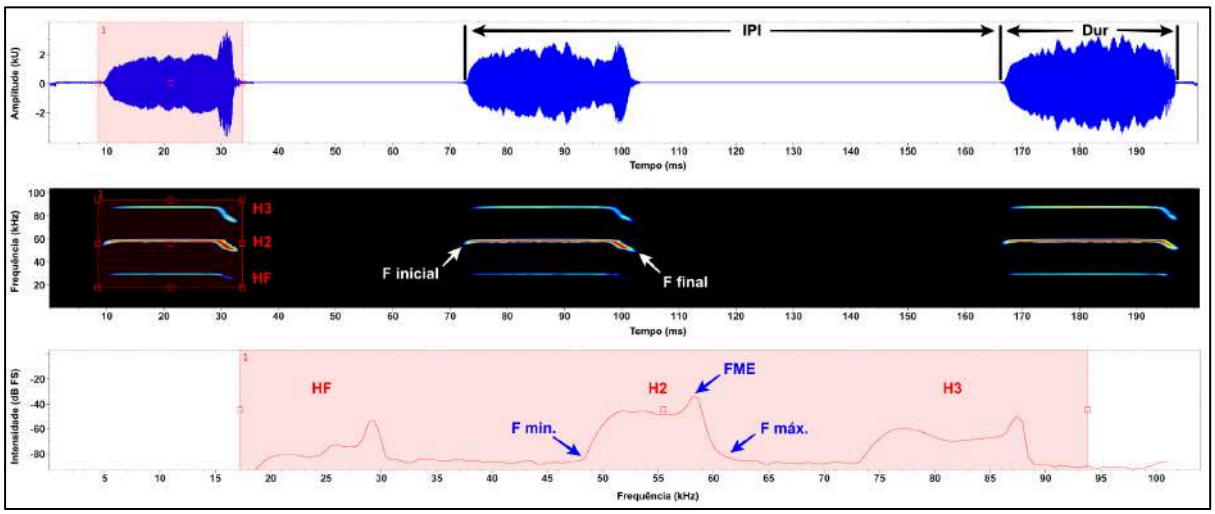
b) **Amostragem passiva:** este tipo de amostragem não implica que o pesquisador esteja presente. O detetor gravará todos os sinais que possuam as características pré-determinadas na configuração feita pelo pesquisador. Mesmo que o pesquisador esteja presente, e esteja fazendo um transecto transportando o detector, a amostragem será considerada passiva caso ele não escolha ativamente quais as gravações do seu interesse.

Para se efetuar análise e identificação acústica laboratorial é indispensável que o pesquisador possua um treinamento para o efeito, uma vez que a análise acústica implica o domínio de vários conceitos e ferramentas específicos (AHLÉN; BAAGOE, 1999; BARCLAY, 1999; PARSONS, 2004; PARSONS; SZEWCZAK, 2009; FENTON et al., 2016). Quando bem usada, esta é uma técnica com muito potencial, não só para descrição das vocalizações ou identificação das espécies, mas também para análises ecológicas e comportamentais dos morcegos. No entanto, o mau uso desta técnica poderá levar à identificação incorreta das espécies, ou a interpretação ecológica e comportamental deficientes, e em última instância provocando problemas ao nível da conservação das espécies (AHLÉN; BAAGOE, 1999; BARCLAY, 1999; PARSONS, 2004; PARSONS; SZEWCZAK, 2009).

A análise acústica de morcegos deve ser realizada com o uso de um software de análise acústica que, através de oscilogramas, espectrogramas e espectros de potência, possua a capacidade de analisar parâmetros essenciais à identificação ou descrição das suas vocalizações. Esta análise acústica baseia-se em parâmetros quantitativos relacionados com frequência, tempo e amplitude [frequências inicial (F inicial), final (F final) e de máxima energia (FME), *bandwidth* (BW); duração (Dur), intervalo entre pulsos (IPI); harmónica mais intensa, etc.] e parâmetros qualitativos (estrutura do sinal, alternância de sinal, etc.) (AHLÉN; BAAGOE, 1999; BARATAUD et al., 2013; FENTON et al., 2016) (Figura 18). Assim, é possível identificar a espécie em questão ou, em determinados casos, identificar um complexo de espécies que partilham características acústicas similares usando a conjugação de vários destes parâmetros (AHLÉN; BAAGOE, 1999; RUSSO; JONES, 2002; KUNZ; PARSONS, 2009; PARSONS; SZEWCZAK, 2009; FENTON et al., 2016). No entanto, algumas espécies apresentam algum tipo de variação regional nas suas vocalizações, por isso, a descrição das vocalizações das espécies em cada região de estudo torna-se fundamental (AHLÉN; BAAGOE, 1999; BARCLAY, 1999; BARCLAY; FULLARD; JACOBS, 1999; OBRIST; BOESCH;

CKIGER, 2004; WATERS; GANNON, 2004; PARSONS; SZEWCZAK, 2009; JIANG; WU; FENG, 2015; FENTON et al., 2016).

Figura 18 – Oscilograma, espectrograma de três pulsos de ecolocalização e espectro de potência do primeiro pulso de um morcego, evidenciando alguns parâmetros usados para a análise acústica (IPI, intervalo entre o segundo e o terceiro pulso; Dur, duração do terceiro pulso; HF, harmónica fundamental; H2, segunda harmónica; H3, terceira harmónica; F inicial, frequência inicial; F final, frequência final; F min., frequência mínima; FME, frequência de máxima energia; F máx., frequência máxima).



Fonte: Frederico Hintze (autor).

Neste aspeto, as bibliotecas regionais de vocalizações de morcegos desempenham um papel vital para o uso de metodologias acústicas no estudo de morcegos, já que usar métodos bioacústicos para a identificação de morcegos implica um bom conhecimento de como as espécies vocalizam na região em estudo (AHLÉN; BAAGOE, 1999; O'Farrell; MILLER; GANNON, 1999; WATERS; GANNON, 2004; PARSONS; SZEWCZAK, 2009; FENTON et al., 2016). Uma boa descrição das vocalizações de morcegos implica que a identificação do indivíduo gravado seja confiável. Para isso, podemos recorrer a várias estratégias de gravação, tais como (BRIGHAM et al., 2004; PARSONS; SZEWCZAK, 2009; FENTON et al., 2016):

1 Emergência de abrigo, através da instalação de detetores junto a abrigos conhecidos das espécies;
2 Instalação de detetor na rede-de-neblina, caso haja a possibilidade de associar a hora de gravação com a hora de captura do indivíduo;
3 Tenda de vôo, após captura e identificação, liberta-se o indivíduo e gravam-se as suas vocalizações dentro de um recinto fechado;
4 Através de libertação em mão (*hand-release*), após captura e identificação do indivíduo gravam-se as suas vocalizações durante a sua libertação;
5 *Light-tag*, marcando as espécies com pequenos marcadores quimiluminescentes (cada cor correspondendo com uma espécie distinta), poderemos gravar o morcego em vôo livre; e

6 *Zipline*, que basicamente é o 'método morcego-pipa'. Antes de soltar o morcego, coloca-se um fio de nylon ligado a uma coleira, e seguramos a outra extremidade do fio para que o morcego não voe para fora do alcance do microfone. Basicamente, faz-se um morcego-pipa. Como o método de *light-tag* possui uma baixa taxa de sucesso, este pode ser um método alternativo para espécies que apresentam vôo alto e rápido.

O uso de metodologias acústicas não só possibilita a caracterização, descrição e identificação das espécies, mas também estudar outros aspetos da ecologia e comportamento dos morcegos tais como padrões espaço-temporais de atividade e de forrageio (AHLÉN; BAAGOE, 1999; BRIGHAM et al., 2004; KUNZ; FENTON, 2006; PARSONS; SZEWCZAK, 2009; OBRIST et al., 2010; DENZINGER; SCHNITZLER, 2013; FENTON et al., 2016). Embora não seja possível determinar se 100 gravações de uma espécie representam 100 indivíduos ou apenas um mesmo individuo detetado 100 vezes, podemos utilizar este número como uma medida de atividade - um *proxy* de abundância. Esta medida de atividade (utilização de espaço) pode ser bastante relevante, já que se poderá deduzir que um local que apresente maior atividade de uma espécie será ecologicamente mais importante do que outro local onde a mesma espécie foi detetada menos vezes (AHLÉN; BAAGOE, 1999; BRIGHAM et al., 2004; FENTON et al., 2016). Além disso, a deteção de um *feeding-buzz* no final de uma sequência de ecolocalização permitir-nos-á inferir que a espécie não só usa aquele habitat para comutar, como também para forragear ou beber água (SCHNITZLER; MOSS; DENZINGER, 2003; PARSONS; SZEWCZAK, 2009; GRIFFITHS, 2013). Já a presença de *social-calls* permitirá assinalar e associar interação entre morcegos, tais como: rituais de acasalamento, coesão social e comportamentos de cooperação ou agonísticos (sinais de stress ou alarme); com determinados habitats e/ou épocas específicas (BARLOW; JONES, 1997; WILKINSON; WENRICK BOUGHMAN, 1998; BEHR; VON HELVERSEN, 2004; KUNZ; FENTON, 2006; FURMANKIEWICZ et al., 2011; FENTON et al., 2016).

Informações acústicas como a estrutura, a frequência e a duração dos pulsos de navegação poderão também revelar-nos o habitat, guilda trófica e estratégias de caça que os morcegos exploram (SCHNITZLER; MOSS; DENZINGER, 2003; JONES; TEELING, 2006; KUNZ; FENTON, 2006; DENZINGER; SCHNITZLER, 2013; DENZINGER; TSCHAPKA; SCHNITZLER, 2017). E, em última instância, diferenças acústicas acentuadas entre indivíduos aparentemente conspecíficos poderão também fornecer-nos pistas essenciais ao delineamento da diversidade críptica existente numa região (JONES; PARIJS, 1993; WATERS; GANNON, 2004; THOISY et al., 2014; LÓPEZ-BAUCELLS et al., 2018; PAVAN; BOBROWIEC;

PERCEQUILLO, 2018). Estas informações fornecidas pela bioacústica poderão ser estudadas e mensuradas de forma não-invasiva, revelando quais os habitats e épocas mais importantes e quais os hábitos e comportamentos, assim como definir e delimitar melhor a distribuição de cada espécie, permitindo-nos assim conhecer aspetos fundamentais à conservação dos morcegos.

2.4 A DISTRIBUIÇÃO DE ESPÉCIES DE MORCEGOS E A MODELAGEM ESPACIAL

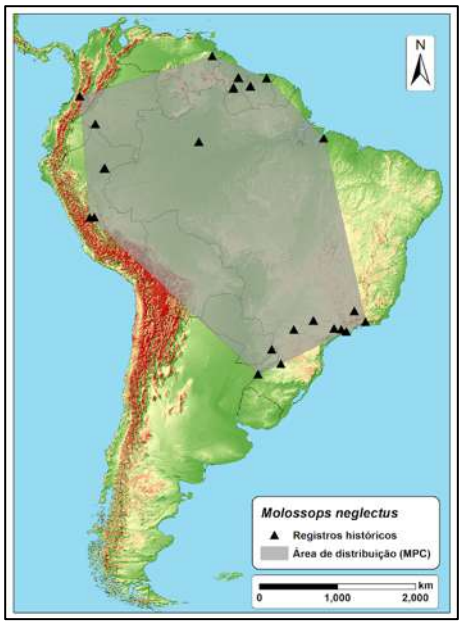
2.4.1 Os SIG e a distribuição de espécies

Desde Carl Nilsson Linnæus, criador da nomenclatura binomial e de fundamental importância para a sistemática, que existe a necessidade de saber como e por onde se distribuem as espécies no nosso planeta. A área de ocorrência é importante, não apenas para o conhecimento biogeográfico e ecológico, mas também para os esforços de conservação das espécies, principalmente numa época onde a biodiversidade do planeta está posta em causa (BURGMAN; FOX, 2003; MOTA-VARGAS; ROJAS-SOTO, 2012). É aqui que entra, por exemplo, o *short-fall* wallaceano que refere a necessidade de se conhecer bem as áreas de ocorrência das espécies. Uma vez que existem grandes diferenças na amostragem de várias regiões do mundo, vários *taxa* sofrem de vieses geográficos, o que faz com que a representação da sua distribuição conhecida seja apenas um reflexo do esforço amostral (HORTAL et al., 2015). Neste sentido, os Sistemas de Informação Geográfica (SIG) têm assumido uma grande importância no desenvolvimento de estudos de distribuição espacial e conservação de espécies animais em todo o mundo (MYERS et al., 2000; BURGMAN; FOX, 2003; ENGLER; GUISAN; RECHSTEINER, 2004; RUSHTON; ORMEROD; KERBY, 2004; GUISAN; THUILLER, 2005; MOTA-VARGAS; ROJAS-SOTO, 2012). Os SIG permitem o uso de várias metodologias para a criação de mapas que delimitem a ocorrência das espécies, tais como o mínimo polígono convexo (MPC), aerogeografia ou a modelagem de nicho ecológico (RAPOPORT, 1975; BURGMAN; FOX, 2003; ENGLER; GUISAN; RECHSTEINER, 2004; MOTA-VARGAS; ROJAS-SOTO, 2012).

O MPC é o método mais simples para estimar a área de ocorrência de uma espécie e é definido pelo menor polígono possível que resulte da união (e contenha) de todos os pontos

conhecidos (BURGMAN; FOX, 2003; NILSEN; PEDERSEN; LINNELL, 2008) (Figura 19).

Figura 19 – Mapa da América do Sul evidenciando os registros históricos e área de distribuição do morcego *Molossops neglectus* usando o método de mínimo polígono convexo (MPC). A escala de cores deste mapa representa a orogenia (baixo relevo, a verde; alto relevo, a marrom).

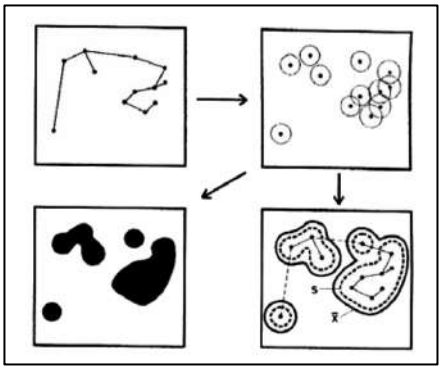


Fonte: Frederico Hintze (autor).

Pela sua simplicidade, e apenas necessitar de dados de presença, é ainda bastante utilizado hoje em dia, onde o maior exemplo são os mapas de distribuição da IUCN (BURGMAN; FOX, 2003; NILSEN; PEDERSEN; LINNELL, 2008; IUCN, 2016). Contudo, possui alguns problemas incontornáveis tais como a ausência de sensibilidade aos habitats, podendo sobrestimar bastante a área de ocorrência de espécies (e.g. BARG; JONES; ROBERTSON, 2005; MOTA-VARGAS; ROJAS-SOTO, 2012), ou levar a enviesamentos consideráveis quando o número de ocorrências de que dispomos é baixo (e.g. BÖRGER et al., 2006), seja devido à raridade ou à dificuldade de registro da espécie em causa.

A aerogeografia, talvez a menos utilizada e conhecida das metodologias, foi proposta por RAPOPORT (1975) e utiliza a média ou o desvio padrão das distâncias entre os registros mais

Figura 20 – Esquema simplificado da estimativa de distribuição de espécies pelo método de aerogeografia.

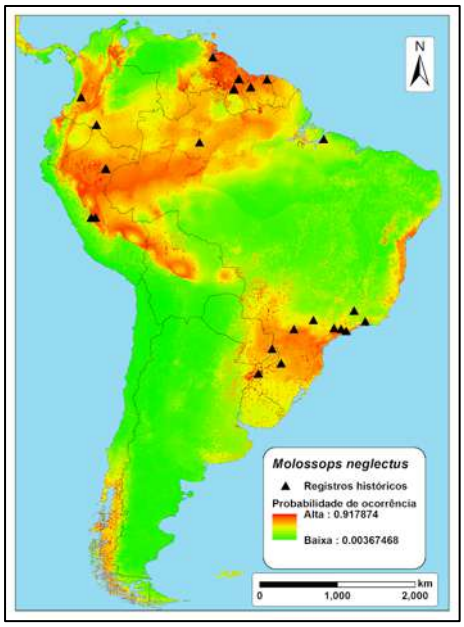


Fonte: Retirado de Rapoport e Monjeau (2001).

próximos. Este método utiliza esses valores de distância para fazer círculos em volta de cada ponto de ocorrência conhecido e o conjunto desses círculos é usado como estimativa das áreas de distribuição das espécies (RAPOPORT, 1975; RAPOPORT; MONJEAU, 2001; MOTA-VARGAS; ROJAS-SOTO, 2012) (Figura 20). Ao contrário do MPC, a aerogeografia tende a aumentar das áreas de ocorrência quando o número de registros é baixo, porém, à medida que o número de registros aumenta, tende a sobreajustar a predição de novas áreas junto aos pontos de registro conhecidos das espécies (MOTA-VARGAS; ROJAS-SOTO, 2012).

Mais recentemente, e amplamente utilizados hoje em dia, surgiu a modelagem de distribuição espacial de espécies (SDM) ou modelagem de nicho ecológico (Figura 21). Os SDM utilizam vários algoritmos matemáticos e computacionais para gerar uma predição probabilística das áreas de distribuição potencial das espécies através dos registros conhecidos das espécies e um set de variáveis biológicas (e.g. disponibilidade de alimentos e fitofisionomias) e dados geológicos e climáticos (e.g. orogenia, presença de corpos d'água, uso de solo, precipitação, temperatura) (PETERSON, 2001; RUSHTON; ORMEROD; KERBY, 2004; GUISAN; THUILLER, 2005; PHILLIPS; ANDERSON; SCHAPIRE, 2006; MEROW; SMITH; SILANDER, 2013).

Figura 21 – Mapa da América do Sul evidenciando os registros históricos e área de distribuição potencial do morcego *Molossops neglectus* utilizando o método de modelagem espacial (SDM). A escala de cores deste mapa representa a probabilidade de ocorrência da espécie (a verde, baixa probabilidade; a vermelho, alta probabilidade).



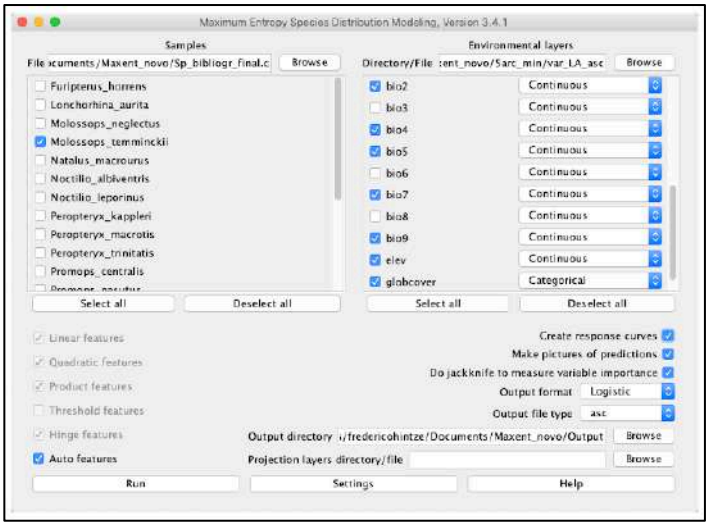
Fonte: Frederico Hintze (autor).

2.4.2 A modelagem de distribuição espacial de espécies

Existem vários tipos de técnicas matemáticas utilizadas nas diversas propostas de SDM's, cada uma possuindo vantagens e desvantagens em relação às outras. Por exemplo, algumas propostas necessitam de registros de presença e ausência (e.g. GLM), enquanto outros necessitam apenas de registros de presença (e.g. MaxENT, ENFA) (GUISAN; THUILLER, 2005). Estes SDM's estão baseados em várias metodologias/técnicas tais como (GUISAN; THUILLER, 2005; ELITH; GRAHAM, 2009): (1) o uso das distâncias ambientais aos registros de ocorrência (envelope climático) (e.g. BIOCLIM); (2) análises fatoriais de nicho ecológico (e.g. BIOMAPPER - ENFA); (3) métodos de regressão, tais como os modelos lineares generalizados (e.g. ECOSPAT); e (4) *machine learning* e redes neurais (e.g. GARP, Random forest, MaxEnt).

Dentro de todas as propostas de SDM's, o MaxEnt (Figura 22) é provavelmente o mais utilizado (ELITH et al., 2006; MEROW; SMITH; SILANDER, 2013), permitindo: (a) alcançar boas taxas preditivas, particularmente com amostras pequenas (ELITH et al., 2006; PHILLIPS; ANDERSON; SCHAPIRE, 2006; PEARSON et al., 2007; ELITH; GRAHAM, 2009); (b) utilizar apenas registros de presença (PHILLIPS; ANDERSON; SCHAPIRE, 2006); (c) a utilização de variáveis contínuas e categóricas, simultaneamente (PHILLIPS; ANDERSON; SCHAPIRE, 2006); (d) a convergência para uma ótima distribuição de probabilidade de ocorrência das espécies (princípio da máxima entropia) (PHILLIPS; ANDERSON; SCHAPIRE, 2006; PEARSON et al., 2007); e (e) utilizar vários tipos de valores limiares (thresholds), convertendo as probabilidades contínuas de ocorrência em mapas binários de presença e ausência das espécies (PHILLIPS; ANDERSON; SCHAPIRE, 2006).

Figura 22 – Interface geral do software MaxEnt, versão 3.4.1.



Fonte: Frederico Hintze (autor).

2.4.3 A importância da validação dos SDM's

Os SDM's assumiram grande importância no desenvolvimento de estudos sobre distribuição e conservação espacial de espécies animais em todo o mundo (ENGLER; GUISAN; RECHSTEINER, 2004; RUSHTON; ORMEROD; KERBY, 2004; GUISAN; THUILLER, 2005), e os morcegos não são exceção (JABERG; GUISAN, 2001; GREAVES; MATHIEU; SEDDON, 2006; SATTLER et al., 2007; REBELO; JONES, 2010; RAZGOUR et al., 2016; DELGADO-JARAMILLO et al., 2020). Como estes modelos de distribuição são criados a partir de registros de ocorrência e um set de variáveis, qualquer imprecisão nestes dados ou mesmo uma limitação no algoritmo poderá ser prejudicial para uma boa predição das áreas de distribuição das espécies (JIMÉNEZ-VALVERDE; LOBO; HORTAL, 2008; ELITH; GRAHAM, 2009; RADOSAVLJEVIC; ANDERSON, 2014; RAZGOUR et al., 2016). Estes modelos poderão excluir locais onde as espécies efetivamente estejam (erros de omissão) ou incluir onde não estejam (erros de comissão) e, portanto, poderão não traduzir corretamente a distribuição das espécies (ELITH et al., 2006; RANDIN et al., 2006; ELITH; GRAHAM, 2009; ANDERSON; GONZALEZ, 2011; BENITO; CAYUELA; ALBUQUERQUE, 2013; RAZGOUR et al., 2016). Minimizar estes erros é um desafio da ciência de modelagem espacial, uma vez que poderão inflar ou reduzir a potencial distribuição e ter um impacto direto na conservação das espécies (JIMÉNEZ-VALVERDE et al., 2008; ANDERSON, 2012; VISCONTI et al., 2013).

Por isso, a avaliação dos modelos gerados é preponderante, já que é necessário saber se estes descrevem adequadamente os requisitos das espécies e, a partir daí, se conseguem estimar corretamente a sua distribuição no espaço (ANDERSON, 2012; YACKULIC et al., 2013; RAZGOUR et al., 2016). Esta avaliação é realizada utilizando métricas teóricas de avaliação que, usando vários tipos de fórmulas estatísticas, verificam a capacidade preditiva dos modelos criados a partir de uma parte dos registros de ocorrência das espécies (normalmente 25%) (JIMÉNEZ-VALVERDE; LOBO; HORTAL, 2008; RADOSAVLJEVIC; ANDERSON, 2014). Vários tipos de métricas teóricas de avaliação dos modelos têm sido propostas, e vários estudos têm revisado e testado os pontos fortes e limitações de cada (e.g., RAES; TER STEEGE, 2007; ELITH; GRAHAM, 2009; MEROW; SMITH; SILANDER, 2013). Estas métricas de avaliação teóricas podem: (1) ser afetadas pelo viés espacial dos registros e não considerar o ajuste excessivo do modelo (e.g. AUC) (BECK et al., 2014; RADOSAVLJEVIC; ANDERSON, 2014); (2) ter a incapacidade de considerar a acurácia esperada de um modelo aleatório (e.g. *overall accuracy*) (ALLOUCHE; TSOAR; KADMON, 2006); (3) não possuir

independência (ou ser afetados) pela prevalência em determinadas condições (e.g. kappa, TSS) (ALLOUCHE; TSOAR; KADMON, 2006; SOMODI; LEPESI; BOTTA-DUKÁT, 2017); (4) beneficiar modelos binários que tenham utilizado um determinado tipo de *threshold* (e.g. TSS quando o threshold utilizado é maxSSS) (WUNDERLICH et al., 2019); (5) não avaliar uniformemente erros de omissão e comissão (e.g. TSS, SEDI) (WUNDERLICH et al., 2019); (6) não poder ser utilizadas caso um dos resultados possíveis do modelo (presença, ausência, erros de comissão ou erros de omissão) seja igual a zero (e.g. SEDI) (WUNDERLICH et al., 2019). Por exemplo, usando dados independentes, BEAN; STAFFORD; BRASHARES (2012) mostraram que muitos modelos obtinham pontuações teóricas mais altas do que quando eram avaliados com dados independentes.

Esses problemas mostram que, devido a estas limitações na avaliação destes modelos de distribuição potencial, a validação *in situ* com dados independentes se torna necessária e, em alguns casos, urgente principalmente no atual contexto de crise de conservação das espécies (GREAVES; MATHIEU; SEDDON, 2006; JIMÉNEZ-VALVERDE et al., 2008; VISCONTI et al., 2013; HERTZOG; BESNARD; JAY-ROBERT, 2014; HIPÓLITO; HASUI; VIANA, 2015). Embora pouco comum, vários autores têm utilizado dados independentes para validar SDM's de vários grupos biológicos (e.g. HERTZOG; BESNARD; JAY-ROBERT, 2014; ROOPER et al., 2016; WEST et al., 2016; ORTEGA-HUERTA; VEGA-RIVERA, 2017; GINÉ; FARIA, 2018), e os morcegos não são exceção (GREAVES; MATHIEU; SEDDON, 2006; REBELO; JONES, 2010).

Esta tese vai ao encontro às iniciativas globais de melhor conhecimento da biodiversidade, em especial de grupos pouco conhecidos e com alto potencial de novas espécies como os morcegos (CEBALLOS; EHRLICH, 2009). Mais além, ele também busca contribuir para o melhor entendimento dos serviços ecológicos prestados por morcegos, considerado uma prioridade em território brasileiro (BERNARD et al., 2012). A adoção de técnicas de bioacústica e modelagem espacial possuem o potencial de complementar e refinar os dados obtidos com redes de neblina (MICKLEBURGH; HUTSON; RACEY, 2002; RYDELL et al., 2002; SAMPAIO et al., 2003; SILVA; BERNARD, 2017). Em função da escassa utilização da bioacústica, permanece um profundo desconhecimento das vocalizações de grande parte das espécies insetívoras que ocorrem no Brasil, assim como da sua distribuição. Com exceção de alguns estudos muito pontuais (FENTON et al., 1999; O'Farrell; MILLER; GANNON, 1999; PORTFORS et al., 2000; BERNARD; FENTON, 2002; JUNG; KALKO; HELVERSEN, 2007; BARATAUD et al., 2013), o conhecimento das vocalizações das espécies brasileiras resulta,

em grande parte, de trabalhos realizados em outros países da América Central e do Sul. No entanto, as diferenças regionais intraespecíficas podem ser bastante acentuadas em algumas espécies ou grupos (JIANG; WU; FENG, 2015), e por este motivo torna-se indispensável que se realize um inventário dos sonótipos das espécies brasileiras.

Assim, os resultados esperados neste trabalho permitirão: 1) em primeira instância, aumentar o conhecimento sobre a distribuição de espécies de morcegos insetívoros no nordeste do Brasil, região com baixa amostragem e alto potencial de riqueza; 2) preencher lacunas de informações necessárias para refinar as distribuições potenciais e reais de algumas espécies, com implicações diretas, por exemplo, para a determinação de seus status de conservação e para o estabelecimento de políticas públicas de conservação; 3) aferir a viabilidade dos SIG para a geração de mapas de distribuição espacial de espécies de quirópteros; e 4) fomentar a implementação definitiva da bioacústica como um dos métodos de estudo de morcegos no Brasil, contribuindo para a difusão de métodos e técnicas ainda pouco empregados em território nacional. Considerando ainda que haverá a validação *in situ* da distribuição potencial de espécies, e que esta validação percorrerá trechos do Nordeste, tais estudos podem ainda ser úteis, por exemplo, nos Estudos de Impacto Ambiental das centenas de parques eólicos que se encontram atualmente em instalação ou projetados para o nordeste brasileiro (BERNARD et al., 2014; VALENÇA; BERNARD, 2015).

3 RESULTADOS

3.1 UMA NOTA DE PRECAUÇÃO SOBRE A IDENTIFICAÇÃO AUTOMÁTICA DE CHAMADOS DE ECOLOCALIZAÇÃO DE MORCEGOS NO BRASIL

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RESUMO

A análise de chamados de ecolocalização é, há muito tempo, utilizada como ferramenta imprescindível no estudo dos quirópteros na Europa, América do Norte e Oceania, por isso tem o potencial de preencher grandes lacunas de informação sobre a riqueza de espécies e atividade de morcegos no Brasil. Existem no mercado vários softwares que identificam automaticamente os chamados produzidos pelos morcegos, prometendo facilidade e rapidez na identificação dos numerosos arquivos gerados durante a gravação. Utilizando uma seleção de 71 arquivos com vocalizações de 43 espécies (9 famílias) de morcegos brasileiros previamente identificadas, testamos dois softwares comerciais de identificação automatizada com classificadores disponíveis para a região Neotropical: Kaleidoscope Pro (Wildlife Acoustics, USA) e SonoChiro® 3.0 (Biotope, France). A análise dos resultados apontou que este método pode levar a erros grosseiros derivados do uso indiscriminado e acrítico por pessoal não qualificado. O nível de acurácia (% de identificações corretas) dos softwares é bastante baixo, assim como o nível de concordância entre os softwares. Também testámos duas versões do Kaleidoscope Pro: a mais recente identificou mais gravações, mas com um menor nível de acurácia, identificando erroneamente gravações que a versão anterior identificou corretamente. Nossos resultados enfatizam que, antes de sua ampla utilização na identificação acústica de morcegos no Brasil, estes softwares automatizados precisarão de muitos testes de melhoria e validação. Concluímos apresentando algumas sugestões de melhores práticas para evitar erros e para permitir que a ecolocalização se torne uma ferramenta fundamental para o avanço do conhecimento sobre os morcegos brasileiros.

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ENSAIOS

Uma nota de precaução sobre a identificação automática de chamados de ecolocalização de morcegos no Brasil

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Resumo: A análise de chamados de ecolocalização é, há muito tempo, utilizada como ferramenta imprescindível no estudo dos quirópteros na Europa, América do Norte e Oceania, por isso tem o potencial de preencher grandes lacunas de informação sobre a riqueza de espécies e atividade de morcegos no Brasil. Existem no mercado vários softwares que identificam automaticamente os chamados produzidos pelos morcegos, prometendo facilidade e rapidez na identificação dos numerosos arquivos gerados durante a gravação. Utilizando uma seleção de 71 arquivos com vocalizações de 43 espécies (9 famílias) de morcegos brasileiros previamente identificadas, testamos dois softwares comerciais de identificação automatizada com classificadores disponíveis para a região Neotropical: Kaleidoscope Pro (Wildlife Acoustics, USA) e SonoChiro® 3.0 (Biotope, France). A análise dos resultados apontou que este método pode levar a erros grosseiros derivados do uso indiscriminado e acrítico por pessoal não qualificado. O nível de acurácia (% de identificações corretas) dos softwares é bastante baixo, assim como o nível de concordância entre os softwares. Também testámos duas versões do Kaleidoscope Pro: a mais recente identificou mais gravações, mas com um menor nível de acurácia, identificando erroneamente gravações que a versão anterior identificou corretamente. Nossos resultados enfatizam que, antes de sua ampla utilização na identificação acústica de morcegos no Brasil, estes softwares automatizados precisarão de muitos testes de melhoria e validação. Concluímos apresentando algumas sugestões de melhores práticas para evitar erros e para permitir que a ecolocalização se torne uma ferramenta fundamental para o avanço do conhecimento sobre os morcegos brasileiros.

Palavras-Chave: Bioacústica; Chiroptera; Kaleidoscope Pro; Identificação acústica; SonoChiro.

Abstract: A precautionary note on the automated identification of bat echolocation calls in Brazil. The analysis of echolocation calls has long been used as an essential tool in the study of bats in Europe, North America and Oceania and, therefore has the potential to fill large gaps in information on species richness and bats activity in Brazil. There are in the market several software that automatically identify the calls produced by bats, promising ease and speed in identifying the numerous files generated during recording. Using a selection of 71 files with vocalizations of 43 species (and 9 families) of previously identified Brazilian bats, we tested two commercial automated identification software with classifiers available for the Neotropical region: Kaleidoscope Pro (Wildlife Acoustics, USA) and SonoChiro 3.0 (Biotope, France). The examination of the results showed that this method can lead to rough errors derived from the indiscriminate and uncritical use by unqualified staff. The level of accuracy (% of correct identifications) of both software is very low, just as the level of agreement between them. We also tested two versions of the Kaleidoscope Pro: the latest one identified more recordings but with a lower level of accuracy, mistakenly identifying recordings that the previous version has correctly identified. Our results emphasize that, before their wide use in acoustic identification of bats in Brazil, automated software will need much improvement and validation tests. We conclude by presenting some suggestions of best practices to avoid errors and to make bat call identification an important tool for the advancement of knowledge on Brazilian bats.

Key-Words: Acoustic identification; Bioacoustics; Chiroptera; Kaleidoscope Pro; SonoChiro.

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A bioacústica no estudo de morcegos é bastante usada na Europa, América do Norte e Oceania há mais de 30 anos (*e.g.,* Fenton *et al.,* 1987; Ahlén & Baag, 1999; Jones, 1999; Schnitzler & Kalko, 2001; Rydell *et al.,* 2002; Obrist *et al.,* 2004; Waters & Gannon, 2004; Roche *et al.,* 2011; Adams *et al.,* 2012; Walters *et al.,* 2013). Uma vez que as vocalizações de morcegos são na maior parte das vezes espécie-específicas, apresentando parâmetros acústicos bem definidos, e à medida que a gravação dessas mesmas vocalizações se torna cada vez mais acessível e precisa, a bioacústica constitui um método não-invasivo e relativamente barato, principalmente em estudo com morcegos de difícil captura por meio de redes de neblina, ou aqueles difíceis de serem detectados em seus abrigos (O'Farrell & Gannon, 1999; Ochoa *et al.,* 2000; Rydell *et al.,* 2002; MacSwiney *et al.,* 2008; Adams *et al.,* 2012). Além da identificação de espécies, crípticas ou não, a bioacústica tem sido amplamente utilizada para estudos ecológicos tais como a diferenciação de nicho ecológico, estudos de comportamento, uso do habitat e determinação de padrões de atividade espaço-temporal, além de servir como suporte para estudos de impacto ambiental (EIA) (*e.g.,* Jones & Parijs, 1993; Ahlén & Baag, 1999; Jensen & Miller, 1999; Arlettaz *et al.,* 2001; Russo & Jones, 2002; Russo & Jones, 2003; Kalcounis-Rueppell *et al.,* 2007; Abbott *et al.,* 2009; Marques *et al.,* 2015). Assim, o emprego da bioacústica tem potencial de preencher grandes lacunas de informação sobre a riqueza de espécies e atividade de morcegos no Brasil, um país com dimensões continentais e onde, até 2011, cerca de 60% do seu território não possuía qualquer registro formal de morcegos (Bernard *et al.,* 2011).

No entanto, vários cuidados são necessários para extrair o melhor na utilização desta técnica, uma vez que as vocalizações dos morcegos possuem muitas especificidades. Morcegos utilizam a ecolocalização para se orientarem no espaço e na busca por alimento em variados tipos de habitats, e as vocalizações de uma espécie podem variar bastante de acordo com os seus objetivos e as características de cada habitat (Ahlén & Baag, 1999; Barclay, 1999). Além disso, uma dada espécie pode apresentar uma grande variabilidade regional das suas vocalizações (*e.g.,* Murray *et al.,* 2001; Law *et al.,* 2002; Jiang *et al.,* 2015), o que tornam necessárias análises cuidadosas das vocalizações das espécies e posterior criação de bibliotecas de vocalizações para cada uma das regiões. Estes cuidados são essenciais para obter identificações robustas e confiáveis, principalmente na região Neotropical onde a diversidade de espécies é muito elevada e, tal como ocorre para outras regiões e em particular para espécies do mesmo gênero, as vocalizações podem ser bastante similares (Waters & Gannon, 2004; Walters *et al.,* 2013). Outra dificuldade adicional em estudos com a bioacústica é a produção de muitos arquivos de som e a necessidade de identificá-los com baixo grau de erro, tendo em consideração as dificuldades acima mencionadas. Neste caso, a identificação manual pode tornar-se inviável por consumir bastante tempo e recursos humanos. A identificação automatizada surgiu como uma ferramenta essencial para o aumento da eficiência deste tipo de estudo (Jennings *et al.,* 2008; Adams *et al.,* 2010; Armitage & Ober, 2010; Walters *et al.,* 2013), uma vez que ela pode ter as vantagens de ser mais rápida em processar os inúmeros arquivos gerados e fornecer resultados mais objetivos e consistentes ao longo do tempo (Jennings *et al.,* 2008).

Baseando-se em bibliotecas de vocalizações das espécies, e utilizando uma grande variedade de algoritmos estatísticos e matemáticos (*e.g.,* análise discriminante, redes neurais e árvores de classificação, aprendizagem computacional, entre outras), tem havido importantes progressos na automatização da identificação acústica de morcegos (Russo & Jones, 2002; Jennings *et al.,* 2008; Armitage & Ober, 2010; Adams *et al.,* 2012; Walters *et al.,* 2012; Walters *et al.,* 2013; Russo & Voigt, 2016). No entanto, publicações recentes já alertam para os perigos do uso indiscriminado e acrítico de softwares de identificação automatizada (Russo & Voigt, 2016). Atualmente, estes softwares baseiam as suas identificações em bibliotecas de vocalizações limitadas quanto ao número de espécies e quanto à amplitude da área amostrada, ou seja, restritas a algumas regiões (Russo & Voigt, 2016). Isto desconsidera a variação regional intraespecífica das vocalizações, o potencial para a ocorrência de espécies crípticas, podendo conduzir a identificações erradas, principalmente se as espécies a serem identificadas são raras ou não ocorrem na região que serviu de suporte à biblioteca de chamados (Russo & Voigt, 2016). Além disso, os softwares existentes no mercado não parecem apresentar alta concordância nas identificações quando testados com o mesmo conjunto de gravações, o que nos leva a suspeitar da alta precisão propagandeada por esses softwares (Lemen *et al.,* 2015). A baixa precisão é exatamente um fator de preocupação para uma das supostas vantagens destes métodos: resultados consistentes e independentes de viés provocado pelo observador (Jennings *et al.,* 2008; Lemen *et al.,* 2015; Russo & Voigt, 2016; Rydell *et al.,* 2017). De fato, Fritsch & Bruckner (2014), Russo & Voigt (2016) e Rydell *et al.* (2017) alertam que as identificações automatizadas geradas por estes softwares devem ser supervisionadas e validadas por pessoal capacitado e experiente em acústica de quirópteros. Uma identificação errônea – seja por considerar a espécie presente quando ela está ausente, ou considerá-la ausente quando está presente – pode ter consequências negativas e de longo prazo no conhecimento, na avaliação de padrões de distribuição, em estimativas de riqueza de espécies, na quantificação de atividade de espécies e na análise da utilização de habitat e, consequentemente na conservação das espécies de morcegos (Russo & Voigt, 2016).

É sobre este conjunto de questões que reside a nossa preocupação na utilização de softwares de identificação automatizada de chamados de ecolocalização de morcegos no Brasil. Os exemplos e as preocupações levantadas por Fritsch & Bruckner (2014), Lemen *et al.* (2015), Russo & Voigt (2016) e Rydell *et al.* (2017) têm por base análises automatizadas sobre espécies da região temperada, onde: (i) a diversidade de morcegos não é muito elevada, (ii) a descrição de chamados de

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espécies é realizada há muitos anos e, consequentemente, encontram-se disponíveis amplas bibliotecas de vocalizações, e (iii) os monitoramentos acústicos de morcegos são prática corrente.

Na região Neotropical, ao contrário, não só a diversidade de morcegos é a mais elevada do planeta (Willig *et al.*, 2003), como – e também por esse motivo – grande parte das vocalizações das espécies são ainda desconhecidas, uma vez que só muito recentemente se iniciaram estudos sistematizados com bioacústica. Dentre as 262 espécies de morcegos neotropicais, apenas 107 possuem registro acústico, ou seja, cerca de 60% das espécies neotropicais não tem seus repertórios acústicos conhecidos. Embora apresentando uma tendência crescente, no Brasil esses trabalhos são ainda muito pontuais (*e.g.*, Fenton *et al.*, 1999; Marques *et al.*, 2015; Hintze *et al.*, 2016) e grande parte das vocalizações disponíveis relativas às espécies que ocorrem no país provém de outros países como México, Costa Rica, Panamá, Chile e Guiana Francesa (*e.g.*, Barclay, 1983; Jennings *et al.*, 2004; Jung *et al.*, 2007; Barataud *et al.*, 2013; Jung *et al.*, 2014). Assim, não só as bibliotecas de vocalizações apresentam um viés distribucional, como são extremamente incompletas.

É previsível que o uso indiscriminado e acrítico destes softwares de análise automatizada por biólogos e profissionais de consultoria ambiental não habilitados e/ou inexperientes no estudo acústico de quirópteros no Brasil conduza a identificações erradas, com consequências desastrosas nos níveis de conhecimento, manejo e conservação de morcegos acima mencionadas. Deste modo, neste ensaio tivemos como objetivo alertar sobre o uso indiscriminado de softwares de identificação automatizada de vocalizações de morcegos no Brasil sem a supervisão por especialistas em bioacústica de morcegos. De uma maneira bem direta, nosso objetivo foi demostrar que a classificação automatizada, em seu estado atual, deve ser vista com ressalvas. Para tanto, realizamos e apresentamos um teste onde utilizamos uma seleção de arquivos com vocalizações previamente identificadas manualmente pelos autores deste ensaio (com validação cega por dois ou mais autores), e testamos dois softwares comerciais de identificação automatizada com classificadores disponíveis para a região Neotropical: Kaleidoscope Pro (Wildlife Acoustics, USA) e SonoChiro® 3.0 (Biotope, France). No caso do Kaleidoscope Pro utilizamos duas versões (2.2.1 com o classificador 2.1.0Beta6 e versão 4.0.3 com o classificador 3.1.3) para aferirmos a sua evolução na correção de identificação das espécies. Foram utilizados 71 arquivos (com 72 identificações possíveis) referentes a um total de 47 taxa pertencentes a 9 famílias (Tabela 1).

As gravações no formato .wav foram renomeadas com códigos para não influenciar o pesquisador, e foram analisadas e classificadas pelas duas versões do Kaleisdoscope Pro e pelo SonoChiro. Nas duas versões do Kaleidoscope Pro, utilizamos o seu classificador correspondente (Bats of Neotropics, região Brasil) em modo *conservador,* definindo os seguintes parâmetros como sinal de interesse: Frequência 8-250 kHz; Duração 1-500 ms; Número mínimo de pulsos = 1. No SonoChiro foram utilizados os seguintes parâmetros: Sensibilidade 7 e Duração mínima do pulso 0,2 ms. O output gerado por cada software foi comparado com a identificação manual já conhecida de cada arquivo, para se verificar as percentagens de identificações corretas, incorretas e não-identificações. Note-se que ambos os softwares retornam um percentual ou índice de confiança na identificação realizada: 0 (confiança mínima) a 1 (confiança máxima) no Kaleidoscope Pro, e 0 (confiança mínima) a 10 (confiança máxima) no SonoChiro. Ao contrário do Kaleisdoscope Pro, o SonoChiro apresenta também resultados ao nível da família, com grau de confiança que pode divergir daquele apresentado para o nível específico. Para efeitos de comparação entre os softwares,

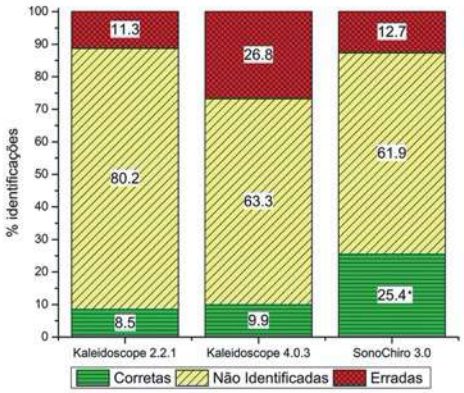

Figura 1: Percentagem de acerto (correta), erro (errada) e sem identificação (não identificada) em todas as gravações testadas nos softwares Kaleisdoscope Pro (versão 2.1.1 com classificador dos morcegos neotropicais 2.1.0beta6 e versão 4.0.3 com classificador dos morcegos neotropicais 3.1.3) e SonoChiro (versão 3.0). (*) 14,1% das identificações corretas do SonoChiro 3.0 são referentes a identificação ao nível de família.

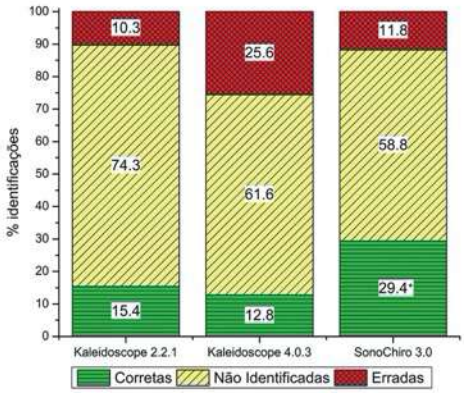

Figura 2: Percentagem de acerto (correta), erro (errada) e sem identificação (não identificada) nas gravações contendo espécies presentes na base de dados dos softwares Kaleisdoscope Pro (versão 2.1.1 com classificador dos morcegos neotropicais 2.1.0beta6 e versão 4.0.3 com classificador dos morcegos neotropicais 3.1.3) e SonoChiro (versão 3.0). (*) 13,7% das identificações corretas do SonoChiro 3.0 são referentes a identificação ao nível de família.

Tabela 1: Lista de espécies e número de gravações utilizadas neste trabalho, com a localidade onde foram gravadas (Localidades: BA = Bahia, Brasil; CE = Ceará, Brasil; ES = Espirito Santo, Brasil; MS = Mato Grosso do Sul, Brasil; GF = Guiana Francesa; PE = Pernambuco, Brasil; RN = Rio Grande do Norte, Brasil. Referências bibliográficas: 1 = Jung *et al.*, 2007; 2 = Barataud *et al.*, 2013; 3 = Hintze *et al.*, 2016; 4 = Jung & Kalko, 2011; 5 = Jung *et al.*, 2014; 6 = Ochoa *et al.*, 2000; 7 = Arias-Aguilar *et al.*, submitted; 8 = Rydell *et al.*, 2002; 9 = Falcão *et al.*, 2015; 10 = Barbier *et al., in prep.;* 11 = López-Baucells *et al.*, 2014; 12 = Guillén-Servent & Ibáñez, 2007; 13 = Mora *et al.*, 2004; 14 = Siemers *et al.*, 2001; 15 = Rodrigues & Bernard, *in prep.;* 16 = Mora & Torres, 2008; 17 = Hintze *et al., in prep.;* 18 = Thoisy *et al.*, 2014; 19 = Smotherman & Guillén-Servent, 2008). [1] Espécie presente na base de dados do Kaleidoscope Pro [2] Espécie presente na base de dados do SonoChiro 3.0.

Espécies	Localidade	n gravações	n sinais total	Referências Bibliográficas
Centronycteris maximiliani[1,2]	GF; PE	2	8	1, 2, 3
Cormura brevirostris[2]	GF	1	62	1, 2, 4
Cynomops abrasus[2]	GF	1	3	2, 5
C. paranus[2]	GF	1	3	2, 5
C. planirostris[2]	GF	1	4	2, 4, 5
Diclidurus albus[1,2]	GF	1	3	1, 2
D. ingens[2]	GF	1	3	1, 2
D. scutatus[2]	GF	1	3	1, 2
Eptesicus brasiliensis[1]	MS	1	4	6, 7
E. furinalis[1,2]	BA	2	32	2, 7, 8
Eumops auripendulus[2]	GF	1	4	2, 5
E. hansae[2]	GF	1	3	7
Eumops sp. 1	PE	1	14	2, 4, 5
Eumops sp. 2	PE	1	11	2, 5
Furipterus horrens[2]	BA; GF	2	14	2, 9
Histiotus diaphanopterus	PE	1	5	10
Lasiurus ega[1,2]	BA	1	7	5, 8, 11
Lonchorhina aurita[2]	PE	1	12	2
Molossops neglectus	GF	1	4	5
M. temminkii[1]	MS	2	6	5, 12
Molossus currentium	PE	1	4	2, 4, 5
M. molossus[1,2]	MS	2	10	2, 4, 5, 13
M. rufus[1,2]	MS; PE	2	6	2, 4, 5
Molossus sp.	PE	1	5	2, 5
Myotis albescens[2]	MS	1	14	7
M. lavali	PE	1	5	7
M. nigricans[1,2]	MS	1	8	2, 4, 7, 14
Myotis sp.	PE	1	7	2, 14
Natalus macrourus	PE	1	8	7
Neoplatymops mattogrossensis	PE	1	8	5, 7, 15
Noctilio albiventris[2]	MS	1	3	2, 4
N. leporinus[1,2]	PE; RN	4	37	2, 4
Nyctinomops laticaudatus[1,2]	MS	2	7	2, 4, 5, 16
Peropteryx macrotis[1,2]	RN	1	5	1, 2, 4, 8
Peropteryx sp.	PE	1	4	1, 2, 3
P. trinitatis[2]	PE	1	5	1, 2, 3
Promops centralis[1,2]	ES; PE; RN	5	36	2, 4, 5, 17
P. nasutus	PE	3	10	2, 5, 7, 15
Pteronotus gymnonotus[1,2]	PE	4	63	4, 7
P. parnellii[1,2]	MS	1	4	4, 8, 18
P. personatus[1,2]	PE	1	3	4, 19
Rhogeessa hussoni	PE	1	5	7, 15
Rhynchonycteris naso[1,2]	GF	1	3	1, 2
Saccopteryx bilineata[1,2]	PE	4	59	1, 2, 3, 4
Saccopteryx leptura[1,2]	CE	1	4	1, 2, 4
Saccopteryx sp.	PE	3	14	3
Thyroptera tricolor	GF	2	4	2

consideramos apenas as identificações ao nível da espécie como "identificação correta". Registramos também os arquivos com um nível de confiança na identificação automatizada superior a 80%, segundo cada software. Foram ainda verificadas as identificações de arquivos contendo espécies que constam da base de dados de cada um dos softwares. Tal como Lemen *et al.* (2015) testamos também o nível de concordância nas identificações positivas (corretas e incorretas) entre as versões do Kaleidoscope Pro e o SonoChiro.

A análise dos resultados apontou que o nível de acurácia (% de identificações corretas) dos softwares

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foi bastante baixo (Figura 1). O software Kaleidoscope Pro (versão atual) apenas identificou corretamente 7 de 72 identificações possíveis (Figura 1; Tabela 2). Enquanto que o SonoChiro, embora tenha tido uma melhor performance, identificou corretamente apenas 8 de 72 identificações possíveis (até 18 identificações corretas, se considerarmos as identificações corretas ao nível da família) (Figura 1; Tabela 2).

Comparando as duas versões do Kaleidoscope Pro, a versão mais recente conseguiu identificar uma maior percentagem de arquivos em relação à versão mais antiga, embora o percentual de identificações corretas entre as duas versões tenha sido similar (Figura 1; Tabela 2). No entanto, e surpreendentemente, o nível de identificações incorretas aumentou muito da versão antiga para a atual (Figura 1; Tabela 2). Em alguns casos, a versão antiga demonstrou um nível de acurácia na identificação muito superior à atual, como no caso de gravações de *Saccopteryx bilineata, Molossus molossus* e *Noctilio leporinus* (Tabela 2). As melhorias registradas da versão antiga para a atual resumiram-se às identificações de *Myotis nigricans, Rhynchonycteris naso* e *Pteronotus gymnonotus* (Tabela 2). O SonoChiro também apresentou um percentual elevado de identificações erradas, onde de um total de 38,1% de arquivos tidos como identificados, 12,7% foram identificados incorretamente (Figura 1).

Se considerarmos apenas os arquivos contendo espécies que constam na base de dados de cada um dos softwares, detectamos apenas uma pequena melhoria na performance (Figura 2; Tabela 2). As versões do Kaleidoscope Pro (antiga e nova) identificaram corretamente apenas seis e cinco espécies, respectivamente, em 39 possíveis (Figura 2; Tabela 2). Enquanto que o SonoChiro identificou corretamente apenas 15 gravações em 51 gravações (Figura 2; Tabela 2). No entanto, as percentagens de identificações incorretas do Kaleidoscope Pro e do SonoChiro continuaram elevadas (Figura 2).

Utilizando apenas os arquivos onde, segundo os softwares, os níveis de confiança na identificação automatizada foram superiores a 80%, a percentagem de identificações incorretas foi de 11,1% na versão mais atual do Kaleidoscope Pro (oito identificações incorretas), enquanto que no SonoChiro foi de 8,3% (seis identificações incorretas) (Tabela 2). A versão mais antiga do Kaleisdoscope só assinalou um nível de confiança superior a 80% numa gravação corretamente identificada como *Eptesicus furinalis* (Tabela 2).

O nível de concordância entre os softwares Kaleidoscope Pro e SonoChiro foi extremamente reduzido. Em apenas uma gravação do total de 71 gravações (1,4%) obtivemos a mesma classificação dos softwares (Tabela 2). Entre a versão antiga do Kaleidoscope Pro e o SonoChiro houve apenas duas identificações concordantes (2,8%) (Tabela 2).

Os resultados aqui apresentados são preocupantes, sublinhando a necessidade destes softwares e seus classificadores passarem por muito aperfeiçoamento e testes de validação antes de serem propagandeados no mercado para amplo uso na identificação acústica de morcegos no Brasil. É, no entanto, de destacar a atenção dos criadores do software SonoChiro para com os seus utilizadores; com efeito, no momento da disponibilização, os criadores reconhecem a limitação do software relativamente a morcegos Neotropicais. Exatamente devido à inexistência de bibliotecas completas de chamados destas espécies, reconhecem ainda que alguns grupos ou gêneros se encontram mais sujeitos a viés de identificação. Preocupante também é o decréscimo no percentual de identificações corretamente identificadas entre as versões do Kaleidoscope Pro, uma vez que se esperaria que versões posteriores fossem capazes de corrigir problemas experimentados por versões mais antigas. Nossa análise não foi exaustiva, mas nos parece claro que, quando não tratados com o devido cuidado e sob supervisão de pessoas experientes e capacitadas em acústica de quirópteros, os resultados produzidos por estes softwares, mesmo quando utilizando apenas as identificações que apresentam grau de confiança elevado, devem ser considerados com muita cautela. Encontramos também um nível extremamente baixo de concordância entre as identificações dos dois softwares analisados. Este resultado ressalta o mesmo tipo de problema já levantado por Lemen *et al.* (2015): a falta de resultados consistentes e livres de viés, que seria uma das supostas vantagens que estes programas poderiam trazer em relação à identificação manual. Sem a devida supervisão, em vez de obter resultados que representam a realidade dos habitats estudados, corremos o risco de efetuar estimativas de diversidade de espécies de quirópteros e seus padrões de atividade que são apenas reflexo do software utilizado (Lemen *et al.*, 2015; Russo & Voigt, 2016). Os riscos da utilização destes softwares diminuem quando os utilizadores têm uma abordagem crítica, verificando quais as espécies que ocorrem na sua área de estudo, região e País. Desta forma, consultando o banco de dados dos softwares em causa, se verificará que nas suas gravações podem constar espécies que o software não tem em conta, identificando erroneamente ou não as assinalando.

Além da qualidade das identificações em si, nos preocupa também as consequências do uso destas identificações errôneas. Hoje, o licenciamento ambiental, seja relacionado à pré- ou pós-instalação de parques eólicos ou outras grandes infraestruturas, ou ainda como o cumprimento de condicionantes de compensação ambiental é um dos maiores mercados para a gravação e análise de sinais de ecolocalização de morcegos no Brasil. Em termos de distribuição e conservação das espécies, identificações incorretas e subestimativas grosseiras podem ser mais lesivas do que uma não-identificação dos arquivos (Russo & Voigt, 2016). De forma similar, a descrição de padrões de atividade ou de uso de habitat baseados em dados incorretos e que subestimem os reais impactos das infraestruturas sobre a fauna de morcegos tem alto potencial de influência sobre processos de liberação de licenças de instalação. Assim, especialmente no caso do licenciamento ambiental, a classificação automatizada de sinais de ecolocalização deve ser vista com mais ressalvas ainda. Os órgãos licenciadores precisam

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Tabela 2: Gravações utilizadas nos testes realizados comparando a identificação acústica prévia e as identificações automatizadas realizadas nas duas versões do Kaleidoscope Pro (2.2.1 e 4.0.3) e no SonoChiro 3.0. Com asterisco (*), estão assinaladas as identificações automatizadas fornecidas por cada software com um nível de confiança mínimo de 80%. (NI = Não identificado). [1] Espécie presente na base de dados do Kaleidoscope Pro [2] Espécie presente na base de dados do SonoChiro 3.0.

Arquivo	ID	Kaleidoscope Pro 2.2.1	Kaleidoscope Pro 4.0.3	SonoChiro 3.0
1	*C. maximiliani*[1,2]	NI	NI	*Saccopteryx bilineata**
2	*C. brevirostris*[2]	*Molossus rufus*	*Promops centralis*	*Cormura brevirostris**
3	*C. maximiliani*[1,2]	NI	NI	NI
4	*F. horrens*[2]	NI	NI	*Natalus* spp.*
5	*C. abrasus*[2]	NI	NI	NI
6	*E. auripendulus*[2]	NI	*Eumops glaucinus**	*Eumops auripendulus**
7	*E. hansae*[2]	NI	*Lasiurus cinereus**	Molossidae*
8	*N. leporinus*[1,2]	NI	NI	NI
9	*P. gymnonotus*[1,2]	NI	*Pteronotus gymnonotus**	NI
10	*E. brasiliensis*[1]	NI	NI	NI
11	*H. diaphanopterus*	NI	NI	NI
12	*M. molossus*[1,2]	NI	NI	NI
13	*M. molossus*[1,2]	*Molossus molossus*	*Peropteryx kappleri*	NI
14	*M. lavali*	NI	NI	*Myotis nigricans*
15	*P. centralis*[1,2]	NI	NI	Vespertilionidae
16	*P. trinitatis*[2]	NI	NI	*Peropteryx trinitatis**
17	*S. leptura*[1,2]	NI	NI	*Saccopteryx leptura**
18	*T. tricolor*	NI	NI	*Thyroptera* sp.*
19	*N. laticaudatus*[1,2]	NI	NI	Molossidae
20	*D. scutatus*[2]	NI	NI	NI
21	*E. furinalis*[1,2]	NI	NI	*Eptesicus furinalis**
22	*F. horrens*[2]	NI	NI	*Natalus* spp.*
23	*D. albus*[1,2]	NI	NI	NI
24	*C. planirostris*[2]	NI	*Lasiurus ega*	NI
25	*P. personatus*[1,2]	NI	NI	Moomopidae
26	*M. rufus*[1,2]	NI	NI	Molossidae
27	*M. rufus*[1,2]	NI	NI	NI
28	*M. temminkii*[1,2]	NI	NI	*Myotis riparius**
29	*C. paranus*[2]	NI	NI	Molossidae*
30	*P. nasutus*	NI	NI	NI
31	*L. ega*[1,2]	*Eptesicus furinalis*	*Eptesicus fuscus**	NI
32	*M. albescens*[2]	NI	NI	NI
33	*N. macrourus*	NI	NI	NI
34	*N. mattogrossensis*	NI	*Molossus molossus*	NI
35	*M. nigricans*[1,2]	*Noctilio leporinus*	*Myotis nigricans*	NI
36	*N. albiventris*[2]	NI	NI	NI
37	*N. leporinus*[1,2]	NI	NI	*Noctilio leporinus**
38	*P. centralis*[1,2]	*Molossus rufus*	*Tadarida brasiliensis*	NI
39	*P. gymnonotus*[1,2]	NI	NI	NI
40	*R. hussoni*	NI	NI	NI
41	*P. parnellii*[1,2]	NI	NI	NI
42	*Saccopteryx* sp.	NI	NI	NI
43	*R. naso*[1,2]	NI	*Rhynchonycteris naso**	NI
44	*N. laticaudatus*[1,2]	NI	NI	NI
45	*Peropteryx* sp.	NI	NI	NI
46	*D. ingens*[2]	*Lasiurus cinereus*	*Lasiurus cinereus*	NI
47	*M. neglectus*	NI	NI	NI
48	*M. currentium*	NI	NI	NI
49	*P. macrotis*[1,2]	NI	*Eptesicus furinalis**	NI
50	*P. nasutus*	NI	*Myotis nigricans*	NI
50	*P. gymnonotus*[1,2]	NI	NI	NI
51	*S. bilineata*[1,2]	NI	NI	*Saccopteryx leptura**
52	*Saccopteryx* sp.	NI	NI	NI
53	*P. nasutus*	NI	*Peropteryx kappleri**	NI
54	*P. centralis*[1,2]	NI	NI	NI
55	*T. tricolor*	NI	NI	NI

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Arquivo	ID	Kaleidoscope Pro 2.2.1	Kaleidoscope Pro 4.0.3	SonoChiro 3.0
56	*M. temminkii*[1]	NI	NI	*Saccopteryx canescens*
57	*Molossus* sp.	NI	NI	NI
58	*P. centralis*[1,2]	NI	NI	NI
59	*Saccopteryx* sp.	*Centronycteris centralis*	*Centronycteris centralis*	NI
60	*P. centralis*[1,2]	NI	NI	NI
61	*Myotis* sp.	NI	NI	NI
62	*Eumops* sp. 1	NI	*Eumops glaucinus*	Molossidae
63	*Eumops* sp. 2	*Nyctinomops laticaudatus*	*Eumops glaucinus**	Molossidae*
64	*E. furinalis*[1,2]	*Eptesicus furinalis**	*Eptesicus furinalis**	*Eptesicus furinalis**
65	*L. aurita*[2]	NI	*Noctilio leporinus**	NI
66	*P. gymnonotus*[1,2]	*Noctilio leporinus*	*Pteronotus gymnonotus*	NI
67	*N. leporinus*[1,2]	*Noctilio leporinus*	*Pteronotus gymnonotus**	*Noctilio leporinus**
68	*N. leporinus*[1,2]	NI	*Pteronotus gymnonotus*	*Noctilio leporinus**
69	*S. bilineata*[1,2]	*Saccopteryx bilineata*	*Noctilio leporinus*	*Saccopteryx* sp.*
70	*S. bilineata*[1,2]	*Saccopteryx bilineata*	*Noctilio leporinus*	*Saccopteryx* sp.*
71	*S. bilineata*[1,2]	*Saccopteryx bilineata*	*Noctilio leporinus*	*Saccopteryx leptura**

ser notificados das grandes lacunas que ainda existem e nas implicações do mau uso destes softwares.

A capacitação de pessoal em bioacústica focada em morcegos é uma condição *sine qua non* para o uso deste tipo de metodologia em qualquer trabalho científico ou técnico no Brasil. A falta de oferta deste tipo de formação não é uma justificativa, uma vez que só entre 2014 e 2016 foram ofertados, pelo menos, seis cursos em Brasília, Minas Gerais, Pernambuco e Rio de Janeiro. Novos cursos serão ofertados e outros mais precisam ser oferecidos em outras regiões do Brasil. Adicionalmente, existe já ampla bibliografia que pode auxiliar na melhoria das identificações manuais ou automáticas supervisionadas, mesmo que ainda tenham restrições em termos de espécies e abrangência geográfica (para uma revisão ver Arias-Aguilar *et al.*, submetido).

Dado o potencial impacto de identificações incorretas, o investimento na difusão da capacitação em gravação e análise de sinais de ecolocalização deveria ser considerado prioridade para a conservação dos morcegos brasileiros. Mesmo no futuro, quando os programas de identificação automatizada estiverem bem afinados, ainda assim será necessário que estes programas sejam utilizados por pessoas experientes de forma a que a validação dos seus resultados tenha viés reduzido e seja realizada de forma crítica (Jennings *et al.*, 2008; Fritsch & Bruckner, 2014; Lemen *et al.*, 2015; Russo & Voigt, 2016; Rydell *et al.*, 2017). Quando em pleno funcionamento, estes softwares terão vantagens óbvias na velocidade de processamento de milhares de arquivos correspondentes a terabytes de informação acústica digital. No entanto, ainda não serão capazes de substituir recursos humanos experientes, essenciais para que os estudos apresentem melhor qualidade (Jennings *et al.*, 2008; Fritsch & Bruckner, 2014; Russo & Voigt, 2016; Rydell *et al.*, 2017).

Até que tenhamos mais pessoal qualificado para a gravação e análise de sinais de ecolocalização no Brasil, e até que a classificação efetuada pelos softwares possa ser considerada confiável, a adoção de melhores práticas precisa ser estimulada. Para evitar erros grosseiros sugerimos que:

- Trabalhos de campo incluindo monitoramentos acústicos devem ser efetuados utilizando metodologias e equipamentos adequados ao trabalho proposto e executado por pessoal experiente no estudo de quirópteros (*e.g.*, Ahlén & Baag, 1999; Barclay, 1999; Kunz & Parsons, 2009; Adams *et al.*, 2012);
- A identificação acústica, mesmo que automatizada não deve ser prontamente acatada como uma verdade absoluta, e deve ser sujeito a análise crítica por parte de pessoal qualificado, habilitado e experiente na área (mínimo de 1 ano de experiência com identificação de espécies) (*e.g.*, Ahlén & Baag, 1999; Jennings *et al.*, 2008; Fritsch & Bruckner, 2014; Russo & Voigt, 2016);
- A identificação acústica deve ter por base a bibliografia existente descrevendo as vocalizações, e suportada por boas bibliotecas de vocalizações da região em estudo, para que as identificações contenham o menor número de erros possível (Ahlén & Baag, 1999; Waters & Gannon, 2004; Russo & Voigt, 2016);
- A literatura de suporte às identificações automatizadas ou à identificação manual deve ser claramente apontada (*e.g.*, Ahlén & Baag, 1999; Barclay, 1999; Waters & Gannon, 2004; Kunz & Parsons, 2009; Walters *et al.*, 2013);
- No caso de licenciamento ambiental, os órgãos competentes devem, por obrigação legal, exigir que os estudos sejam assinados por técnicos/biólogos experientes e devidamente capacitados em bioacústica de morcegos;
- A criação de uma comissão de Bioacústica de Morcegos dentro da Sociedade Brasileira para o Estudo de Quirópteros, para a definição de métodos/práticas adequadas a cada tipo de estudo de licenciamento ambiental no Brasil é urgente;
- Ainda no licenciamento ambiental, tanto os sinais originalmente gravados quanto o output de identificação devem ser organizados em um repositório público (biblioteca de sons), sem restrições e passíveis de validação por pessoal qualificado.

Ressaltamos que acreditamos que a utilização de sinais de ecolocalização é uma ferramenta fundamental para o avanço do conhecimento sobre os morcegos brasileiros. Seu uso (mas não o mau uso!) deve ser estimulado e constantemente melhorado no país. Neste processo, ganharão os morcegos e a ciência brasileira.

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3.2 BIOACOUSTICS AS A NON-INVASIVE METHOD FOR THE STUDY OF CAVE-DWELLING BAT SPECIES IN BRAZIL´S DRYLANDS

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RESUMO

Devido à dependência muito específica de abrigos, os morcegos que vivem em cavernas são espécies particularmente vulneráveis e algumas encontram-se ameaçadas nacional ou globalmente. A maioria dos estudos focados em morcegos cavernícolas utiliza métodos de captura e visitação - mesmo para fins de pesquisa - que frequentemente perturba as colônias. Métodos menos invasivos de amostragem e monitoramento são, portanto, altamente desejáveis, especialmente quando estão envolvidas espécies ameaçadas. Nós avaliamos o uso da bioacústica como um método de baixo impacto, não invasivo e útil para a identificação de espécies de morcegos cavernícolas insetívoros no Brasil e nos Neotrópicos. Nossas espécies-focais foram *Lonchorhina aurita* e *Natalus macrourus* (ambas ameaçadas de extinção no Brasil), além de *Pteronotus gymnonotus* e *Pteronotus personatus*, conhecidas por formarem grandes colônias. Usando o método de *hand-release,* descrevemos suas chamadas de ecolocalização e comparamos suas características com as chamadas de vôo livre. Verificamos que as vocalizações das quatro espécies podem ser identificáveis de forma correta e inequívoca. Descrevemos as chamadas de ecolocalização para *N. macrourus* (sem efeitos de *aliasing*) e *L. aurita* pela primeira vez no Brasil. Além das implicações para a ciência básica, verificamos que o método pode ser prontamente aplicado em situações em que a detecção de espécies é obrigatória, como em avaliações de impacto ambiental envolvendo espécies de morcegos ameaçadas de extinção, ou quando o monitoramento de longo prazo é necessário. Dada a confiabilidade e eficácia deste tipo de amostragem, sugerimos que o registro das chamadas de ecolocalização deva agora ser considerado obrigatório para avaliações de impacto ambiental envolvendo morcegos no Brasil.

Bioacoustics as a non-invasive method for the study of endangered and cave-dwelling bat species in Brazil

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Abstract

Due to highly specific roost dependence, cave-dwelling bats are particularly vulnerable species, some nationally or globally threatened. Most studies focused on cave-dwelling bats uses capture methods, and visitation – even for research purposes – frequently stresses colonies. Less invasive sampling and monitoring methods are, therefore, highly desirable, especially when threatened species are involved. We evaluated the use of bioacoustics as a lower impact, non-invasive, useful method for the identification of insectivorous cave-dwelling bat species in Brazil and the Neotropics. Our focal species were *Lonchorhina aurita* and *Natalus macrourus* (both endangered in Brazil), plus *Pteronotus gymnonotus* and *Pteronotus personatus*, known to form extensive colonies. We described their echolocation calls using hand-release methods and compare their characteristics with free-flight calls, and the calls of the four species can be correctly and unequivocally identifiable. We described the echolocation calls for *N. macrourus* (with no *aliasing* effects) and *L. aurita* for the first time for Brazil. Besides the implications for basic science, our findings are readly applied in situations when species detection is mandatory, like in environmental impact assessments involving endangered bat species, or when long-term monitoring is required. Given the plausibility and the effectiveness of such sampling, we suggest that the echolocation calls' recording should now be considered as mandatory for environmental impact assessments involving bats in Brazil.

Key words: bioacoustics; Chiroptera monitoring; echolocation calls; *Lonchorhina aurita*; *Natalus macrourus*; *Pteronotus gymnonotus*; *Pteronotus personatus*; tropical dry forest.

Introduction

Cave-dwelling bats are particularly vulnerable species due to their strong dependence on caves with specific characteristics to shelter these species, particularly considering the growing of anthropogenic pressures such as underground habitats face globally (Furey and Racey 2016; Glover and Altringham 2008; McCracken 2011; Rodríguez-Durán 2009; Trajano 2012). Most of the cave-dwelling bat species strictly shelters in caves, making them highly dependent on the availability of caves with specific conditions, such as temperature or humidity. Those caves shelters against adverse weather or predators, but are also social centers and nurseries (Glover and Altringham 2008; Kunz and Fenton 2006; Rodríguez-Durán 2009).

Caves are sensitive habitats whose biotas are frequently composed of very specialized organisms (Culver et al. 2000; Halse 2018). Worldwide, karstic areas are under pressure, and the most common anthropogenic threatens on caves are related to mining, vandalism, and unregulated visitation (Furey and Racey 2016; Halse 2018; Trajano 2012). Although usually controlled, research methods used to study cave-dwelling bat species may also alter cave conditions and stress their biotas, including bat colonies. Some practices often involve invasive capture and handling techniques such as hand nets, mist nets, and harp-traps inside or close to the roosts (Furey and Racey 2016; Halse 2018; McCracken 2011; Rodríguez-Durán 2009; Trajano 2012; Warren and Witter 2002). Therefore, the search for less intrusive research methods is highly desired or even mandatory in some cases (Sikes et al. 2016), especially when threatened species are involved.

Non-invasive techniques like bioacoustics surveys are long available for echolocating bats and are broadly used to assess activity and species richness in several countries and regions with success (e.g., Ahlén and Baagoe 1999; Fenton 1999; Fenton et al. 1987; Russo and Jones 2002). However, to fully take advantage of this method, the bats' echolocation calls in a given region of study need to be minimally recognized (Ahlén and Baagoe 1999; Barclay 1999). Unfortunately, the majority of the Neotropical bat calls are still not fully described, and consequently, the use of bioacoustics frequently requires more information on how these species vocalize (Arias-Aguilar et al. 2018; López-Baucells et al. 2016). This situation is not different for Brazil, a continental-sized, species-rich country that harbors more than 180 species of bats (Nogueira et al. 2018). Formal and systematic efforts have been carried out in Brazil to

assess and describe its vibrant bat echolocation repertoire, but still a long way to be completed (Arias-Aguilar et al. 2018; Hintze et al. 2019).

Even if now more affordable, bioacoustics still has some limitations for bats as some species are difficult to be recorded and their calls precisely identified. For example, the acoustic identification of most of the Phyllostomidae species is problematic, since their calls have high directionality, low intensity and are similar in structure, making it challenging to discriminate species (Barataud et al. 2013; Kalko 2004; Yoh et al. 2020). However, considering the Brazilian bat fauna is composed of species from nine families, a large set of species can still be easily identified by their echolocation calls, enabling the use of acoustics methods for several purposes (Arias-Aguilar et al. 2018; Hintze et al. 2019; López-Baucells et al. 2016).

Found across the Neotropical region, *Pteronotus gymnonotus* (Wagner, 1843)*, P. personatus* (Wagner, 1843) *and Lonchorhina aurita* Tomes, 1863 are medium-sized species belonging to the Moormopidae and Phyllostomidae families, respectively, while *Natalus macrourus* (Gervais, 1856) is a small-sized Natalidae species restricted to Bolivia, Brazil and Paraguay (Delgado-Jaramillo et al. 2020; Delgado-Jaramillo et al. 2017; Gardner 2008; Guilherme and Tejedor 2013; Simmons and Cirranello 2019; Simmons et al. 2005). All these four species are considered very dependent on caves (de la Torre and Medellín 2010; Gardner 2008; Guilherme and Tejedor 2013; Lassieur and Wilson 1989; Mena 2016). Moreover, *L. aurita* and *N. macrourus* are nationally endangered species in Brazil (ICMBio 2018), and *Pteronotus gymnonotus* and *P. personatus* are strictly cave-dwelling species, known to form extensive colonies in several parts of the Neotropics (Rodríguez-Durán 1998; Rodríguez-Durán 2009). In Northeastern Brazil, some caves harbor more than 200,000 bats (Azevedo and Bernard 2015), and such large colonies inside a single roost make them vulnerable to disturbance.

Therefore, some caves in Brazil – and the Neotropics as well – frequently harbor a combination of threatened and exceptionally large populations of other cave dependent species, making such sites of particular conservation concerns (Bernard et al., 2012; Medellin et al., 2017; Jaramillo, 2018). This is particularly true considering that caves and their associated biota are frequently the subjects of environmental impact assessments related to mining activities (Bernard et al., 2012), an essential economic sector not just in Brazil, but elsewhere in the Neotropics.

So, facing such a scenario, could bioacoustics be used as a lower impact, non-invasive, useful method for the identification of insectivorous cave-dwelling bat species in Brazil and the

Neotropics? To answer this question, we recorded the echolocation calls of *P. gymnonotus*, *P. personatus*, *L. aurita,* and *N. macrourus* and compared their calls using two different methods to sample the calls, the hand-release method and free-flight, assessing if these species are easily and unequivocally identified based solely on their acoustic characters.

Materials and methods

Study area and species sampled

We recorded echolocation calls of *P. gymnonotus*, *P. personatus*, *L. aurita,* and *N. macrourus* in "Meu Rei" and "Furna do Gato" caves, both located in Catimbau National Park, Pernambuco State, Northeastern Brazil (8° 29.225'S; 37° 16.747'W). Meu Rei cave (~162.6 m of length) shelters up to 10 bat species, with populations reaching up to 120,000 individuals on some occasions, where *P. gymnonotus* is, qualitatively, the most abundant species (Azevedo and Bernard, 2015; Delgado-Jaramillo et al., 2017). With ~35 m of length, "Furna do Gato" cave is smaller than Meu Rei, and houses < 1000 individuals of six species (Azevedo and Bernard, 2015). Bat capture was conducted during inventories in the two caves, using hand nets. We identified the bats at species-level based on Gardner (2008) and Díaz et al. (2016). Vouchers of the species were collected and deposited in the Mammal Collection of the Federal University of Pernambuco (*P. gymnonotus*: UFPE 3643; *P. personatus*: UFPE 3645; *L. aurita*: UFPE 3644; *N. macrourus*: UFPE 3317). This study was carried out following the recommendations of the Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education (Sikes et al., 2016), and approved by Brazilian ICMBio/MMA under permits 43816-1, 43816-2 and 59743-1.

Acoustics sampling and analysis

Individuals of *P. gymnonotus*, *P. personatus,* and *L. aurita* were both recorded free-flying during their roost emergence and by hand-release after capture. We recorded the calls from the hand-released bats using the Dodotronic Ultramic 384K microphone (Dodotronic di Ivano Pelicella, Italy) with 384 kHz sampling rate linked to an Apple iPad Air 2. To avoid aliasing, in the case of *Natalus macrourus*' calls, we used one Wildlife Acoustics SM4BAT FS with 500 kHz sampling rate. To ensure proper performance on recordings and to mitigate hypothetical

bias on data collection, we only recorded during nights with good weather conditions, without strong winds or rain (Kunz and Parsons, 2009).

For acoustic analysis, we only considered sequences containing a minimum of three consecutive calls, with appropriate signal-to-noise ratio and without clipping (Lloyd et al., 2006; Ratcliffe et al., 2011), excluding feeding-buzzes or social-calls. We analyzed the calls using CallViewer18, a MATLAB based software (Skowronski and Fenton, 2008), with spectrogram parameters set to Fast Fourier Transformation size 1024, 1 ms of windows length and a background threshold of 10 dB, using Hanning windows. Using the CallViewer´18´s Auto Detection function, we extracted seven acoustic variables: inter-pulse interval (IPI, in ms), call duration (Dur, in ms), minimum frequency (Fmin, in kHz), maximum energy frequency (FME, in kHz), and maximum frequency (Fmax, in kHz). We set the parameters for the Auto Detection function following Hintze et al. (2016). For each species, we calculated the mean ± standard deviation for all analyzed parameters. We used Raven Pro 1.5 Build 29 (Cornell, 2014) to build the sonograms showed in this study, adopting a Hann window, 512 DFT size with 98% overlap, and clipping values under 20 dB. To improve visualization and comparison of the species´ call structures, we limited the displayed frequency values up to 175 kHz, except for sequences from *N. macrourus*.

To test if calls of those four species recorded in Northeastern Brazil are undoubtedly species-specific, we performed a linear Discriminant Function Analysis (DFA) using Past 3.14 software (Hammer et al., 2001). We compared each call parameter, using free-flying and hand-released recordings of each species as a group. The parameters we used for generating the DFA were FME, Fmin, Fmax, Duration, slope, bandwidth (BW), and duty-cycle (DC).

Results

In total, we analyzed 349 calls of 41 sequences belonging to the four selected species, both obtained from hand-released (153 calls) and free-flying individuals (196 calls) (Table 1). The two *Pteronotus* species exhibited a similar call structure with multi-harmonic calls with a 'lazy-z' shape (i.e., downward qCF component followed by a downward FM component and a final downward qCF component – qCFd-FMd-qCFd), exhibiting the FME on the second harmonic (Fig. 1A and 1B). *P. gymnonotus*' calls final qCF component is less prominent (Fig. 1A) or often inexistent in several calls (Fig. 1B). *L. aurita* also exhibited multi-harmonic calls, but with an initial downward qCF component followed by a downward FM component (qCFd-FMd) and presented the FME on the third harmonic during the hand-released recordings (Fig.

1C). However, in recordings from free-flying individuals, we noticed that occasionally the calls' FMd component is absent and, except the third, all other harmonics have low energy or are not recorded at all (Fig. 2).

Excluding *N. macrourus*, *P. personatus* emitted calls with the highest frequencies: the Fmax of its most energetic harmonic (H2) averaged 80 kHz, while Fmin averaged 65 kHz, and FME averaged 69 kHz (Table 1). For *P. gymnonotus,* the Fmax of its most energetic harmonic (H2) averaged 61 kHz, while Fmin averaged 49 kHz, and FME averaged 54 kHz (Table 1). *L. aurita* emitted calls with the lowest frequencies among the studied species: the Fmax of its most energetic harmonic (H3) averaged 49 kHz, while Fmin averaged 40 kHz, and FME averaged 46 kHz (Table 1). Duty cycle and Dur showed to be similar for the three species calls: lower than 10% and averaging 6 ms, respectively (Table 1).

Calls structure of *N. macrourus* was different from those of *Pteronotus* and *Lonchorhina*: the species emitted steep-FM calls with a subtle qCF final component (stFMd-qCFd), exhibiting the FME on the second harmonic (Fig. 1D; Fig. 3). *Natalus macrourus* Fmax´s most energetic harmonic (H2) averaged 141 kHz, the Fmin averaged 97 kHz, and FME averaged 114 kHz. Duration and IPI were short, averaging 2 ms and 27 ms, respectively (Table 1).

All four species were easily identifiable based on their echolocation calls (with 100% certainty), with significant differences among their calls (Fig. 4; Supplementary Material). We found no significant differences comparing hand-released and free-flying recordings within species (Table I; Fig. 4; Supplementary Material). Call structure, FME, and Fmax of the most energetic harmonic are the best acoustic parameters to be used in order to easily discriminate calls from these four species (Table I; Fig. 4; Supplementary Material).

Discussion

The importance of regional bat calls libraries

Here we presented the first description of *L. aurita´*s echolocation calls for Brazil. The genus *Lonchorhina* is composed by at least seven species (Gardner, 2008; Mantilla-Meluk and Montenegro, 2016) and although poorly studied concerning their echolocation calls, some species might be also acoustically differentiated. Comparing to a recent first vocalizations' description of *L. aurita,* recorded in Costa Rica by Gessinger et al. (2019), we found that *L. aurita*'s individuals from Brazil vocalize with similar maximum energy frequency. Gessinger et al. (2019) did not measured maximum frequency, but here we found that such information is a more stable variable, provides easier identification of *L. aurita* vocalizations and discriminate

198 from other similar species vocalizations. When comparing to its sibling species *L. inusitata,*
199 recorded in French Guiana (Barataud et al., 2013), we found that *L. aurita* calls are 10-12 kHz
200 higher in frequency. This suggests that the two *Lonchorhina* species occurring in Brazil [*L.*
201 *aurita* and *L. inusitata* (Nogueira et al., 2018)] should be easily discriminated by acoustic
202 methodologies.
203 Several bat species occurring in Brazil have their calls described based on acoustical data
204 recorded outside the country, including data from Belize (e.g. O'Farrell and Miller, 1999), Costa
205 Rica and Panama (Jung et al., 2007; Jung et al., 2014) or French Guiana (Barataud et al., 2013).
206 Special care needs to be taken when using acoustic data from other regions due to, for example,
207 intraspecific regional calls variations (Barclay, 1999; Jiang et al., 2015). We have found that
208 this is the case for *Pteronotus* species. Comparing our recordings from the drylands of
209 Northeastern Brazil to those made in French Guiana by Barataud et al. (2013), we found
210 similarities in call structure but also differences in terms of the frequencies on the calls of *P.*
211 *gymnonotus* and *P. personatus*. The 5 kHz (*P. gymnonotus*) and 4 kHz (*P. personatus*)
212 difference of maximum frequency between calls here presented and from those from French
213 Guiana and the Brazilian Amazonia points out that intraspecific regional variation of bat calls
214 should be expected for some widely distributed species (Murray et al., 2001; Jiang et al., 2015;
215 Arias-Aguilar et al., 2018). This raises the attention for the necessity of regional bat call
216 libraries when dealing with species-rich bat faunas, such as that from the Neotropics (Arias-
217 Aguilar et al. 2018). In fact, the assemble of good regional bat calls libraries for the Neotropics
218 is a herculean task which will require a quantitative leap for the continuous description of calls
219 from the hundreds of species there. But this is a goal that must be pursued and could take
220 advantage of the good momentum bioacoustics experiences, supported by large technological
221 developments and falling prices over the last decade, and especially by citizen science
222 initiatives (e.g. Deichmann et al., 2018; Burivalova et al., 2019).
223
224 ***Bioacoutics as essential method to bat caves monitoring***
225 We found that calls from the cave-dwelling *Pteronotus gymnonotus*, *P. personatus*,
226 *Lonchorhina aurita,* and *Natalus macrourus* in the Northeastern Brazil drylands have very
227 distinctive structure or frequencies, allowing an unproblematic and unequivocal acoustic
228 identification of these species during cave emergence. Call structure, FME and maximum
229 frequency of the strongest harmonic are the best acoustic parameters to be used in order to
230 discriminate the *Pteronotus* and *Lonchorhina* species, characteristics which were previously

pointed by Barataud et al. (2013) and (Gessinger et al. 2019). We identified that calls from these *taxa* also differ on the strongest harmonic – second in *Pteronotus* and third in *Lonchorhina* -, however the fundamental harmonic of *Lonchorhina* calls is often missing or dissipated (Gessinger et al. 2019). Due to its very high frequencies and distinct call structure, calls from *N. macrourus* are unmistakable: this is the species with the second highest call frequency in Brazil, after *Furipterus horrens* (Falcão et al., 2015, Arias-Aguilar et al. 2018). In *F. horrens*, however, the FME is on the first harmonic, opposite to the second harmonic in calls from *N. macrourus*. Moreover, *F. horrens*'s highest and lowest frequencies (~190 kHz and 135 kHz, respectively - (Falcão et al., 2015) are very different from those from *N. macrourus* here detected (141 kHz and 97 kHz, respectively). Therefore, the two bat species with highest frequency in Brazil are also acoustically unambiguous.

The four species here studied are not easily captured in mist-netting samplings (Silva and Bernard, 2017; Gonçalves et al., 2018), and given that netting is still the main method used in bat studies the Neotropics, they are frequently under recorded, undersampled and understudied. However, their calls showed to be easily identifiable and discriminated, and such an unequivocal acoustic identification definitely allows the use of passive acoustic monitoring for these species.

Additionally, given the good capabilities of acoustic monitoring to measure bat activity or to access potential foraging sites (e.g. Vaughan et al., 1997; Sherwin et al., 2000; Rainey et al., 2009), we recommend that bioacoustics should be considered an useful and adequate technique not only to assess presence/absence of those species in cave habitats, but also to assess roost emergence patterns during the night. In addition to a better detection, using acoustic devices in roost entrances would also considerably reduce disturbances in caves, which have direct conservation and behavioural implications (e.g. Dittmar and Mayberry, 2010; Cardiff et al., 2012; Paksuz and Özkan, 2012; Luo et al., 2013; Halse, 2018).

Besides the implications for basic science, our findings are also especially useful in situations when species detection is mandatory, like in environmental impact assessments involving endangered species, or when long-term monitoring is required (RELCOM, 2016; Barros et al., 2017; MMA, 2017; Pereira et al., 2017). Currently, seven species of bats are recognized as endangered in Brazil, and *N. macrourus* and *L. aurita* are among them (MMA, 2014). We have shown that bioacoustics can be unambiguously used to detect the presence of these two endangered species and, therefore, we strongly recommend that the recording of echolocation calls should be now considered as mandatory for environmental impact

assessments involving bats in Brazil. Besides complementing the role mist nets already play, bioacoustics could be more effective for recording these two species since bats flying high above or in places where nets could not be set would be recorded.

Environmental licensing process involving bats in the Neotropics needs improvement, and bioacoustics could and should be key. Estimates points out that Brazil may harbour nearly 310,000 caves (Piló and Auler, 2011) and the number of bat species recorded in caves in the country is currently high (72 spp.) and increasing (Oliveira et al., 2018). However, only ~16,000 caves are formally known in Brazil (http://www.icmbio.gov.br/cecav/canie.html). An analysis on the conservation situation of bats in Brazil has shown that ~20% of the known caves in the country are in areas under active mining and ~55% of the Brazilian strict protected federal areas are < 5 km away from mining operations (Jaramillo, 2018).

The Brazilian cave protection legislation, for example, requires that caves passive to licensing (for mining or other commercial uses, for example) must be classified according to their relevance and only those classified as having "maximum relevance" would be fully protected (Brasil, 2008; MMA, 2017). The presence of endangered species of bats, and/or the existence of exceptionally large bat populations in a given cave are among the criteria used to classify caves as maximum relevance (MMA, 2017). Therefore, concerning the mining licensing, the use of bioacoustics can definitively improve the detection in caves and their surroundings of two endangered species in Brazil – *N. macrourus* and *L. aurita*. The same applies for *P. gymnonotus* and *P. personatus*, known to form exceptionally large colonies. Thus, bioacoustics should be considered as a mandatory complementary approach for the classification of cave relevance in Brazil. Similar considerations stressing the gaps bioacoustics could fill have been already raised for the licensing of wind farms not just in Brazil (Barros et. al., 2017; Pereira et al., 2017), but elsewhere in Latin America (RELCOM, 2016). Considering prices have severely dropped in the last decade and that recordings equipment has never been as accessible as now (Deichmann et al., 2018; Hill et al., 2018; Burivalova et al., 2019; Prince et al., 2019), there is no reason to not incorporate such techniques and raise the bar in the environmental licensing process affecting bats in the region (e.g. Valença and Bernard, 2015; Arias-Aguilar et al., 2018).

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507

508 ## Tables

509 **Table 1.** Calls acoustic characteristics for the most intense harmonic of four cave-dwelling bats species recorded in Catimbau National Park, Pernambuco state, Northeastern
510 Brazil. Mean ± Standard deviation. MIH = most intense harmonic, Dur = call duration, IPI = inter-pulse interval, Fmin = minimum frequency, FME = frequency with maximum
511 energy, Fmax = maximum frequency, BW = bandwidth, NC = number of analyzed calls, NS = number of analyzed sequences, NI = number of individuals recorded.

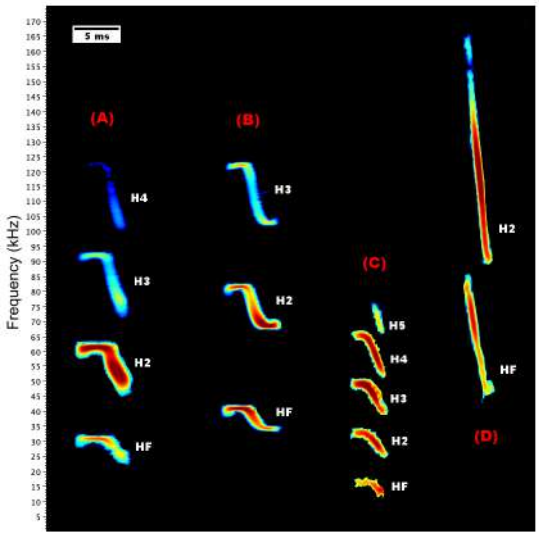
Species	Recording	Call structure	MIH	Dur (ms)	IPI (ms)	Fmin (kHz)	FME (kHz)	Fmax (kHz)	BW (kHz)	DC (%)	NC	NS	NI
Lonchorhina aurita	Hand-release	qCFd-(FMd)	3	5.1 ± 0.7	52.0 ± 14.8	38.3 ± 0.8	46.9 ± 1.7	50.3 ± 0.9	12.0 ± 0.8	9.4 ± 1.9	40	5	5
	free flying	qCFd-(FMd)	3	6.8 ± 1.2	54.9 ± 30.1	39.1 ± 1.3	45.7 ± 2.8	49.5 ± 0.8	10.4 ± 0.8	12.6 ± 3.9	47	8	-
	All	qCFd-(FMd)	3	6.6 ± 1.2	56.1 ± 27.1	39.1 ± 1.2	45.8 ± 2.6	49.6 ± 0.9	10.5 ± 1.6	11.8 ± 3.8	87	13	-
Pteronotus gymnonotus	Hand-release	qCFd-FMd-(qCFd)	2	5.2 ± 0.5	79.0 ± 42.6	48.2 ± 1.6	52.6 ± 2.4	60.7 ± 1.1	12.5 ± 1.8	7.5 ± 2.9	82	6	6
	free flying	qCFd-FMd-(qCFd)	2	5.5 ± 0.6	72.4 ± 57.1	49.5 ± 1.2	55.1 ± 2.8	60.8 ± 0.6	11.3 ± 1.1	9.2 ± 3.3	65	8	-

	All	qCFd-FMd-(qCFd)	2	5.4 ± 0.6	76.2 ± 49.1	48.8 ± 1.6	53.7 ± 2.9	60.8 ± 0.9	12.0 ± 1.6	8.3 ± 3.2	147	14	-
Pteronotus personatus	Hand-release	qCFd-FMd-qCFd	2	6.1 ± 0.9	59.2 ± 23.7	67.2 ± 0.5	72.5 ± 3.0	80.0 ± 1.6	12.5 ± 0.9	10.0 ± 3.0	10	1	1
	free flying	qCFd-FMd-qCFd	2	5.1 ± 0.8	55.4 ± 28.0	65.3 ± 1.6	68.7 ± 3.1	79.7 ± 0.8	14.7 ± 1.6	9.4 ± 2.5	61	7	-
	All	qCFd-FMd-qCFd	2	5.3 ± 0.9	55.9 ± 27.3	65.6 ± 2.3	69.3 ± 3.4	80.0 ± 1.5	14.4 ± 1.7	9.5 ± 2.6	71	8	-
Natalus macrourus	Hand-release	stFM-qCFd	2	2.1 ± 0.3	27.4 ± 2.6	97.2 ± 4.3	115.7 ± 2.7	141.0 ± 9.3	43.8 ± 12.4	7.0 ± 1.2	21	2	2
	free flying	stFM-qCFd	2	2.9 ± 0.5	29.7 ± 15.6	100.1 ± 1.7	110.3 ± 8.9	127.7 ± 3.2	27.6 ± 3.4	10.6 ± 4.9	23	4	-
	All	stFM-qCFd	2	2.4 ± 0.6	28.2 ± 9.2	98.3 ± 3.8	113.7 ± 6.2	136.2 ± 10.0	37.9 ±12.7	8.3 ± 3.4	44	6	-

Fonte: Frederico Hintze (autor).

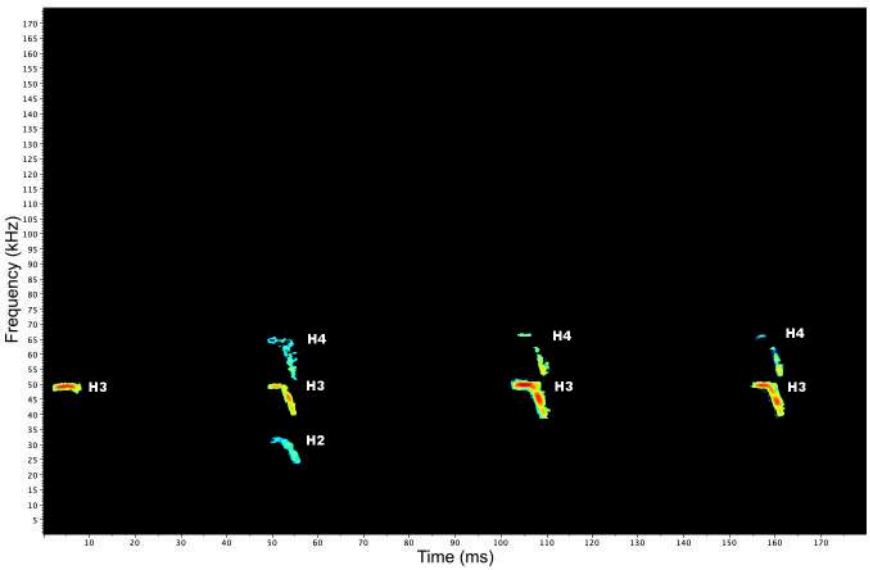
Figures

Fig. 1. Representation of search-phase echolocation calls of the bats *Pteronotus gymnonotus* (A), *P. personatus* (B), *Lonchorhina aurita* (C) and *Natalus macrourus* (D) recorded in Northeastern Brazil. Fundamental harmonic (first harmonic, HF); Second harmonic (H2); Third harmonic (H3), Forth harmonic (H4), Fifth harmonic (H5).



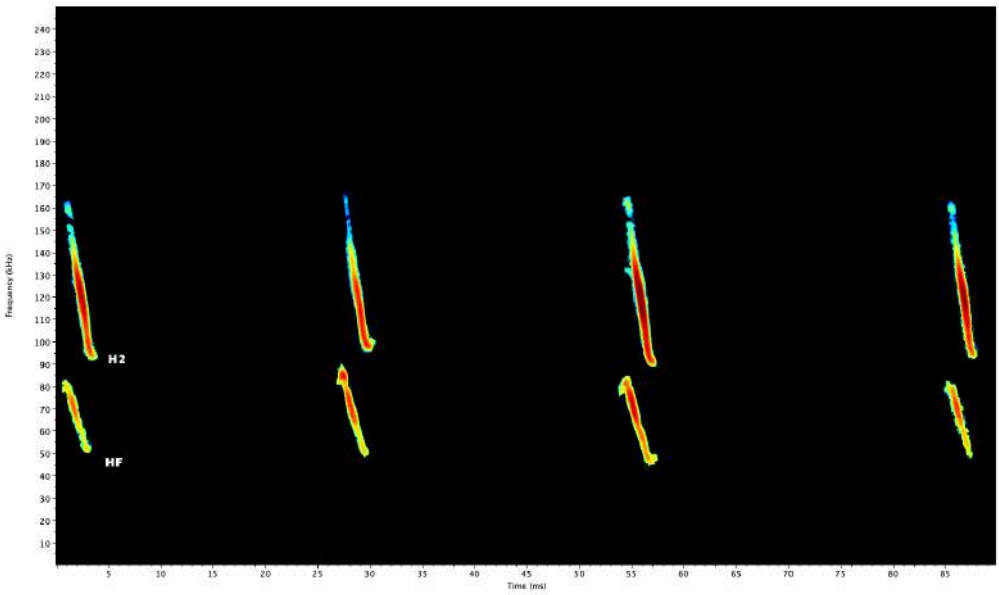
Fonte: Frederico Hintze (autor).

Fig. 2. Portion of a search-phase echolocation sequence of the bat *Lonchorhina aurita* recorded in Northeastern Brazil, evidencing the absence of the FMd component of the first call, the absence of the fundamental harmonic (first harmonic) and the low energy of the H2 (second harmonic) and H4 (forth harmonic). H3 = Third harmonic.



Fonte: Frederico Hintze (autor).

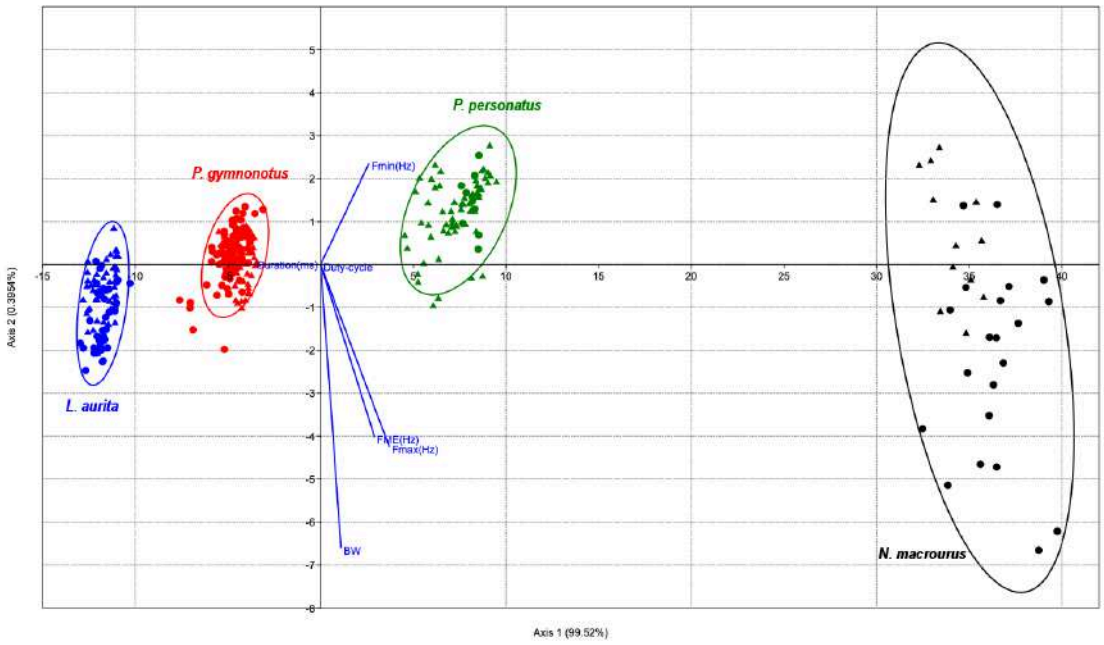
524 **Fig. 3.** Portion of a search-phase echolocation sequence of the bat *Natalus macrourus* recorded in Northeastern
525 Brazil, evidencing steep-FM calls with a subtle qCF final component and the frequency of maximum energy on
526 the second harmonic (H2).



527 **Fonte:** Frederico Hintze (autor).

528

Fig. 4. Linear Discriminant function analysis (DFA), using frequencies of maximum energy (FME), minimum frequencies (Fmin), maximum frequencies (Fmax), duration, bandwidth (BW) and duty-cycle values extracted from echolocation calls of the bats *Lonchorhina aurita* (in blue), *Pteronotus gymnonotus* (in red), *P. personatus* (in green) and *Natalus macrourus* (in black), all recorded in Northeastern Brazil. Dots represent calls from hand-released bats and triangles calls from free-flying individuals. Ellipses contain 95% of the values. Jackkniffed correctly classified calls equals to 100%.



Fonte: Frederico Hintze (autor).

3.3 MOLOSSID UNLIMITED: OUTSTANDING RANGE EXPANSION AND UNUSUAL VOCALIZATION PATTERN OF *PROMOPS CENTRALIS*

Artigo publicado no periódico *Journal of Mammalogy* (volume 101, edição 2, páginas 417-432), em 2020.

RESUMO

O morcego *Promops centralis* Thomas, 1915 ocorre nas Américas Central e do Sul, no entanto a sua estratégia de caça, com vôo alto e em espaço aberto, torna a sua captura muito desafiante, o que contribui para o conhecimento atual limitado da sua distribuição e ecologia. Porém, *P. centralis* apresenta chamadas de ecolocalização presumivelmente fáceis de identificar, o que permite o seu estudo através de métodos acústicos. Após a gravação de chamados de *P. centralis* a 1.500 km de distância de sua área de distribuição conhecida no Brasil, levantamos a hipótese de que, provavelmente, a mesma se encontraria muito subestimada. Para então melhorar o conhecimento sobre sua distribuição real, empregamos levantamentos acústicos em várias partes do Brasil e, após uma revisão bibliográfica para reunir outros registros da literatura, adotamos o software MaxEnt para modelar a distribuição potencial da espécie. Neste estudo, verificamos que *P. centralis* tem uma distribuição muito mais ampla na América do Sul do que o previsto anteriormente, expandindo sua área de distribuição em mais de 3,8 milhões de km^2. Ainda, descrevemos e discutimos um padrão de vocalização incomum da espécie, com indivíduos emitindo pelo menos três vocalizações muito distintas e altamente variáveis. Este estudo demonstra que inventários acústicos e modelagem da distribuição potencial podem desempenhar um papel fundamental ao complementar outras metodologias tradicionais para o estudo de espécies de difícil captura, como *P. centralis*, potencialmente contribuindo para planos de conservação e manejo mais eficazes.

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Molossid unlimited: extraordinary extension of range and unusual vocalization patterns of the bat, *Promops centralis*

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The big crested mastiff bat, *Promops centralis*, occurs in Central and South America, but knowledge of its ecology is limited due to its open space hunting strategy, making captures extremely challenging. Notwithstanding, members of the species produce echolocation calls that are easy to identify. After recording calls of *P. centralis* 1,500 km away from its known range in Brazil, we hypothesized that the distribution range of this species was probably greatly underestimated. To improve the accuracy of *P. centralis*' real distribution, we employed acoustic surveys throughout parts of Brazil, conducted after a bibliographic review to gather additional records, and used MaxEnt to model the species' potential distribution. We have found that *P. centralis* has a much wider distribution in South America than previously thought, adding more than 3.8 million km^2 to its former known area. We also describe an unusual vocalization pattern of *P. centralis*, with individuals emitting at least three very distinct but highly variable calls. This study shows that bioacoustic surveys and species distribution models can complement traditional methodologies in studying species that are difficult to capture, such as *P. centralis*, potentially contributing to more effective conservation and management plans.

O morcego *Promops centralis* Thomas, 1915 ocorre nas Américas Central e do Sul, no entanto a sua estratégia de caça, com vôo alto e em espaço aberto, torna a sua captura muito desafiante, o que contribui para o conhecimento atual limitado da sua distribuição e ecologia. Porém, *P. centralis* apresenta chamadas de ecolocalização

presumivelmente fáceis de identificar, o que permite o seu estudo através de métodos acústicos. Após a gravação de chamados de *P. centralis* a 1.500 km de distância de sua área de distribuição conhecida no Brasil, levantamos a hipótese de que, provavelmente, a mesma se encontraria muito subestimada. Para então melhorar o conhecimento sobre sua distribuição real, empregamos levantamentos acústicos em várias partes do Brasil e, após uma revisão bibliográfica para reunir outros registros da literatura, adotamos o software MaxEnt para modelar a distribuição potencial da espécie. Neste estudo, verificamos que *P. centralis* tem uma distribuição muito mais ampla na América do Sul do que o previsto anteriormente, expandindo sua área de distribuição em mais de 3,8 milhões de km^2. Ainda, descrevemos e discutimos um padrão de vocalização incomum da espécie, com indivíduos emitindo pelo menos três vocalizações muito distintas e altamente variáveis. Este estudo demonstra que inventários acústicos e modelagem da distribuição potencial podem desempenhar um papel fundamental ao complementar outras metodologias tradicionais para o estudo de espécies de difícil captura, como *P. centralis*, potencialmente contribuindo para planos de conservação e manejo mais eficazes.

Key words: Chiroptera, big crested mastiff bat, duty cycle, echolocation calls, frequency, MaxEnt, Molossidae, social calls, species distribution modeling, vocalizations

The big crested mastiff bat, *Promops centralis*, is one of three recognized species of the genus *Promops*, along with the brown mastiff bat, *P. nasutus*, and *P. davisonii* (Gregorin and Taddei 2000; Simmons 2005; Gregorin and Chiquito 2010). This species is thought to be restricted to Central America and the northern, western, and central regions of South America (e.g., Nowak 1994; Gardner 2008). However, records of *P. centralis* in South America are rare, and the species' natural history remains unclear (Gregorin and Taddei 2000; Sampaio et al. 2003; Gregorin and Chiquito 2010; Flores et al. 2015). In South America, *P. centralis* occurs from French Guiana to Venezuela, and from Colombia to northern Argentina, including the Brazilian Amazon Basin, with recent capture records from the Brazilian state of Mato Grosso do Sul, near Paraguay (e.g., Nogueira et al. 1999; Gregorin and Taddei 2000; Simmons 2005; Bernard et al. 2011; Fischer et al. 2015). Like many other molossids, *P. centralis* is a fast-flying insectivorous species, usually capturing its prey while flying several meters above the ground in open landscapes and above the tree canopy (Nowak 1994; Reis et al. 2007; Gardner 2008; Kalko et al. 2008). *Promops centralis* individuals have been recorded in a wide range of habitat types, from tropical forests, such as the Amazonian forest (e.g., Gregorin and Taddei 2000; Lim and Engstrom 2001) and tropical wetlands like the Pantanal region (Fischer et al. 2015), to arid environments, like the Sonora Desert (González-Terrazas et al. 2016), or even urban areas (Jung and Kalko 2010, 2011). Individuals of the genus *Promops* roost under palm trees leaves, inside hollow trees, and under house roofs (Nowak 1994). Contrary to other molossids, this species does not appear to be gregarious because known roosts are composed of only up to six individuals (Nowak 1994; Reis et al. 2007; Gardner 2008). Studying bat species that exhibit behaviors such as those described for *P. centralis* is quite challenging, especially when using only traditional methods such as ground mist nets and roost searches. In South America, mist nets are usually placed on the ground up to 3–4 m high and, when executed, the majority of the roost searches are in caves (e.g., Sampaio et al. 2003; Bernard et al. 2011). This has resulted in the low number of individuals of *P. centralis* recorded throughout the continent.

Species distribution modeling (SDM) has developed into an important tool for biodiversity conservation worldwide (Engler et al. 2004; Rushton et al. 2004; Guisan and Thuiller 2005), and bats are no exception to this pattern (Jaberg and Guisan 2001; Greaves et al. 2006; Sattler et al. 2007; Razgour et al. 2016; Delgado-Jaramillo et al. 2017). Distribution models predict the geographical distribution of a given species on the basis of a mathematical depiction of their environmental space represented by biotic and abiotic data collected at points of known occurrence of that species (Rushton et al. 2004; Guisan and Thuiller 2005). However, model accuracy and predictive power depend on the quality of the input data and on the appropriate use of specific software and their parameters (Elith et al. 2006; Jiménez-Valverde et al. 2008a, 2008b; Anderson and Gonzalez 2011; Syfert et al. 2013; Radosavljevic and Anderson 2014). Omission and commission errors may result in significant negative impacts on species conservation, as they may reduce or inflate the predicted distribution affecting, for example, the determination of the species' conservation status (Rondinini et al. 2006; Jiménez-Valverde et al. 2008a, 2008b; Anderson 2012; Visconti et al. 2013).

Although documenting the presence of *P. centralis* is difficult using traditional methods, their echolocation calls are quite distinctive, with upward modulated lower frequency calls (~30 kHz) that irregularly alternate with downward modulated higher frequency calls (~35 kHz—Jung and Kalko 2011; Barataud et al. 2013; Jung et al. 2014). This allows the use of acoustic methods for the study of this elusive species. Indeed, the use of acoustic monitoring for species identification and the refinement of distribution patterns is widely and successfully used in Europe, North America, and Australia, particularly for species that are hard to capture using mist nets (Fenton et al. 1987; Ahlén and Baagoe 1999; Schnitzler and Kalko 2001; Rydell et al. 2002; Adams et al. 2012). Brazil is the fifth largest country in the world, with 8.516 million km^2, and although notoriously rich in bat species, up to 60% of the country has no formal records of bats (Bernard et al. 2011). Given the foregoing, acoustic-monitoring programs may improve bat species detection, help fill data gaps for species presence, and produce a better description of the ecology and behavior of species

(Kunz and Parsons 2009; Jung and Kalko 2011; Barataud et al. 2013, Jung et al. 2014; Arias-Aguilar et al. 2018).

We recorded calls of *P. centralis* 1,500 km from its known range, in Brazil and hypothesized that the distribution of this species probably was greatly underestimated. Because this is a high-flying species that is difficult to capture with traditional techniques, we used information gathered with acoustic monitoring to improve the definition and accuracy of the species' range. We analyzed and compiled acoustic records from several Brazilian localities and used these data to model and update the species' potential distribution throughout South America. Moreover, during the acoustic data compilation, we found an unusual *P. centralis* vocalization pattern; we describe this pattern and discuss its probable function within the vocal repertoire of the species.

Materials and Methods

Study area.—During acoustic surveys in northeastern Brazil, two of the authors (FH, EB) found typical calls of *P. centralis* in three localities. Since the species had not yet been recorded in those regions, contacts were made with colleagues conducting acoustics surveys in other regions of the country asking for calls similar to those previously recorded. The remaining authors confirmed similar vocalizations in their recordings in the other seven localities of this study. Our survey therefore resulted in recordings covering a large environmental and geographic range, including both protected and highly human-modified areas (Fig. 1B; see Supplementary Data SD1 for more detailed descriptions of each site):

- Locality 1—Mata da Cristal (hereafter MC); an Atlantic Forest remnant adjacent to Cristal mining company, in the municipality of Mataraca, Paraíba state (6°29′43.92″S, 34°58′58.62″W) (Cristal 2016). Calls were recorded in an area under reforestation since 1988.
- Locality 2—Estação Ecológica do Seridó (SER); an IUCN category Ia protected area of Caatinga, in Serra Negra do Norte, Rio Grande do Norte state (6°34′29.52″S; 37°16′2.04″W) (ICMBio 2004). Calls were recorded near rocky outcrops with understory scrubland and sparse foliage cover.
- Locality 3—Aeroporto Internacional de Recife (REC); the international airport located in the southern part of the capital Recife, Pernambuco state (8°7′38.22″S, 34°55′25.44″W). Calls were recorded in the two main runways' heads.
- Locality 4—Parque Nacional do Catimbau (CNP); an IUCN category II protected area in Pernambuco state (8°29′14.10″S; 37°16′48.80″W) located in the Caatinga biome (Azevedo and Bernard 2015; ICMBio 2016). Calls were recorded near an arboreal dry forest with shrubby, spine-free vegetation immersed in a matrix of sandy soils and rock outcrops.
- Locality 5—Área de Proteção Ambiental da Serra do Lajeado (LAJ); 10°2′43.98″S; 48°15′15.00″W; an environmental protection area in Tocantins state fully within the Cerrado biome (ICMBio 2014). Calls were recorded in areas of Cerrado sensu stricto, Cerradão and Gallery Forest, typical phytophysiognomies of the biome.
- Locality 6—municipality of Mambaí (MAM), in Goiás state, near the border of Bahia state, Central Brazil (14°28′59.7″S; 46°06′46.9″W), is located within the Nascentes do Rio Vermelho Environmental Protection Area, encompassing the Pequi Municipal Natural Park. The area is within the Cerrado biome (ICMBio 2017). Calls were recorded in areas with low shrub vegetation in well-preserved savanna regions, but near areas with some grazing and agriculture.
- Locality 7—Parque Nacional da Serra do Cipó (SCP); a national park in Minas Gerais state (19°20′37.10″S; 43°36′38.84″W) is located in a transition zone between Cerrado and Atlantic Forest biomes (ICMBio 2009a, 2009b). Calls were recorded in a riparian gallery, near the Atlantic Forest biome portion of the park, and in a cave exit during emergence from the roost (19°30′11.31″S; 43°26′21.87″W) in *Campos Rupestres* phytophysiognomy surrounded by Atlantic Forest.
- Locality 8—Campus of the Universidade Federal de Espírito Santo (UFES), a federal university in Vitória, Espírito Santo state (20°16′52.70″S, 40°18′21.50″W). The campus is divided into two main areas, a building zone and an environmental protection zone of Atlantic Forest (UFES 2005). Calls were recorded in a narrow strip of Atlantic Forest bordering the mangrove.
- Locality 9—A 138-ha island in the reservoir of the Funil Hydroelectric Dam (FHD), municipality of Ijaci, Minas Gerais state (21°10′3.31″S, 44°51′59.62″W). The landscape is part of the Cerrado biome and is facing strong anthropogenic pressures from urbanization, agriculture, and pasture (Coelho and Pereira 2010). Calls were recorded near the reservoir margin in a fishing pier.
- Locality 10—Parque Nacional dos Aparados da Serra (PNA), a national park located in the eastern limit of the Araucaria Plateau (29°14′53.42″S, 50°14′49.61″W), in the border of the states of Rio Grande do Sul and Santa Catarina. This park is located in the southernmost region of the Atlantic Forest (IBAMA/MMA 2004); calls were recorded in open areas near the edge of secondary growth forest patches.

Distribution modeling.—We gathered *P. centralis* distribution records from the literature and from the acoustic sampling sites described above (Supplementary Data SD1). We searched for published papers through November 2017 using the keywords: "Promops," "Promops centralis," "P. centralis," and "big crested mastiff bat" in online databases and search engines such as Google Scholar (scholar.google.com), Web of Science (www.webofknowledge.com), Scopus (www.scopus.com), Periódicos CAPES (www.periodicos.capes.gov.br), SciELO (www.scielo.br), Vertebrate Zoology Database of American Museum of Natural History (http://sci-web-001.amnh.org/db/emuwebamnh/index.php), and Global Biodiversity Information Facility (www.gbif.org). We also reviewed occurrences in sources not available online such as Barquez et al. (2006) and

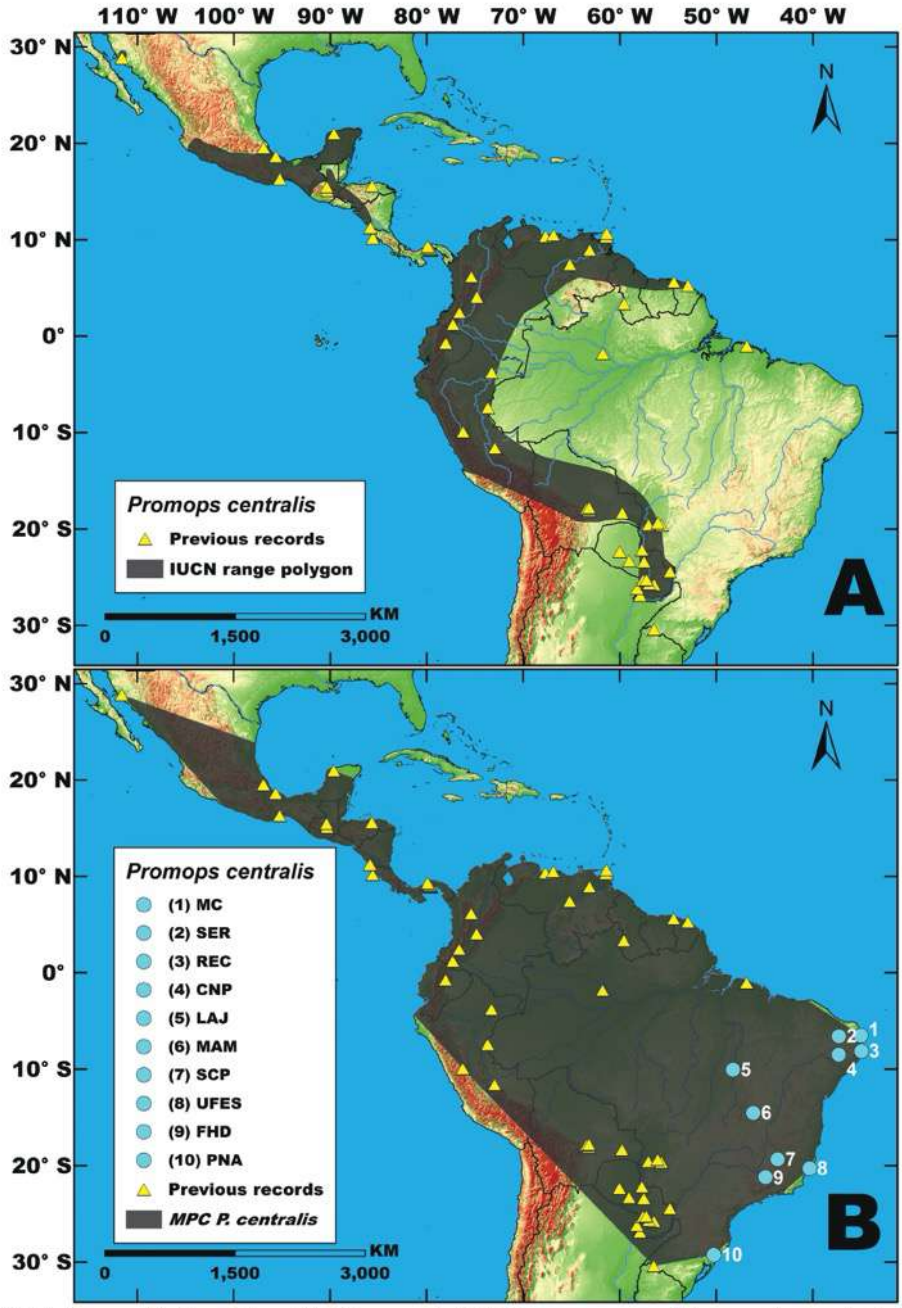

Fig. 1.—Distribution maps of the big crested mastiff bat, *Promops centralis*. (A) The gray area represents the range polygon used by the IUCN for threat assessment of *P. centralis* (Solari 2019). Triangles represent the former records for the species. (B) The gray area represents new proposed

Gardner (2008). Each occurrence point was checked to detect duplication of localities and eventually correct any location or taxonomic errors (Peterson et al. 2011). For example, following Gregorin and Chiquito (2010), the literature records of *Promops centralis davisoni* were not used in this study because it currently is considered a distinct species (*P. davisoni*). This resulted in a total of 53 occurrences in the literature, in addition to the 10 sites from this study (Supplementary Data SD2).

To reduce potential bias and avoid inflation of accuracy measurements due to spatial autocorrelation (Veloz 2009), we used the Spatial Rarefy Occurrence Data tool in SDMtoolbox for ArcGIS (Brown 2014; Coxen et al. 2017). This tool produced an environmental heterogeneity map with the bioclimatic variables of WorldClim (Hijmans et al. 2017), and subsequently eliminated records under the same environmental conditions within 25 km of each other (Coxen et al. 2017). Although the 25 km rule may be considered arbitrary, as other studies usually use 10 km (e.g., Hidalgo-Mihart et al. 2004; Pearson et al. 2007; Radosavljevic and Anderson 2014), we amplified to 25 km to avoid spatial bias on point localities, adjusting the distance to a species with high flight capacity and large home ranges such as *P. centralis*, and to the topographic and environmental heterogeneity of the country (Fourcade et al. 2014). This procedure ensured that our localities corresponded to a unique spatial sample but reduced the number of localities from 63 to 51 localities.

Species distribution modeling are increasingly used to estimate potential species distribution and environmental suitable regions or habitats (Elith and Leathwick 2009; Booth et al. 2014; Booth 2016). We opted for MaxEnt (Phillips et al. 2006) for the following reasons: i) presence-only input data; ii) the ability to include both categorical and continuous covariables; and iii) the possibility of creating a spatially explicit suitability map for the focal species. We generated several distribution models for *P. centralis* based on a set of variables at 5 km^2 resolution. To avoid collinearity among the bioclimatic variables we first ran a preliminary model using all variables to check the weight of each according to the variable contributions table and Jackknife tests. Then, we used the Correlations and Summary Stats tool of the SDMtoolbox package for ArcGIS to obtain correlation and covariance matrices and remove highly correlated variables among the 19 variables available in WorldClim (Snedecor and Cochran 1980; Brown 2014). When pairwise correlation was > 0.7, the variable that provided the lowest contribution to the model was discarded. This resulted in nine variables derived from temperature and rainfall variables: mean daily temperature range; isothermality; temperature seasonality; maximum temperature in the warmest month; mean temperature in the wettest quarter; mean temperature in the coldest quarter; annual rainfall; rainfall in the driest quarter; and rainfall in the warmest quarter. Because knowledge of the ecology and biology of *P. centralis* is highly limited and the species is a habitat generalist, we chose to use temperature and precipitation variables and assumed they affected the species' distribution (Gaston 2003). These variables have successfully predicted suitable areas for other bats in this region (Aguiar et al. 2016; Delgado-Jaramillo et al. 2017; Silva et al. 2018).

We employed a logistic output to produce our models and obtain values for habitat suitability (continuous probability from 0 to 1—Phillips et al. 2006, 2009). We also used MaxEnt's regularization multiplier parameters to reduce the negative effects of spatial autocorrelation. Default regularization values lead to overfitted models when spatial filtering is used (Radosavljevic and Anderson 2014). To limit model complexity and mitigate these overfitting problems, we therefore calibrated models within the MaxEnt software package with different values for the regularization multiplier (default setting 1.0, 2.0, 3.0, 4.0, and 5.0). We then evaluated the best models produced for each regularization multiplier as recommended by Radosavljevic and Anderson (2014) and Merow et al. (2013). To generate overall predictive distribution models, we used 75% of the data for calibration and 25% for internal evaluation (testing data). To produce more robust results to random events linked to the selection of localities we performed 10 cross-validation replicates to calculate confidence intervals.

MaxEnt produces continuous models of environmental suitability that are interpreted as the probability of occurrence, with values ranging from 0 (no environmental suitability for the presence of the species) to 1 (100% suitability). To generate a probable presence–absence output from those continuous suitability models, we needed to calculate the "thresholds" values which support a certain location to be suitable or unsuitable for a given species (Pearson et al. 2007; Liu et al. 2013, 2016). We chose two widely used approaches to calculate those thresholds: 1) the lowest presence threshold (LPT—Pearson et al. 2007) and 2) maxSSS (Liu et al. 2013, 2016). LPT is the minimum predicted suitability value of a model where the species' presence was observed and maxSSS is based on the maximum sum of sensitivity and specificity of the model. Using these two threshold calculation methods, we converted the continuous suitability outputs of the models into binary presence–absence, generating presence–absence maps. Finally, we used the area under the curve (AUC) to assess the models' predictive abilities. However, due to the limitations of AUC to evaluate models (Lobo et al. 2008) we also assessed the models' predictive ability employing the True Skill Statistic (TSS) tests using "ecospat" R package (Di Cola et al. 2017) and calculated the false-negative rate. Since AUC does not directly quantify

range polygon for IUCN's threat assessment of *P. centralis* for South America. Triangles represent the former records for the species and, dots are new records from this study: 1—Mata da Cristal, Paraíba, Brazil (MC); 2—Estação Ecológica do Seridó, Rio Grande do Norte, Brazil (SER); 3—Aeroporto Internacional de Recife, Pernambuco, Brazil (REC); 4—Parque Nacional do Catimbau, Pernambuco, Brazil (CNP); 5—Área de Proteção Ambiental da Serra do Lajeado, Tocantins, Brazil; 6—Mambaí municipality, Goiás, Brazil (MAM); 7—Parque Nacional da Serra do Cipó, Minas Gerais, Brazil (SCP); 8—Universidade Federal de Espírito Santo, Espírito Santo, Brazil (UFES); 9—Funil Hydroelectric Dam, Minas Gerais, Brazil (FHD); 10—Parque Nacional dos Aparados da Serra, Rio Grande do Sul, Brazil (PNA).

overfitting we quantified overfitting by calculating the difference between the calibration and evaluation AUCs: the smaller this difference, the less overfitting in the model (Warren and Seifert 2011). We also evaluated models by visual examination of the resulting maps based on expert knowledge of the known species distribution.

Acoustic sampling and identification.—Between August 2012 and August 2016, we made recordings using a 16-bit full spectrum Batbox Griffin ultrasound detector (Batbox, Ltd, United Kingdom) in UFES, Wildlife Acoustics SM2Bat+ detectors (Wildlife Acoustics, Inc., Concord, Massachusetts) in MC, SER, and CNP, a combination of Wildlife Acoustics SM2Bat+ and SM3BAT (both from Wildlife Acoustics) detectors in REC, the Dodotronic Ultramic 200K (Dodotronic di Ivano Pelicella, Castel Gandolfo, Italy) in FHD, Pettersson D500X in LAJ, PNA, and MAM, and Pettersson D1000x (Pettersson Elektronik AB, Uppsala, Sweden) in SCP. Given the different recording systems used, some slight differences in detection among sites might have occurred due to the frequency sensitivity and range detection performance of each detector (Limpens and McCracken 2004; Adams et al. 2012). However, calls of the Molossidae are characterized by low frequency, low slope, and high intensity, and are therefore easily detected and recorded at longer distances than calls of species emitting at higher frequencies (Adams et al. 2012). Consequently, we did not expect significant differences in detection among the different recorders (Adams et al. 2012). To mitigate hypothetical bias in data collection and ensure good recordings of *P. centralis* calls, we used a minimum sampling rate of 192 kHz in all recording situations. Because *P. centralis* typically emits at frequencies below 40 kHz, this sampling rate is more than enough to detect and record the calls of this species. We recorded only during nights without strong winds or rain (Parsons and Szewczak, 2009). To maximize reception of bat vocalizations, we placed the detectors at a 45° angle relative to the ground and avoided areas with dense vegetation (Seidman and Zabel 2001; Kunz and Parsons 2009; Jung and Kalko 2011; Adams et al. 2012).

We used CallViewer18, a MATLAB based software (Skowronski and Fenton 2008) for acoustic analyses. Spectrogram parameters were set to fast Fourier transformation size 1024, window length to 1 ms, and a background threshold of 10 dB using Hamming windows. Using CallViewer18's Auto Detection function, we extracted seven variables for each call detected in a file: call duration (Dur, in ms), minimum frequency (Fmin, in kHz), maximum energy frequency (FME, in kHz), maximum frequency (Fmax, in kHz), initial frequency (F initial), final frequency (F final), and inter-pulse interval (IPI, in ms). The parameters for the Auto Detection function were set following Hintze et al. (2016). To reduce unwanted noise, we used an upper cutoff frequency of 50 kHz and a lower cutoff frequency of 20 kHz.

We calculated mean ± *SD* and range for all analyzed parameters and calculated the duty cycle (DC, in %) according to Lazure and Fenton (2011). Only sequences containing a minimum of three good quality calls were analyzed (Lloyd et al. 2006; Ratcliffe et al. 2011). Feeding buzzes (and pulses emitted immediately after or before) and social calls were not considered for analysis. Examples of recordings containing all described calls in this study are provided in Supplementary Data SD3–SD11.

Similar to species of the genus *Molossops*, but differing from other molossids, *Promops* produce upward modulated FM-qCF calls (type I calls), occasionally alternating with higher frequency and downward modulated FM-qCF calls (type II calls—Barataud et al. 2013; Jung et al. 2014; Oliveira et al. 2018). Nevertheless, *Molossops* and *Promops* can be easily distinguished by significant differences in their call frequency and duration (Jung et al. 2014; Oliveira et al. 2018). In addition, the two *Promops* species, *P. centralis* and *P. nasutus*, are distinguished by the maximum energy frequency and call duration (Jung et al. 2014; Arias-Aguilar et al. 2018): *P. centralis* typically emits calls of lower frequency and higher duration (type I calls FME averaging 30 kHz and duration > 16 ms), while *P. nasutus* emits at higher frequency and lower duration (type I calls FME averaging 35 kHz and duration < 12 ms—Barataud et al. 2013; Jung et al. 2014). Therefore, although *P. centralis*, *P. nasutus*, the dwarf dog-faced bat *Molossops temminckii*, and the rufous dog-faced bat *M. neglectus* are sympatric in many regions of their ranges, characteristics of their calls enable easy discrimination among them. By using literature information (e.g., Jung and Kalko 2011; Barataud et al. 2013; Jung et al. 2014; Arias-Aguilar et al. 2018) and recordings made by us outside a known *P. centralis* roost in SCP, we were able to unambiguously identify all the species' calls based on signal structure, frequency, and duration parameters of search-phase calls.

Nevertheless, to test if *P. centralis* calls recorded in Brazil are indubitably species-specific, we performed a linear discriminant function analysis (DFA) using Past 3.10 (Hammer et al. 2001), comparing each of the abovementioned call parameters with those of acoustically similar species (*P. nasutus*, *M. temminckii*, and *M. neglectus*) and with those of an outgroup (*Eumops* sp.). We used calls from our own library and, in the case of *M. neglectus*, M. Barataud's library from French Guiana. The parameters we used for generating the DFA were FME, Fmin, Fmax, F initial, F final, Dur, slope, bandwidth (BW), and duty cycle (DC).

To build the sonograms for the figures exhibited in this study, we used Raven Pro 1.5, Build 29 (Cornell Lab of Ornithology 2014). We built sonograms using a Hamming window, 1024 or 2048 DFT size with 96% or 98% overlap, respectively.

All fieldwork procedures used during this study were in compliance with the American Society of Mammalogists (ASM) guidelines for the use of wild mammals in research and education (Sikes et al. 2016).

Results

Distributional records, potential distribution, and environmental suitability.—We recorded the first records of *P. centralis* in the Brazilian states of Rio Grande do Norte, Paraíba, Pernambuco, Tocantins, Minas Gerais, Espírito Santo, Goiás,

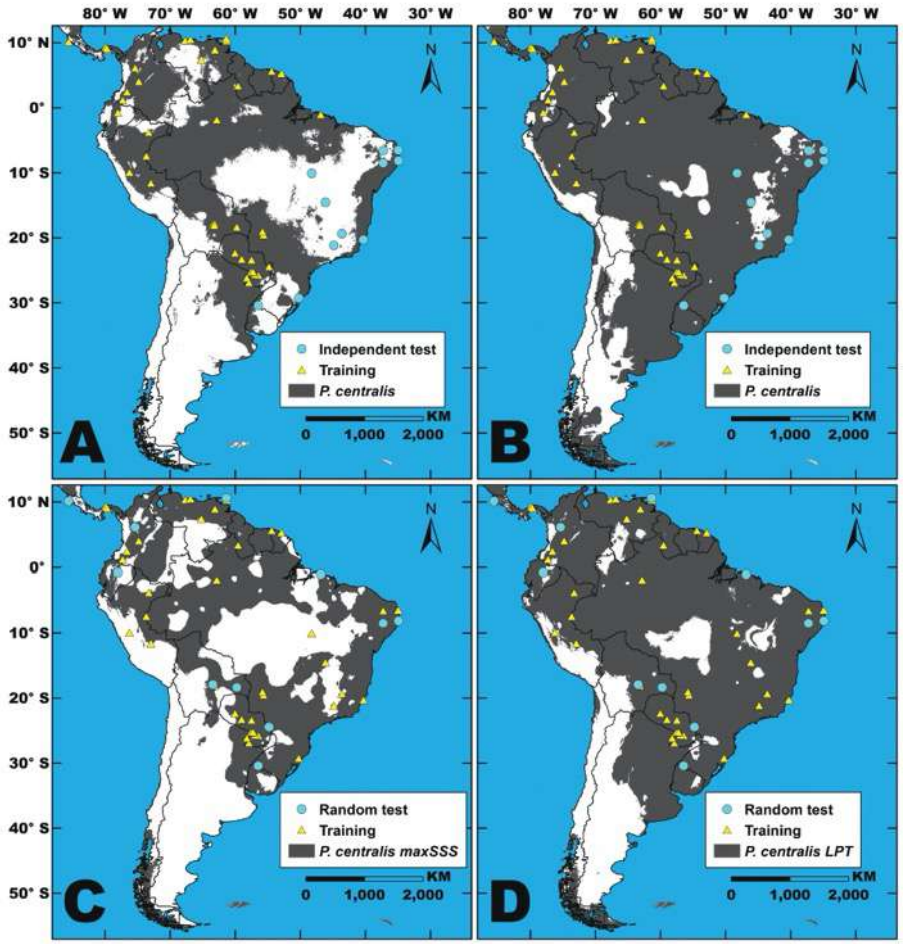

Fig. 2.—Potential distribution maps for *Promops centralis* in South America based on MaxEnt models using (A) a regularization multiplier of 1.0 and our acoustics record as independent test points (light gray dots), (B) regularization multiplier of 3.0 using our acoustics record as independent test points (light gray dots), (C) a regularization multiplier of 3.0 with random points used for model testing (light grey dots) and using maximum sum of sensitivity and specificity (maxSSS) threshold, and (D) a regularization multiplier of 3.0 with random points used for model testing (light grey dots) and using the lowest presence threshold (LPT).

and Rio Grande do Sul, extending the range of the species by 3,866,733 km^2 (Fig. 1B), and confirmed its presence in the Atlantic Forest, Caatinga, and Cerrado biomes.

Using the new occurrence points from acoustic surveys as independent test points, the best distribution models were those using the 3.0 regularization multiplier, accomplishing a zero omission rate (false-negative rate) of test points (Fig. 2B–D). The default multiplier (1.0) produced overfitted models (Fig. 2A), with a 60% omission rate of the test points. TSS for the threshold LPT (Fig. 2D) was 0.21 while the maxSSS was 0.53 (Fig. 2D). The potential distribution of *P. centralis* (AUCtraining = 0.83 ± *SD* 0.02; AUCtest = 0.80 ± *SD* 0.05), showed a wide distribution both in South America and part of Central America and in the countries where it had already been recorded. Additionally, our models extended the probability of occurrence to the mid-eastern part of Argentina. Within Brazil, *P. centralis*' presence was predicted in all states including the Pampa biome, which was not sampled during this study. The models' predictive power, however, was not enough to fill data gaps in the southern portions of the Amazonia biome, and in the

transition zones between Amazonia and Cerrado and between Cerrado and Caatinga, where the occurrence of *P. centralis* was not predicted (Fig. 2).

Precipitation of the driest month (27.4%) and mean diurnal temperature range [monthly mean (max temp – min temp)] (24.2%) had the highest contributions to the model; the highest suitability values were negatively associated with high precipitation levels and wider temperature variations during the day. The variable with the third highest contribution was mean temperature of the wettest quarter (15.6%), and the highest suitability values were positively associated with this variable.

Vocalization patterns.—We analyzed 203 calls from 44 sequences of *P. centralis* recorded in our acoustic surveys. *P. centralis* showed great vocal plasticity (Fig. 3A). We recorded sequences with typical upward frequency modulated calls (low type I calls) occasionally alternating with higher frequency calls and downward modulated FM-qCF calls (high calls) (Fig. 3B; Table 1; Supplementary Data SD3). Nevertheless, we found variation in the call behavior of the species (Fig. 4A; Supplementary Data SD4 and SD5), where low type I calls were switched to longer duration calls presenting a long initial CF component, whereas inter-pulse intervals between calls decrease (low type II calls) (Figs. 3C and 4B; Table 1; Supplementary Data SD4–SD7).

The recordings containing low type II sequences lasted for 1–10 s and were recorded in five locations (CNP, MC, REC, SCP, and MAM) at different periods of the night (Supplementary Data SD8 and SD9). Occasionally buzzes were also recorded in the terminal phase of the same sequences (Fig. 5A; Supplementary Data SD10). In some sequences, bats again emitted low type I calls of low duty cycle following the buzzes (Fig. 5B; Supplementary Data SD11).

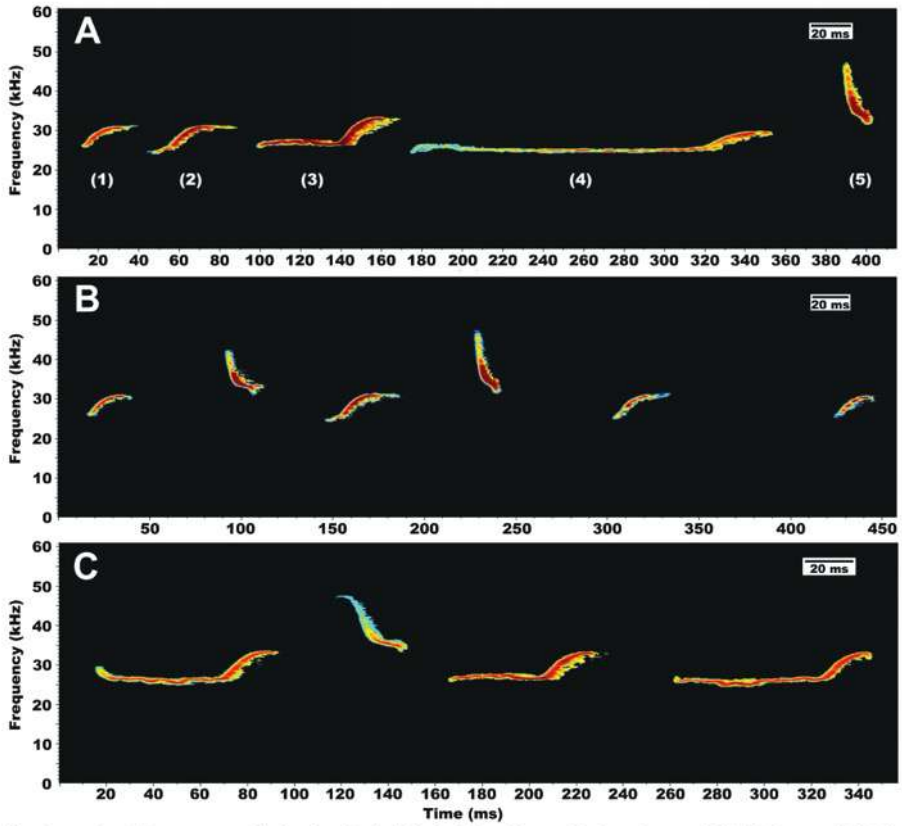

Fig. 3.—Vocal repertoire of *Promops centralis* showing (A) the high plasticity of the vocalizations [low type I (1) (2), low type II (3) (4), and high (5) calls], (B) search-phase echolocation sequence showing the typical irregular alternation of low type I calls and high calls. Inter-pulse intervals between calls were preserved, and (C) call sequence showing the longer low calls (low type II), occasionally alternating with high calls. Inter-pulse intervals between calls were preserved. Time scale (20 ms) is in the upper right corner of the figure.

Table 1.—Call characteristics of *Promops centralis* recorded in this study compared to the calls available in literature. Mean ± *SD* and the minimum–maximum ranges of the parameters (in parenthesis). IPI = inter-pulse interval, Duration = call duration, Fmin = minimum frequency, FME = frequency with maximum energy, Fmax = maximum frequency, DC = duty cycle, NC = number of analyzed calls, NS = number of analyzed sequences. Call structure: FMu = upward modulated frequency, qCFu = upward quasi-constant frequency, FMd = downward modulated frequency, qCFd = downward quasi-constant frequency, CF = constant frequency.

Call type	Call structure	IPI (ms)	Duration (ms)	Fmin (kHz)	FME (kHz)	Fmax (kHz)	DC (%)	NC	NS	Location	Reference
Low	FMu-qCFu	?	?	?	28	?	?	?	?	Panama	Jung and Kalko (2011)
High	FMd-qCFd	?	?	?	32	?	?	?	?		
Low	qCFu	?	21.2 (17.5–35)	26.3	29.3	32.3	?	33	10	French Guiana	Barataud et al. (2013)
High	FMd-qCFd	?	14.1 (13.2–14.8)	33.7	35.4	36.7	?	3	10		
Low	FMu-qCFu	276.9 ± 91.2	17.8 ± 3.3	25.8 ± 0.8	≈ 28	28.0 ± 0.7	7.1 ± 2.0	12	13	Neotropics	Jung et al. (2014)
High	FMd-qCFd	158.9 ± 88.8	17.1 ± 7.8	30.4 ± 1.1	?	35.7 ± 6.5	11.8 ± 0.6	7	9		
Low type I	(qCFu)-FMu-qCFu	244.7 ± 114.8 (71.2–671.0)	23.4 ± 9.7 (14.4–86.5)	26.4 ± 1.5 (23.3–29.7)	29.7 ± 1.1 (25.5–31.5)	31.8 ± 0.9 (30.0–33.8)	10.4 ± 6.0 (2.5–29.8)	104	24	Brazil	Our recordings
Low type II	CF-FMu-qCFu	90.2 ± 88.3 (23.4–423.9)	105.1 ± 36.7 (22.0–178.2)	24.8 ± 0.7 (22.5–27.8)	28.9 ± 1.4 (24.8–31.5)	31.4 ± 0.9 (27.8–33.8)	53.3 ± 20.9 (17.5–87.2)	88	20		
High	FMd-qCFd	71.3 ± 32.0 (49.4–159.2)	16.8 ± 5.3 (9.9–27.0)	33.3 ± 1.2 (30.8–36.0)	35.4 ± 1.3 (33.0–38.7)	44.8 ± 2.7 (39.8–48.3)	19.2 ± 6.3 (5.9–31.1)	19	11		

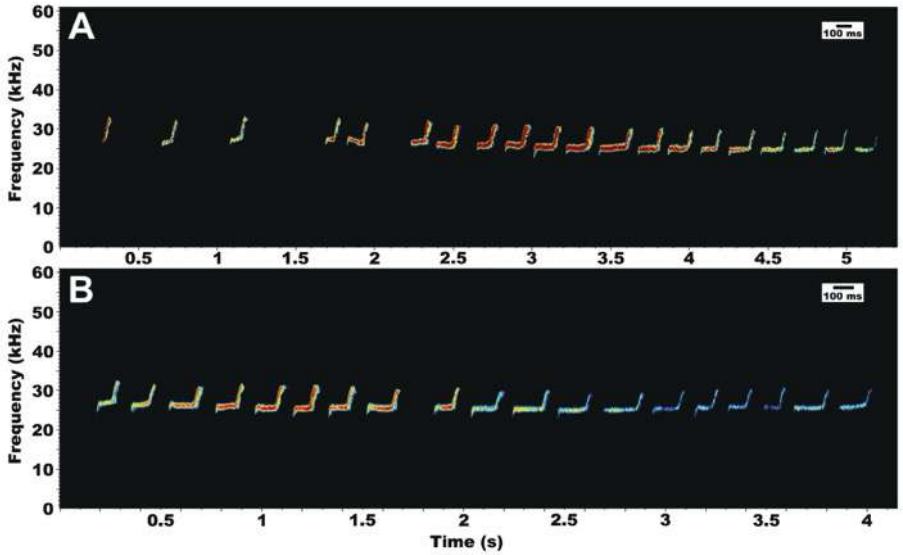

Fig. 4.—Call sequence of *Promops centralis* showing (A) a change in the pattern of its calls pattern, where the monotone low type I calls change to low type II calls, with an increase of its duty cycle, and (B) a monotone sequence of the longer low calls (low type II) with a high duty cycle. Note the very long calls and small inter-pulse interval are very unusual call patterns for a molossid. Inter-pulse intervals between calls were preserved. Time scale (100 ms) in the upper right corner of the figure.

In this study, we found that frequencies of maximum energy (FME) averaged 30 kHz (low type I) and 35 kHz (high calls), the minimum frequency (Fmin) averaged 26 kHz (low type I) and 33 kHz (high calls) while the maximum frequency (Fmax) averaged 32 kHz (low type I) and 45 kHz (high calls) (Table 1). Duration averaged 23 ms and 17 ms for low type I call and high calls, respectively. Duty cycle (DC) averaged 10% when high calls were not emitted and 19% when high calls were emitted (Table 1). Low type II call frequencies were similar to low type I calls, but presented longer duration (~100 ms) and shorter inter-pulse interval (less 60% compared to type I calls) leading to a duty cycle average of 53% (Table 1).

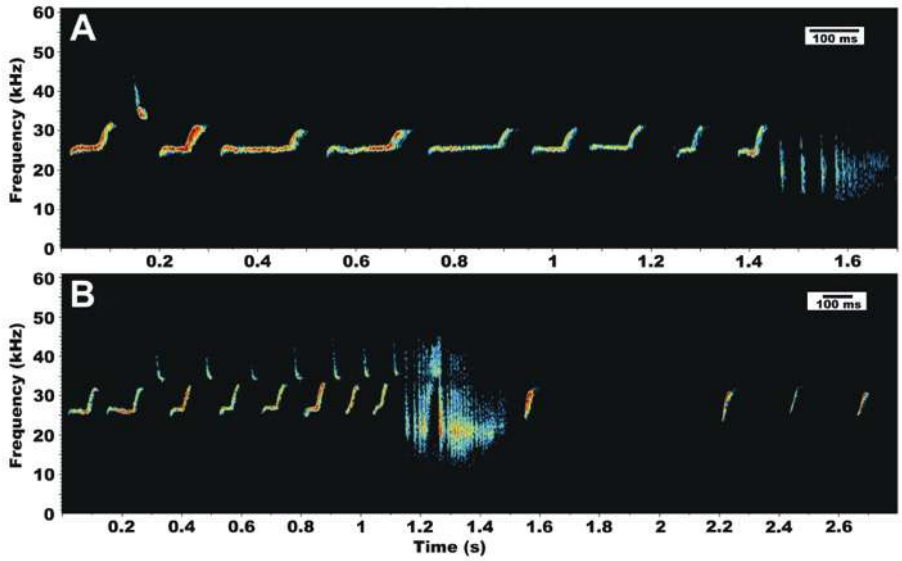

Fig. 5.—Call sequences of *Promops centralis* showing (A) longer low calls (low type II) alternating with high calls, terminating with a buzz, and (B) longer low calls (low type II) alternating with high calls, terminating with a buzz followed by initiation of vocalizations with low type I calls. Inter-pulse intervals between calls were preserved. Time scale (100 ms) in the upper right corner.

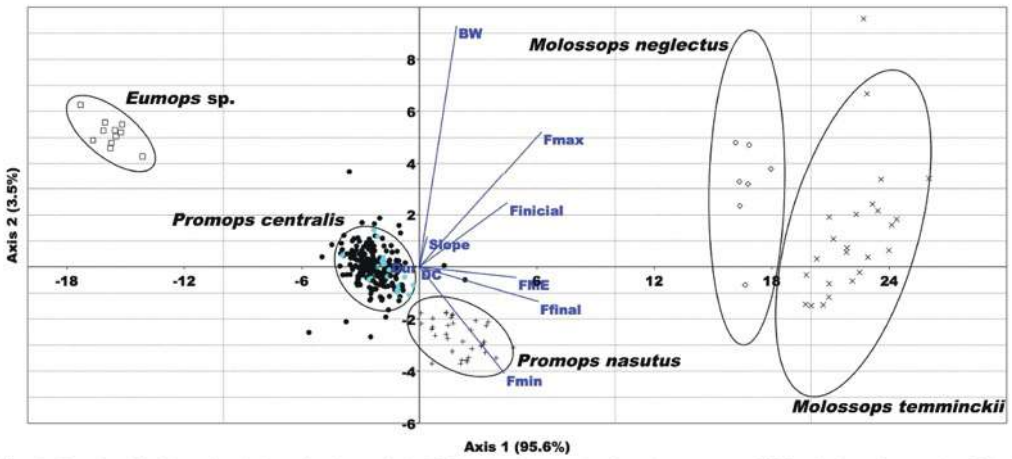

Fig. 6.—Results of the linear discriminant function analysis (DFA) using frequencies of maximum energy (FME), minimum frequencies (Fmin), maximum frequencies (Fmax), initial frequencies (F inicial), final frequencies (F final), duration (Dur), slope, bandwidth (BW), and duty cycle (DC) values extracted from calls of *Promops centralis* (dots; gray dots are calls from roost emergence in SCP) recorded in this study, *P. nasutus* (plus), *Molossops temminckii* (cross), *Eumops* sp. (square), and *M. neglectus* (diamond). Ellipses contain 95% of the values.

Calls from *P. centralis* were easily separated from the other acoustically similar (*P. nasutus*, *M. temminckii*, or *M. neglectus*) with great confidence (Jackknife correct identifications = 98.75%; Fig. 6; Supplementary Data SD12).

Discussion

Species distribution models.—Using acoustic sampling, we increased the knowledge of *P. centralis*' distribution, adding new records to the eastern region of South America, with an

area extension by more than 3.8 million km². Until this study, the known distribution of *P. centralis* in South America was restricted to the northern and western regions (i.e., locations in French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, Paraguay, Uruguay, northern Argentina, and the Brazilian states of Pará, Amazonas, Acre—mostly within the Amazonia biome—and Mato Grosso do Sul, within the Pantanal biome; e.g., Gregorin and Taddei 2000; Simmons 2005; Fischer et al. 2015; Fig. 1A). Based on our records in Caatinga, a semiarid Brazilian biome, we confirmed that South American *P. centralis* individuals also tolerate arid environments. This was also recently observed in Mexico (González-Terrazas et al. 2016; Alavez Tadeo et al. 2017). We further found that the current IUCN range polygon for *P. centralis* is inaccurate (see Fig. 1A), failing to include several known valid records, some that are ~20 years old (e.g., Gregorin and Taddei 2000; Lim and Engstrom 2001; Barnett et al. 2006; Botto et al. 2008; Jung and Kalko 2010), thus hampering the correct assessment of the species' extent of occurrence and area of occupancy, information used by the IUCN to categorize the level of threat to a species.

Although *P. centralis* was recorded in six protected areas, some of our recordings are from sites within large metropolitan areas, such as the International Airport in Recife (3.6 million inhabitants), and the UFES *campus*, in the city of Vitória (1.9 million habitants). We also detected the species in a fragment of secondary Atlantic Forest, but in a matrix of sugarcane and abandoned mining areas. Therefore, *P. centralis* appears to be somewhat tolerant of anthropogenic changes (Jung and Kalko 2011), similar to other molossids that are classified as "urban adapters." These species are able to easily adapt to urban matrices because of the availability of roosts in buildings, house roofs, bridges, or other structures (Avila-Flores and Fenton 2005; Jung and Kalko 2010; Araújo and Bernard 2016) and the attraction of insects by city lights (Jung and Kalko 2010).

Using SDM we predicted a potentially wide distribution of *P. centralis* in South America and also extended its range in Central America. Our results extended the potential occurrence of the species to the mid-eastern part of Argentina. Within Brazil, its presence was predicted in all the Brazilian biomes, including the Pampa, where it has not been recorded so far. It is very likely that *P. centralis* occurs across most of South America, and in other biomes of the continent, in particular the Chaco and the Pampa. To date, our southernmost records were retrieved from the Parque Nacional dos Aparados da Serra, in the extreme southern range of the Atlantic Forest biome (López-González 1998; Gregorin and Taddei 2000; Barquez et al. 2006), but we have acoustic monitoring programs planned further south in Brazil up to Uruguay and Argentina, including Pampa locations in the three countries.

Although our models predicted a vast range extension, they also predicted potential distribution gaps for *P. centralis* in southern Amazonia, and the transition zones between the Cerrado and both Amazonia and the Caatinga. Due to the few bat studies, combined with intensive crop and cattle production in those areas, we believe this distribution gap is more likely to be an omission error of the models than true absence (Silva et al. 2006; Costa and Pires 2010; Bernard et al. 2011; Aldrich et al. 2012; Aguiar et al. 2016). A similar result was obtained by Delgado-Jaramillo et al. (2017) for the Brazilian funnel-eared bat *Natalus macrourus*. Therefore, ground validation of our models is necessary (Greaves et al. 2006; Jiménez-Valverde et al. 2008a, 2008b; Buckman-Sewald et al. 2014; Hipólito et al. 2015). Bioacoustics surveys can play an important role in that validation (Greaves et al. 2006; Rebelo and Jones 2010).

A good data set of species records is important for the production of good species distribution models leading to more suitable conservation actions (López-González 1998; Phillips et al. 2009; Aguiar et al. 2016; Delgado-Jaramillo et al. 2017), but other factors can negatively influence species distribution models, such as inadequate choice of MaxEnt parameters (Anderson and Gonzalez 2011; Radosavljevic and Anderson 2014; Morales et al. 2017). Contrary to other studies of bats that have adopted the default regularization multiplier (1.0; e.g., de Moraes Weber and Viveiros Grelle 2012; Roscioni et al. 2013; Buckman-Sewald et al. 2014), we found that in the case of *P. centralis* the best model produced was using 3.0 regularization multiplier. MaxSSS is less sensitive to lower sample sizes than LPT (Liu et al. 2013), but in our study, omission rates using maxSSS were greater than using LPT. When considering generalist bat species with great mobility, such as molossids, using MaxEnt's default parameters and more conservative thresholds like maxSSS might lead to overfitted distribution models. This reinforces that species-specific adjustments of MaxEnt parameters are essential for highly predictive and accurate distribution models (Anderson and Gonzalez 2011; Syfert et al. 2013; Radosavljevic and Anderson 2014; Gottwald et al. 2017), and that uncritically employing default parameters might lead to biased results.

Promops centralis' diverse vocal repertoire.—The calls of *P. centralis* in Brazil proved to be species-specific and easily distinguishable from other acoustically similar molossid species. Despite slight differences, low type I calls recorded in Brazil were very similar to *P. centralis* calls from French Guiana and Central America (see Jung and Kalko 2011; Barataud et al. 2013), with an upward modulated FM-qCF calls (low type I calls) that occasionally alternated with higher frequency and downward modulated FM-qCF calls (high calls).

Further, the repertoire of *P. centralis* was more diverse than previously thought. These bats produced at least three highly variable calls, including an unusual call type (low type II calls) that are very a long calls with a prominent constant frequency component and short inter-pulse intervals. This latter call type is difficult to definitively label as either echolocation or social call. Although the buzzes found at the end of several 'low type II' sequences seemed very similar to feeding buzzes—suggesting an echolocation nature—we nevertheless cannot exclude a potential communication function of these buzzes. Molossidae is a socially structured bat family, not only inside the roosts but also in flight, exhibiting complex social-calls, "syllabs" and songs (Gelfand and McCracken

1986; Fenton et al. 2004; Ratcliffe et al. 2004; Schwartz et al. 2007; Bayefsky-Anand et al. 2008; Bohn and Gillam 2018). Indeed, social buzzes are often used by Brazilian free-tailed bat *Tadarida brasiliensis* when stationary, and these are similar to feeding buzzes used for insect capture (Schwartz et al. 2007). But social buzzes are not only emitted when bats are stationary: some molossids, such as the Florida bonneted bat *Eumops floridanus* (Bohn and Gillam 2018), *T. brasiliensis* (Bohn and Gillam 2018), European free-tailed bat *T. teniotis* (Bayefsky-Anand et al. 2008), and Pallas's mastiff bat *Molossus molossus* (K. M. Bohn, Johns Hopkins University, pers. comm.), produce buzz-like vocalizations when flying. However, shifts from the typical echolocation "low type I" calls to the distinctive novel call pattern (low type II calls) described herein were observed during both roost emergence and free flight. Therefore, these "low type II calls" may be used for navigation and foraging (as search calls). If so, to our knowledge, this would be the first description of echolocation calls of this nature among the Molossidae. However, if used as echolocation calls, they probably present some challenges to the bats. Due to the short inter-pulse intervals in comparison to the length of the calls, there could overlap between the outgoing calls and their returning echo. If these calls are indeed used for echolocation, *P. centralis* would belong to the restricted group of high duty cycle (HDC) bats that have adaptations in the auditory fovea enabling them to distinguish the incoming weaker echoes from the stronger simultaneous outgoing calls (Neuweiler 1990, 2000; Schnitzler and Denzinger 2011; Bohn and Gillam 2018). To fully satisfy the HDC criteria, a bat must emit calls with a dominant CF component, have evolved auditory fovea, and be able to use Doppler shift compensation (Lazure and Fenton 2011; Fenton et al. 2012). Our low type II calls sequences present duty cycle over 20% (see Lazure and Fenton 2011) and a dominant CF component, but our study was neither focused on anatomical aspects of the species, nor on aspects of echo intensity of their calls. We therefore were not able to definitively state if *P. centralis* fully satisfies those criteria. Even so, as with other molossids (e.g., Mora et al. 2011; Jung et al. 2014; Oliveira et al. 2018), *P. centralis* show great vocalization plasticity, probably enabling individuals of this species to explore distinct types of habitats or prey. However, we lack experimental evidence to determine if the "low type II" calls are echolocation or social calls. This should be a research priority in future studies on the species.

Our research demonstrated that the combination of acoustic surveys and SDM are very useful for research and conservation of poorly known, hard to capture bat species, with the potential to refine knowledge of the species' distribution, ecology, and behavior. Like anywhere in the Neotropics, most bat inventories are still based on the sole use of understory mist netting or roost searches (Sampaio et al. 2003; Bernard et al. 2011; Silva and Bernard 2017). Here we have shown that for elusive, high-flying species such as *P. centralis*, these limited surveys simply are not sufficient, and must be complemented with acoustic monitoring.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Detailed description of the study sites.

Supplementary Data SD2.—Table. Distribution records of *Promops centralis* gathered from the literature review and from the acoustic sampling performed in this study.

Supplementary Data SD3.—Audio. *Promops centralis*' "low type I" calls alternating with "high calls."

Supplementary Data SD4.—Audio. *Promops centralis*' search-phase echolocation changing from "low type I" to "low type II" calls.

Supplementary Data SD5.—Audio. *Promops centralis*' search-phase echolocation changing from "low type I" to "low type II" calls, increasing duty cycle.

Supplementary Data SD6.—Audio. *Promops centralis*' "low type II" calls alternating with "high calls."

Supplementary Data SD7.—Audio. *Promops centralis*' "type II" calls alternating with "high calls."

Supplementary Data SD8.—Audio. *Promops centralis*' monotone low type II calls search-phase sequence.

Supplementary Data SD9.—Audio. *Promops centralis*' monotone low type II calls search-phase sequence.

Supplementary Data SD10.—Audio. *Promops centralis*' calls sequence with a buzz.

Supplementary Data SD11.—Audio. *Promops centralis*' low type II calls sequence with a buzz.

Supplementary Data SD12.—Discriminant function analysis (DFA) tables.

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SUPPLEMENTARY DATA

Supplementary Data SD1.—Detailed description of study sites.

1- In the Mata da Cristal (hereafter MC), an Atlantic Forest remnant (936 ha) adjacent to Cristal mining company in the municipality of Mataraca, Paraíba state (6°29'43.92"S, 34°58'58.62"W) (Cristal 2016). The annual average temperature is around 25ºC and the average annual precipitation rain is 1725 mm (Cunha et al. 2003, Cristal 2016). Calls were recorded in an area under reforestation since 1988.

2- In the Reserva Ecológica do Seridó (SER), a IUCN category Ia protected area (1123 ha), in Serra Negra do Norte, Rio Grande do Norte state (6°34'29.52"S; 37°16'2.04"W). This location is characterized by an arid climate with annual average temperatures between 20.3º C and 35.2º C and monthly average precipitation of 45.4 mm (ICMBio, 2004). However, during the driest months the precipitation can be minimal or none. Although SER has no residents within its area, this reserve has been facing human pressure due to its small size surrounded by a highly anthropized matrix. Calls were recorded near rocky outcrops with arbustive scrubland and sparse foliage cover.

3- In the Recife International Airport (REC), located in southern part of the capital Recife, Pernambuco state (8° 7'38.22"S, 34°55'25.44"W). With an area of 263 ha (INFRAERO 2016) REC is in a region once dominated by Atlantic Forest, but the area now presents a low level of vegetation structure due to severe urbanization (Costa Filho 1997, Oliveira et al. 2011). The annual average temperature is around 25ºC and the average annual precipitation rain is around 2,500 mm (Costa Filho 1997, Oliveira et al. 2011). Calls were recorded at the two main headings of the airport's runway.

4- In the Catimbau National Park (CNP), a IUCN category II protected area in the municipalities of Buíque, Ibimirim, Sertânia, and Tupanatinga, in Pernambuco state

(8°29'14.10"S; 37°16'48.80"W). Located in the Caatinga biome, CNP has a total area of 62,294 ha and the altitude ranges from 400 m to 1,000 m, with frequent occurrence of canyons and caves (ICMBio 2016). The annual average temperature is around 23ºC and average annual precipitation rain between 500 and 600 mm (Souza Cavalcanti & Barros Corrêa 2015). The vegetation includes dense arboreal Caatinga dry forests and shrubby spineless vegetation, immersed in a matrix of sandy soils and rock outcrops. Although not supposed to have human residents within its limits, the land regularization process was not concluded in the park and ~1,100 people still live inside the park, causing direct impacts on the vegetation (Azevedo & Bernard 2015).

5- The Serra do Lajeado (LAJ) Environmental Protection Area (10° 2'43.98"S; 48°15'15.00"W), Tocantins state, Central Brazil is a partially protected area located near the geodesic centre of Brazil and comprises the Lajeado State Park, a fully protected area only opened to controlled visitation and where no human economic activities are allowed (ICMBio 2014). The Environmental Protection Area has a total area of 1,214,177,659 ha and ranges from about 200 m to 600 m altitude (ICMBio 2014). The area is fully within the Cerrado biome, and here the main natural phytophysiognomies include Cerrado *sensu stricto*, Cerradão and semideciduous and evergreen alluvial forests occurring in richer soils or located in the proximity of watercourses (ICMBio 2014). A few other formations typical of the Cerrado biome, such as campo rupestre, campo limpo, and vereda occupy a smaller fraction of the area. The climate is tropical with high and relatively constant thermal averages along the year, a great contrast between very humid and rainy summers and prolonged drought (ICMBio 2014). The regional climate corresponds to the humid tropical climate of the tropical savannas (Aw) of the classification of Köppen, characterized by rainy summer and dry winter. The average temperature of the hottest month is above 22°C and that of the coldest month, less than 18 °C. Calls were recorded in a 'Cerrado *sensu lato*' habitat.

6- In the municipality of Mambaí (MAM) (14°28'59.7"S; 46°06'46.9"W), Goiás state, near the border of Bahia state, Central Brazil, located within the "Nascentes do Rio Vermelho" Environmental Protection Area and encompassing the Pequi Municipal Natural Park (ICMBio 2017). The Environmental Protection Area has a total area of 176,322.22 ha and is a region of sustainable use with a certain degree of human occupation. The Pequi Municipal Natural Park has a total area of approximately 2,300 ha and is an integral protection unit which allows indirect use of resources as ecological tourism and scientific research, among others (ICMBio 2017). The area is within the Cerrado biome and includes main natural phytophysiognomies as Cerrado *sensu stricto*, gallery forest, and veredas. Its natural cover is rather well preserved but has been almost completely destroyed by intensive plantations on its east side (state of Bahia). The regional climate corresponds to the humid tropical climate of the tropical savannas (Aw) of the classification of Köppen. The local climate is characterized by high temperatures throughout the year with average annual temperature that ranges between 21 and 25°C and by a pronounced pluviometric seasonality of 1,200 to 1,450 mm/yr with concentration of precipitation occurring between October and April (ICMBio 2017). Calls were recorded in areas with low shrub vegetation, in well-preserved Cerrado conditions, but near areas with some level of land use such as grazing and agriculture.

7- In the Serra do Cipó National Park (SCP), a protected area in the Jaboticatubas, Morro do Pilar, Itambé do Mato Dentro, and Santana do Riacho municipalities, in Minas Gerais state (19°20'37.10"S; 43°36'38.84"W). Located in a transition zone between Cerrado and Atlantic Forest biomes, SCP has a total area of 31,639 ha and the altitude ranges from 700 m to 1,670 m, with frequent occurrence of karst areas, riparian forests, 'Campos Rupestres' montane savanna, and caves (ICMBio 2009a, b). The annual average temperature is around 18ºC and average annual precipitation rain between 1,200 and 1,700 mm (ICMBio 2009b). Calls were recorded in a riparian gallery, near to the Atlantic Forest biome portion of the park, and calls

were also recorded in a cave exit from free-flying individuals during emergence from its roost (19°30'11.31"S; 43°26'21.87"W) in a 'Campos Rupestres' habitat surrounded by Atlantic Forest.

8- In the *campus* of the Federal University of Espírito Santo (UFES), in Vitória, Espírito Santo state (20°16'52.70"S, 40°18'21.50"W). The *campus* is divided into two main areas (a building zone and an environmental protection zone) and recordings were obtained in the last one, which consists of ~ 89 ha composed by mangroves, forests over very moist clay soils ('tabuleiro' forest), rocky outcrop vegetation and transition vegetation (UFES 2005). The annual average temperature is around 25ºC and average annual precipitation rain between 1,300 and 1,400 mm (INCAPER 2011, de Souza et al. 2013). Calls were recorded in a narrow strip of forest bordering the mangrove (UFES 2005).

9- In a 138 ha island in the reservoir of the Funil Hydroelectric Dam (FHD), in the municipality of Ijaci, Minas Gerais state (21°10'3.31"S, 44°51'59.62"W). The construction of this dam was concluded in 2002 and was built in the upper part of the Rio Grande (Alves et al. 2007, Coelho & Pereira 2010). The landscape is part of the Cerrado biome and is facing strong anthropogenic pressures due to urbanization, agriculture and pasture (Coelho & Pereira 2010). The annual average temperature is around 20ºC and the average annual precipitation rain is 1,460 mm. Calls were recorded near to the reservoir' margin in a fishing pier.

10- The Aparados da Serra National Park (PNA) located in the eastern limit of the Araucaria Plateau (29°14'53.42"S, 50°14'49.61"W), in the border of the states of Rio Grande do Sul and Santa Catarina (Brazil), has an area of 10,250 ha, contributing with approximately 0.02% of the 2.44% of Atlantic Forest territory classified as a Federal Conservation Unit (IBAMA/MMA 2004). It harbours three of the eight plant formations encompassed by that biome: Mixed Ombrophilous Forest or Araucaria Forest, Dense Ombrophilous Forest, and High Altitude Fields (IBAMA/MMA 2004). A relief deeply cut by some rivers characterizes the region. The

climate is moist mesothermic, with precipitation well distributed along the year and mild summers (classified as Cfb in the Köppen system). This type of climate is characteristic of the higher altitudes (700 m) (IBAMA/MMA 2004). Negative temperatures can occur in the months of April to November, the formation of frosts is very frequent and in more rigorous winters it may snow. Frequent and intense fogs, especially in the vicinity of the river valleys, also affect the region (IBAMA/MMA 2004). Precipitation is high in all months with an annual average of 2,252 mm (IBAMA/MMA 2004). Calls were recorded in open areas near the edge of secondary growth forest patches.

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SUPPLEMENTARY DATA

Supplementary Data SD2.—Distribution records information of *Promops centralis* gathered from the literature revision and from acoustic sampling performed in this study.

#	Latitude	Longitude	Location	State	Country	Source
1	-26.172073°	-58.213824°	Formosa	Formosa	Argentina	(Barquez et al. 2006, Gregorin & Chiquito 2010)
2	-18.088972°	-63.209556°	Guirapembi	Santa Cruz	Bolivia	(Anderson 1997)
3	-17.901989°	-63.437727°	Espejillos	Santa Cruz	Bolivia	(Anderson 1997)
4	-18.341996°	-59.754770°	Roboré	Santa Cruz	Bolivia	(Gregorin & Chiquito 2010)
5	-7.448611°	-73.661389°	Rio Moa, Serra da Jaquirana	Acre	Brazil	(Nogueira et al. 1999)
6	-1.816667°	-61.766667°	Campina do Patauá, Ajú	Amazonas	Brazil	(Barnett et al. 2006)
7	-1.028940°	-46.851051°	Bragança	Pará	Brazil	(Gregorin & Taddei 2000)
8	-19.079430°	-56.526479°	Pantanal	Mato Grosso do Sul	Brazil	(Fischer et al. 2015)
9	-6.574867°	-37.267233°	ESEC Seridó (SER)	Rio Grande do Norte	Brazil	Present study
10	-8.487250°	-37.280222°	Parque Nacional do Catimbau (CNP)	Pernambuco	Brazil	Present study

#	Latitude	Longitude	Location	State	Country	Source
11	-6.495533°	-34.982950°	Mina da Cristal (MC)	Paraíba	Brazil	Present study
12	-21.167587°	-44.866560°	Albufeira Barragem do Funil (FHD)	Minas Gerais	Brazil	Present study
13	-8.127283°	-34.923733°	Aeroporto Internacional de Recife (REC)	Pernambuco	Brazil	Present study
14	-20.281306°	-40.305972°	Universidade Federal de Espírito Santo (UFES)	Espírito Santo	Brazil	Present study
15	-14.522409°	-46.140293°	Mambaí (MAM)	Goiás	Brazil	Present study
16	-10.045550°	-48.254167°	Serra do Lageado (LAJ)	Tocantins	Brazil	Present study
17	-29.250000°	-50.250000°	Parque Nacional dos Aparados da Serra (PNA)	Rio Grande do Sul	Brazil	Present study
18	-19.283794°	-43.629429°	Parque Nacional da Serra do Cipó (SCP)	Minas Gerais	Brazil	Present study
19	4.033333°	-74.816667°	Suárez y Gualanday	Tolima	Colombia	(Bejarano-Bonilla et al. 2007)
20	1.199906°	-77.290273°	Pasto	Nariño	Colombia	(Gardner 2008)
21	2.434069°	-76.621787°	Popayán	Cauca	Colombia	(Marinkelle & Cadena 1972)

#	Latitude	Longitude	Location	State	Country	Source
22	6.144837°	-75.375085°	Río Negro	Antioquia	Colombia	(Gardner 2008)
23	10.173333°	-85.594167°	Parque Nacional Diriá	Guanacaste	Costa Rica	(Rodríguez-Herrera et al. 2014)
24	-0.743315°	-78.040448°	Orellana, 1 km. S of Estación Científica Yasuní	Napo	Ecuador	(Reid et al. 2000, Gardner 2008)
25	15.465059°	-90.384253°	Cobán	Alta Verapaz	Guatemala	(Gregorin & Chiquito 2010)
26	15.099152°	-90.312119°	Salamá	Baja Verapaz	Guatemala	(Gregorin & Chiquito 2010)
27	5.274118°	-52.923870°	Domaine Experimental Paracou	Paracou	French Guiana	(Simmons & Voss 1998)
28	3.350000°	-59.566667°	Iwokrama Field Station	Potaro-Siparuni	Guyana	(Lim & Engstrom 2001)
29	15.567824°	-85.682721°	El Pedrero	La Paz	Honduras	(Gregorin & Chiquito 2010)
30	21.016039°	-89.614908°	Country Club Campestre, Merida	Yucatan	Mexico	(Bowles et al. 1990)
31	21.004617°	-89.563639°	Colegio Peninsular, Merida	Yucatan	Mexico	(Bowles et al. 1990)
32	16.322699°	-95.242330°	Tehuantepec	Oaxaca	Mexico	(Gregorin & Chiquito 2010)
33	28.833636°	-111.599222	Bahía de Kino	Sonora	Mexico	(González-Terrazas et al. 2016)

#	Latitude	Longitude	Location	State	Country	Source
		°				
34	19.516667°	-96.916667°	Xalapa	Veracruz	Mexico	(Alavez Tadeo et al. 2017)
35	18.600000°	-95.650000°	Plaza San Miguelito, Tlacotalpan	Veracruz	Mexico	(Alavez Tadeo et al. 2017)
36	9.116020°	-79.697861°	Gamboa	Colón	Panama	(Jung & Kalko 2010)
37	8.953720°	-79.563504°	Ancón	Panamá	Panama	(Gregorin & Chiquito 2010)
38	8.988003°	-79.575743°	Corozal	Veraguas	Panama	(Gregorin & Chiquito 2010)
39	8.914397°	-79.525229°	Fort Amador	Panamá	Panama	(Gregorin & Chiquito 2010)
40	9.001405°	-79.581417°	Fort Clayton	Panamá	Panama	(Gregorin & Chiquito 2010)
41	9.293780°	-79.912202°	Fort Gulick	Colón	Panama	(Gregorin & Chiquito 2010)
42	-24.437167°	-54.666333°	Estancia Rivas	Canindeyú	Paraguay	(Lopez-Gonzalez 1998)
43	-25.776062°	-56.449592°	Villa Rica	Guairá	Paraguay	(Lopez-Gonzalez 1998, Gregorin & Chiquito 2010)
44	-23.408680°	-57.495240°	8 km E Concepción	Concepción	Paraguay	(Lopez-Gonzalez 1998)
45	-22.181822°	-57.702609°	Estancia Estrellas	Concepcion	Paraguay	(Lopez-Gonzalez 1998)
46	-25.085369°	-57.266327°	20 km N Altos	Cordillera	Paraguay	(Lopez-Gonzalez 1998, Gregorin &

#	Latitude	Longitude	Location	State	Country	Source
						Chiquito 2010)
47	-25.666633°	-56.956590°	Sapucay	Paraguarí	Paraguay	(Lopez-Gonzalez 1998, Gregorin & Chiquito 2010)
48	-26.884675°	-57.904830°	18 km E San Lorenzo	Ñeembucú	Paraguay	(Lopez-Gonzalez 1998)
49	-23.303115°	-59.020610°	Rincón Charrúa	Presidente Hayes	Paraguay	(Lopez-Gonzalez 1998)
50	-22.354073°	-60.030921°	Filadelfia	Boquerón	Paraguay	(Gregorin & Chiquito 2010)
51	-3.797326°	-73.276927°	RNAM, Iquitos	Loreto	Peru	(Hice et al. 2004)
52	-11.588641°	-72.951319°	Camisea, San Martin 3	Cuzco	Peru	(Gregorin & Chiquito 2010)
53	-4.916667°	-73.750000°	Jenaro Herrera	Loreto	Peru	(Ascorra et al. 1993)
54	5.689120°	-54.415517°	10 km N, 24 km W Moengo (river margin)	Marowijne	Suriname	(Genoways & Williams 1979, Gardner 2008)
55	10.645658°	-61.365190°	St. George	Tunapuna-Piarco	Trinidad and Tobago	(Carter et al. 1981, Gardner 2008)
56	10.285619°	-61.315444°	Princes Town	Princes town	Trinidad and Tobago	(Gregorin & Chiquito 2010)

#	Latitude	Longitude	Location	State	Country	Source
57	10.285724°	-61.446275°	San Fernando	San Fernando	Trinidad and Tobago	(Gregorin & Chiquito 2010)
58	-30.402828°	-56.458425°	Artigas	Artigas	Uruguay	(Botto et al. 2008)
59	7.412673°	-65.188798°	Hato La Florida, 47 Km ESE Caicara	Bolivar	Venezuela	(Ochoa & García 2009)
60	10.349316°	-67.685238°	Parque Nacional Henri Pittier	Aragua	Venezuela	(Fernández-Badillo & Ulloa 1990)
61	10.486118°	-66.887390°	Caracas	Distrito Federal	Venezuela	(Ochoa G & Ibáñez 1985)
62	8.917434°	-63.122703°	Puente Morichal Largo	Monagas	Venezuela	(Ochoa G & Ibáñez 1985)
63	11.232998°	-85.864364°	San Juan del Sur	Rivas	Nicaragua	(Medina-Fitoria 2014)

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SUPPLEMENTARY DATA

Supplementary Data SD12.—Table A. Eigenvalues and variation percentage of the linear Discriminant function analysis (DFA) performed for the echolocation calls of: *Promops centralis* recorded in this study, and *P. nasutus*, *Molossops temminckii*, and *Eumops* sp. calls from our bat call libraries and *M. neglectus* from a bat call library from French Guiana. We used frequencies of maximum energy (FME), minimum frequencies (Fmin), maximum frequencies (Fmax), initial frequencies (F initial), final frequencies (F final), duration (Dur), slope, bandwidth (BW), and duty-cycle (DC), values extracted from the echolocation calls.

Axis	Eigenvalues	Percentage
1	56.741	95.63
2	2.0639	3.478
3	0.35803	0.6034
4	0.17406	0.2933

Supplementary Data S12.—Table B. Confusion matrix of the linear Discriminant function analysis (DFA) for the echolocation calls of: *Promops centralis* recorded in this study, and *P. nasutus*, *Molossops temminckii*, and *Eumops* sp. calls from our bat call libraries and *M. neglectus* from a bat call library from French Guiana, using frequencies of maximum energy (FME), minimum frequencies (Fmin), maximum frequencies (Fmax), initial frequencies (F initial), final frequencies (F final), duration (Dur), slope, bandwidth (BW), and duty-cycle (DC) values extracted from the echolocation calls.

	P. nasutus	*P. centralis*	*Eumops sp.*	*M. temminckii*	*M. neglectus*	Total
P. nasutus	34	1	0	0	0	35
P. centralis	3	240	0	0	0	243
Eumops sp.	0	0	11	0	0	11
M. temminckii	0	0	0	24	0	24
M. neglectus	0	0	0	0	7	7

Total	37	241	11	24	7	320
Jackknifed % correctly classification = 98,75						

Supplementary Data S12.—Table C. Loadings of the linear Discriminant function analysis (DFA) performed for the echolocation calls of: *Promops centralis* recorded in this study, and *P. nasutus*, *Molossops temminckii*, and *Eumops* sp. calls from our bat call libraries and *M. neglectus* from a bat call library from French Guiana, using frequencies of maximum energy (FME), minimum frequencies (Fmin), maximum frequencies (Fmax), initial frequencies (F initial), final frequencies (F final), duration (Dur), slope, bandwidth (BW), and duty-cycle (DC) values extracted from the echolocation calls.

	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**
Dur	-1,388	-1,4334	22,889	4,9279
Fmin	597,16	-560,51	-1972,2	517,33
FME	681,87	-55,823	-1270,5	1329,6
Fmax	859,75	716,99	-1484,2	1794,7
BW	262,6	1277,5	487,94	1277,5
Slope	54,479	159,57	-131,94	50,271
DC	-0,51593	0,33574	11,117	4,0732
F initial	619,33	339,53	-3573,2	2064,4
F final	837,58	-183,05	116,75	247,6

3.4 THE IMPORTANCE OF *IN SITU* VALIDATION FOR SPECIES DISTRIBUTION MODELLING: AN EXAMPLE WITH BIOACOUSTICS AND BATS IN BRAZIL

Manuscrito submetido para publicação

RESUMO

A modelagem de distribuição de espécies (SDM) ganhou importância nos estudos de distribuição e conservação da biodiversidade em todo o mundo, incluindo a priorização de áreas para políticas públicas e tratados internacionais. SDM é útil para abordagens e estimativas em grande escala, uma vantagem considerando que uma pequena fração do planeta é adequadamente amostrada. No entanto, a SDM precisa ser o mais confiável possível. Minimizar erros é desafiador, mas essencial, considerando os usos e as consequências dos modelos gerados. A validação *in situ* das saídas SDM deve ser uma etapa-chave - em alguns casos, urgente e a bioacústica pode ser usada para validar e refinar SDMs, especialmente se as vocalizações das espécies forem conspícuas e específicas (*e.g.* morcegos). Aqui, usamos monitoramento acústico *in situ* extenso (>120 pontos de validação, cobrindo uma área de >758.000 km^2, e >300.000 arquivos de som) para validar modelos do MaxEnt, o algoritmo SDM mais usado, para seis espécies de morcegos neotropicais numa região mal amostrada do Brasil. Com base nesta validação *in situ*, avaliamos a capacidade de quatro métricas de avaliação teórica *threshold*-dependentes em predizer o desempenho dos modelos. Também avaliamos o desempenho de três *thresholds* amplamente utilizados para converter SDMs contínuos em mapas de presença-ausência. Demonstramos que o MaxEnt pode produzir resultados muito diferentes, exigindo uma escolha cuidadosa de thresholds e outros parâmetros. Embora todas as métricas de avaliação teórica estudadas foram positivamente correlacionadas com a acurácia, sabendo que a maioria dos SDMs são baseados em dados não-balanceados, demonstramos empiricamente que as métricas baseadas em sensibilidade-especificidade e precisão-sensibilidade são melhores, já que não são afetados por conjuntos de dados não-balanceados. Sem a validação de campo independente dos resultados, descobrimos que usar *thresholds* arbitrários pode ser uma abordagem precária, mesmo se obtendo boa avaliação. A bioacústica se mostrou muito útil para validar SDMs das seis espécies de morcegos analisadas, permitindo um melhor refinamento dos SDMs em regiões extensas e subamostradas, com esforço amostral relativamente baixo. Independente do método de avaliação usado, nossa pesquisa destacou a importância e a necessidade da validação *in situ* para SDM.

The importance of *in situ* validation for species distribution modelling: An example with bioacoustics and bats in Brazil

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Abstract

Species distribution modelling (SDM) gained importance on biodiversity distribution and conservation studies worldwide, including prioritizing areas for public policies and international treaties. SDM is useful for large-scale approaches and estimates, a plus considering that a minor fraction of the planet is adequately sampled. However, SDM needs to be as reliable as possible. Minimizing errors in SDM is challenging, but essential, considering the uses and consequences of such models. *In situ* validation of the SDM outputs should be a key-step – in some cases, urgent. Bioacoustics can be used to validate *in situ* and refine SDM outputs, especially if the focal species' vocalizations are conspicuous and species-specific. This is the case of echolocating bats. Here, we used extensive *in situ* acoustic monitoring (>120 validation points, covering an area of >758,000 km^2, and >300,000 sound files) to validate MaxEnt outputs, the most used SDM algorithm, for six neotropical bat species in a poorly-sampled part of Brazil. Based on *in situ* validation, we evaluated four threshold-dependent theoretical evaluation metrics' ability in predicting models' performance. We also assessed the performance of three widely used thresholds to convert continuous SDMs into binary (presence/absence) maps. We demonstrated that MaxEnt could produce very different outputs, requiring a careful thresholds and modeling parameters choice. Although all the theoretical evaluation metrics studied were positively correlated with accuracy, considering that most SDMs are based on unbalanced data, we empirically demonstrated that metrics based on specificity-sensitivity and sensitivity-precision are better for testing models since they are not affected by sets of unbalanced class data. Without independent field validation of the results, we found that using an arbitrary threshold for modelling can be a precarious approach with many possible outcomes, even if getting good evaluation scores. Bioacoustics proved to be very

useful for validating SDMs for the six bat species analyzed, allowing a better refinement of distribution models in large and under-sampled regions, with relatively low sampling effort. Due to inherent limitations, and independent of the species assessing method used, our research highlighted the importance and necessity of *in situ* validation for SDM.

Keywords: accuracy, echolocation calls, MaxEnt, predictive distribution maps, thresholds, SDM.

Introduction

Species distribution modelling (SDM) gained importance in the development of studies on biodiversity distribution and conservation worldwide (Domisch et al., 2019; Zimmermann et al., 2010). These distribution models can be produced and refined by crossing species presence records with biological and non-biological variables and environmental data (e.g., Phillips et al., 2006). Such modelling can be beneficial for large-scale approaches and estimates, a plus considering that fewer parts of planet Earth were adequately sampled (Anderson, 2012; Guisan et al., 2013). Moreover, SDM has been used to support decision-making processes, including prioritizing areas and regions in public policies and international treaties (Domisch et al., 2019; Guisan et al., 2013).

For biodiversity conservation purposes, SDM should be as reliable as possible. For instance, imprecise models can undermine the calculation/estimate of a species' occupancy, a criterion used to assess its conservation status, for example (Fourcade et al., 2018). Depending on the quality of the input data and modelling parameters chosen, the predictions created may not translate precisely the species' distribution (Benito et al., 2013; Jiménez-Valverde et al., 2008). Known as commission (false positives) and omission (false negatives) errors, they can inflate or reduce a given *taxon*'s potential distribution. Minimizing such errors is a challenge for the spatial modelling science (Anderson, 2012; Jiménez-Valverde et al., 2008; Visconti et al., 2013), but essential considering the uses and consequences such models may have (Greaves et al., 2006). Therefore, *in situ* validation of the SDM outputs should be a critical step – in some cases, urgent (Greaves et al., 2006; Hipólito et al., 2015).

Certifying that a species is present in a given area is not always straightforward, and different and innovative approaches have been proposed for such task [e.g., e-DNA (Carraro et al., 2020) or satellite images (Cubaynes et al., 2019)]. Bioacoustics is one of such techniques

and has been used for a long time to record species presence/absence for birds, cetaceans, and amphibians (Laiolo, 2010). Bats are a widespread group, using many habitats and resources, and most of the 1400 known species depend on echolocation for navigation and food acquisition (Schnitzler et al., 2003). The bats' echolocation system is based on ultrasonic signals which, although above the human hearing capacity, thanks to recent electronics advances, can be easily recorded (Parsons and Szewczak, 2009). Moreover, most bats have conspicuous and species-specific calls, allowing precise identification of the emitter's identity and making the record of its presence accurate (Parsons and Szewczak, 2009). Therefore, bioacoustics can be a useful technique applied to the *in situ* validation and refinement of SDM outputs for echolocating bats.

Here, we used extensive *in situ* monitoring (> 120 validation points, covering > 758,000 km^2, and > 300,000 sound files) of echolocation calls to validate the outputs of the most used SDM algorithm (MaxEnt; Phillips et al., 2006) for six neotropical bat species in a poorly-sampled part of Brazil. Using independent acoustic data collected, we (a) evaluated the ability of four threshold-dependent theoretical evaluation metrics in predicting models' performance, and (b) assessed the performance of three widely used thresholds to convert continuous species habitat suitability models into binary (presence/absence) maps.

Materials and Methods

Historical species records

In our analysis, we selected six neotropical bat species whose echolocation calls are well-known, species-specific and unequivocally identifiable: *Noctilio leporinus*, *Promops centralis*, *Promops nasutus*, *Pteronotus gymnonotus*, *Pteronotus personatus*, and *Saccopteryx leptura* (Arias-Aguilar et al., 2018; Barataud et al., 2013; Hintze et al., 2020). We gathered distribution records for these species from a bibliographic revision using the following online databases and search engines: the Vertebrate Zoology Database of the American Museum of Natural History (http://sci-web-001.amnh.org/db/emuwebamnh/index.php); the database of the Division of Mammals Collections of the Smithsonian National Museum of Natural History (https://collections.nmnh.si.edu/search/mammals/); the Global Biodiversity Information Facility (www.gbif.org); the SpeciesLink network (http://www.splink.org.br); Google Scholar (scholar.google.com); the Web of Science (www.webofknowledge.com); Scopus (www.scopus.com); the Periódicos CAPES (www.periodicos.capes.gov.br); and the Scientific Electronic Library Online (www.scielo.br). We also reviewed occurrences in studies available online such as Barquez et al. (2006) and Gardner (2008). Each record was checked for

duplication of localities and, eventually, to correct location or taxonomy problems (Peterson et al., 2011). For example, following Gardner (2008), we treated *P. nasutus* as a monotypic species (considering *Promops nasutus ancilla, P. nasutus pamana, P. nasutus fosteri* or *P. nasutus downsi* as simply *Promops nasutus*). Overall, we worked with 1277 single records for the six studied bat species: 590 records for *Noctilio leporinus*, 70 for *Promops centralis*, 71 for *Promops nasutus*, 120 for *Pteronotus gymnonotus*, 95 for *Pteronotus personatus*, and 331 for *Saccopteryx leptura* (Figure 1; Table S1 in supplementary material).

Distribution modelling procedure

We used SDMtoolbox 2.4 for ArcGIS (Brown, 2014) to create an environmental heterogeneity map with the bioclimatic variables of Worldclim (Fick and Hijmans, 2017). To reduce the potential bias caused by autocorrelation, we then used the Spatial Rarefy Occurrence Data tool of the SDMtoolbox 2.4 package to delete records under the same environmental conditions within 25 km from each other (Coxen et al., 2017). Other studies usually use a 10km distance between points (e.g. Hidalgo-Mihart et al., 2004; Pearson et al., 2007; Radosavljevic and Anderson, 2014), but given the topographic and environmental heterogeneity of the studied region, we chose 25 km as a spatial filter to avoid eventual spatial bias on historical records (Fourcade et al., 2014). This process ensured that all historical records gathered in our revision corresponded to a unique spatial sample, reducing occurrence data from 1684 to 1157 single localities.

We used MaxEnt 3.4 (Phillips et al., 2006) to generate potential species distribution models for the six selected species based on a set of variables at a 5 km^2 resolution. We used the 19 bioclimatic variables plus elevation available at the Worldclim data website (Fick and Hijmans, 2017) and Globcover 2009 (Arino et al., 2012) as a categorical variable for land cover. To reduce the multicollinearity among the predictor variables, we performed a preliminary model with all variables and checked the weight of each according to their contributions, using Jackknife tests. Next, using the Correlations and Summary Stats tool of the SDMtoolbox 2.4 package, we obtained the correlation and covariances matrices and removed highly correlated variables (i.e., those with the lowest value when the pairwise correlation was > 0.7) (Snedecor and Cochran, 1980). Therefore, we used different variables for each modelled species (Table S2, in supplementary material).

We used a logistic output to produce our models and obtain continuous suitability values for species habitat suitability, which varies from 0 (lowest suitability) to 1 (highest

suitability) (Phillips et al., 2006; Phillips et al., 2009). Since default regularization values lead to overfitted models when using spatial filtering (Radosavljevic and Anderson, 2014), we calibrated the models with different regularization multiplier values (default 1.0, 2.0, 3.0, and 4.0) (Merow et al., 2013; Radosavljevic and Anderson, 2014). To generate overall predictive distribution models, we used 75% of the data for calibration and 25% for internal evaluation (testing data).

We used ten cross-validation replications to test all models and calculate confidence intervals, resulting in 40 models for each species, and a total of 240 continuous models for all species. Since we aimed to use bioacoustics data to validate binary maps (presence-absence), we used three widely used thresholds to convert the continuous suitability values of each model: lowest presence threshold (hereafter LPT) (Pearson et al., 2007); 10^{th} percentile of the predicted values (hereafter P10) (Pearson et al., 2007); and maximum sum of sensitivity and specificity (hereafter maxSSS) (Liu et al., 2016; Liu et al., 2013). LPT is considered the least conservative threshold, whereas maxSSS the most (Jiménez-Valverde and Lobo, 2007; Liu et al., 2016). We produced a total of 720 binary models, 120 for each species.

We then evaluated each species binary models for their predicting performance using four threshold-dependent theoretical evaluation metrics: (1) overall accuracy (hereafter OAcc) (Allouche et al., 2006; Brooner, 1976); (2) Cohen's maximized kappa statistics (hereafter P-kappa) (Cohen, 1960; Mingyang et al., 2008); (3) True Skill Statistics (hereafter TSS) (Allouche et al., 2006; Peirce, 1884); and, (4) Symmetric Extremal Dependence Index (hereafter SEDI) (Wunderlich et al., 2019). OAcc measures the model predicted accuracy using the rate of correct classifications (true positive + true negative) and ranges from 0 to 1; while P-kappa, TSS and SEDI range from -1 to +1, where values ≤ 0 suggest a performance equal or worse than random, and as close the values get to +1, the better the prediction (Allouche et al., 2006; Wunderlich et al., 2019).

For each species, we selected the two best-scored binary models based on the OAcc, P-kappa, TSS, and SEDI for each of the thresholds used (LPT, P10, and maxSSS), resulting in 24 models for each species, 144 in total.

Field validation sampling and acoustic identification

For the selection of the sampling points for field validation, we stacked the average potential distribution outputs of the six species to identify regions with higher predicted species richness and the highest suitability of species occurrence, but without historical records.

Considering the potential distribution of those species covered extensive areas, we focused our field validation on 129 randomly-selected sampling points along 1000 km from east to west and 1000 km from north to south, covering an area of 758,193 km^2, in the Northeastern part of Brazil.

Between March 2014 and January 2020, we employed passive acoustic monitoring to sample bat echolocation calls in the 129 sampling points (Figure 1; Table S3 in supplementary material), using a combination of SM2Bat+, SM3BAT, and SM4BAT-FS ultrasound recorders (Wildlife Acoustics Inc., Massachusetts, USA). Since the highest frequency used by the studied species is ~60 kHz (*Noctilio leporinus*) (Arias-Aguilar et al., 2018), we configured the bat detectors with a minimum sampling rate of 384 kHz, enough to detect and record our focal species without distortions (e.g., aliasing). Each sampling point was acoustically monitored for at least two nights, from 30 minutes before sunset until 30 minutes after sunrise. Since bat activity and the reception of the calls can be affected by weather and local conditions, we sampled only during nights with temperature > 15ºC, without strong winds (< 5 m/s) or rain (Adams et al., 2012; Parsons and Szewczak, 2009; Ratcliffe and Jakobsen, 2018). We set the microphones at 45º to the ground, avoiding highly cluttered areas (Adams et al., 2012; Parsons and Szewczak, 2009; Ratcliffe and Jakobsen, 2018).

We used Raven Pro 1.5 (The Cornell Lab of Ornithology 2014) for the acoustic analysis performed in the laboratory. We configured the spectrograms to DFT equals 1024, 96% overlap, window length to 1 ms, using Hamming windows. We only analyzed sequences containing a minimum of three search calls with a good signal-to-noise ratio (> 15 dB) (Jung et al., 2014; Lloyd et al., 2006). We followed previously published studies on neotropical bat echolocation for species identification (e.g., Arias-Aguilar et al., 2018; Barataud et al., 2013; Hintze et al., 2020; Jung et al., 2007; Jung et al., 2014; López-Baucells et al., 2016). We did not use feeding-buzzes (and calls immediately before and after) or social-calls for identification purposes. Although the chosen species have different natural histories, all are considered as common in the monitored region and can be easily detected and identified by acoustics. All fieldwork procedures complied with the American Society of Mammalogists´ guidelines for the use of wild mammals in research and education (Sikes et al., 2016) and were previously approved by the Brazilian Ministry of the Environment (SISBIO n.º 59743-1).

Models' field validation

We evaluated the 144 selected binary models for the six focal species against the results from the acoustic monitoring performed in the field. We used a confusion matrix to compare the accuracy of the binary maps, where the observed presence and absence cases from the acoustic monitoring were compared against the predicted presence and absence of the models. This procedure allowed us to quantify true positives, true negatives, false negatives (omission errors, type I errors), and false positives (commission errors, type II errors).

We used six metrics for the model performance evaluation: (1) Accuracy, to quantify how often the model is correct in the overall prediction; (2) Precision, to quantify how often is the model correct when it predicts the occurrence of the species; (3) Sensitivity (true positive rate, or recall), to quantify the ability of the model to predict species occurrence; (4) Specificity (or true negative rate), which quantifies the ability of the model to predict species absence; (5) geometric mean of sensitivity and specificity (g-mean), is a performance metric for imbalanced classifications, high g-mean indicates a right balance between sensitivity and specificity. If the species presence classification performance is weak, the g-mean will be low even with an excellent species absence classification performance (Branco et al., 2016); and (6) harmonic mean of precision and sensitivity (f-score), gives the same importance to precision and sensitivity, i.e., high F-score indicates excellent model performance on the minority class (Branco et al., 2016; Daskalaki et al., 2006). The commission error rate is inversely proportional to sensitivity (= 1 - sensitivity), whereas the omission error rate is inversely proportional to specificity (= 1 - specificity).

To assess the overall performance of the theoretical evaluation metrics (OAcc, P-kappa, TSS, and SEDI), we performed a Spearman rank-order correlation between those scores and the post-validation performance metrics scores (accuracy, precision, sensitivity, specificity, g-mean, and f-score). To test differences in the prediction performances (using the post-validation performance metrics scores) between the thresholds used (LPT, maxSSS, and P10), we employed the Kruskal-Wallis test with Mann-Whitney pairwise *post hoc* test. The thresholds were tested with both all species together and separately for each one.

Results

SDM's and acoustic field validation

The acoustics sampling performed in this study resulted in more than 1.5 TB of raw sound files, where more than 300,000 sound files contained bat calls. We identified

echolocation calls of *Noctilio leporinus* in 38 points (29,4%), of *Promops centralis* in 23 (17,8%), *Promops nasutus* in 44 (34,1%), *Pteronotus gymnonotus* in 53 (41,1%), *Pteronotus personatus* in 21 (16,3%), and *Saccopteryx leptura* in 24 of the 129 sampled points (18,6%) (Table S3, in supplementary material).

After field validation, the performance scores varied considerably between the 144 binary models: accuracy varied from 0.16 to 0.81, precision varied between 0.09 and 0.59, sensitivity varied from 0.17 to 1, specificity from 0 to 0.86, g-mean from 0 to 0.75 and f-score from 0.12 to 0.60 (Table S4, in supplementary material). We registered the highest accuracy score (0.81) in a maxSSS thresholded map of *Saccopteryx leptura*, the highest precision score (0.59) in a maxSSS thresholded map of *Noctilio leporinus*, and the highest sensitivity score (= 1) in LPT thresholded maps of four species (*Noctilio leporinus*, *Pteronotus gymnonotus*, *Promops nasutus*, and *Pteronotus personatus*) (Table S4 and Maps S5, in supplementary material). The highest specificity score (0.86) was recorded in maxSSS thresholded maps of two species (*Noctilio leporinus* and *Saccopteryx leptura*), the highest g-mean score (0.75) in a P10 thresholded map of *Saccopteryx leptura*, and the highest f-score score (0.60) in a maxSSS thresholded maps of *Pteronotus gymononotus* (Table S4 and Maps S5, in supplementary material).

Model evaluation vs. field validation

All theoretical model evaluation metrics analysed exhibited a significant monotonic positive correlation with accuracy and specificity (Table I). However, the evaluation metrics exhibited an overall significant negative correlation with sensitivity (Table I). We also found very weak monotonic correlations between the evaluation metrics and precision (Table I). Although negative, the correlation between the theoretical evaluation metrics and f-score was not significant (Table I). Only TSS and overall accuracy exhibited significant monotonic positive correlations with g-mean (Table I).

Thresholds vs. validation

Based on the output maps of all species together, LPT threshold maps exhibited significantly the lowest overall average accuracy, precision, specificity, and g-mean scores of the three thresholds tested (Table II). While P10 exhibited a significantly higher average f-score than maxSSS, we found no significant differences between the f-score results between P10 and

LPT, and between maxSSS and LPT (Table II). P10 obtained overall average sensitivity and specificity scores between the other two thresholds (Table II). LPT maps scored the highest average sensitivity but also presented low average specificity scores. Note that while LPT's sensitivity scores near one, its specificity scores are also near zero (Table II). We found this same LPT and maxSSS behavior when we analyzed all species separately (Table II). One LPT map for *N. leporinus* (Figure 2) exemplifies this odd behavior, where omission errors are minimal, but commission errors are maximum (sensitivity = 1, specificity = 0, and g-mean = 0). Even the LPT map with the highest g-mean score (*P. nasutus*, Figure 3) represented a commission error rate of ~81% and an omission error rate of ~7% (sensitivity = 0.93, specificity = 0.19, and g-mean = 0.42). While maxSSS scored the highest overall average accuracy and specificity, its maps also exhibited the lowest average sensitivity scores (Table II). Nevertheless, in contrast to LPT, maxSSS' sensitivity and specificity average scores are similar, thus presenting higher g-mean scores than LPT (Table II). This was clear when the maxSSS with the highest g-mean (Figure 4), represented an omission error of ~29% and a commission error of ~25% (sensitivity = 0.71, specificity = 0.75, and g-mean = 0.73). All thresholds significantly presented different specificity and specificity scores, but we found no significant differences between the overall accuracy, precision, and g-mean scores of maxSSS and P10 threshold maps (Table II).

Analyzing species by species, LPT maps once again significantly exhibited the highest average sensitivity scores. However, it also showed significantly the lowest average accuracy, specificity, and g-mean scores for all six species studied (Table II). In the cases of *N. leporinus* and *S. leptura*, LPT maps also significantly exhibited the lowest average precision and f-score, and the lowest average precision scores for *P. nasutus* and *P. personatus* among the three thresholds tested (Table II). Thresholded maps based on maxSSS significantly exhibited the lowest average sensitivity scores among the three thresholds tested for *N. leporinus* and *P. gymnonotus* (Table II). Still, maxSSS also showed significantly the highest average specificity and g-mean scores for the same species. The maxSSS maps also presented the highest average accuracy for *N. leporinus* and *P. personatus*, and the highest average g-mean for *S. leptura* among the three thresholds tested (Table II). *Saccopteryx leptura*'s P10 maps significantly exhibited the highest average g-mean of the three thresholds tested (Table II). We found no differences between the performance scores based on maxSSS and P10 in all *P. centralis* and *P. nasutus* maps. We also found no differences between the three thresholds in precision and f-score for *P. centralis* and *P. personatus*, f-score of *P. nasutus*, and precision scores of *P. gymnonotus* maps (see Maps S5 in supplementary material for the best performing binary maps for the six species).

Discussion

This study evaluated and validated species binary distribution models using a combination of acoustic data collected in the field and simple performance metrics. Bioacoustics proved to be a very effective method for the *in situ* validation of SDM for six neotropical bat species in a large and poorly-sampled area in Brazil. For species with conspicuous vocalizations – like bats – this method has the potential to better refine SDMs in large and under-sampled regions, requiring relatively low sampling effort. This is quite useful in tropical areas, usually bat species-rich, but frequently understudied (Bernard et al., 2011;

316 Delgado-Jaramillo et al., 2020). However, we also demonstrated that a careful decision on the
317 modelling parameters and thresholds used is pivotal since, depending on the combination, they
318 can produce very different outputs. Our observations highlight the importance and necessity of
319 *in situ* validation of SDM' outputs.
320 Field validation of SDM is unusual (e.g., Giné and Faria, 2018; Hertzog et al., 2014),
321 and very rare for bats (e.g., Greaves et al., 2006; Razgour et al., 2016; Rebelo and Jones, 2010).
322 Still, we empirically demonstrated that independent field surveys are the best approach to
323 corroborate the predictions made by modelling, especially in subsampled regions with high
324 biodiversity like the Neotropics. We are aware that *in situ* validation of SDM is not always
325 possible, as that will depend on the focal species, its extension of occurrence, survey methods,
326 and the type and accessibility of the potential area modelled. However, field validation of SDM
327 – in smaller or focally-selected parts of the predicted distribution, or randomly-selected regions
328 – should be imperative. This is especially important in a conservation-focused scenario dealing
329 with such high habitat changes due to anthropogenic causes. Modelling species distributions
330 without proper *in situ* validation may result in inaccurate outputs, compromising the
331 implementation of better conservation policies or species management plans, for example
332 (Guisan et al., 2013; Razgour et al., 2016; Visconti et al., 2013). This can be particularly serious
333 in the case of models with actual low sensibility (high omission errors).
334
335 ***Theoretical model evaluation metrics and thresholds vs. validation***
336
337 We found that all theoretical model evaluation metrics studied here correlated positively
338 with accuracy. However, caution is necessary, since the most detected species (*P. gymnonotus*)
339 was recorded in only 41% of the sampled points (meaning an unbalanced class data, i.e., in this
340 case absences are higher than presences). In situations like this, any random model predicting
341 more absences than presences would be benefited by an evaluation metric that does not take
342 into account results by chance – this is the case of accuracy (Ferri et al., 2009). Therefore,
343 accuracy should not be used when data used to train and/or test the models is unbalanced. Here,
344 we empirically demonstrated that sensitivity-specificity and precision-sensitivity metrics, as g-
345 mean and f-score, are better performance measures for the SDMs evaluation than accuracy
346 (Branco et al., 2016; Ferri et al., 2009). For example, the *Pteronotus gymnonotus'* distribution
347 output with the highest accuracy also had the third-highest omission rate. In opposition, the
348 model with the highest g-mean and f-score also presented low omission scores. These results

were not a threshold-related since it occurred in two different maxSSS models, evidencing the unbalanced nature of our SDM outputs and the problem of using accuracy to measure model performance. Considering the majority of SDM are based on unbalanced data, instead of accuracy, the use of sensitivity-specificity and precision-sensitivity metrics should be mandatory to test the models as they are not affected by unbalanced class data sets (Branco et al., 2016; Ferri et al., 2009).

Surprisingly, we also found that all theoretical threshold-dependent evaluation metrics tested here exhibited an overall significant negative correlation with sensitivity and a significant positive correlation with specificity. This means that models with higher evaluation scores predicted better locations with actual species absence than species presence. West et al. (2016) reported similar findings after field validation of MaxEnt's invasive cheatgrass species models. This is probably because bioclimatic variables' values are more homogeneous in species presence locations than in absence. Nevertheless, this 'issue' will be less a concern if the modeler's goal is to balance actual presences and absences, as we found positive correlations between evaluation metrics and g-mean or f-score.

We found that threshold performances varied largely. Despite having almost no omission errors, the LPT models exhibited higher commission error rates and lower accuracy, g-mean and precision scores. Thus, at least for the six widespread neotropical bat species studied here, we were able to empirically confirm Liu et al. (2013)’s findings: maps based on the LPT threshold are unsuitable for species distribution modelling. In our study, LPT-thresholded maps of the two species with the most historical records (*N. leporinus* and *S. leptura*) also had a worse performance than the other four LPT-modeled scores. Although widespread and common, *N. leporinus* is a piscivorous bat species, strongly related to water bodies, and *S. leptura* is a forest-dwelling species that forage next to edges (Hood and Jones, 1984; Yancey et al., 1998). Thus, these two species as less generalist than the other four we analyzed and the use of a less conservative threshold can be detrimental in those cases. Therefore, knowledge of the species' natural history and the use of land cover data in the models might be fundamental for best SDM practices and the better output results (Wilson et al., 2013).

But contrary to Liu et al. (2013), we also found that some maxSSS maps with high accuracy scores were highly overfitted (exhibiting low sensitivity/high omission rates), sometimes excluding historical locations for some species. Nevertheless, we also found that some maxSSS and P10 thresholded maps performed reasonably well, exhibiting balanced results between sensitivity and specificity (displaying high g-mean scores). In general, even

showing higher omission errors than LPT, P10 thresholded models performed best in predicting actual species occurrences, while maxSSS models performed best in predicting where we did not record the species in the field. Several authors agree that threshold selection (as other parameters) has a high impact on the binary map (presence/absence) outputs and the models' predictive capacity (e.g., Benito et al., 2013; Fourcade et al., 2018). Several thresholds have been proposed and evaluated; however, most of those evaluations are based on theoretical evaluation metrics without independent field validation data. After using *in situ* validation in our study, we are cautionary about some studies still proposing to model species distribution using a single threshold. Without independent field validation of the results, we found that using an arbitrary threshold for modelling can be a precarious approach with many possible outcomes, even if getting good evaluation scores. Undoubtedly, validating the models using part of the historical occurrence points is faster and less laborious than using independent data collected in the field. However, one cannot guarantee if the species are still present in historical points in databases such as GBIF (Beck et al., 2014). Hence, independent field data are the safest way to validate the species´ presence in the modelled region.

Authors' contributions

Frederico Hintze: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Project administration; **Ricardo B. Machado:** Conceptualization, Methodology, Formal analysis, Data curation, Writing - Review & Editing; **Enrico Bernard:** Conceptualization, Resources, Writing - Original Draft, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

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415

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578

Tables

Table I – Spearman rank-order correlation results of the theoretical evaluation metrics and the post-validation performance metric scores for the distribution modelling of six neotropical bats based on bioacoustics field validation in northeastern Brazil (rs = Spearman correlation coefficient; n = number of pairwise comparisons).

Theoretical evaluation metric	Validation performance metric	rs	n	p (w/ Bonferroni correction)
TSS	**Accuracy**	0.36	144	<0.001
	Precision	0.08	144	1
	Sensitivity	-0.54	144	<0.001
	Specificity	0.47	144	<0.001
	G-mean	0.43	144	<0.001
	F-score	-0.09	144	1
OAcc	**Accuracy**	0.56	144	<0.001
	Precision	0.15	144	1
	Sensitivity	-0.86	144	<0.001
	Specificity	0.74	144	<0.001
	G-mean	0.57	144	<0.001
	F-score	-0.19	144	0.91
P-kappa	**Accuracy**	0.27	144	<0.05
	Precision	0.06	144	1
	Sensitivity	-0.37	144	<0.001
	Specificity	0.35	144	<0.001
	G-mean	0.38	144	<0.001
	F-score	-0.02	144	1
SEDI	**Accuracy**	0.26	97	0.31
	Precision	0.00	97	1.00
	Sensitivity	-0.38	97	<0.05
	Specificity	0.35	97	<0.05
	G-mean	0.29	97	0.18
	F-score	-0.18	97	1

Fonte: Frederico Hintze (autor).

585 **Table II –** Average ± standard deviation scores of accuracy, precision, sensitivity, specificity, g-mean, and f-score
586 of the three thresholds tested for SDMs of six neotropical bat species after a field validation in northeastern Brazil
587 using bioacoustics. Kruskal-Wallis test results for the comparisons between the thresholds' performance scores is
588 also presented. The Mann-Whitney pairwise post hoc test results are presented by letters next to average ± standard
589 deviation (different letters indicate significant differences between groups, $p < 0.05$).
590

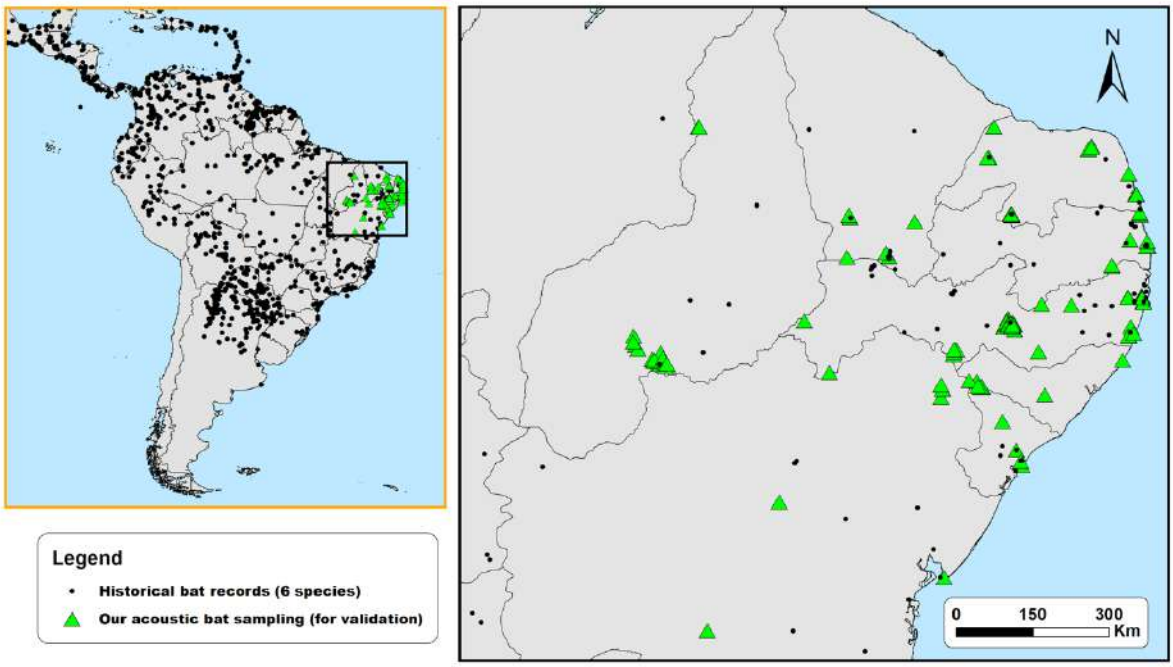
Species	Validation performance metric	Threshold			Kruskal-Wallis test results	
		LPT	maxSSS	P10	χ^2	p
All species	Accuracy	0.31 ± 0.09^{b}	0.53 ± 0.15^{a}	0.49 ± 0.14^{a}	62.28	<0.001
	Precision	0.28 ± 0.11^{b}	0.33 ± 0.12^{a}	0.33 ± 0.11^{a}	9.629	<0.05
	Sensitivity	0.95 ± 0.08^{a}	0.58 ± 0.21^{c}	0.73 ± 0.16^{b}	90.83	<0.001
	Specificity	0.05 ± 0.05^{c}	0.51 ± 0.26^{a}	0.39 ± 0.23^{b}	92.18	<0.001
	G-mean	0.16 ± 0.14^{b}	0.49 ± 0.14^{a}	0.49 ± 0.14^{a}	83.84	<0.001
	F-score	$0.43 \pm 0.13^{a,b}$	0.40 ± 0.13^{b}	0.44 ± 0.12^{a}	6.244	<0.05
Noctilio leporinus	Accuracy	0.3 ± 0.02^{c}	0.67 ± 0.05^{a}	0.57 ± 0.02^{b}	20.48	<0.001
	Precision	0.3 ± 0^{c}	0.47 ± 0.07^{a}	0.38 ± 0.02^{b}	19.86	<0.001
	Sensitivity	1 ± 0.01^{a}	0.59 ± 0.08^{c}	0.74 ± 0.08^{b}	19.42	<0.001
	Specificity	0.01 ± 0.03^{c}	0.71 ± 0.09^{a}	0.5 ± 0.03^{b}	20.48	<0.001
	G-mean	0.05 ± 0.1^{c}	0.64 ± 0.02^{a}	0.61 ± 0.02^{b}	18.36	<0.001
	F-score	0.46 ± 0^{b}	0.52 ± 0.02^{a}	0.5 ± 0.03^{a}	15.66	<0.001
Promops centralis	Accuracy	0.28 ± 0.01^{b}	0.44 ± 0.14^{a}	0.34 ± 0.02^{a}	16.27	<0.001
	Precision	0.19 ± 0^{a}	0.2 ± 0.04^{a}	0.19 ± 0.01^{a}	0.6563	0.7164
	Sensitivity	0.95 ± 0.03^{a}	0.67 ± 0.17^{b}	0.83 ± 0.05^{b}	16.34	<0.001
	Specificity	0.13 ± 0.02^{b}	0.38 ± 0.21^{a}	0.23 ± 0.03^{a}	16.41	<0.001
	G-mean	0.36 ± 0.02^{b}	0.47 ± 0.06^{a}	0.44 ± 0.02^{a}	15.81	<0.001
	F-score	0.32 ± 0.01^{a}	0.3 ± 0.02^{a}	0.31 ± 0.01^{a}	4.884	0.0835
Promops nasutus	Accuracy	0.38 ± 0.03^{b}	0.58 ± 0.02^{a}	0.55 ± 0.03^{a}	17.67	<0.001
	Precision	0.35 ± 0.01^{b}	0.38 ± 0.05^{a}	0.41 ± 0.02^{a}	9.251	<0.05
	Sensitivity	0.97 ± 0.04^{a}	0.42 ± 0.25^{b}	0.74 ± 0.07^{b}	17.78	<0.001
	Specificity	0.08 ± 0.05^{b}	0.67 ± 0.15^{a}	0.45 ± 0.07^{a}	18	<0.001
	G-mean	0.26 ± 0.08^{b}	0.49 ± 0.1^{a}	0.57 ± 0.04^{a}	15.31	<0.001
	F-score	0.52 ± 0.01^{a}	0.38 ± 0.14^{a}	0.53 ± 0.02^{a}	5.071	0.0787
Pteronotus gymnonotus	Accuracy	0.42 ± 0.01^{b}	0.48 ± 0.05^{a}	0.44 ± 0.02^{a}	12.31	<0.05
	Precision	0.41 ± 0^{a}	0.37 ± 0.07^{a}	0.42 ± 0.01^{a}	1.046	0.5895
	Sensitivity	1 ± 0^{a}	0.47 ± 0.34^{c}	0.91 ± 0.03^{b}	19.42	<0.001
	Specificity	0.01 ± 0.02^{c}	0.49 ± 0.28^{a}	0.11 ± 0.02^{b}	19.57	<0.001

	G-mean	0.06 ± 0.09^{c}	0.39 ± 0.06^{a}	0.31 ± 0.03^{b}	18.87	<0.001
	F-score	0.58 ± 0^{a}	0.38 ± 0.16^{b}	0.57 ± 0.01^{b}	10.28	<0.05
Pteronotus personatus	Accuracy	0.19 ± 0.02^{c}	0.42 ± 0.11^{a}	0.32 ± 0.04^{b}	18.12	<0.001
	Precision	0.15 ± 0.01^{a}	0.15 ± 0.03^{a}	0.15 ± 0.01^{a}	2.205	0.3301
	Sensitivity	0.82 ± 0.11^{a}	0.55 ± 0.2^{b}	0.7 ± 0.06^{b}	12.88	<0.001
	Specificity	0.07 ± 0.04^{a}	0.4 ± 0.17^{b}	0.25 ± 0.06^{b}	17.78	<0.001
	G-mean	0.22 ± 0.08^{b}	0.43 ± 0.07^{a}	0.41 ± 0.04^{a}	16.64	<0.001
	F-score	0.25 ± 0.02^{a}	0.23 ± 0.05^{a}	0.25 ± 0.01^{a}	0.9237	0.6293
Saccopteryx leptura	Accuracy	0.2 ± 0.02^{b}	0.69 ± 0.17^{a}	0.74 ± 0.01^{a}	15.38	<0.001
	Precision	0.17 ± 0.01^{b}	0.38 ± 0.1^{a}	0.4 ± 0.01^{a}	14.03	<0.001
	Sensitivity	0.89 ± 0.03^{a}	0.68 ± 0.07^{b}	0.73 ± 0.02^{b}	16.34	<0.001
	Specificity	0.04 ± 0.03^{b}	0.69 ± 0.22^{a}	0.75 ± 0.01^{a}	15.36	<0.001
	G-mean	0.16 ± 0.09^{c}	0.67 ± 0.12^{b}	0.74 ± 0.01^{a}	18.36	<0.001
	F-score	0.29 ± 0.01^{b}	0.47 ± 0.08^{a}	0.51 ± 0.02^{a}	13.03	<0.05

Fonte: Frederico Hintze (autor).

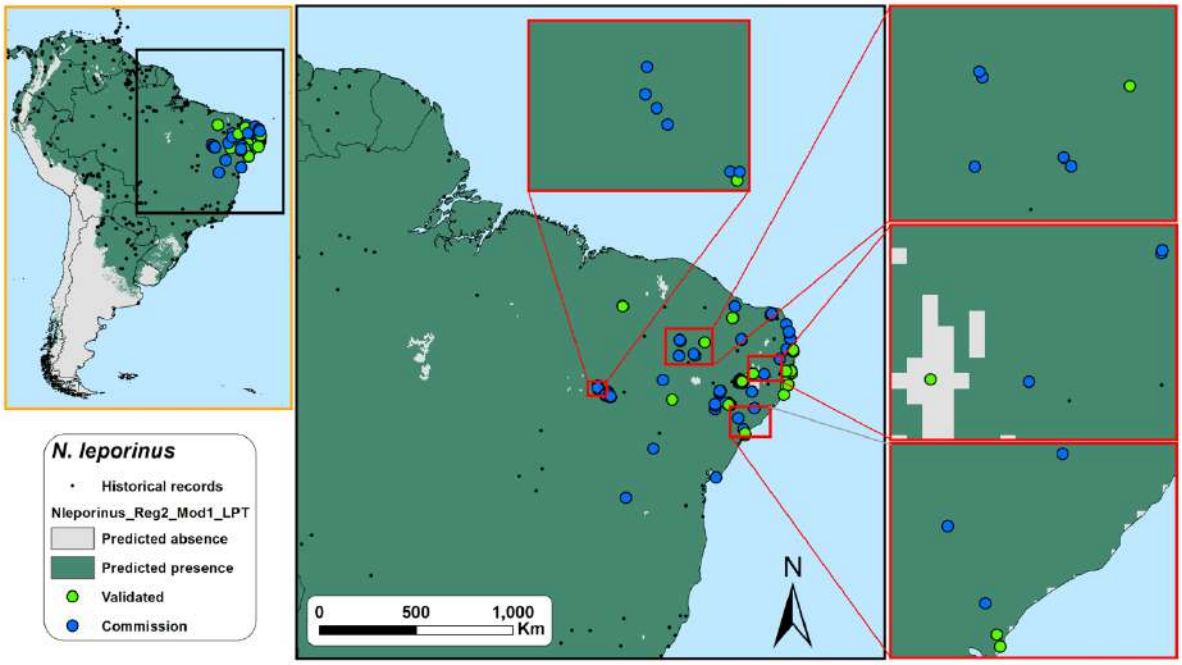
Figures

Figure 1. Historical distribution records assembled from the literature review and the 129 acoustic sampling points used for the validation of SDM of six neotropical bat species (*Noctilio leporinus*, *Promops centralis*, *Promops nasutus*, *Pteronutus gymnonotus*, *Pteronotus personatus,* and *Saccopteryx leptura*).



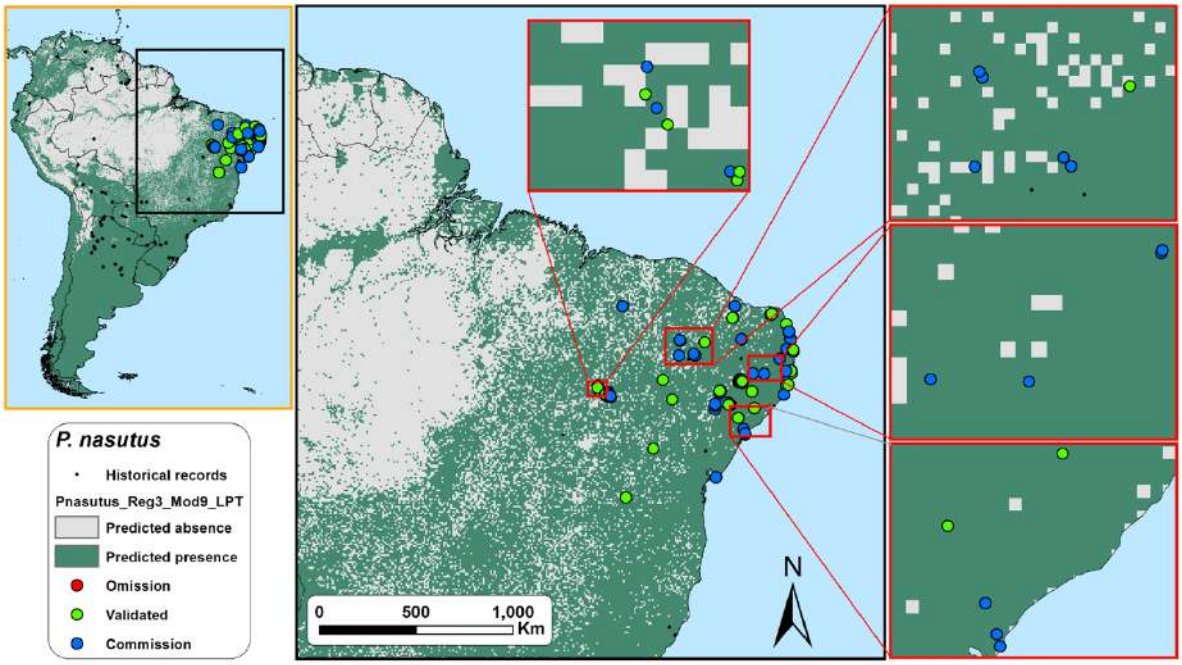
Fonte: Frederico Hintze (autor).

Figure 2. Field validation results for the LPT binary map with the highest accuracy score (= 1) for *Noctilio leporinus* in northeastern Brazil. Omission errors are minimal but commission errors are maximum (sensitivity = 1, specificity = 0, and g-mean = 0). 'Omission' points represent locations where the model did not predict the species occurrence, but the species was detected during the acoustics monitoring; 'Validated' points represent locations where the model predict the species occurrence and the species was detected during the acoustics monitoring or locations where the model did not predict the species occurrence, and the species was detected during the acoustics monitoring; 'commission' points represent locations where the model predict the species occurrence but the species was not detected during the acoustics monitoring.



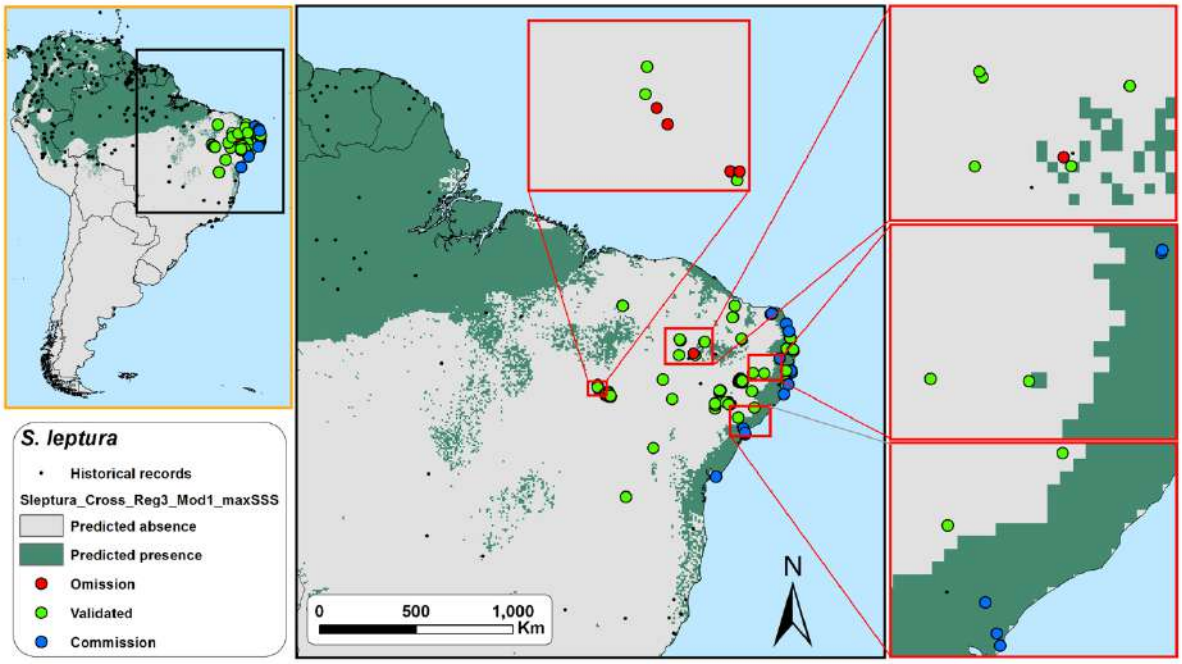
Fonte: Frederico Hintze (autor).

Figure 3. Field validation results for the LPT binary map with the highest g-mean score (= 0.42) for *Promops nasutus* in northeastern Brazil. Omission errors are low but commission errors are very high (sensitivity = 0.93, specificity = 0.19). See Figure 2 caption for the explanation on omission, validation and commission points.



Fonte: Frederico Hintze (autor).

Figure 4. Field validation results for the maxSSS binary map with the highest g-mean score (= 0.73) for *Saccopteryx leptura* in northeastern Brazil. Omission errors and commission errors are balanced (sensitivity = 0.71, specificity = 0.75). See Figure 2 caption for the explanation on omission, validation and commission points.



Fonte: Frederico Hintze (autor).

Supplementary material

Table S1. Location of the 129 acoustic sampling points used for the validation of SDM's of six neotropical bat species in northeastern Brazil.

Table S2. Presence/absence obtained in the acoustic monitoring of 129 acoustic sampling points used for the validation of SDM's of six neotropical bat species in northeastern Brazil.

Table S3. Theoretical model evaluation scores, validation confusion matrix, and performance scores of the 144 binary distribution models of six neotropical bat species validated with field acoustics sampling in northeastern Brazil.

Maps S4. Field validation results for the binary maps with the highest accuracy, precision, sensitivity, specificity, gmean, and f-score scores for the six studied species in northeastern Brazil.

636 **Table S1**

Point code	State	Longitude	Latitude
AL05	Alagoas	-37.768914	-9.632000
AL06	Alagoas	-37.862792	-9.514665
AL09	Alagoas	-36.664135	-9.764121
AL10	Alagoas	-37.771937	-9.616187
AL12	Alagoas	-38.000018	-9.511357
AL13	Alagoas	-35.288368	-9.149152
BA01	Bahia	-38.466833	-9.664500
BA06	Bahia	-41.353222	-11.647884
BA07	Bahia	-42.623600	-13.920304
BA08	Bahia	-38.438775	-12.983319
BA09	Bahia	-38.492167	-9.810167
BA10	Bahia	-38.470167	-9.664167
BA11	Bahia	-38.491333	-9.581500
CE01	Ceará	-39.412750	-7.333050
CE02	Ceará	-39.470920	-7.262414
CE03	Ceará	-40.099220	-6.643240
CE04	Ceará	-40.122150	-6.599320
CE08	Ceará	-38.958460	-6.711420
CE09	Ceará	-40.157800	-7.335310
CE11	Ceará	-38.958070	-6.713060
PB01	Paraíba	-34.968523	-6.591269
PB04	Paraíba	-34.986479	-6.561144
PB05	Paraíba	-34.985715	-6.544311
PB07	Paraíba	-35.159644	-7.037235
PB08	Paraíba	-34.843553	-7.138299
PB09	Paraíba	-34.860729	-7.136494
PB10	Paraíba	-34.856539	-7.063408
PB11	Paraíba	-34.856651	-7.061206
PE01	Pernambuco	-34.950029	-8.047590
PE02	Pernambuco	-34.946591	-8.050039
PE04	Pernambuco	-34.949200	-8.011520
PE07	Pernambuco	-36.720278	-8.168611
PE08	Pernambuco	-35.484444	-7.492500
PE09	Pernambuco	-37.196997	-8.615513
PE10	Pernambuco	-36.775767	-9.004091
PE11	Pernambuco	-37.394600	-8.572290
PE12	Pernambuco	-37.389500	-8.570820
PE13	Pernambuco	-40.469440	-9.374355

PE14	Pernambuco	-40.908716	-8.456792
PE15	Pernambuco	-37.382990	-8.570400
PE16	Pernambuco	-35.176375	-8.730576
PE19	Pernambuco	-35.143484	-8.558122
PE20	Pernambuco	-34.957204	-8.037036
PE21	Pernambuco	-34.945367	-8.042630
PE22	Pernambuco	-34.927463	-8.115085
PE23	Pernambuco	-34.919447	-8.139625
PE24	Pernambuco	-36.193063	-8.181557
PE25	Pernambuco	-35.196017	-8.041218
PE26	Pernambuco	-35.194651	-8.039689
PE27	Pernambuco	-37.279118	-8.487088
PE28	Pernambuco	-37.248488	-8.580039
PE29	Pernambuco	-37.196837	-8.531343
PE30	Pernambuco	-37.355059	-8.507242
PE31	Pernambuco	-37.299343	-8.449588
PE32	Pernambuco	-37.230109	-8.535398
PE33	Pernambuco	-37.224777	-8.516704
PE34	Pernambuco	-37.304636	-8.427781
PE35	Pernambuco	-37.317409	-8.413305
PE36	Pernambuco	-37.325939	-8.465797
PE37	Pernambuco	-37.241889	-8.567333
PE38	Pernambuco	-37.322206	-8.485380
PE39	Pernambuco	-37.296306	-8.520858
PE40	Pernambuco	-37.342813	-8.483051
PE41	Pernambuco	-37.311786	-8.517770
PE42	Pernambuco	-37.236917	-8.479111
PE43	Pernambuco	-37.234629	-8.494245
PE44	Pernambuco	-37.276981	-8.511267
PE45	Pernambuco	-37.309575	-8.537189
PE46	Pernambuco	-37.247456	-8.570823
PE47	Pernambuco	-37.244943	-8.516634
PE48	Pernambuco	-37.234833	-8.534472
PE49	Pernambuco	-35.186593	-8.723416
PE50	Pernambuco	-35.088720	-8.683133
PE51	Pernambuco	-34.953021	-8.052687
PE54	Pernambuco	-35.479167	-7.477778
PE55	Pernambuco	-38.247743	-8.963358
PE56	Pernambuco	-38.274771	-9.052005
PE57	Pernambuco	-38.265107	-9.021227
PE58	Pernambuco	-38.217852	-8.979184

PE59	Pernambuco	-38.272760	-8.967920
PE61	Pernambuco	-34.949068	-8.053206
PE65	Pernambuco	-35.196774	-8.045321
PI01	Piauí	-43.318453	-9.259312
PI02	Piauí	-43.370155	-9.254109
PI03	Piauí	-43.490148	-9.219221
PI04	Piauí	-43.463348	-9.226200
PI05	Piauí	-43.427874	-9.048640
PI06	Piauí	-43.888544	-8.888955
PI07	Piauí	-43.570771	-9.173204
PI08	Piauí	-43.443955	-9.022384
PI09	Piauí	-43.844594	-8.953189
PI10	Piauí	-43.360817	-9.190529
PI11	Piauí	-43.926115	-8.726366
PI12	Piauí	-43.932104	-8.834702
PI13	Piauí	-43.597790	-9.138420
PI14	Piauí	-43.561070	-9.140210
PI15	Piauí	-43.402909	-9.114661
PI16	Piauí	-43.335854	-9.213573
PI17	Piauí	-42.780195	-5.036261
PI18	Piauí	-42.769370	-5.041710
RN01	Rio Grande do Norte	-35.059700	-6.228400
RN04	Rio Grande do Norte	-35.893660	-5.443390
RN06	Rio Grande do Norte	-37.560150	-5.036850
RN10	Rio Grande do Norte	-35.836936	-5.377448
RN11	Rio Grande do Norte	-37.248427	-6.597874
RN12	Rio Grande do Norte	-37.652460	-5.573010
RN13	Rio Grande do Norte	-37.674150	-5.579020
RN14	Rio Grande do Norte	-35.895750	-5.443270
RN15	Rio Grande do Norte	-35.894773	-5.431502
RN16	Rio Grande do Norte	-35.842450	-5.397869
RN17	Rio Grande do Norte	-35.179726	-5.865478
RN18	Rio Grande do Norte	-35.060500	-6.228200
RN19	Rio Grande do Norte	-35.044400	-6.229800
RN20	Rio Grande do Norte	-35.043000	-6.233900
RN21	Rio Grande do Norte	-35.049816	-6.229111
RN22	Rio Grande do Norte	-37.248667	-6.594183
RN23	Rio Grande do Norte	-37.245000	-6.595333
RN24	Rio Grande do Norte	-37.267167	-6.574833
RN25	Rio Grande do Norte	-37.255567	-6.579375
RN26	Rio Grande do Norte	-37.255988	-6.581566

RN27	Rio Grande do Norte	-37.270647	-6.572836
RN28	Rio Grande do Norte	-37.248667	-6.577500
RN29	Rio Grande do Norte	-37.257505	-6.579240
SE01	Sergipe	-37.409946	-10.232622
SE02	Sergipe	-37.071004	-11.014655
SE03	Sergipe	-37.799900	-9.627592
SE05	Sergipe	-37.165560	-10.732830
SE06	Sergipe	-37.846063	-9.606472
SE07	Sergipe	-37.091966	-10.935127

Fonte: Frederico Hintze (autor).

639 **Table S2**

Point code	Longitude	Latitude	*Noctilio leporinus*	*Promops centralis*	*Promops nasutus*	*Pteronotus gymnonotus*	*Pteronotus personatus*	*Saccopteryx leptura*
AL05	-37.768914	-9.632000	1	0	0	0	1	0
AL06	-37.862792	-9.514665	1	1	1	1	1	0
AL09	-36.664135	-9.764121	0	1	1	0	0	0
AL10	-37.771937	-9.616187	1	0	0	1	1	0
AL12	-38.000018	-9.511357	0	0	0	0	0	0
AL13	-35.288368	-9.149152	1	1	0	0	0	0
BA01	-38.466833	-9.664500	0	0	1	1	0	0
BA06	-41.353222	-11.647884	0	0	1	0	0	0
BA07	-42.623600	-13.920304	0	0	1	0	0	0
BA08	-38.438775	-12.983319	0	0	0	0	0	0
BA09	-38.492167	-9.810167	0	0	0	0	0	0
BA10	-38.470167	-9.664167	0	0	0	1	0	0
BA11	-38.491333	-9.581500	0	0	0	0	0	0
CE01	-39.412750	-7.333050	0	0	0	1	0	1
CE02	-39.470920	-7.262414	0	0	0	0	0	1
CE03	-40.099220	-6.643240	0	0	0	1	1	0
CE04	-40.122150	-6.599320	0	0	0	1	0	0
CE08	-38.958460	-6.711420	1	0	0	1	1	0
CE09	-40.157800	-7.335310	0	0	0	1	0	0
CE11	-38.958070	-6.713060	1	0	0	1	1	0
PB01	-34.968523	-6.591269	0	0	0	0	0	0
PB04	-34.986479	-6.561144	1	1	1	1	0	1
PB05	-34.985715	-6.544311	0	0	0	1	0	1

PB07	-35.159644	-7.037235	0	0	0	0	0	1
PB08	-34.843553	-7.138299	0	0	0	0	0	1
PB09	-34.860729	-7.136494	1	1	0	0	0	1
PB10	-34.856539	-7.063408	1	1	0	0	0	1
PB11	-34.856651	-7.061206	1	1	1	0	0	1
PE01	-34.950029	-8.047590	1	0	0	0	0	0
PE02	-34.946591	-8.050039	1	0	0	0	0	1
PE04	-34.949200	-8.011520	0	1	0	0	0	1
PE07	-36.720278	-8.168611	0	0	0	0	0	0
PE08	-35.484444	-7.492500	0	0	0	0	0	0
PE09	-37.196997	-8.615513	1	0	1	1	1	0
PE10	-36.775767	-9.004091	0	0	1	0	0	0
PE11	-37.394600	-8.572290	0	0	0	1	1	0
PE12	-37.389500	-8.570820	0	0	0	1	1	0
PE13	-40.469440	-9.374355	1	1	1	0	0	0
PE14	-40.908716	-8.456792	0	0	1	1	0	0
PE15	-37.382990	-8.570400	0	0	0	0	0	0
PE16	-35.176375	-8.730576	0	0	0	0	0	1
PE19	-35.143484	-8.558122	1	0	0	0	0	1
PE20	-34.957204	-8.037036	0	0	0	0	0	0
PE21	-34.945367	-8.042630	0	0	0	0	0	0
PE22	-34.927463	-8.115085	0	1	1	0	0	0
PE23	-34.919447	-8.139625	1	1	1	0	0	0
PE24	-36.193063	-8.181557	0	0	0	0	0	0
PE25	-35.196017	-8.041218	0	0	0	0	0	1
PE26	-35.194651	-8.039689	0	0	0	0	0	1
PE27	-37.279118	-8.487088	0	0	0	1	1	0

PE28	-37.248488	-8.580039	0	0	1	1	0	0
PE29	-37.196837	-8.531343	0	0	0	1	0	0
PE30	-37.355059	-8.507242	0	0	1	0	0	0
PE31	-37.299343	-8.449588	0	0	0	1	0	0
PE32	-37.230109	-8.535398	0	0	1	1	0	0
PE33	-37.224777	-8.516704	0	0	1	1	0	0
PE34	-37.304636	-8.427781	0	0	0	0	0	0
PE35	-37.317409	-8.413305	0	0	0	1	0	0
PE36	-37.325939	-8.465797	0	1	1	0	0	0
PE37	-37.241889	-8.567333	0	0	1	1	0	0
PE38	-37.322206	-8.485380	0	0	1	1	0	0
PE39	-37.296306	-8.520858	0	0	0	1	0	0
PE40	-37.342813	-8.483051	0	0	1	1	0	0
PE41	-37.311786	-8.517770	0	0	1	1	0	0
PE42	-37.236917	-8.479111	0	0	0	1	0	0
PE43	-37.234629	-8.494245	0	0	0	1	0	0
PE44	-37.276981	-8.511267	0	0	0	1	0	0
PE45	-37.309575	-8.537189	0	0	0	0	0	0
PE46	-37.247456	-8.570823	0	0	1	1	0	0
PE47	-37.244943	-8.516634	0	0	1	0	0	0
PE48	-37.234833	-8.534472	1	0	1	1	0	0
PE49	-35.186593	-8.723416	1	1	0	1	0	1
PE50	-35.088720	-8.683133	1	1	1	0	0	0
PE51	-34.953021	-8.052687	1	0	0	0	0	0
PE54	-35.479167	-7.477778	0	0	0	0	0	0
PE55	-38.247743	-8.963358	0	0	1	0	0	0
PE56	-38.274771	-9.052005	1	0	1	1	1	0

PE57	-38.265107	-9.021227	0	0	0	0	0	0
PE58	-38.217852	-8.979184	0	0	1	0	0	0
PE59	-38.272760	-8.967920	0	1	1	1	0	0
PE61	-34.949068	-8.053206	1	0	1	0	0	0
PE65	-35.196774	-8.045321	1	1	0	1	0	1
PI01	-43.318453	-9.259312	0	0	0	0	1	0
PI02	-43.370155	-9.254109	0	0	0	0	0	0
PI03	-43.490148	-9.219221	1	0	0	1	1	1
PI04	-43.463348	-9.226200	1	0	1	1	1	1
PI05	-43.427874	-9.048640	0	0	0	0	0	0
PI06	-43.888544	-8.888955	0	0	0	0	0	1
PI07	-43.570771	-9.173204	1	0	1	1	1	0
PI08	-43.443955	-9.022384	0	0	0	0	0	0
PI09	-43.844594	-8.953189	0	0	0	0	0	1
PI10	-43.360817	-9.190529	0	0	1	0	1	0
PI11	-43.926115	-8.726366	0	1	0	1	0	0
PI12	-43.932104	-8.834702	0	0	0	0	0	0
PI13	-43.597790	-9.138420	0	0	0	1	0	1
PI14	-43.561070	-9.140210	0	0	1	0	0	1
PI15	-43.402909	-9.114661	0	0	0	0	0	0
PI16	-43.335854	-9.213573	0	0	0	0	0	0
PI17	-42.780195	-5.036261	1	0	0	0	0	0
PI18	-42.769370	-5.041710	1	0	0	0	0	0
RN01	-35.059700	-6.228400	1	0	0	0	0	1
RN04	-35.893660	-5.443390	0	0	0	1	0	0
RN06	-37.560150	-5.036850	0	1	0	1	0	0
RN10	-35.836936	-5.377448	0	0	1	0	0	0

RN11	-37.248427	-6.597874	0	0	0	1	0	0
RN12	-37.652460	-5.573010	0	0	1	1	1	0
RN13	-37.674150	-5.579020	1	1	1	1	0	0
RN14	-35.895750	-5.443270	0	0	0	1	0	0
RN15	-35.894773	-5.431502	0	0	0	1	0	0
RN16	-35.842450	-5.397869	0	1	0	1	0	0
RN17	-35.179726	-5.865478	0	0	0	0	0	0
RN18	-35.060500	-6.228200	1	0	0	0	0	0
RN19	-35.044400	-6.229800	0	0	0	0	0	0
RN20	-35.043000	-6.233900	1	0	1	0	0	0
RN21	-35.049816	-6.229111	0	0	0	0	0	0
RN22	-37.248667	-6.594183	0	0	0	0	0	0
RN23	-37.245000	-6.595333	0	0	1	0	0	0
RN24	-37.267167	-6.574833	0	1	0	0	0	0
RN25	-37.255567	-6.579375	1	0	0	0	0	0
RN26	-37.255988	-6.581566	1	1	1	0	0	0
RN27	-37.270647	-6.572836	0	0	0	0	0	0
RN28	-37.248667	-6.577500	0	0	0	0	0	0
RN29	-37.257505	-6.579240	0	0	0	0	0	0
SE01	-37.409946	-10.232622	0	0	1	0	0	0
SE02	-37.071004	-11.014655	1	0	0	0	0	0
SE03	-37.799900	-9.627592	1	0	1	1	1	0
SE05	-37.165560	-10.732830	0	0	0	1	1	0
SE06	-37.846063	-9.606472	1	0	1	1	1	0
SE07	-37.091966	-10.935127	1	1	0	0	1	0

Fonte: Frederico Hintze (autor).

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Species	Binary Model	Threshold used	Theoretical model evaluation scores				Validation (confusion matrix)					Models validation performance scores				
			TSS	OAcc	Kappa	SEDI	True Positives	False Positives	True Negatives	False Negatives	Accuracy	Precision	Sensitivity	Specificity	G-mean	F-score
Noctilio leporinus	Nleporinus_Cross_Reg1_Mod1_maxSSS	maxSSS	0.653	0.807	0.359	0.804	24	30	61	14	0.659	0.444	0.632	0.670	0.651	0.522
Noctilio leporinus	Nleporinus_Cross_Reg1_Mod1_P10	P10	0.571	0.630	0.348	0.760	27	46	45	11	0.558	0.370	0.711	0.495	0.593	0.486
Noctilio leporinus	Nleporinus_Cross_Reg1_Mod2_LPT	LPT	0.297	0.300	0.227		38	91	0	0	0.295	0.295	1.000	0.000	0.000	0.455
Noctilio leporinus	Nleporinus_Cross_Reg1_Mod2_P10	P10	0.484	0.658	0.290	0.645	25	42	49	13	0.574	0.373	0.658	0.538	0.595	0.476
Noctilio leporinus	Nleporinus_Cross_Reg1_Mod3_LPT	LPT	0.300	0.304	0.229		38	91	0	0	0.295	0.295	1.000	0.000	0.000	0.455
Noctilio leporinus	Nleporinus_Cross_Reg1_Mod4_maxSSS	maxSSS	0.706	0.785	0.393	0.853	24	29	62	14	0.667	0.453	0.632	0.681	0.656	0.527
Noctilio leporinus	Nleporinus_Cross_Reg1_Mod4_P10	P10	0.604	0.625	0.370	0.818	27	48	43	11	0.543	0.360	0.711	0.473	0.579	0.478
Noctilio leporinus	Nleporinus_Cross_Reg1_Mod5_LPT	LPT	0.330	0.353	0.243	0.606	37	83	8	1	0.349	0.308	0.974	0.088	0.293	0.468
Noctilio leporinus	Nleporinus_Cross_Reg1_Mod5_maxSSS	maxSSS	0.528	0.938	0.270	0.723	19	13	78	19	0.752	0.594	0.500	0.857	0.655	0.543
Noctilio leporinus	Nleporinus_Cross_Reg1_Mod6_P10	P10	0.585	0.626	0.358	0.784	27	43	48	11	0.581	0.386	0.711	0.527	0.612	0.500
Noctilio leporinus	Nleporinus_Cross_Reg1_Mod7_P10	P10	0.445	0.662	0.266	0.599	25	44	47	13	0.558	0.362	0.658	0.516	0.583	0.467
Noctilio leporinus	Nleporinus_Cross_Reg2_Mod0_LPT	LPT	0.295	0.298	0.226		38	91	0	0	0.295	0.295	1.000	0.000	0.000	0.455
Noctilio leporinus	Nleporinus_Cross_Reg2_Mod1_LPT	LPT	0.301	0.324	0.226	0.578	38	90	1	0	0.302	0.297	1.000	0.011	0.105	0.458

Noctilio leporinus	Nleporinus_Cross_Reg2_Mod3_maxSSS	maxSSS	0.493	0.933	0.253	0.690	18	14	77	20	0.736	0.563	0.474	0.846	0.633	0.514
Noctilio leporinus	Nleporinus_Cross_Reg2_Mod6_LPT	LPT	0.296	0.299	0.227		38	91	0	0	0.295	0.295	1.000	0.000	0.000	0.455
Noctilio leporinus	Nleporinus_Cross_Reg2_Mod7_LPT	LPT	0.294	0.298	0.226		38	91	0	0	0.295	0.295	1.000	0.000	0.000	0.455
Noctilio leporinus	Nleporinus_Cross_Reg2_Mod7_maxSSS	maxSSS	0.655	0.812	0.359	0.806	22	31	60	16	0.636	0.415	0.579	0.659	0.618	0.484
Noctilio leporinus	Nleporinus_Cross_Reg2_Mod7_P10	P10	0.537	0.597	0.334	0.732	28	45	46	10	0.574	0.384	0.737	0.505	0.610	0.505
Noctilio leporinus	Nleporinus_Cross_Reg3_Mod4_LPT	LPT	0.287	0.310	0.218	0.563	38	91	0	0	0.295	0.295	1.000	0.000	0.000	0.455
Noctilio leporinus	Nleporinus_Cross_Reg3_Mod5_maxSSS	maxSSS	0.653	0.810	0.359	0.804	22	32	59	16	0.628	0.407	0.579	0.648	0.613	0.478
Noctilio leporinus	Nleporinus_Cross_Reg3_Mod5_P10	P10	0.535	0.576	0.338	0.746	33	46	45	5	0.605	0.418	0.868	0.495	0.655	0.564
Noctilio leporinus	Nleporinus_Cross_Reg3_Mod6_maxSSS	maxSSS	0.655	0.773	0.367	0.809	27	34	57	11	0.651	0.443	0.711	0.626	0.667	0.545
Noctilio leporinus	Nleporinus_Cross_Reg3_Mod6_P10	P10	0.551	0.592	0.344	0.759	33	51	40	5	0.566	0.393	0.868	0.440	0.618	0.541
Noctilio leporinus	Nleporinus_Cross_Reg4_Mod5_maxSSS	maxSSS	0.644	0.820	0.352	0.796	24	31	60	14	0.651	0.436	0.632	0.659	0.645	0.516
Promops centralis	Pcentralis_Cross_Reg1_Mod0_maxSSS	maxSSS	0.639	0.782	0.345	0.793	15	73	33	8	0.372	0.170	0.652	0.311	0.451	0.270
Promops centralis	Pcentralis_Cross_Reg1_Mod1_LPT	LPT	0.274	0.417	0.184	0.415	22	93	13	1	0.271	0.191	0.957	0.123	0.343	0.319
Promops centralis	Pcentralis_Cross_Reg1_Mod1_P10	P10	0.553	0.696	0.313	0.717	19	79	27	4	0.357	0.194	0.826	0.255	0.459	0.314
Promops centralis	Pcentralis_Cross_Reg1_Mod2_LPT	LPT	0.379	0.379	0.261		22	93	13	1	0.271	0.191	0.957	0.123	0.343	0.319
Promops centralis	Pcentralis_Cross_Reg1_Mod2_P10	P10	0.283	0.712	0.159	0.399	17	76	30	6	0.364	0.183	0.739	0.283	0.457	0.293

Promops centralis	Pcentralis_Cross_Reg1_Mod3_LPT	LPT	0.268	0.412	0.181	0.407	20	87	19	3	0.302	0.187	0.870	0.179	0.395	0.308
Promops centralis	Pcentralis_Cross_Reg1_Mod4_P10	P10	0.526	0.669	0.302	0.692	19	80	26	4	0.349	0.192	0.826	0.245	0.450	0.311
Promops centralis	Pcentralis_Cross_Reg1_Mod7_LPT	LPT	0.398	0.398	0.269		22	93	13	1	0.271	0.191	0.957	0.123	0.343	0.319
Promops centralis	Pcentralis_Cross_Reg1_Mod7_maxSSS	maxSSS	0.647	0.647	0.374		19	83	23	4	0.326	0.186	0.826	0.217	0.423	0.304
Promops centralis	Pcentralis_Cross_Reg1_Mod7_P10	P10	0.618	0.618	0.363		19	84	22	4	0.318	0.184	0.826	0.208	0.414	0.302
Promops centralis	Pcentralis_Cross_Reg1_Mod8_LPT	LPT	0.390	0.391	0.265		22	93	13	1	0.271	0.191	0.957	0.123	0.343	0.319
Promops centralis	Pcentralis_Cross_Reg1_Mod8_P10	P10	0.610	0.610	0.360		19	81	25	4	0.341	0.190	0.826	0.236	0.441	0.309
Promops centralis	Pcentralis_Cross_Reg1_Mod9_LPT	LPT	0.393	0.394	0.266		22	93	13	1	0.271	0.191	0.957	0.123	0.343	0.319
Promops centralis	Pcentralis_Cross_Reg1_Mod9_maxSSS	maxSSS	0.751	0.918	0.375	0.882	13	45	61	10	0.574	0.224	0.565	0.575	0.570	0.321
Promops centralis	Pcentralis_Cross_Reg2_Mod0_maxSSS	maxSSS	0.669	0.812	0.355	0.818	17	73	33	6	0.388	0.189	0.739	0.311	0.480	0.301
Promops centralis	Pcentralis_Cross_Reg2_Mod0_P10	P10	0.529	0.672	0.303	0.694	19	81	25	4	0.341	0.190	0.826	0.236	0.441	0.309
Promops centralis	Pcentralis_Cross_Reg2_Mod1_P10	P10	0.604	0.604	0.361		20	81	25	3	0.349	0.198	0.870	0.236	0.453	0.323
Promops centralis	Pcentralis_Cross_Reg2_Mod4_LPT	LPT	0.268	0.411	0.181	0.406	22	93	13	1	0.271	0.191	0.957	0.123	0.343	0.319
Promops centralis	Pcentralis_Cross_Reg2_Mod9_maxSSS	maxSSS	0.443	0.943	0.219	0.651	8	21	85	15	0.721	0.276	0.348	0.802	0.528	0.308
Promops centralis	Pcentralis_Cross_Reg3_Mod1_maxSSS	maxSSS	0.731	0.731	0.405		16	78	28	7	0.341	0.170	0.696	0.264	0.429	0.274
Promops centralis	Pcentralis_Cross_Reg3_Mod5_LPT	LPT	0.013	0.441	0.008	0.019	22	89	17	1	0.302	0.198	0.957	0.160	0.392	0.328

Promops centralis	Pcentralis_Cross_Reg3_Mod5_maxSSS	maxSSS	0.182	0.895	0.092	0.312	14	62	44	9	0.450	0.184	0.609	0.415	0.503	0.283
Promops centralis	Pcentralis_Cross_Reg3_Mod6_maxSSS	maxSSS	0.698	0.698	0.395		21	87	19	2	0.310	0.194	0.913	0.179	0.405	0.321
Promops centralis	Pcentralis_Cross_Reg4_Mod6_P10	P10	0.576	0.576	0.350		21	87	19	2	0.310	0.194	0.913	0.179	0.405	0.321
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg1_Mod0_P10	P10	0.542	0.724	0.306	0.702	48	67	9	5	0.442	0.417	0.906	0.118	0.327	0.571
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg1_Mod1_LPT	LPT	0.528	0.529	0.336		53	76	0	0	0.411	0.411	1.000	0.000	0.000	0.582
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg1_Mod1_P10	P10	0.627	0.718	0.355	0.791	49	69	7	4	0.434	0.415	0.925	0.092	0.292	0.573
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg1_Mod2_LPT	LPT	0.522	0.522	0.333		53	75	1	0	0.419	0.414	1.000	0.013	0.115	0.586
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg1_Mod3_LPT	LPT	0.468	0.559	0.292	0.652	53	74	2	0	0.426	0.417	1.000	0.026	0.162	0.589
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg1_Mod4_LPT	LPT	0.533	0.533	0.338		53	73	3	0	0.434	0.421	1.000	0.039	0.199	0.592
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg1_Mod4_maxSSS	maxSSS	0.762	0.943	0.383	0.893	9	21	55	44	0.496	0.300	0.170	0.724	0.351	0.217
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg1_Mod5_LPT	LPT	0.411	0.512	0.263	0.591	53	76	0	0	0.411	0.411	1.000	0.000	0.000	0.582
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg1_Mod6_LPT	LPT	0.576	0.576	0.354		53	76	0	0	0.411	0.411	1.000	0.000	0.000	0.582
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg1_Mod6_P10	P10	0.717	0.718	0.406		49	68	8	4	0.442	0.419	0.925	0.105	0.312	0.576
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg1_Mod8_maxSSS	maxSSS	0.729	0.829	0.388	0.866	45	53	23	8	0.527	0.459	0.849	0.303	0.507	0.596
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg1_Mod8_P10	P10	0.714	0.714	0.405		50	70	6	3	0.434	0.417	0.943	0.079	0.273	0.578
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg1_Mod9_LPT	LPT	0.458	0.558	0.285	0.638	53	76	0	0	0.411	0.411	1.000	0.000	0.000	0.582

Pteronotus gymnonotus	Pgymnonotus_Cross_Reg2_Mod1_maxSSS	maxSSS	0.719	0.901	0.370	0.859	17	38	38	36	0.426	0.309	0.321	0.500	0.400	0.315
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg2_Mod6_P10	P10	0.671	0.671	0.390		49	64	12	4	0.473	0.434	0.925	0.158	0.382	0.590
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg2_Mod8_maxSSS	maxSSS	0.654	0.953	0.326	0.827	10	11	65	43	0.581	0.476	0.189	0.855	0.402	0.270
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg3_Mod1_maxSSS	maxSSS	0.705	0.705	0.403		48	65	11	5	0.457	0.425	0.906	0.145	0.362	0.578
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg3_Mod1_P10	P10	0.690	0.690	0.398		48	69	7	5	0.426	0.410	0.906	0.092	0.289	0.565
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg3_Mod2_LPT	LPT	0.421	0.513	0.270	0.606	53	76	0	0	0.411	0.411	1.000	0.000	0.000	0.582
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg3_Mod3_maxSSS	maxSSS	0.582	0.945	0.292	0.770	9	21	55	44	0.496	0.300	0.170	0.724	0.351	0.217
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg3_Mod4_P10	P10	0.357	0.721	0.202	0.492	45	67	9	8	0.419	0.402	0.849	0.118	0.317	0.545
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg3_Mod7_maxSSS	maxSSS	0.725	0.725	0.408		45	67	9	8	0.419	0.402	0.849	0.118	0.317	0.545
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg3_Mod8_P10	P10	0.606	0.706	0.345	0.772	48	69	7	5	0.426	0.410	0.906	0.092	0.289	0.565
Pteronotus gymnonotus	Pgymnonotus_Cross_Reg4_Mod0_maxSSS	maxSSS	0.815	0.906	0.418	0.922	16	34	42	37	0.450	0.320	0.302	0.553	0.408	0.311
Promops nasutus	Pnasutus_Cross_Reg1_Mod0_LPT	LPT	0.148	0.291	0.109	0.245	40	76	9	4	0.380	0.345	0.909	0.106	0.310	0.500
Promops nasutus	Pnasutus_Cross_Reg1_Mod0_P10	P10	0.098	0.812	0.052	0.158	29	43	42	15	0.550	0.403	0.659	0.494	0.571	0.500
Promops nasutus	Pnasutus_Cross_Reg1_Mod1_LPT	LPT	0.119	0.262	0.089	0.202	44	82	3	0	0.364	0.349	1.000	0.035	0.188	0.518
Promops nasutus	Pnasutus_Cross_Reg1_Mod1_P10	P10	0.081	0.795	0.043	0.129	29	42	43	15	0.558	0.408	0.659	0.506	0.577	0.504
Promops nasutus	Pnasutus_Cross_Reg1_Mod3_LPT	LPT	0.221	0.364	0.154	0.346	44	77	8	0	0.403	0.364	1.000	0.094	0.307	0.533

Promops nasutus	Pnasutus_Cross_Reg1_Mod4_LPT	LPT	0.261	0.262	0.196		44	81	4	0	0.372	0.352	1.000	0.047	0.217	0.521
Promops nasutus	Pnasutus_Cross_Reg1_Mod4_P10	P10	0.703	0.703	0.396		32	46	39	12	0.550	0.410	0.727	0.459	0.578	0.525
Promops nasutus	Pnasutus_Cross_Reg1_Mod5_LPT	LPT	0.245	0.245	0.184		44	81	4	0	0.372	0.352	1.000	0.047	0.217	0.521
Promops nasutus	Pnasutus_Cross_Reg1_Mod5_maxSSS	maxSSS	0.736	0.903	0.371	0.871	18	25	60	26	0.605	0.419	0.409	0.706	0.537	0.414
Promops nasutus	Pnasutus_Cross_Reg1_Mod5_P10	P10	0.732	0.732	0.403		33	41	44	11	0.597	0.446	0.750	0.518	0.623	0.559
Promops nasutus	Pnasutus_Cross_Reg1_Mod6_maxSSS	maxSSS	0.711	0.711	0.396		33	44	41	11	0.574	0.429	0.750	0.482	0.601	0.545
Promops nasutus	Pnasutus_Cross_Reg1_Mod6_P10	P10	0.640	0.640	0.371		34	54	31	10	0.504	0.386	0.773	0.365	0.531	0.515
Promops nasutus	Pnasutus_Cross_Reg1_Mod7_maxSSS	maxSSS	0.661	0.827	0.346	0.810	24	34	51	20	0.581	0.414	0.545	0.600	0.572	0.471
Promops nasutus	Pnasutus_Cross_Reg1_Mod8_LPT	LPT	0.245	0.246	0.185		44	81	4	0	0.372	0.352	1.000	0.047	0.217	0.521
Promops nasutus	Pnasutus_Cross_Reg1_Mod8_P10	P10	0.517	0.684	0.293	0.679	36	47	38	8	0.574	0.434	0.818	0.447	0.605	0.567
Promops nasutus	Pnasutus_Cross_Reg1_Mod9_maxSSS	maxSSS	0.728	0.728	0.402		34	48	37	10	0.550	0.415	0.773	0.435	0.580	0.540
Promops nasutus	Pnasutus_Cross_Reg1_Mod9_P10	P10	0.601	0.768	0.325	0.759	31	45	40	13	0.550	0.408	0.705	0.471	0.576	0.517
Promops nasutus	Pnasutus_Cross_Reg2_Mod6_P10	P10	0.630	0.630	0.368		38	59	26	6	0.496	0.392	0.864	0.306	0.514	0.539
Promops nasutus	Pnasutus_Cross_Reg3_Mod6_maxSSS	maxSSS	0.449	0.948	0.221	0.662	8	18	67	36	0.581	0.308	0.182	0.788	0.379	0.229
Promops nasutus	Pnasutus_Cross_Reg3_Mod7_maxSSS	maxSSS	0.762	0.928	0.379	0.890	8	14	71	36	0.612	0.364	0.182	0.835	0.390	0.242
Promops nasutus	Pnasutus_Cross_Reg3_Mod8_maxSSS	maxSSS	0.452	0.952	0.222	0.669	8	18	67	36	0.581	0.308	0.182	0.788	0.379	0.229

Promops nasutus	Pnasutus_Cross_Reg3_Mod9_LPT	LPT	0.270	0.437	0.178	0.401	41	69	16	3	0.442	0.373	0.932	0.188	0.419	0.532
Promops nasutus	Pnasutus_Cross_Reg4_Mod3_maxSSS	maxSSS	0.684	0.827	0.360	0.830	15	26	59	29	0.574	0.366	0.341	0.694	0.486	0.353
Promops nasutus	Pnasutus_Cross_Reg4_Mod8_LPT	LPT	0.225	0.391	0.152	0.342	6	81	4	2	0.357	0.341	0.955	0.047	0.212	0.503
Pteronotus personatus	Ppersonatus_Cross_Reg1_Mod0_LPT	LPT	0.585	0.585	0.356		16	99	9	5	0.194	0.139	0.762	0.083	0.252	0.235
Pteronotus personatus	Ppersonatus_Cross_Reg1_Mod1_maxSSS	maxSSS	0.737	0.848	0.387	0.871	14	73	35	7	0.380	0.161	0.667	0.324	0.465	0.259
Pteronotus personatus	Ppersonatus_Cross_Reg1_Mod1_P10	P10	0.670	0.781	0.365	0.821	14	78	30	7	0.341	0.152	0.667	0.278	0.430	0.248
Pteronotus personatus	Ppersonatus_Cross_Reg1_Mod2_LPT	LPT	0.574	0.574	0.352		16	97	11	5	0.209	0.142	0.762	0.102	0.279	0.239
Pteronotus personatus	Ppersonatus_Cross_Reg1_Mod2_maxSSS	maxSSS	0.832	0.943	0.416	0.933	9	48	60	12	0.535	0.158	0.429	0.556	0.488	0.231
Pteronotus personatus	Ppersonatus_Cross_Reg1_Mod3_LPT	LPT	0.586	0.586	0.356		16	97	11	5	0.209	0.142	0.762	0.102	0.279	0.239
Pteronotus personatus	Ppersonatus_Cross_Reg1_Mod3_P10	P10	0.341	0.841	0.179	0.490	14	75	33	7	0.364	0.157	0.667	0.306	0.451	0.255
Pteronotus personatus	Ppersonatus_Cross_Reg1_Mod5_maxSSS	maxSSS	0.707	0.957	0.350	0.864	8	48	60	13	0.527	0.143	0.381	0.556	0.460	0.208
Pteronotus personatus	Ppersonatus_Cross_Reg1_Mod6_LPT	LPT	0.487	0.613	0.291	0.658	16	96	12	5	0.217	0.143	0.762	0.111	0.291	0.241
Pteronotus personatus	Ppersonatus_Cross_Reg1_Mod7_P10	P10	0.478	0.853	0.250	0.643	12	75	33	9	0.349	0.138	0.571	0.306	0.418	0.222
Pteronotus personatus	Ppersonatus_Cross_Reg1_Mod9_P10	P10	0.772	0.772	0.421		15	81	27	6	0.326	0.156	0.714	0.250	0.423	0.256
Pteronotus personatus	Ppersonatus_Cross_Reg2_Mod1_LPT	LPT	0.579	0.580	0.354		16	99	9	5	0.194	0.139	0.762	0.083	0.252	0.235
Pteronotus personatus	Ppersonatus_Cross_Reg2_Mod3_maxSSS	maxSSS	0.860	0.860	0.447		14	67	41	7	0.426	0.173	0.667	0.380	0.503	0.275

Pteronotus personatus	Ppersonatus_Cross_Reg2_Mod3_P10	P10	0.764	0.764	0.418		15	80	28	6	0.333	0.158	0.714	0.259	0.430	0.259
Pteronotus personatus	Ppersonatus_Cross_Reg2_Mod7_maxSSS	maxSSS	0.930	0.930	0.467		4	40	68	17	0.558	0.091	0.190	0.630	0.346	0.123
Pteronotus personatus	Ppersonatus_Cross_Reg2_Mod8_LPT	LPT	0.460	0.586	0.279	0.631	16	103	5	5	0.163	0.134	0.762	0.046	0.188	0.229
Pteronotus personatus	Ppersonatus_Cross_Reg3_Mod2_P10	P10	0.685	0.796	0.370	0.833	15	80	28	6	0.333	0.158	0.714	0.259	0.430	0.259
Pteronotus personatus	Ppersonatus_Cross_Reg3_Mod4_LPT	LPT	0.437	0.562	0.269	0.607	21	107	1	0	0.171	0.164	1.000	0.009	0.096	0.282
Pteronotus personatus	Ppersonatus_Cross_Reg3_Mod8_maxSSS	maxSSS	0.767	0.892	0.393	0.891	12	72	36	9	0.372	0.143	0.571	0.333	0.436	0.229
Pteronotus personatus	Ppersonatus_Cross_Reg3_Mod9_maxSSS	maxSSS	0.746	0.746	0.412		16	95	13	5	0.225	0.144	0.762	0.120	0.303	0.242
Pteronotus personatus	Ppersonatus_Cross_Reg4_Mod1_P10	P10	0.776	0.776	0.424		16	91	17	5	0.256	0.150	0.762	0.157	0.346	0.250
Pteronotus personatus	Ppersonatus_Cross_Reg4_Mod4_maxSSS	maxSSS	0.786	0.786	0.425		15	76	32	6	0.364	0.165	0.714	0.296	0.460	0.268
Pteronotus personatus	Ppersonatus_Cross_Reg4_Mod8_P10	P10	0.782	0.782	0.424		16	91	17	5	0.256	0.150	0.762	0.157	0.346	0.250
Pteronotus personatus	Ppersonatus_Cross_Reg4_Mod9_LPT	LPT	0.443	0.569	0.272	0.614	21	107	1	0	0.171	0.164	1.000	0.009	0.096	0.282
Saccopteryx leptura	Sleptura_Cross_Reg1_Mod0_P10	P10	0.628	0.693	0.368	0.801	18	26	79	6	0.752	0.409	0.750	0.752	0.751	0.529
Saccopteryx leptura	Sleptura_Cross_Reg1_Mod6_P10	P10	0.514	0.715	0.297	0.673	18	26	79	6	0.752	0.409	0.750	0.752	0.751	0.529
Saccopteryx leptura	Sleptura_Cross_Reg1_Mod7_P10	P10	0.635	0.702	0.370	0.805	18	26	79	6	0.752	0.409	0.750	0.752	0.751	0.529
Saccopteryx leptura	Sleptura_Cross_Reg1_Mod8_maxSSS	maxSSS	0.743	0.876	0.392	0.874	14	17	88	10	0.791	0.452	0.583	0.838	0.699	0.509
Saccopteryx leptura	Sleptura_Cross_Reg1_Mod8_P10	P10	0.662	0.696	0.387	0.841	18	27	78	6	0.744	0.400	0.750	0.743	0.746	0.522

Saccopteryx leptura	Sleptura_Cross_Reg1_Mod9_maxSSS	maxSSS	0.616	0.617	0.377	0.963	18	41	64	6	0.636	0.305	0.750	0.610	0.676	0.434
Saccopteryx leptura	Sleptura_Cross_Reg2_Mod0_LPT	LPT	0.423	0.457	0.287	0.663	21	94	11	3	0.248	0.183	0.875	0.105	0.303	0.302
Saccopteryx leptura	Sleptura_Cross_Reg2_Mod1_LPT	LPT	0.447	0.448	0.305	0.938	21	102	3	3	0.186	0.171	0.875	0.029	0.158	0.286
Saccopteryx leptura	Sleptura_Cross_Reg2_Mod2_LPT	LPT	0.451	0.452	0.307	0.939	21	102	3	3	0.186	0.171	0.875	0.029	0.158	0.286
Saccopteryx leptura	Sleptura_Cross_Reg2_Mod3_LPT	LPT	0.450	0.451	0.307	0.939	21	100	5	3	0.202	0.174	0.875	0.048	0.204	0.290
Saccopteryx leptura	Sleptura_Cross_Reg2_Mod4_LPT	LPT	0.449	0.451	0.306	0.938	21	104	1	3	0.171	0.168	0.875	0.010	0.091	0.282
Saccopteryx leptura	Sleptura_Cross_Reg2_Mod7_P10	P10	0.545	0.712	0.315	0.706	17	28	77	7	0.729	0.378	0.708	0.733	0.721	0.493
Saccopteryx leptura	Sleptura_Cross_Reg2_Mod8_LPT	LPT	0.447	0.448	0.305	0.938	23	105	0	1	0.178	0.180	0.958	0.000	0.000	0.303
Saccopteryx leptura	Sleptura_Cross_Reg2_Mod8_P10	P10	0.633	0.701	0.369	0.804	17	26	79	7	0.744	0.395	0.708	0.752	0.730	0.507
Saccopteryx leptura	Sleptura_Cross_Reg3_Mod0_LPT	LPT	0.398	0.466	0.269	0.599	21	102	3	3	0.186	0.171	0.875	0.029	0.158	0.286
Saccopteryx leptura	Sleptura_Cross_Reg3_Mod1_maxSSS	maxSSS	0.684	0.717	0.395	0.855	17	26	79	7	0.744	0.395	0.708	0.752	0.730	0.507
Saccopteryx leptura	Sleptura_Cross_Reg3_Mod1_P10	P10	0.644	0.677	0.381	0.830	17	26	79	7	0.744	0.395	0.708	0.752	0.730	0.507
Saccopteryx leptura	Sleptura_Cross_Reg3_Mod2_maxSSS	maxSSS	0.632	0.858	0.337	0.787	15	17	88	9	0.798	0.469	0.625	0.838	0.724	0.536
Saccopteryx leptura	Sleptura_Cross_Reg3_Mod3_LPT	LPT	0.442	0.444	0.303	0.937	21	99	6	3	0.209	0.175	0.875	0.057	0.224	0.292
Saccopteryx leptura	Sleptura_Cross_Reg3_Mod4_maxSSS	maxSSS	0.668	0.669	0.397	0.969	17	27	78	7	0.736	0.386	0.708	0.743	0.725	0.500
Saccopteryx leptura	Sleptura_Cross_Reg3_Mod4_P10	P10	0.658	0.659	0.393	0.968	17	29	76	7	0.721	0.370	0.708	0.724	0.716	0.486

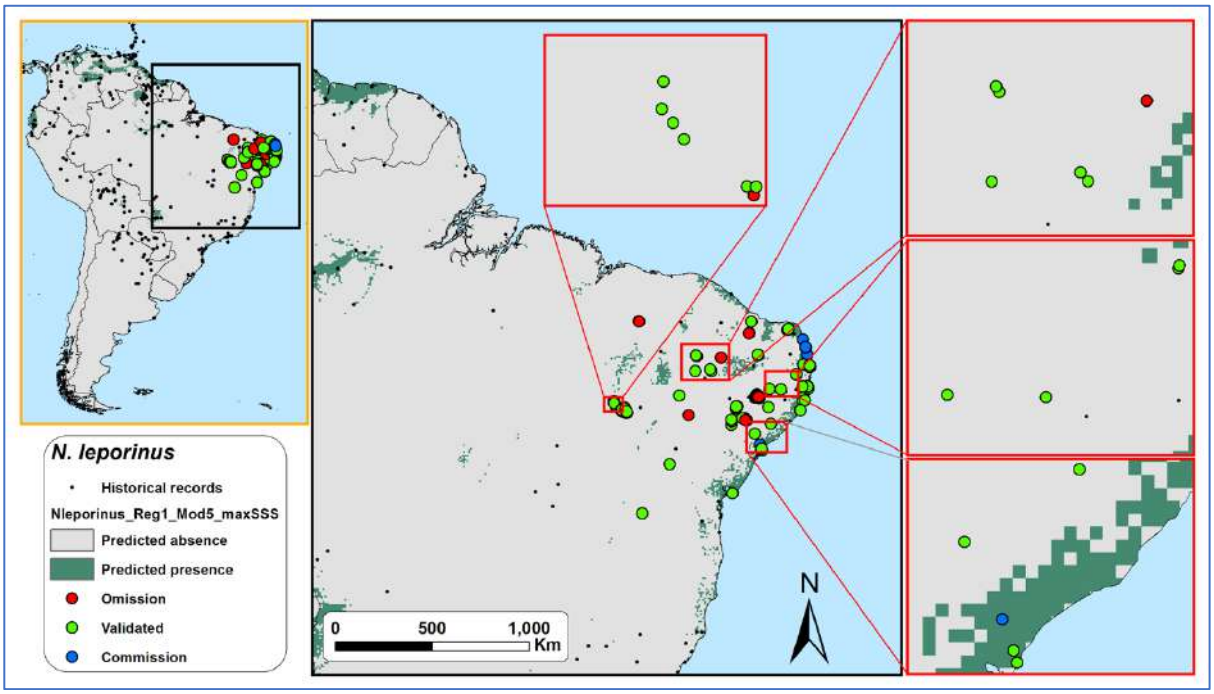
Saccopteryx leptura	Sleptura_Cross_Reg3_Mod5_maxSSS	maxSSS	0.552	0.554	0.352	0.954	18	85	20	6	0.295	0.175	0.750	0.190	0.378	0.283
Saccopteryx leptura	Sleptura_Cross_Reg4_Mod0_maxSSS	maxSSS	0.596	0.886	0.313	0.761	14	15	90	10	0.806	0.483	0.583	0.857	0.707	0.528
Saccopteryx leptura	Sleptura_Cross_Reg4_Mod4_maxSSS	maxSSS	0.647	0.648	0.389	0.967	17	29	76	7	0.721	0.370	0.708	0.724	0.716	0.486

643 **Fonte:** Frederico Hintze (autor).
644

Maps S4

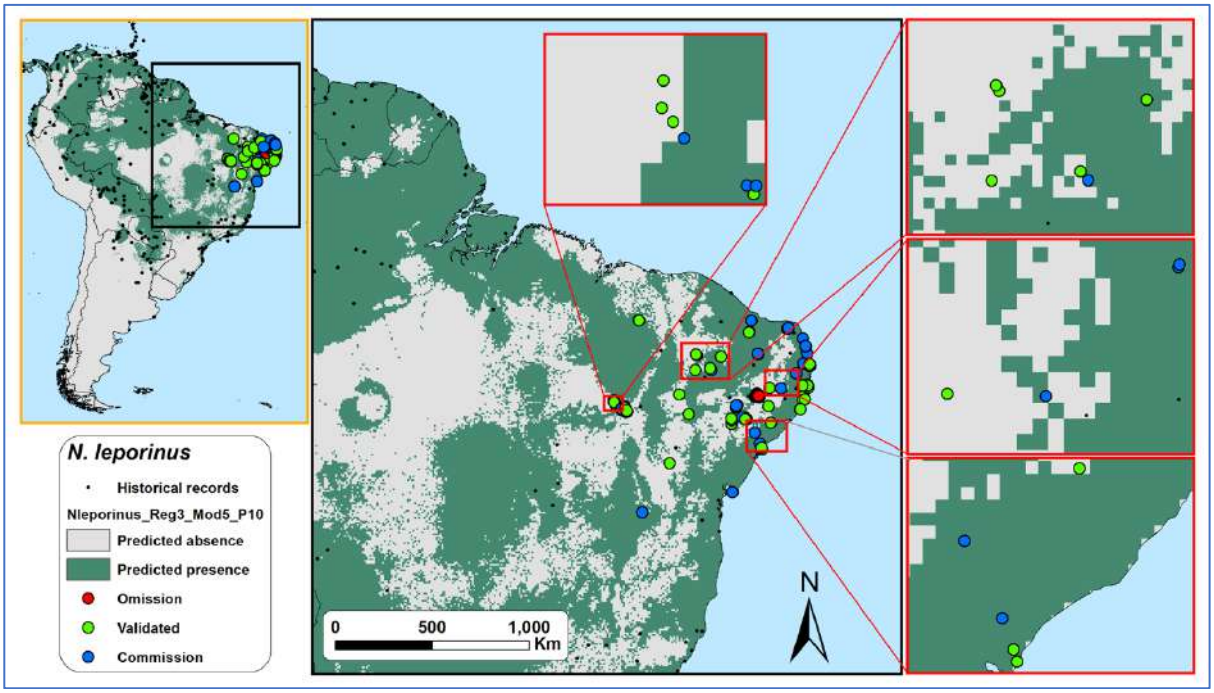
Noctilio leporinus

Figure A - Field validation results for the binary maps with the highest accuracy, precision, and specificity scores for *Noctilio leporinus* in northeastern Brazil. 'Omission' points represent locations where the model did not predict the species occurrence, but the species was detected during the acoustics monitoring; 'Validated' points represent locations where the model predict the species occurrence and the species was detected during the acoustics monitoring or locations where the model did not predict the species occurrence, and the species was detected during the acoustics monitoring; 'commission' points represent locations where the model predict the species occurrence but the species was not detected during the acoustics monitoring.



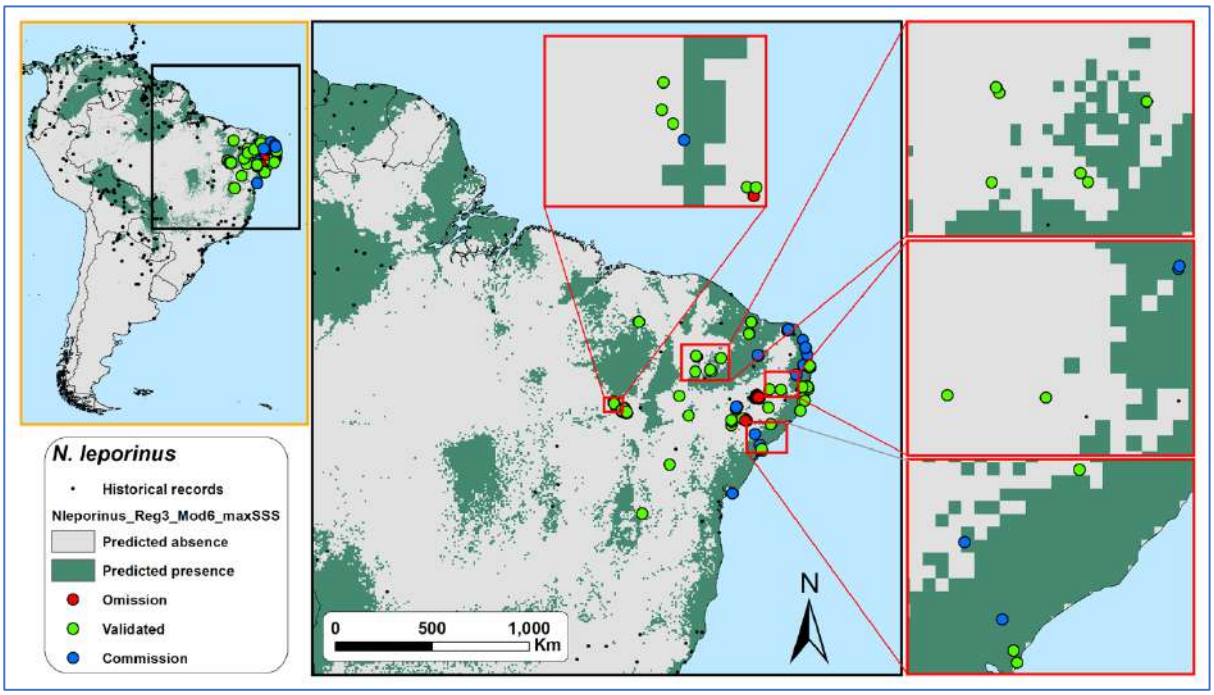
Fonte: Frederico Hintze (autor).

Figure B - Field validation results for the binary maps with the highest f-score score for *Noctilio leporinus* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



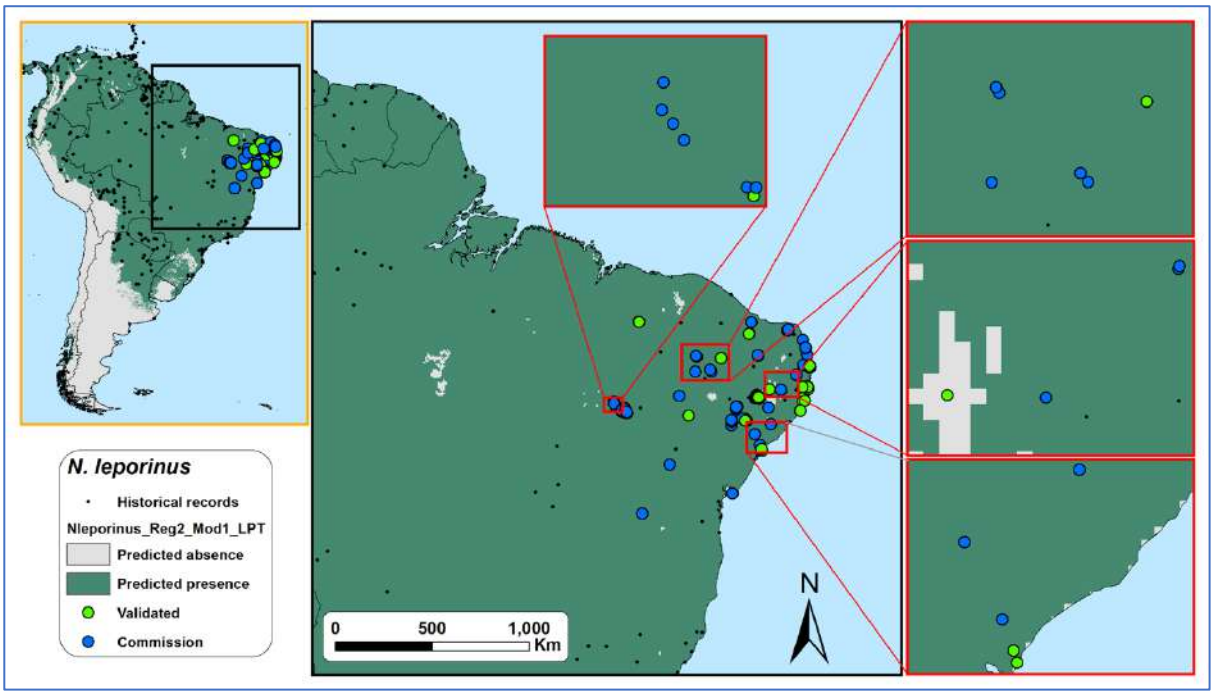
Fonte: Frederico Hintze (autor).

Figure C - Field validation results for the binary maps with the highest g-mean score for *Noctilio leporinus* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



Fonte: Frederico Hintze (autor).

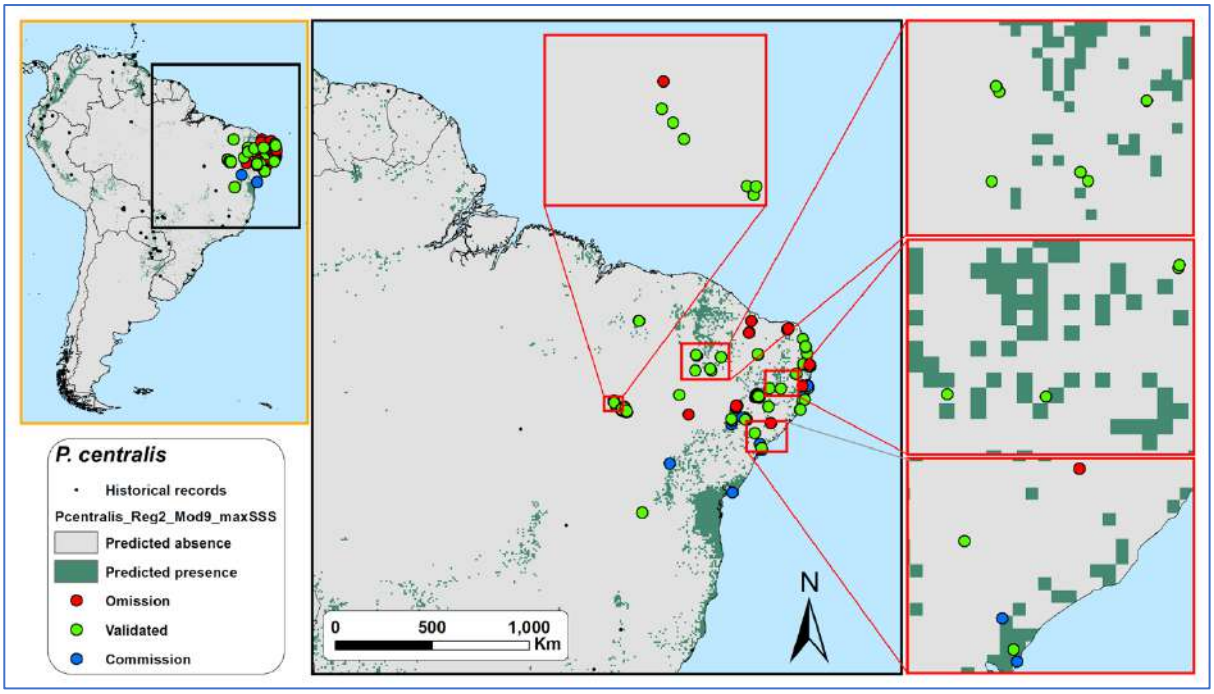
Figure D - Field validation results for the binary maps with the highest sensitivity score for *Noctilio leporinus* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



Fonte: Frederico Hintze (autor).

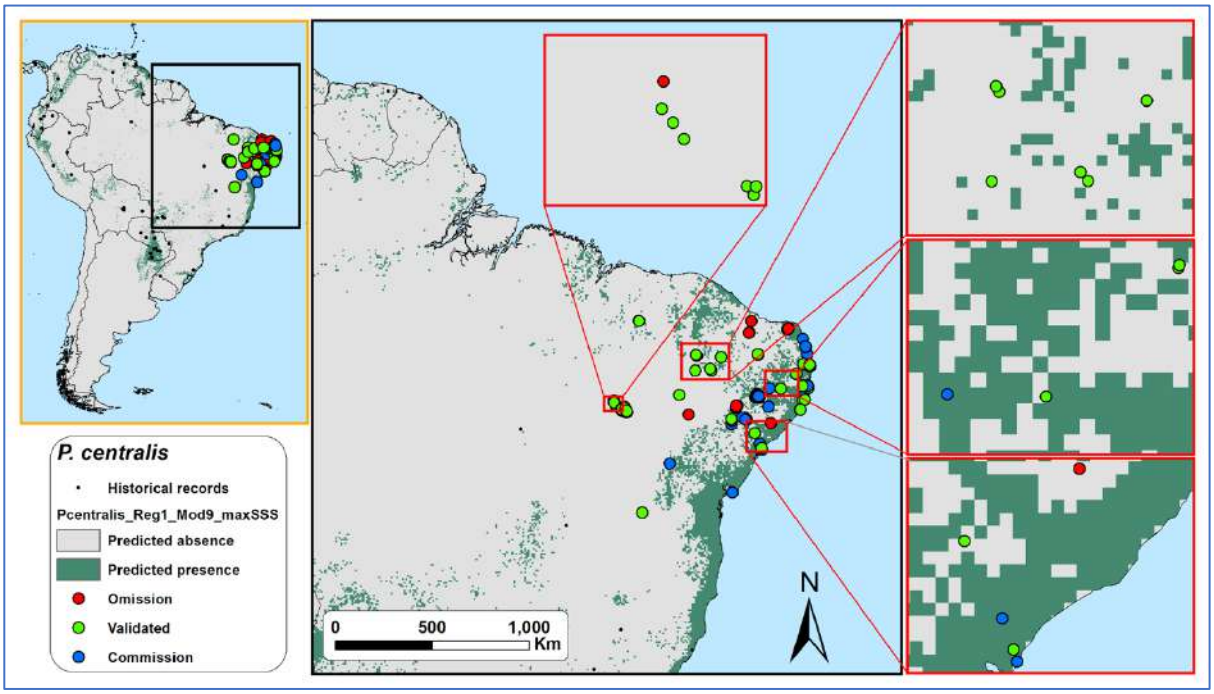
Promops centralis

Figure E - Field validation results for the binary maps with the highest accuracy, precision, and specificity scores for *Promops centralis* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



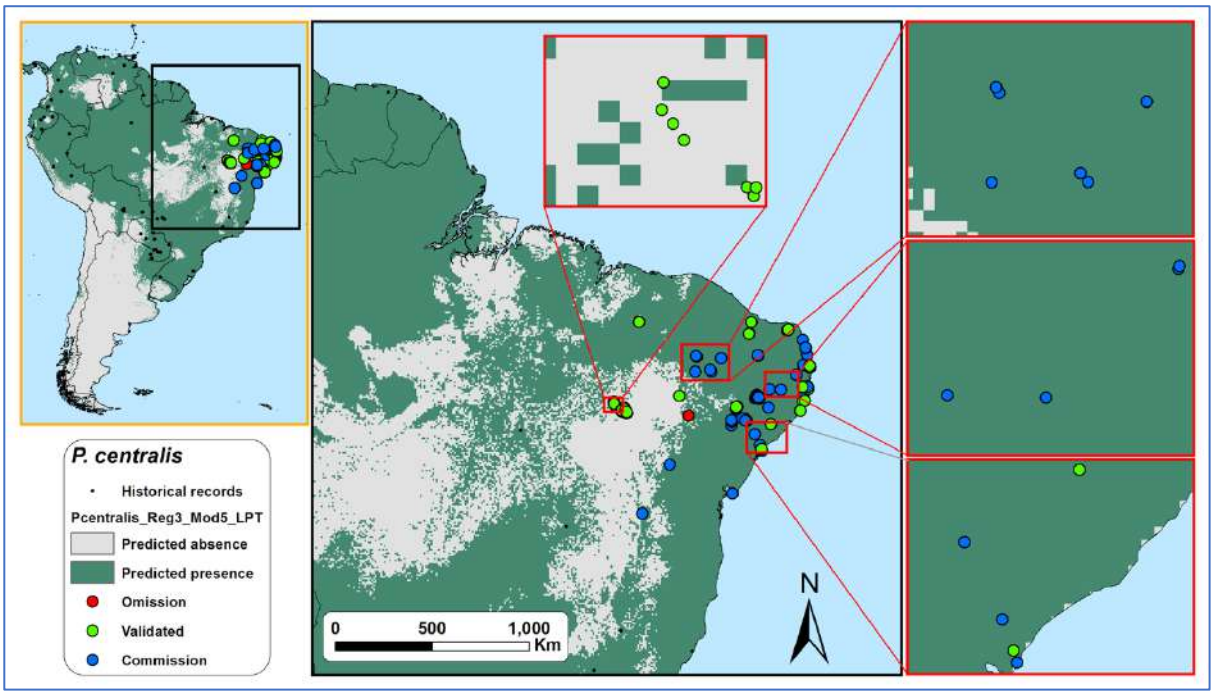
Fonte: Frederico Hintze (autor).

Figure F - Field validation results for the binary maps with the highest g-mean score for *Promops centralis* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



Fonte: Frederico Hintze (autor).

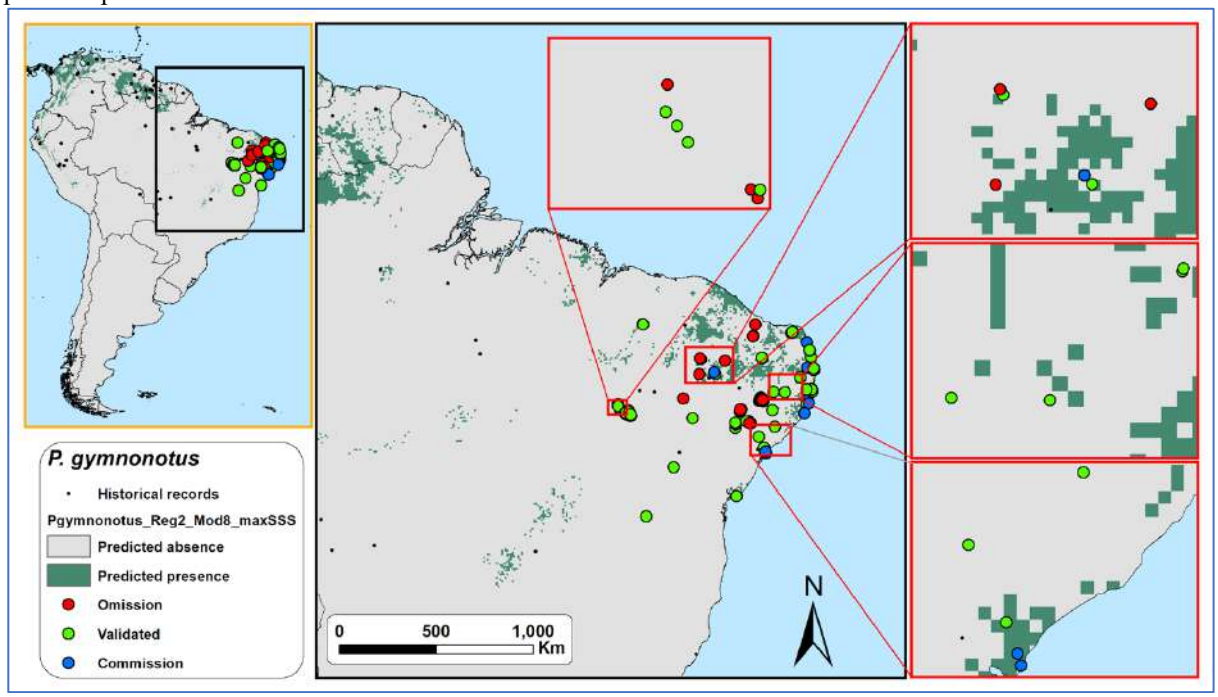
Figure G - Field validation results for the binary maps with the highest sensitivity and f-score scores for *Promops centralis* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



Fonte: Frederico Hintze (autor).

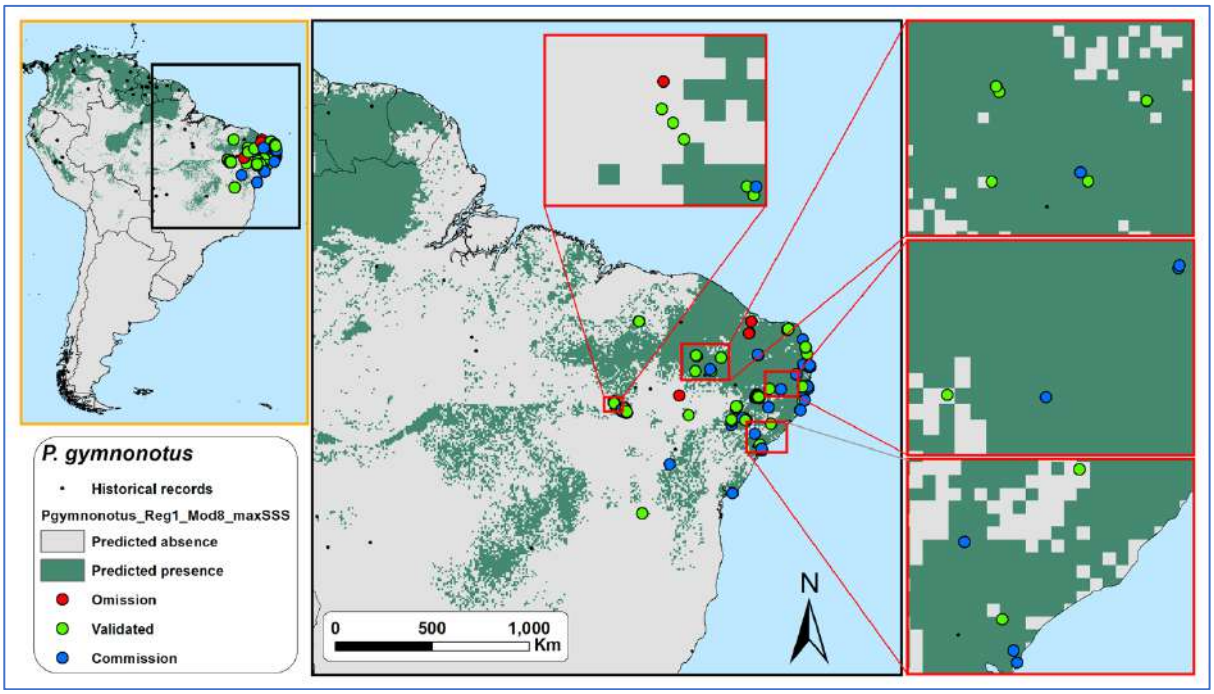
Pteronotus gymnonotus

Figure H - Field validation results for the binary maps with the highest accuracy, precision, and specificity scores for *Pteronotus gymnonotus* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



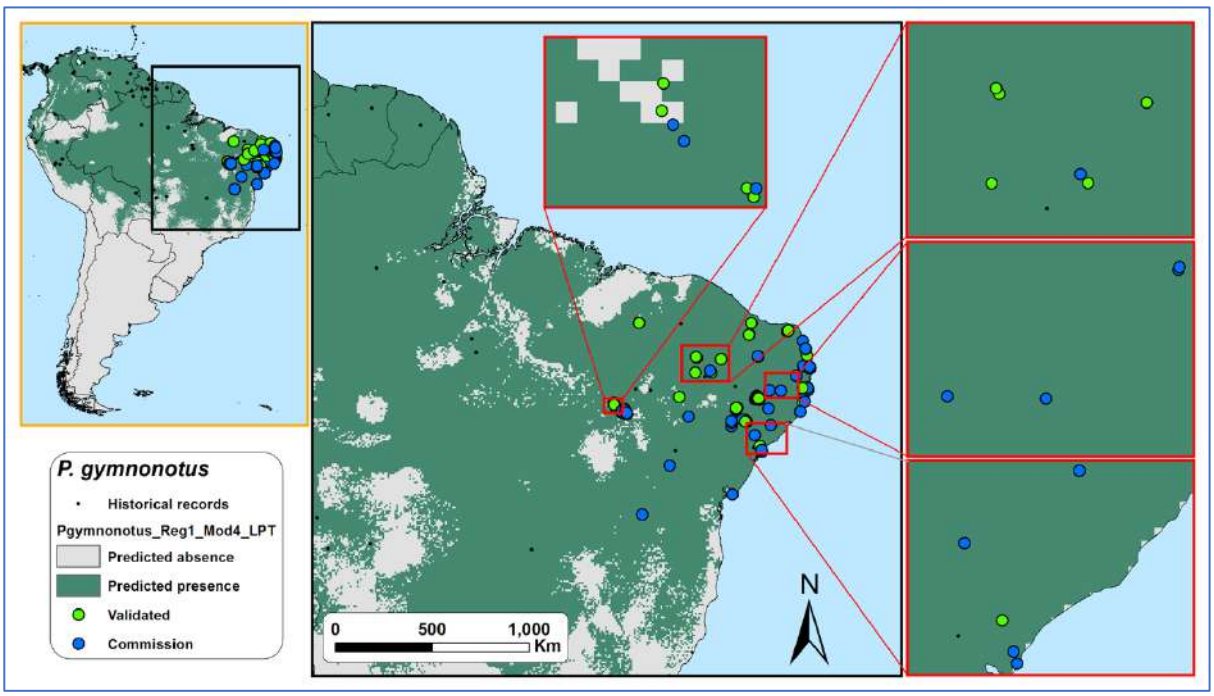
Fonte: Frederico Hintze (autor).

Figure I - Field validation results for the binary maps with the highest g-mean and f-score scores for *Pteronotus gymnonotus* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



Fonte: Frederico Hintze (autor).

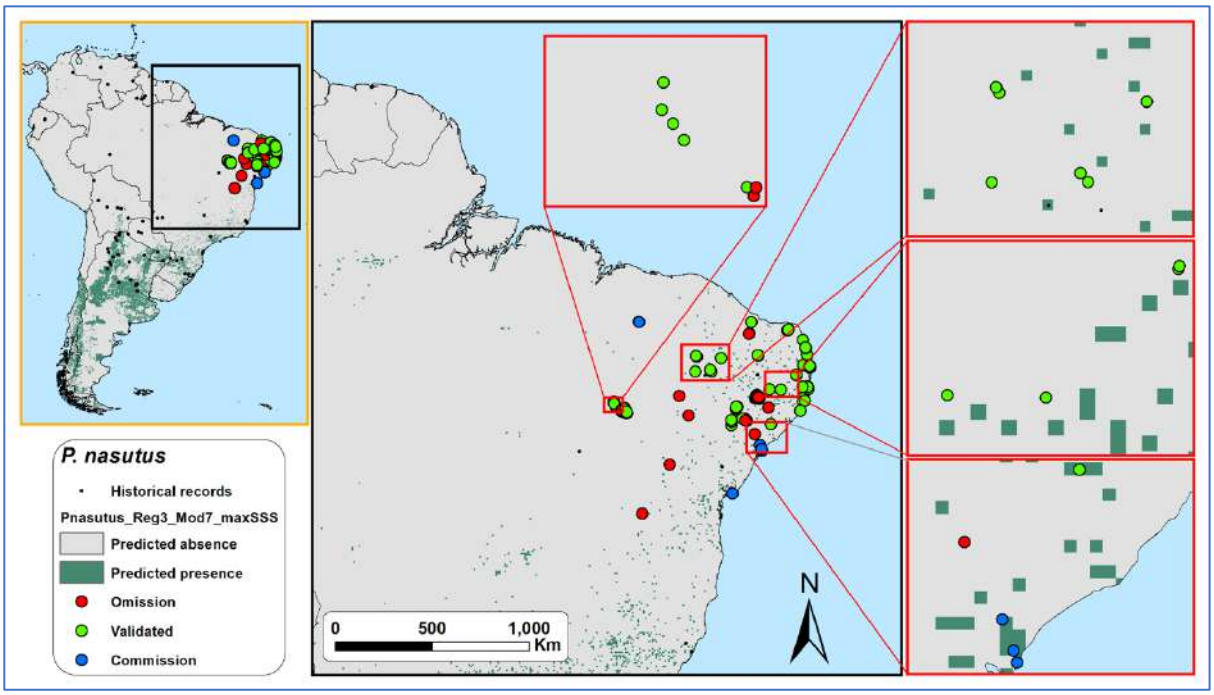
Figure J - Field validation results for the binary maps with the highest sensitivity score for *Pteronotus gymnonotus* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



Fonte: Frederico Hintze (autor).

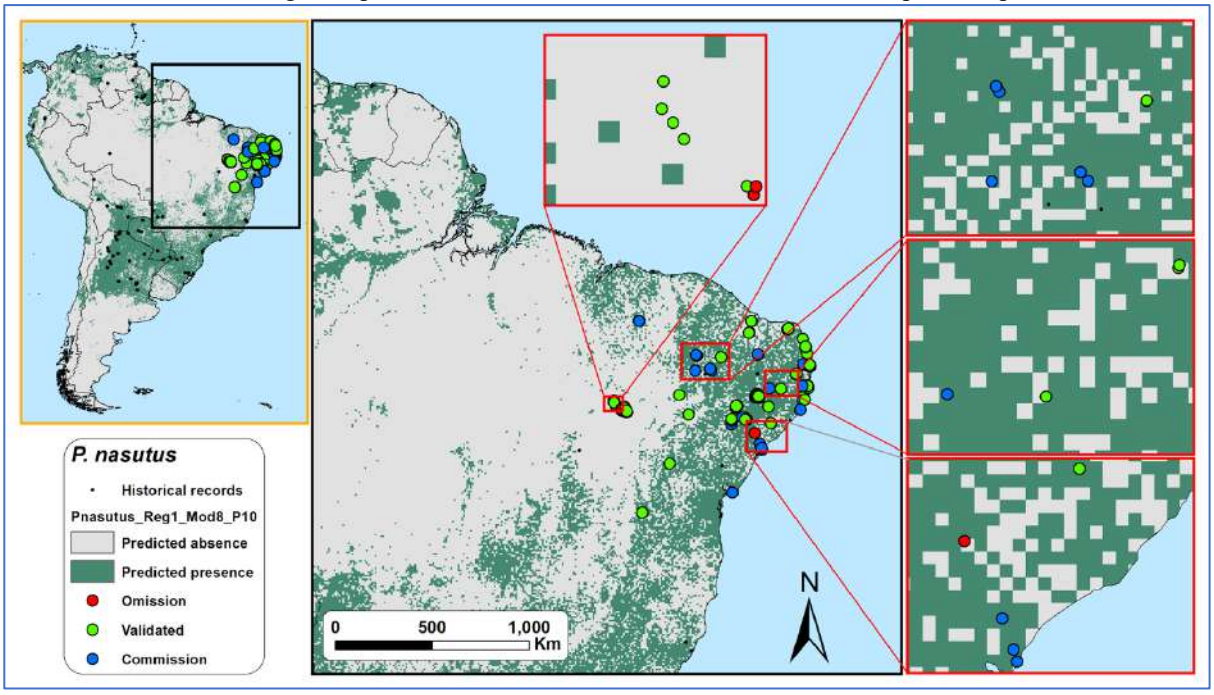
Promops nasutus

Figure K - Field validation results for the binary maps with the highest accuracy and specificity scores for *Promops nasutus* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



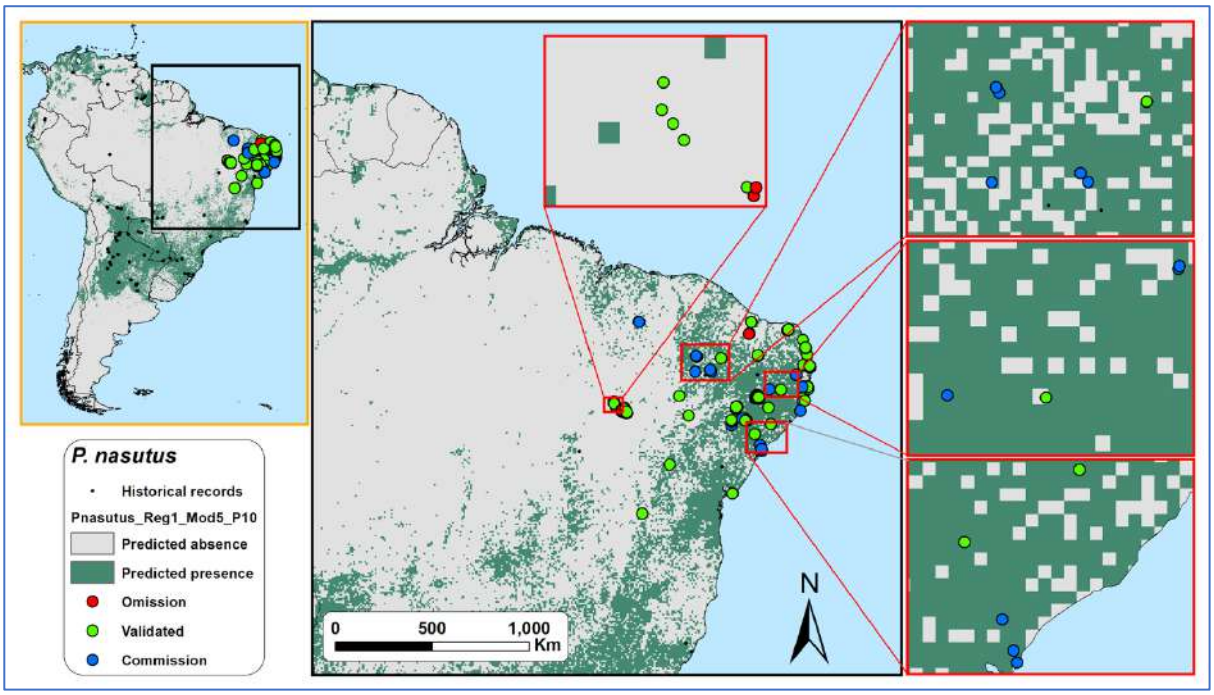
Fonte: Frederico Hintze (autor).

Figure L - Field validation results for the binary maps with the highest f-score score for *Promops nasutus* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



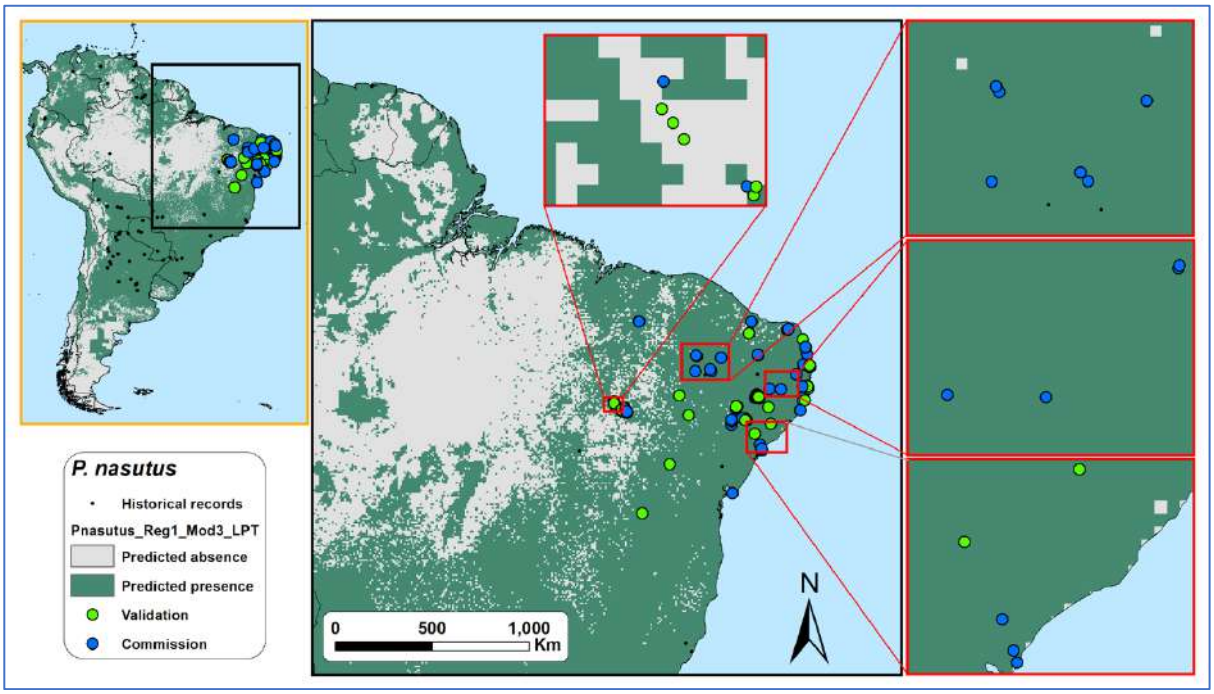
Fonte: Frederico Hintze (autor).

Figure M - Field validation results for the binary maps with the highest g-mean score for *Promops nasutus* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



Fonte: Frederico Hintze (autor).

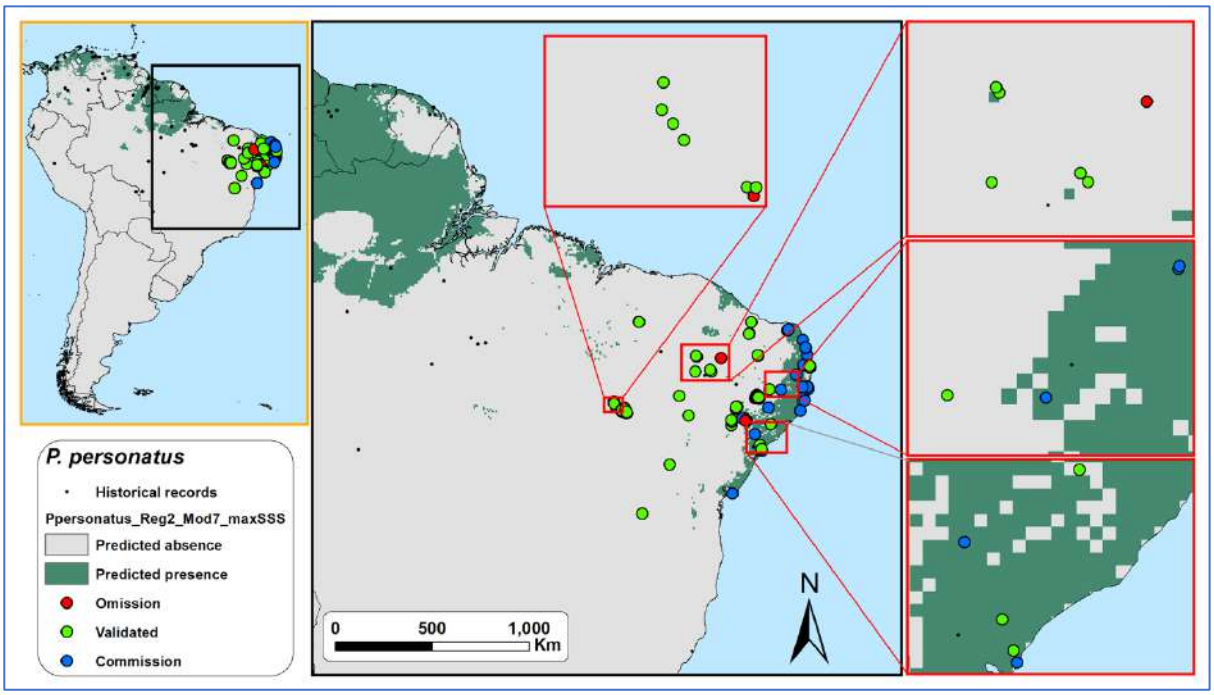
Figure N - Field validation results for the binary maps with the highest sensitivity score for *Promops nasutus* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



Fonte: Frederico Hintze (autor).

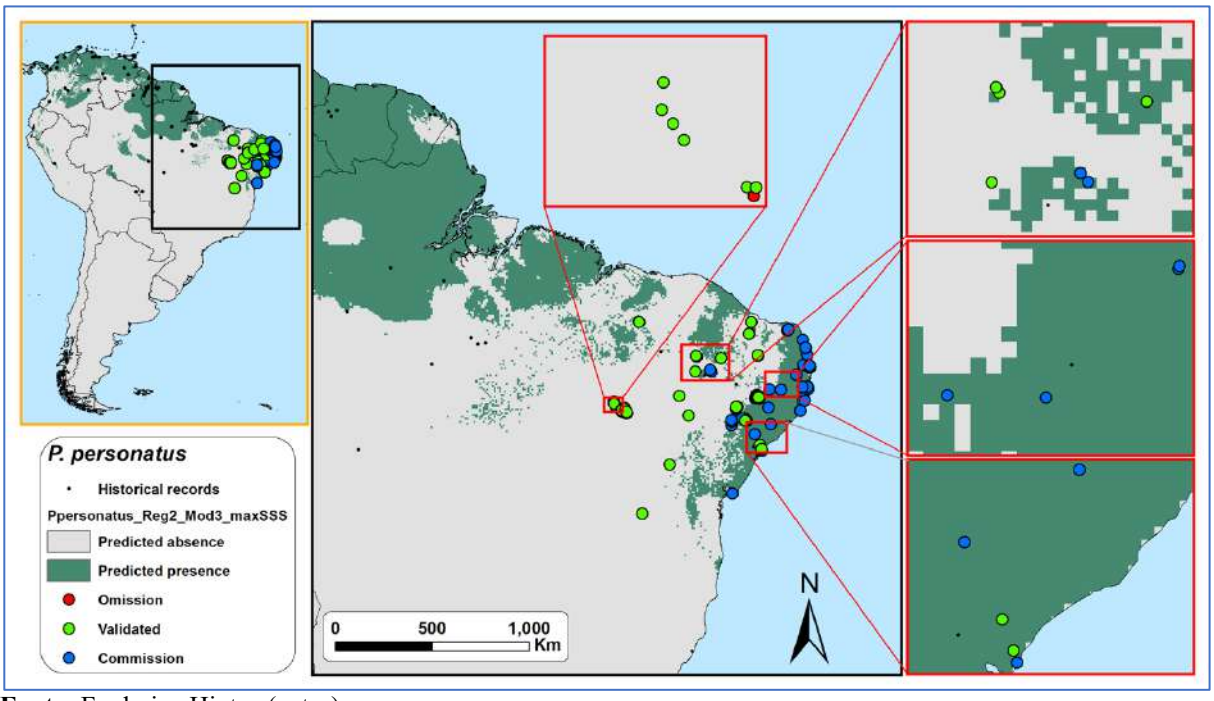
Pteronotus personatus

Figure O - Field validation results for the binary maps with the highest accuracy and specificity scores for *Pteronotus personatus* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



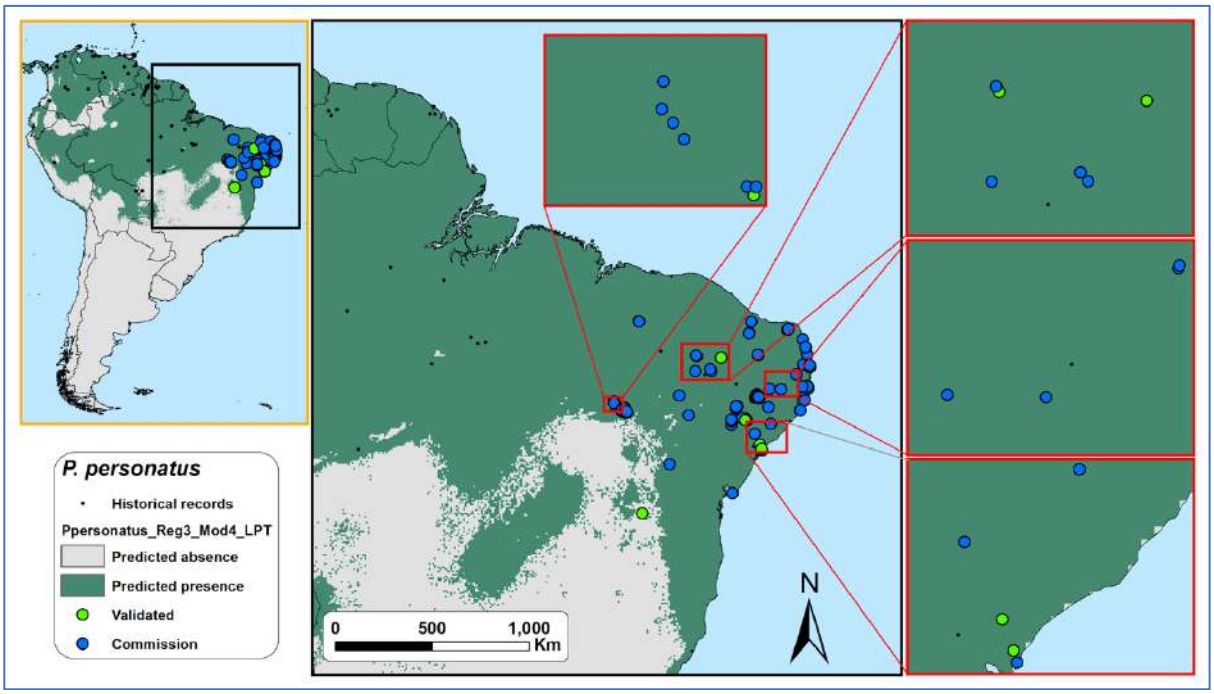
Fonte: Frederico Hintze (autor).

Figure P - Field validation results for the binary maps with the highest precision and g-mean scores for *Pteronotus personatus* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



Fonte: Frederico Hintze (autor).

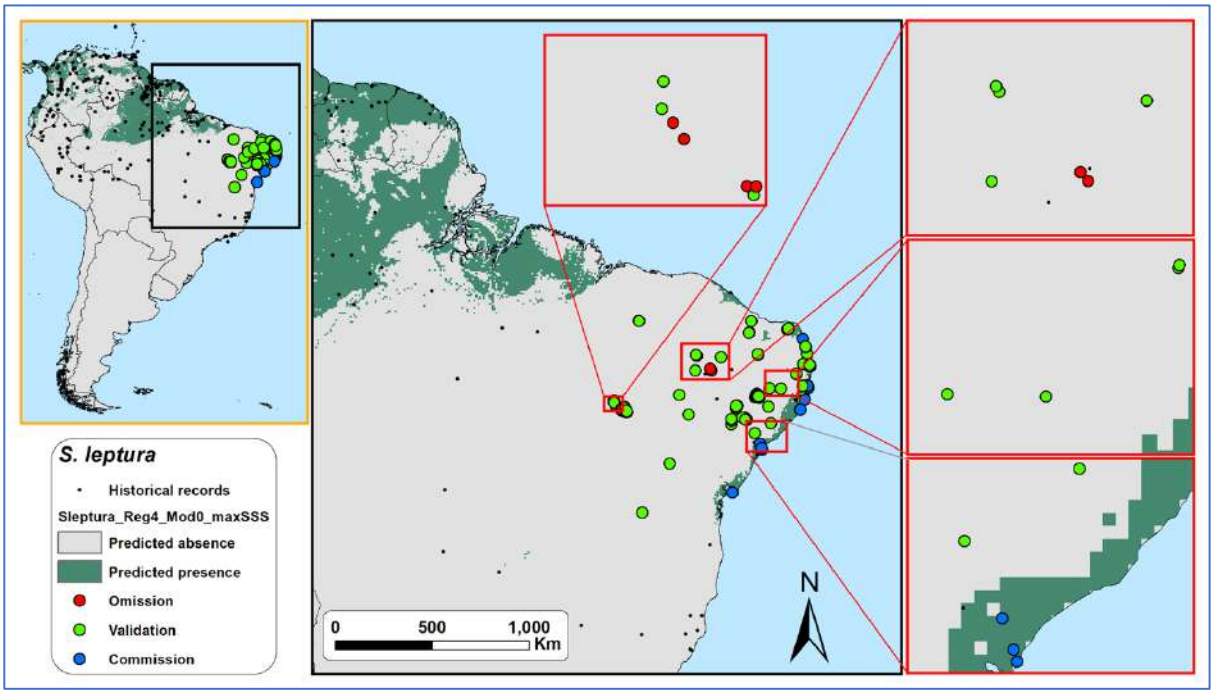
Figure Q - Field validation results for the binary maps with the highest sensitivity and f-score scores for *Pteronotus personatus* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



Fonte: Frederico Hintze (autor).

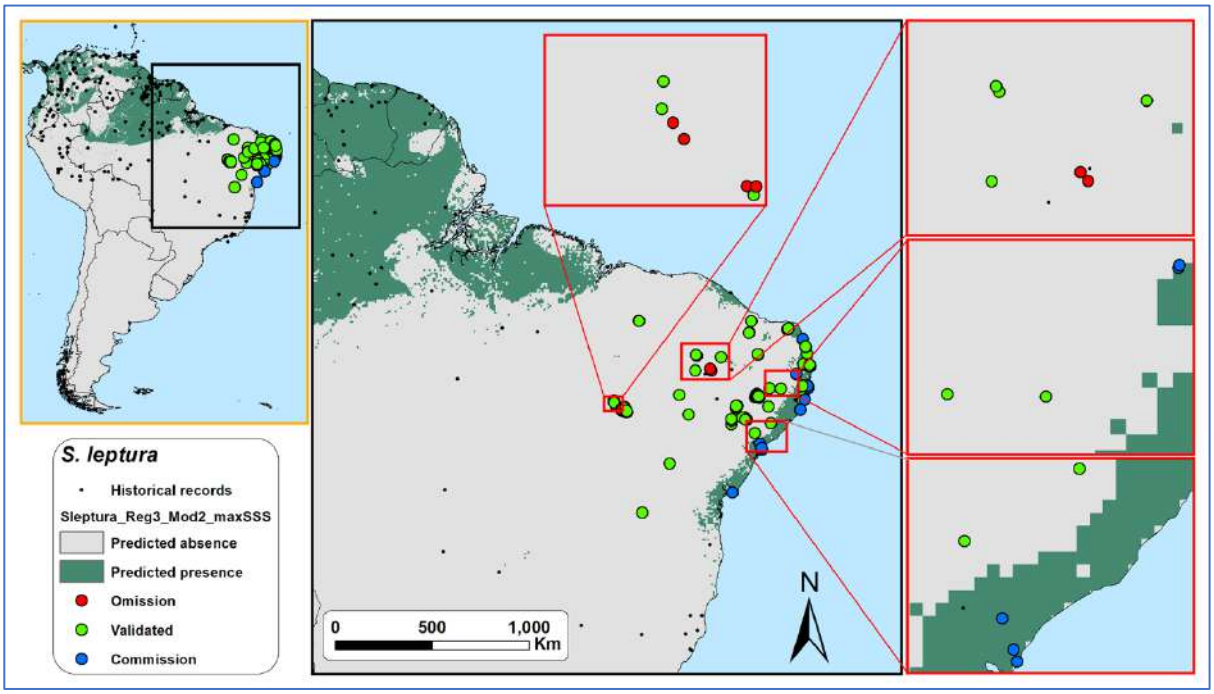
Saccopteryx leptura

Figure R - Field validation results for the binary maps with the highest accuracy, precision, and specificity scores for *Saccopteryx leptura* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



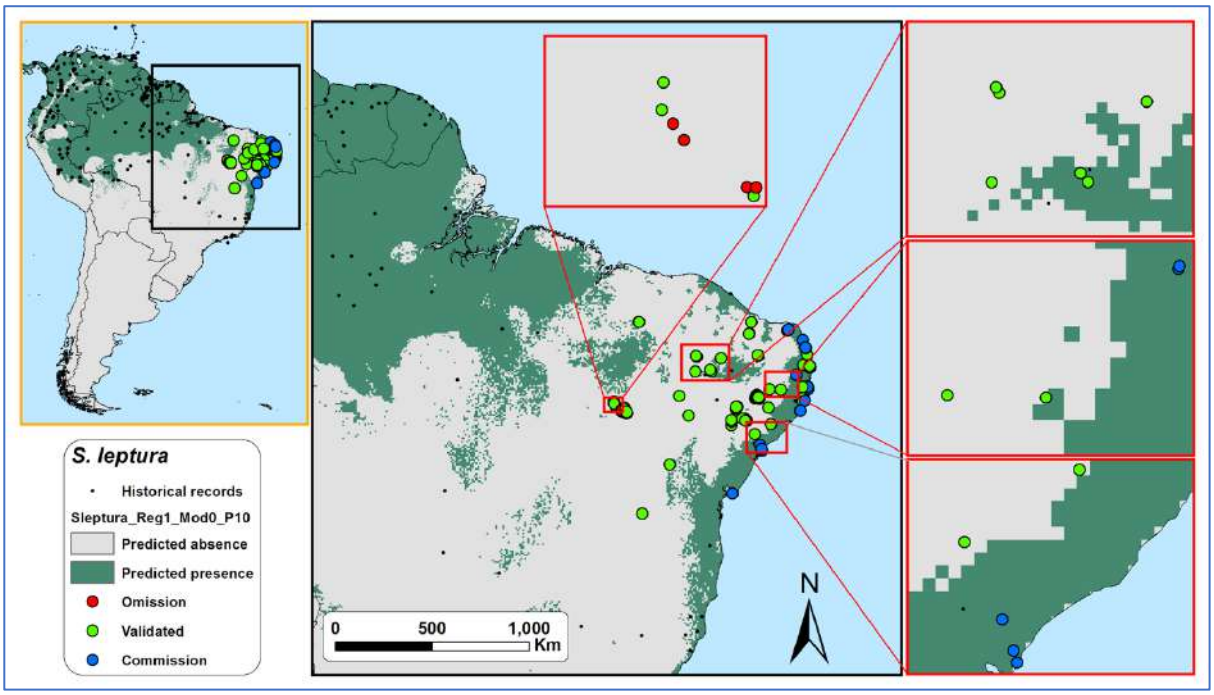
Fonte: Frederico Hintze (autor).

Figure S - Field validation results for the binary maps with the highest f-score score for *Saccopteryx leptura* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



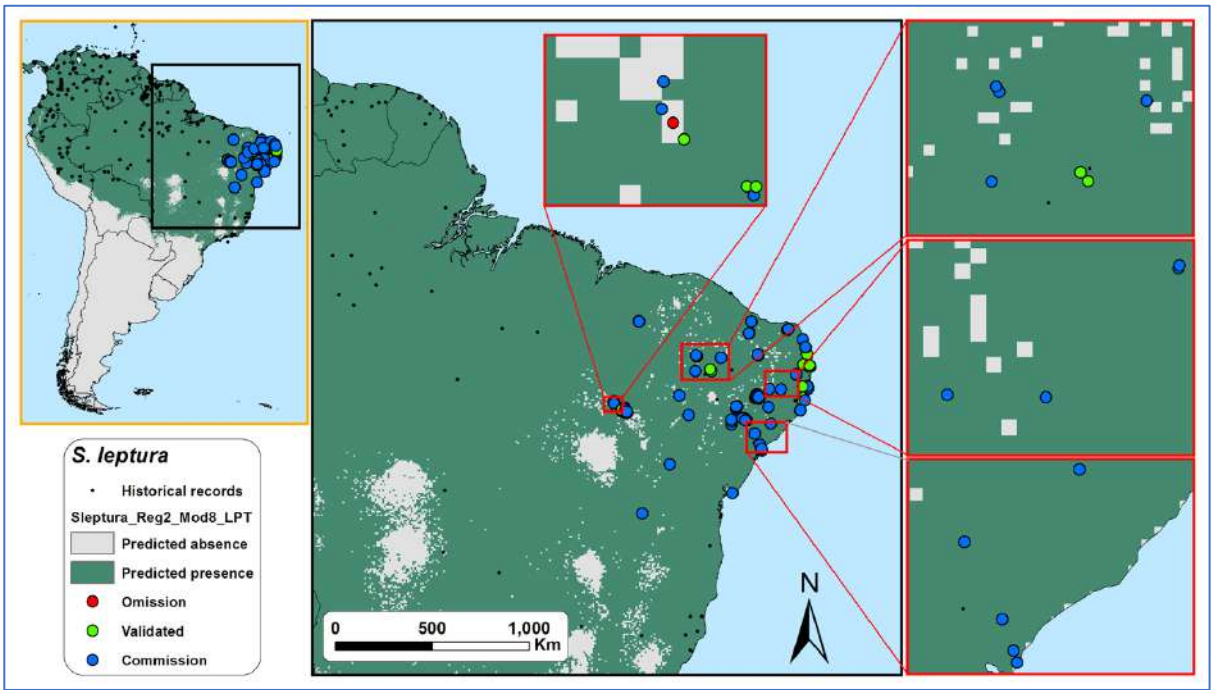
Fonte: Frederico Hintze (autor).

Figure T - Field validation results for the binary maps with the highest g-mean score for *Saccopteryx leptura* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



Fonte: Frederico Hintze (autor).

Figure U - Field validation results for the binary maps with the highest sensitivity score for *Saccopteryx leptura* in northeastern Brazil. See Fig. A caption for the omission, validation and commission points explanation.



Fonte: Frederico Hintze (autor).

4 CONCLUSÕES GERAIS E PERSPECTIVAS FUTURAS

Nesta tese demonstrei o ótimo desempenho dos métodos bioacústicos no estudo das espécies de morcegos do Brasil quando bem empregues, mas mostrei também que existem muitas lacunas e oportunidades neste assunto para se estudar e explorar no futuro. Para que erros básicos não sejam cometidos, e após a baixíssima acurácia dos softwares automatizados evidenciada neste estudo, há uma urgência na criação e adopção de protocolos de análise e monitoramento acústicos rigorosos. Além do treinamento de pessoal qualificado, a criação de bibliotecas regionais de vocalizações e de regras e protocolos mínimos adaptados para cada região irá permitir a maximização das potencialidades deste método no estudos dos morcegos. Durante este estudo, contribuí para um esforço de compilação de todas as informações disponíveis sobre as vocalizações conhecidas das espécies brasileiras, o que nos permitiu apontar quais espécies eram acusticamente reconhecíveis, potencial diversidade críptica e subsidiou a criação de uma chave de identificação acústica (ver anexo). Porém, para o uso pleno das potencialidades da bioacústica, ficou evidente que as lacunas no conhecimento acústico de algumas espécies necessitam ser preenchidas com urgência. Nesta tese avaliei também, com sucesso, três potenciais aplicações práticas da bioacústica (estudos de distribuição, na validação de mapas preditivos de distribuição das espécies e identificação de espécies abrigadas em cavernas). Oferecendo uma solução eficaz para as limitações dos métodos tradicionais utilizados nesse tipo de estudos, estes resultados demonstram inequivocamente que a bioacústica não pode mais ser desconsiderada no estudo de morcegos no Brasil. No que concerne à modelagem espacial da distribuição das espécies de morcegos, após os resultados obtidos nesta tese de doutorado, não parece mais ser razoável a criação de mapas preditivos sem de uma validação dos mesmos com dados independentes coletados em campo.

Com dados adquiridos através de bioacústica, será possível responder também como a grande maioria das espécies de morcegos ocorrendo no Brasil utilizam os habitats e como respondem às alterações nestes ambientes. Estas respostas poderão ser especialmente importantes em regiões subamostradas e impactadas, tal como o Nordeste Brasileiro. Além das espécies de morcegos cujas vocalizações são ainda desconhecidas, necessitamos também esclarecer a função das 'novas' vocalizações de *Promops centralis* que descrevi durante este projeto. Este aspecto pode fornecer-nos respostas valiosas no conhecimento da sua ecologia e resolver alguns questionamentos evolutivos da espécie. Com este projeto e parcerias ao longo de todo o Brasil, foi possível iniciar a construção da primeira biblioteca de vocalizações de

morcegos de âmbito nacional, disponível publicamente na página do comité de bioacústica da Sociedade Brasileira para o Estudo de Quirópteros (https://www.sbeq.net/bioacustica). No futuro, e ainda com dados recolhidos durante este projeto, será possível refinar áreas de distribuição de outras espécies cujas vocalizações são espécie-específicas e de identificação inequívoca. Através de gravações obtidas nesta tese, será também possível sinalizar casos de potenciais novas espécies (e.g. *Noctilio albiventris*) que necessitam ser esclarecidas no futuro, já que poderemos estar nos deparando com espécies endêmicas e de distribuição bastante restrita e, eventualmente, sob um grau variado de ameaça. Neste caso específico, e no âmbito desta tese, o impacto da pandemia de COVID-19 impossibilitou uma resposta cabal sobre cripticidade entre as populações da espécie *Noctilio albiventris* no Brasil. Porém, todas as potenciais respostas que advirão destes questionamentos futuros serão essenciais ao conhecimento ecológico e aos nossos esforços de conservação das espécies de morcegos neotropicais.

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ANEXO A - WHO'S CALLING? ACOUSTIC IDENTIFICATION OF BRAZILIAN BATS & ILLUSTRATED IDENTIFICATION KEY TO THE CALLS OF BRAZILIAN BATS

Publicado como parte do artigo "Who's calling? Acoustic Identification of Brazilian Bats" no periódico *Mammal Research* (volume 77, páginas 163-171), em 2018.

Nota: Embora o artigo tenha Adriana Arias-Aguilar como primeira autora, eu, como segundo autor, fui corresponsável pela compilação de toda a bibliografia na qual este artigo se baseia, assim como na criação e complementação das tabelas, gravações e espectrogramas incluídos no mesmo. Além disso, contribuí com dados acústicos, alguns deles inéditos, resultantes de cerca de 300 gravações de 27 taxa por mim realizadas. Especificamente, a chave de identificação acústica incluída neste trabalho é da minha autoria, com a importante colaboração dos restantes autores. A minha participação como coautor deste artigo foi também ativa nas várias fases de edição e revisão do manuscrito, e da sua informação durante todo o processo de submissão e pós *peer-review.*

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REVIEW ARTICLE

Who's calling? Acoustic identification of Brazilian bats

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Abstract
Brazil is a megadiverse country with more than 180 bat species. However, most inventories have been mostly made using mist-net sampling and roost search and due to the lack of bioacoustics studies, the bat fauna is certainly subrepresented and biased. The knowledge on distribution and ecology of Brazilian bats is mainly within the Phyllostomidae. Reliable data on bat echolocation calls is the key to improve the knowledge on the distribution patterns and foraging ecology of the remaining eight bat families present in the country. Our work aims to (i) integrate information on echolocation calls of non-phyllostomids occurring in Brazil; (ii) detect regional changes in the acoustic profile of those species; (iii) identify gaps in knowledge both in terms of species and regions sampled; and (iv) to point out which species are acoustically recognizable in a reliable way. Finally, we present a key to supporting the acoustic identification of non-phyllostomids in Brazil. We compiled publications on echolocation calls of Neotropical bat species occurring in Brazil and summarized qualitative and quantitative information of acoustic parameters used in call descriptions. We considered 93 non-phyllostomid bat species to occur in Brazil of which 65 have been acoustically described but for 28 we found no published information. Information on echolocation calls was retrieved from 47 publications and acquired in 17 countries. The use of bioacoustics can be a fundamental tool to expand the knowledge on Brazilian bats and improve their conservation.

Keywords Bat bioacoustics · Chiroptera · Echolocation calls · Insectivorous bats · Neotropical bats

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Introduction

With more than 9.5 million square kilometers, Brazil occupies more than 53% of South America and is considered a megadiverse country (Mittermeier et al. 1998; Lewinsohn and Prado 2005). More than 700 species of mammals are known to occur in Brazil (Paglia et al. 2012) and Chiroptera accounts for nearly 25% of those species. Currently, more than 180 species of bats are known in Brazil (Nogueira et al. 2014; Feijó et al. 2015; Fischer et al. 2015; Gregorin et al. 2016).

However, inventories of bat fauna in Brazil have been mostly made using mist-net sampling and roost search (Willig 1985; Sampaio et al. 2003; Bernard et al. 2011; see Alho et al. 2011 for more details), potentially leaving behind many species of difficult capture or species which require well-defined locations for capture by mist-nets (e.g., drinking sites and commuting corridors) or roosting in unknown or inaccessible sites (Rydell et al. 2002; Kunz and Parsons 2009). Most knowledge on distribution and ecology of Brazilian bats is within the Phyllostomidae which comprises 92 species (Nogueira et al. 2014) while there is still a significant lack of knowledge on the ecology and distribution of the remaining eight families occurring in the country—Emballonuridae, Furipteridae, Molossidae, Mormoopidae, Natalidae, Noctilionidae, Thyropteridae, and Vespertilionidae (Cunto and Bernard 2012).

Phyllostomids are much more easily captured using mist-nets and are known to use a combination of clues to explore the environment, including echolocation, olfaction and vision, while species of the other families use almost exclusively echolocation to navigate and find prey (Kalko and Schnitzler 1998; Schnitzler et al. 2003; Denzinger and Schnitzler 2013). Ecologically, most of these bats fall into the category of aerial foragers (Kalko et al. 2008); in fact, the only exceptions to this pattern are Noctilionids, which are trawling foragers, and the Mormoopid *Pteronotus* cf. *parnellii*, which is a narrow space-fluttering forager(Denzinger and Schnitzler 2013). Therefore, non-phyllostomid bat species have specialized echolocation calls and are able to easily detect and avoid mist-nets or fly too high to be captured by these (Kalko and Handley 2001; Marques et al. 2015). Due to the lack of bioacoustics studies in Brazil (but see López-Baucells et al. 2016), the bat fauna inventories are certainly subrepresented (e.g., Bernard et al. 2011) and biased (e.g., Cunto and Bernard 2012).

In temperate regions, the use of ultrasound detectors to assess bat diversity has a few decades and is widespread (Ahlén and Baag 1999; Kunz and Parsons 2009). Curiously, although Neotropical bats have been the object of acoustic studies since the mid-1960s (see Grinnell et al. 2016), only recently, researchers started to use bioacoustics as a monitoring tool in that region systematically (Jung and Kalko 2011; Marques et al. 2015; Hintze et al. 2016c). Still, these studies have been restricted to a few localities in some countries: Mexico (e.g., Briones-Salas et al. 2013; Kraker-Castañeda et al. 2013; Orozco-Lugo et al. 2013; Zamora-Gutierrez et al. 2016), Panama (see the works of Elisabeth Kalko and collaborators; Estrada-Villegas et al. 2012; Bader et al. 2015; Gager et al. 2016), Honduras (Espinal and Mora 2015), Costa Rica (e.g., Jung et al. 2014; Arias-Aguilar et al. 2015), French Guiana (e.g., Barataud et al. 2013; Thoisy et al. 2014), Ecuador (e.g., Rivera-Parra and Burneo 2013), Chile (e.g., Rodríguez-San Pedro and Simonetti 2013; Ossa et al. 2015), and Brazil (Borloti et al. 2014; Heer et al. 2015; Marques et al. 2015; Hintze et al. 2016c).

Early descriptions of echolocation bat calls made in the Neotropics were mostly from Central America and Venezuela. Moreover, most used zero-crossing recording systems (aka ANABAT; e.g., O'Farrell and Miller 1997; O'Farrell et al. 1999; Ochoa et al. 2000), which although useful, usually, results in a lack of the resolution of some of the calls' variables and the lack of information about the time amplitude of the calls and multiple harmonics if present (e.g., Fenton et al. 1999, 2001).

Recently, there has been an increase in the description of ultrasound bat calls, with larger datasets and important additions to the knowledge of some bat families such as the Emballonuridae and the Molossidae (Jung et al. 2007; Jung et al. 2014). In 2013, Barataud et al. (2013) published a comprehensive compilation of echolocation calls of French Guiana bats, including species of the Emballonuridae, Furipteridae, Molossidae, Mormoopidae, Natalidae, Noctilionidae, Thyropteridae, and Vespertilionidae. These authors found the identification of the species of those families reasonably reliable using ultrasound recordings while considering the Phyllostomidae acoustically too homogeneous, deeming this family problematic to identify using bat detectors. Descriptions for call belonging to 38 non-phyllostomids bats are available (Jung et al. 2007; Barataud et al. 2013; Jung et al. 2014), but a close comparison with the Brazilian species list indicates that echolocation calls of *ca*. 60 species of non-phyllostomids remains to be described.

Reliable data on bat echolocation calls is a key to improve the knowledge on the distribution patterns and foraging ecology of non-phyllostomids in Brazil. In addition, changes in Brazilian federal and state laws have led to an increase of demands of bat inventories in Environmental Impact Assessments (EIA) using comprehensive sampling schemes including mist-net captures, roost searches, and acoustic monitoring; the use of acoustic monitoring has been required, or at least suggested in some states (Ramos Pereira et al. 2017) especially for impact assessments of wind farms (Valença and Bernard 2015). Acoustic monitoring is a fundamental tool in EIA in several countries (Government of Alberta Fish and Wildlife Division 2006; Ontario Ministry of Natural Resources 2011; Rodrigues et al. 2015), underlining the need to better know the acoustic profile of Brazilian bats. Moreover, acoustic monitoring can be very useful in the study of spatial-temporal activity and habitat use, niche differentiation, foraging behavior, species distribution, and even the

discovery of cryptic diversity (e.g., Vaughan et al. 1997; Arlettaz et al. 2001; Greif and Siemers 2010; Russo et al. 2012; Thoisy et al. 2014; Hintze et al. 2016b, c).

Therefore, considering the high bat species richness in Brazil, the need for the use of bioacoustics for several purposes in the country—some with legal implications, like incomplete EIA—and the lack of a systematized data bank on the echolocation calls of several Brazilian bats, here we aim to (i) integrate information on echolocation calls of non-phyllostomids occurring in Brazil from published works and our own data; (ii) detect acoustic variation and possible regional changes in the acoustic profile of those species; (iii) identify gaps in knowledge both in terms of species and regions sampled; and (iv) to point out which species are acoustically recognizable in a reliable way. Finally, we present a key to supporting the acoustic identification of non-phyllostomids in Brazil.

Methods

We looked for publications containing quantitative information on echolocation call parameters or pulse descriptions for bat species potentially identifiable through their echolocation calls known to occur or potentially occurring in Brazil (Nogueira et al. 2014; Feijó et al. 2015; Fischer et al. 2015; Gregorin et al. 2016) according to their known distribution. All selected publications included information on bat families of the Neotropical region except the Phyllostomidae. We used the Internet search engine Google Scholar. Our search terms included the union of the terms "Chiroptera," "bat," and "insectivorous," with "acoustic identification," "echolocation calls," "recordings," "bioacoustics" and so forth. We used no date range restriction. We retrieved all quantitative (frequency and time parameters) and qualitative information (type and structure) of search echolocation calls as it was reported in the literature, and then we summarized them by species (parameter selection varied per family according to the relevance for identification purposes). For several species, we also included unpublished acoustic information from our own recordings. We used CallViewer18 (Skowronski and Fenton 2008) Auto Detection function using a Hamming window, FFT = 1024, windows length of 1 ms, and a background threshold of 10 dB, to obtain the acoustic parameters of the search phase calls of the echolocation call sequences. All figures (spectrograms and oscillograms) were created with the Avisoft SasLabPro Software (Version 5.2.09, Raimund Specht, Berlin), using a Hamming window, FFT = 512 and overlap 93%, from our own or donated recordings obtained mainly in Brazil.

For each species and study, we retrieved information on year of publication, recording method, and recording location. We collected information on the conservation status of all species using the IUCN (2016) database. Then, we calculated the number of publications per family and region and counted the number of times each species had been acoustically studied.

While all bat species occurring in the New World do not occur anywhere else, many species occurring in Brazil present wide distribution ranges, ranging from South to North America. For this reason, regions of origin of publications were defined as North, Central, and South America; Caribbean Islands; and their respective main classes of Köppen climate classification: tropical, arid, warm temperate, and cold climate (Peel et al. 2007).

Acoustic information

We considered 93 non-phyllostomid bat species to occur in Brazil. Information on echolocation calls of those species was retrieved from 47 publications ranging between 1997 and 2016 and acquired in 17 countries (Appendix 1). Of the list of 93 species, 65 have been acoustically described but for 28 we found no published information.

Most publications came from tropical region of Central, South (14 publications each), and North America (eight publications), warm temperate North American region (seven publications), Caribbean Islands (five publications), arid North American region (four publications). Accounting the fewest publications were the arid and the warm temperate South American regions (two publications each). Detailed information on the origin and composition of the information used for each bat family is provided below.

Emballonuridae

Echolocation calls of 15 species have been described in the literature (Table 1). Most described species were *Saccopteryx bilineata*, *Peropteryx macrotis*, and *Saccopteryx leptura*. We did not find any acoustic information for *Diclidurus isabella*, *Peropteryx leucoptera* and *Peropteryx pallidoptera*. For some species information on echolocation calls were given as a complex including *Diclidurus scuttatus/albus* and *Centronycteris maximiliani/centralis*. IUCN (2016) data and (Nogueira et al. 2014) recognize only one species of the genus *Centronycteris* in Brazil: *C. maximiliani*. However, comparisons of our own data collected in the state of Pernambuco with that of Jung et al. (2007), Jung and Kalko (2011), and (Barataud et al. 2013) suggest the existence of *Centronycteris centralis* at least in the northeastern region of the Brazilian territory. For this reason, we decided to consider this species as potentially occurring in Brazil. We also included information from our own recordings of potentially new species of *Saccopteryx* and *Peropteryx*.

Echolocation calls of this family are multi-harmonic, with most energy (peak frequency or frequency of maximum energy (FME)) in the quasi-constant frequency (qCF) part of second harmonic (Table 1 and Fig. 1). Sometimes, but rarely, *Diclidurus*, *Saccopteryx*, and

Table 1 Summary of echolocation call parameters as retrieved from the literature and our own data for species of the Emballonuridae known to occur, or potentially occurring, in Brazil, with information on region of recording and IUCN status of each species

Species	IUCN status	Region	Structure	Call type	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	CD (ms)	PI (ms)	SI
Cenmax (?)	LC	SA-Tr	Qcf/fm down	mono			40.6 (39–41.3)					3
			fm up/qcf/fm down (qcf convex)				41.5 ± 0.2	38.1 ± 1.1	41.6 ± 0.3	5.2 ± 0.4	154.8 ± 56.9	17
Cenmax/cen		SA-Tr	Convex qcf up with 2 fm down	single			~ 40					25
Cencen	LC	NA-Tr						39.29 ± 0.61	41.63 ± 0.37	6.98 ± 0.73		8
		CA-Tr	Straight				41.3 ± 0.3			5.9 ± 1.4	119 ± 10	20 21
							43.5					44
Corbre	LC	CA-Tr	Qcf up	low			25.2 ± 1.5			8.2 ± 2.0	119 ± 45	20 21
				middle			28.1 ± 0.6			8.2 ± 1.8	100 ± 21	
				high			31.4 ± 0.4			8.6 ± 1.6	107 ± 38	
							25 28 31					44
		SA-Tr	Qcf convex	low			26 (24.5–26.5)					3
				middle			29.4 (27.5–30)					
				high			32.3 (30.5–33.5)					
					29.39 (27.43–31.89)	30.11 (27.09–34.52)	31.36 (29.59–33.67)	29.01 (27.09–31.70)	32.52 (30.39–35.31)	11.97 (9.03–11.97)		38
			Convex qcf up with 2 fm down	low			~ 25					25
				middle			~ 28					
				high			~ 30					
Cytale	LC	CA-Tr	Qcf up				35.9 ± 0.4			9.8 ± 1.6	154 ± 22/265 ± 68	20 21
		SA-Tr	Qcf	mono			35.4 (34.5–35.4)					3
		SA-Tr	Convex qcf up with 2 fm down	single			~ 35					25
Dicalb	LC	CA-Tr	Qcf (down)	low			23.5 ± 0.3			9.4 ± 4.7/9.6 ± 5.7	162 ± 28/317 ± 43	20 21
				middle			25.8			9.7	249	
Dicing	DD	SA-Tr	Qcf	low			19.6 (18.8–21.8)					3
				high			21.8 (20.3–23.3)					
			Convex qcf down with 2 fm down	low			~ 19					25
				high			~ 22					
Dicisa	LC											
Dicscu/alb	LC	SA-Tr	Qcf/ fm down	low			26.5 (24.7–29.4)					3
				high			30.6 (27.8–31.2)					
			Convex qcf down with 2 fm down	low			26					25
				high			30					
Perkap	LC	CA-Tr	Qcf (down)				31.6 ± 1.6			9.6 ± 2.2	170 ± 34/280 ± 31	20 21
		SA-Tr	Qcf	mono			31.3 (30.7–33)					3
			Convex qcf down with 2 fm down	single			~ 29–33					25
Perleu	LC											
Permac	LC	NA-Tr-Ar-WT			41.71 ± 2.49 (5.97)	37.56 ± 2.32 (6.18)	41.61 ± 2.38 (5.72)	37.54 ± 2.30 (6.13)	41.87 ± 2.48 (5.92)	7.30 ± 1.30 (17.81)		47
		NA-Tr-Ar	Cf/start or end shallow down-sweeps				38.6 ± 0.4	33.1 ± 1.4		5.2 ± 0.5		40
		NA-Tr						35.56 ± 0.86	38.81 ± 0.41	6.14 ± 1.98		8
							39.6 ± 1.8	39.1 ± 1.8	40 ± 1.8	8.8 ± 1.2	152 ± 59.5	28
		CA-Tr	Qcf (down)				38.9 ± 0.9			9.3 ± 1.0	139 ± 14/215 ± 34	20 21
		SA-Tr	Qcf	mono			38.4(36.7–39.7)					3
			Convex qcf down with 2 fm down	single			~ 37–39					25
					38.15 (36.56–40.21)	36.33 (32.46–39.52)	39.58(37.50–42.58)	36.0 (32.46–39.04)	40.16 (39.12–42.62)	7.29 (4.85–10.69)		38
			(fm up)/qcf/fm down	mono			39.2 ± 0.7	37.2 ± 1.1	39.5 ± 0.9	8.2 ± 2.3	193.2 ± 123.3	°
Perpal	NA											
Pertri	LC	SA-Tr	Qcf/ fm down	mono			43.9					3
				single			~ 42–44					25

Table 1 (continued)

Species	IUCN status	Region	Structure	Call type	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	CD (ms)	PI (ms)	SI
			Convex qcf down with 2 fm down									
			Fm up-qcf down-fm down	mono			43.5 ± 0.8	40.4 ± 1.1	43.8 ± 0.7	5.9 ± 1.1	98.3 ± 21.8	°
Per sp.	NA	SA-Tr	Fm up-qcf down-fm down	mono			41.4 ± 0.5	38.8 ± 0.8	41.6 ± 0.6	7.1 ± 1.4	112.3 ± 24.4	°
Rhynas	LC	NA-Tr-Ar-WT			98.25 ± 1.16 (1.18)	81.84 ± 4.88 (5.96)	95.79 ± 4.45 (4.65)	81.84 ± 4.88 (5.96)	98.71 ± 1.03 (1.04)	4.38 ± 0.69 (15.75)		47
		CA-Tr						40.2 (0.53)	47.2 (0.06)	6.7 (0.12)	60.8(2.99)	29
			Straight/up				98.2 ± 2.3			4.8 ± 0.9	58 ± 12	21
		SA-Tr	Qcf/ fm down	mono			95.6(80.2–98.2)					3
			Straight/up	mono			89.6 ± 0.5	88.1 ± 0.6	91.0 ± 1.0	5.6 ± 0.3	74.5 ± 50.0	°
					93.65 (93.19–94.0)	77.0 (73.75–81.49)	87.34(83.53–93.83)	77.0 (73.75–81.49)	94.27 (94.03–94.61)	5.89 (5.17–6.70)		38
		CI-Tr		a			51.3 ± 0.8	42.2 ± 1.4	52.2 ± 0.9	5.3 ± 1.0	29.3 ± 13.7	35
				b			100 ± 2.0	74.8 ± 7.6	101.3 ± 1.6	5.9 ± 1.2	25.9 ± 6.7	
Sacbil	LC	NA-Tr-Ar-WT			45.38 ± 8.10 (17.85)	45.78 ± 4.60 (10.05)	47.29 ± 5.68 (12.01)	44.10 ± 5.11 (11.59)	48.55 ± 7.33 (15.1)	7.40 ± 1.58 (21.35)		47
		NA-Tr		low			44.5 ± 0.7	43.7 ± 0.7	45 ± 0.8	9.2 ± 1.1	181.1 ± 33.56	28
				high			46.8 ± 0.8	46 ± 0.8	47.2 ± 0.8	8.8 ± 1.0	180.3 ± 39.07	
								44.24	47.41			23
		CA-Tr		a				44.5 (0.21)	46.6 (0.18)	6.7 (0.21)	55.8 (1.85)	29
				b				46.6 (0.19)	48.6 (0.17)	6.6 (0.15)	82.5 (3.09)	
								45.1 ± 2.02	47.0 ± 2.35	6.1 ± 1.58		30
			Qcf up	low			44.5 ± 1.3			7.5 ± 1.5	73 ± 17	20 21
				middle			46.8 ± 1.1			7.6 ± 1.3	105 ± 25	
							45 48					44
				alternating			45			8.26 ± 0.22	60.9 ± 5.9	37
							48			8.22 ± 0.18	88.0 ± 4.9	
				monotonous			48			6.43 ± 0.16	93.0 ± 4.4	
		SA-Tr	Qcf convex	low			42.1(41.2–42.2)					3
				high			44.1(44–44.3)					
					43.73 (42.89–44.28)	43.89 (43.17–44.73)	46.46(46.04–46.81)	43.41 (42.59–43.96)	46.81 (46.51–47.08)	7.22 (6.65–7.84)		38
			Fm up/qcf/fm down (qcf convex)	low			45.0 ± 0.7	41.3 ± 1.6	46.3 ± 0.9	8.3 ± 1.9	75.3 ± 11.1	17
				high			47.9 ± 0.6	45.0 ± 0.7	49.3 ± 0.7	8.6 ± 1.4	53.5 ± 12.6	
			Convex qcf up with 2 fm down	low			~ 42					25
				high			~ 45					
		CI-Tr					42 ± 1.6	32.8 ± 3.2	43.9 ± 1.4	5.2 ± 1.1	56.2 ± 24.2	35
Saccan	LC	SA-Tr	Qcf/ fm down	mono			52.5(52.3–54.3)					3
Saccan/gym		SA-Tr	Convex qcf up with 2 fm down	single			~ 54					25
Sacgym	DD	SA-Tr	Qcf/ fm down	mono			53.9					3
Saclep	LC	NA-Tr-Ar-WT			48.35 ± 2.98 (6.16)	47.69 ± 3.77 (7.91)	50.58 ± 2.48 (4.9)	46.66 ± 3.84 (8.23)	51.27 ± 2.50 (4.88)	6.78 ± 2.28 (33.63)		47
		CA-Tr	Qcf up	low			51.3 ± 1.8			7.2 ± 1.5	68 ± 24	20 21
				middle			54.61 ± 1.8			6.8 ± 1.2	90 ± 28	
							52.5 55.5					44
		SA-Tr	Qcf convex	low			47.4(46.6–48.7)					3
				high			49.8(48.5–50.4)					
					51.47 (50.97–51.93)	52.5 (51.75–53.20)	53.31(53.54–54.25)	51.16 (50.58–51.64)	54.52 (54.27–54.79)	6.76 (6.25–7.32)		38
			Convex qcf up with 2 fm down	low			~ 48					25
				high			~ 55					
			Fm up/qcf up/fm down (qcf convex)	low			48.2 ± 0.6	44.5 ± 2.8	49.5 ± 0.6	7.3 ± 1.5	76.6 ± 16.7	°
				high			50.2 ± 0.3	48.2 ± 0.6	51.9 ± 0.8	5.8 ± 0.5	49.6 ± 8.5	
		CI-Tr					51.1 ± 1.2	42.9 ± 1. + 3	53.3 ± 1.4	4.9 ± 1.1	66.7 ± 30.2	35

SF start frequency, *EF* end frequency, *FME* frequency of maximum energy, *LF* lowest frequency, *HF* highest frequency, *CD* call duration, *PI* pulse interval, *SI* reference number and species name abbreviations in Appendix 1

Rhynchonycteris can produce calls with FME on the fundamental harmonic. With the exception of *Rhynchonycteris naso*, pulses are usually narrow band. Genera *Cormura*, *Diclidurus*, and *Saccopteryx* present frequency alternation but one of the pulses may be omitted at some circumstances, e.g., when foraging close to their roost. The other genera produce monotone frequency calls. Peak frequency, the direction of call modulation, and the presence of alternation are important parameters for species identification (O'Farrell and Miller 1999; Jung et al. 2007; Barataud et al. 2013; see Appendix 2 for further details).

Furipteridae

Furipterus horrens is found from Costa Rica to Peru, the Guianas, Brazil, and Trinidad (Nowak 1994; Simmons et al. 2005; Novaes et al. 2012). Nevertheless, acoustic information on this species was compiled only from four localities of the tropical and warm temperate South American regions (three and one publication, respectively; Table 2 and Fig. 2). However, the authors were not aware of the very high frequencies emitted by this species, so the recorded calls presented some artifacts due to aliasing—to accurately measure the frequency of any signal, the sampling rate of the equipment must be at least double of that frequency; otherwise the signal will be aliased, or false images of the signal will be created as mirror images of the original frequency. This situation is called "aliasing back" or "folding back" and can be seen in Fig. 2, where the highest frequencies of the calls were not registered (Falcão et al. 2015).

Echolocation calls of this species present FME in the fundamental harmonic and above 100 kHz. Pulses are broadband with steep modulation and show an inflection point (Appendix 1).

Natalidae

Natalus macrourus is the only species of this family reported to occur in Brazil (Garbino and Tejedor 2013; Tejedor and Davalos 2016; Delgado-Jaramillo et al. 2017). Even if widely distributed in the country (Rocha et al. 2013; Delgado-Jaramillo et al. 2017), there is no published acoustic information for this species. Besides, *Natalus tumidirostris* occurs north of the Amazon River (Garbino and Tejedor 2013) and has been acoustically described in French Guiana (Barataud et al. 2013). So we consider this species to potentially occur in Brazil; also, information on the echolocation call parameters of *N. tumidirostris* (Table 2 and Fig. 2) may give some insight on the acoustic profile of *N. macrourus*. In this paper, we present the first spectrogram (Fig. 2) and describe quantitative information on echolocation call parameters for *N. macrourus* recorded in Northeastern Brazil.

Echolocation calls of this family present FME in the second harmonic and above 100 kHz. Pulses are steep modulated with a very short qCF termination (Appendix 2 and Fig. 2).

Thyropteridae

The genus *Thyroptera* occurs from Mexico to south Brazil (Simmons et al. 2005; Passos et al. 2010). In spite of its wide distribution, acoustic information on the species of the genus is very limited. Echolocation calls are described only for two of the five species occurring in Brazil: *Thyroptera tricolor* (from three localities including French Guiana, Mexico and Ecuador), and *Thyroptera discifera* (from French Guiana) (Table 2 and Fig. 2). Knowledge of the echolocation calls of the remaining species (*Thyroptera devivoi*, *Thyroptera lavali*, and the recently described *Thyroptera wynneae*) (Velazco et al. 2014) is inexistent.

Echolocation calls of this family can present FME in the fundamental or in the second harmonic. Pulses show elevated initial amplitude and are of short duration (< 4 ms) (Appendix 2).

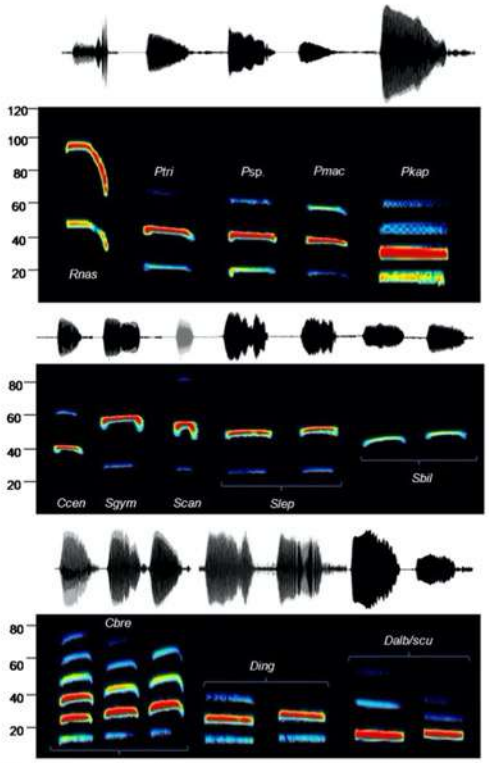

Fig. 1 Echolocation calls for species of the Emballonuridae known to occur, or potentially occurring, in Brazil. Call duration and pulse intervals are not scaled. Rnas *Rhynchonycteris naso*, Ptri *Peropteryx trinitatis*, Psp *Peropteryx* sp., Pmac *Peropteryx macrotis*, Pkap *Peropteryx kappleri*, Ccen *Centronycteris centralis*, Sgym *Saccopteryx gymnura*, Scan *Saccopteryx canescens*, Slep *Saccopteryx leptura*, Sbil *Saccopteryx bilineata*, Cbre *Cormura brevirostris*, Ding *Diclidurus ingens*, Dalb/scu *Diclidurus albus/scutatus*

Table 2 Summary of echolocation call parameters as retrieved from the literature and our own data for species of the Furipteridae, Natalidae and Thyropteridae known to occur, or potentially occurring, in Brazil, with information on region of recording and IUCN status of each species

Species	IUCN	Region	Call type	Structure	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
Furhor	LC	SA-Tr	I				161.3 ± 10.3	128.6 ± 7.6	190.5 ± 3.1	61.9 ± 8.5	3.7 ± 0.5		11
			II				158.4 ± 12.7	122.8 ± 14.5	191.2 ± 2.7	68.4 ± 14.9	2.6 ± 0.5	13.1 ± 7.5	
			II				157.2 ± 14.4	135.1 ± 6.6	191.3 ± 1.7	56.2 ± 6.6	2.3 ± 0.5	15 ± 1.1	
				Steep fm			152 ± 9.6				3.8 ± 0.7		3
				Fm			130–170						25
		SA-WT						120	150		< 1		12
Natmac	NT												
Natlun	LC	SA-Tr	H1	Qcf-fm-qcf			120.2± 5.8			77.4 ± 29.5	3.5 ± 0.1		3
Thydec	DD												
Thydis	LC	SA-Tr	FH	Fm			53 ± 2.7				2.9 ± 0.5		3
			H1	Fm			112.5 ± 7.3				2.5 ± 0.3		
Thylav	DD												
Thyri	LC	NA-Tr-Ar-WT			66.38 ± 2.02 (3.04)	43.50 ± 1.87 (4.30)	53.09 ± 2.46 (4.63)	43.50 ± 1.87 (4.3)	66.38 ± 2.02 (3.04)	22.88 ± 2.32 (10.14)	2.76 ± 0.37 (13.41)		47
		SA-Tr			123.26 (116.93–127.14)	91.95 (89.64–96.66)	103.12 (98.70–108.83)	91.95 (89.64–96.66)	123.26 (116.93–127.14)	31.31 (25.94–37.19)	1.1 (0.78–1.30)		38
			H1	Fm			51 ± 2.2				3.2 ± 0.4		3
Thyoyn	NA												

SF start frequency, *EF* end frequency, *FME* frequency of maximum energy, *LF* lowest frequency, *HF* highest frequency, *BW* bandwidth, *CD* call duration, *PI* pulse interval, *SI* reference number and species name abbreviations in Appendix 1

Molossidae

Twenty-one species occurring in Brazil have been acoustically described in 24 publications mostly originated in the tropical South, North, and Central American regions (Table 3 and Fig. 3). Only one publication including molossids was found for the warm temperate South American region and two for the Caribbean Islands.

Molossus molossus, *Molossus rufus*, and *Tadarida brasiliensis* were the most studied within the family (Table 3). We found no information on the echolocation calls of 11 species registered or possibly occurring in Brazil: *Cynomops mastivus*, *Eumops bonariensis*, *Eumops delticus*, *Eumops hansae*, *Eumops maurus*, *Eumops patagonicus*, *Eumops trumbulli*, *Molossus aztecus*, *Molossus pretiosus*, and *Nyctinomops aurispinosus*. If we follow Moras et al. (2016), *Cynomops paranus* described by Barataud et al. (2013) could relate to *Cynomops milleri*. However, if these are not synonyms, then the echolocation calls of *C. milleri* remain non-described.

We considered *C. mastivus*(Moras et al. 2016), *Eumops dabbenei*, *Eumops nanus* (Bartlett et al. 2013) and *Eumops patagonicus* (Bernardi et al. 2009) as full species. Also, we considered *Molossus barnesi* as a synonym of *Molossus coibensis* (Catzeflis et al. 2016).

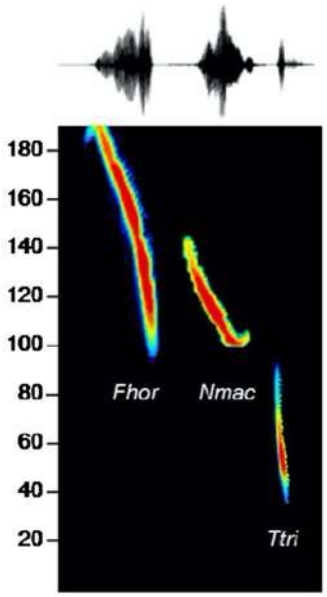

Fig. 2 Echolocation calls for species of the Furipteridae, Natalidae, and Thyropteridae known to occur, or potentially occurring, in Brazil. Call duration and pulse intervals are not scaled. Fhor *Furipterus horrens*, Nmac *Natalus macrourus*, Ttri *Tyroptera tricolor*

Table 3 Summary of echolocation call parameters as retrieved from the literature and our own data for species of the Molossidae known to occur, or potentially occurring, in Brazil, with information on region of recording and IUCN status of each species

Species	IUCN	Region	Call type	Structure	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
Cynabr	LC	SA-Tr	Low	Qcf			22.3 (18.8–26.5)				12.5 (9–20)		3
			Middle				30 (28.2–32)				10.2 (7.7–14.8)		
Cyngre/abr		SA-Tr	Low	Sinuous qcf		~17							25
			High	down		~21							
Cyngre	LC	CA-Tr		Qcf down			21–24						20
		CA_SA-Tr	Low		25.2 ± 1.3	17.4 ± 3.6				7.8 ± 3.1	15.9 ± 2.1	297.2 ± 115.0	22
			High		29 ± 1.5	21.1 ± 4.6				7.9 ± 4.1	14.8 ± 2.4	190.3 ± 61.0	
Cynmas													
Cynmil	NA												
Cynpar	DD	SA-Tr	Low	Qcf			26.5 (23.1–27.8)				15.5 (10.2–18.1)		3
			Middle	Fm down/qcf			31.6 (27.8–32.4)				13.9 (10.8–17.3)		
Cynpar/plan		SA-Tr	Low	Sinuous qcf		~21							25
			High	down		~24							
Cynplan	LC	CA-Tr		Qcf down			25–28						20
		CA_SA-Tr	Low		28.8 ± 1.3	21.1 ± 2.4				7.6 ± 1.9	16.1 ± 1.9	236.4 ± 79.1	22
			High		32.9 ± 1.1	24.3 ± 4.6				8.7 ± 4.5	15.9 ± 2.3	165.1 ± 50.8	
		SA-Tr	Low	Qcf concave/ convex			27.8 (24.7–30.7)				13.6 (9.9–17.1)		3
			Middle	Steep fm			33.9 (32.4–35.8)				10 (6.9–13.3)		
Eumaur	LC	CA_SA-Tr	Low	Fm qcf down	32.4 ± 4.3	18.2 ± 1.6				14.3 ± 3.9	20.3 ± 6.9	269.4 ± 68.9	22
			High		35.8 ± 4.1	21.9 ± 1.6				13.8 ± 4.0	19.3 ± 4.0	215.9 ± 61.0	
		SA-Tr	Low	Qcf concave			18.7 (17.3–21.8)				21.8 (19–27.4)		3
			Middle	Fm down/qcf			23.3 (20.1–25.7)				19.5 (15.1–23.4)		
			High				26.7 (26.3–27)				18.4 (17.5–19.3)		
Eumbon	LC												
Eumnan		CA_SA-Tr	Low	Fm qcf down	27.9 ± 0.1	25.2 ± 0.2				2.8 ± 0.3	15.6 ± 2.4	294.6 ± 32.1	22
Eumdab	LC	CA_SA-Tr	Low	Fm qcf down	21.3 ± 1.2	13.7 ± 0.5				7.6 ± 1.1	28.3 ± 2.8	379.9 ± 123.6	22
			High		24.6	15.8				8.9	25.6	332.7	
Eumdel	LC												
Eumgla	LC	CA_SA-Tr	Low	Fm qcf down	27.4 ± 3.4	19 ± 0.4				8.4 ± 3.5	16.2 ± 4.5	321.1 ± 102.7	22
			High		29.3 ± 4.2	20.3 ± 0.3				8.9 ± 4.1	16.7 ± 4.5	270.9 ± 92.8	
Eumhan	LC												
Eummau	DD												
Eumpat	LC												
Eumper	LC	NA-WT-Sn		Simple sweeps with slight curvature			13.2	9.4	19.8		15.4		18
		NA-WT					7.4 (5.0)	6.8 (4.0)	8.2 (5.9)		57.9 (39.4)	1369 (21.5)	1
Eumtru	LC												
Eumaur/gla/ dab/han/mau		SA-Tr	Low	Concave qcf		~18	<30						25
			High			~22							
Molneg	DD	CA_SA-Tr	Low	Fm up qcf	32.5 ± 3.3	44.3 ± 1.9				11.8 ± 1.9	10.5 ± 0.9	107.2 ± 3.8	22
			High		38.3 ± 2.4	46.9 ± 0.8				8.5 ± 3.0	9.4 ± 0.4	107 ± 17.1	
			High II	Fm down qcf	56.2 ± 2.9	48.9 ± 0.2				7.3 ± 3.0	6.1 ± 1.3	62.2 ± 6.5	
		SA-Tr	Low	Convex qcf up		~44							25
			High	Concave qcf down		~46							
Moltem	LC	CA_SA-Tr	Low	Fm up qcf	42.8 ± 2.6	54.2 ± 1.2				11.4 ± 1.7	8.3 ± 1.2	79.3 ± 5.4	22
			High		45.5 ± 2.4	54.8 ± 1.4				9.3 ± 1.5	7.6 ± 1.1	82.9 ± 3.8	
			High II	Fm down qcf	75.9 ± 9.9	55.4 ± 1.5				20.5 ± 10.3	7.2 ± 1.0	55.2 ± 3.9	
		SA-Tr		Fm up	40.4 ± 3.5	50.4 ± 1.5	50.4 ± 1.4narrow/ 45.1 ± 2.6 broad			10.3 ± 3.1	7.8 ± 1.6	97 ± 29.9	15
			Closed space	Fm up			51.30 ± 0.18	44.06 ± 0.43	52.92 ± 0.21	8.86 ± 0.41	3.99 ± 0.35	61.76 ± 4.33	31
				Fm down			52.99 ± 0.22	40.08 ± 0.27	66.30 ± 0.21	26.21 ± 0.34	2.05 ± 0.02	47.48 ± 0.97	

Table 3 (continued)

Species	IUCN	Region	Call type	Structure	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
			Hand release	Fm up			49.38 ± 0.15	43.98 ± 0.20	51.74 ± 0.14	7.76 ± 0.12	4.11 ± 0.11	118.63 ± 4.52	
				Fm down			45.62 ± 0.81	43.31 ± 0.51	58.82 ± 0.63	16.51 ± 0.45	3.23 ± 0.15	99.66 ± 4.69	
			Low	Convex qcf up		~ 54							25
			High	Concave qcf down		~ 55							
			Low (type I)	Fm up-qcf			46.5 ± 2.1	39.3 ± 2.4	52.1 ± 1.2	12.8 ± 2.3	8.1 ± 0.7	73.8 ± 10.1	*
			High (type II)	Fmd-qcfd			54.7 ± 0.9	52.7 ± 0.6	85.0 ± 7.1	32.2 ± 7.6	8.2 ± 0.4	48.3 ± 4.4	
Neomat	LC	CA_SA-Tr	Low	(Fm) qcf down	32.6 ± 1.7	28.2 ± 1.3				4.3 ± 0.7	12.2 ± 2.9	160.9 ± 40.5	22
			High		36.9 ± 0.9	33.6 ± 1.2				3.4 ± 1.2	11.9 ± 3.6	105.1 ± 22.5	
		SA-Tr	Low	Shallow fm or fm up-qcf down			32.3 ± 1.3	27.7 ± 0.9	34.3 ± 0.9		6.5 ± 0.8	10.0 ± 0.9	*
			High II	Fm down - qcf down			35.8 ± 1.8	34.1 ± 1.5	37.9 ± 1.7		3.9 ± 0.5	10.0 ± 1.0	
Molazt	LC												
Molbar	LC	SA-Tr	Low	Qcf concave/ convex			32.4 (29.4–41.5)				12.8 (5.8–16.9)		3
			Middle				34.9 (35.3–48.7)				11.5 (5.5–15.3)		
Molcoi		CA-Tr	I		35.4 ± 1.3	29.8 ± 1.9				5.6 ± 1.3	0.4 ± 0.4	76.2 ± 23.6	13
			II		39.7 ± 2.1	35 ± 1.8				4.7 ± 1.2	0.3 ± 0.3	153.8 ± 58.9	
Molcur	LC	CA-Tr		Qcf down			28/30/33						20
		CA_SA-Tr	Low		29.7 ± 1.3	24.4 ± 2.2				4.3 ± 3.3	13.9 ± 1.7	205.8 ± 57.9	22
			Middle		32.9 ± 1.6	28.2 ± 2.7				4.4 ± 3.0	14.1 ± 1.8	134.9 ± 31.5	
			High		35.1 ± 0.7	30.3 ± 2.0				3.2 ± 4.3	14.4 ± 1.9	126.4 ± 34.3	
Molmol	LC	NA-Tr-Ar-WT			37.45 ± 4.55 (12.15)	34.95 ± 4.03 (11.53)	38.38 ± 4.59 (11.96)	34.71 ± 4.09 (11.78)	38.93 ± 4.57 (11.74)	4.22 ± 1.55 (36.73)	8.72 ± 2.49 (28.56)		47
		NA-Tr						33.65 ± 2.82	38.55 ± 3.17		9.54 ± 2.06		8
		CA-Tr						30.3 ± 4.76	33.9 ± 4.52		9.3 ± 2.97		30
				Qcf down			35/39/42						20
			I		39.1 ± 3.6	34.4 ± 3.8				4.7 ± 2.0	0.6 ± 0.3	75.4 ± 24.6	13
			II		42.8 ± 2.9	39.1 ± 3.0				3.8 ± 1.4	0.6 ± 0.3	117.6 ± 44.5	
		CA_SA-Tr	Low	Qcf down	35.6 ± 0.9	33.5 ± 1.2				2.2 ± 0.8	10.4 ± 1.4	143.1 ± 25.4	22
			Middle		39.1 ± 0.9	36.8 ± 1.0				2.2 ± 0.6	10.2 ± 1.3	109.2 ± 44.7	
			High		42.8 ± 0.8	39.8 ± 1.2				3 ± 1.2	10.4 ± 2.2	82.8 ± 12.2	
		SA-Tr	Low	Qcf convex			37.5 (32.4–38.4)				10.5 (7.3–14)		3
			Middle				41.4 (38.4–42.7)				10 (6.7–12.9)		
			High	Steep fm			44.3 (44.3–44.3)				8.6 (7.9–9.2)		
					37.59 (35.02–40.42)	35.8 (33.24–38.70)	38.16 (35.72–40.76)	35.59 (32.94–38.38)	38.78 (36.64–41.36)	3.17 (2.41–4.09)	12.01 (10.50–13.43)		38
			1	Narrow bandwidth			42.445	31.601	45.743		5.7		7
			2	Slightly modulated			42.376	32.201	45.934		6.2		
			3	Modulated			42.69	30.507	43.283		5.2		
			Low	Fm up convex			~ 33–35						25
			Middle	qcf down			~ 35–40						
			High				~ 40–45						
			Low	Qcf down or qcf			33.0 ± 0.6	29.9 ± 0.8	33.8 ± 1.0	3.9 ± 1.5	10.1 ± 1.3	175.5 ± 56.4	*
			Middle	convex			37.1 ± 1.9	33.6 ± 2.1	39.7 ± 6.3	6.0 ± 4.9	10.3 ± 2.6	88.2 ± 15.7	
		CI-Tr					47 ± 6.0	22.7 ± 2.6	50.3 ± 5.1		4.8 ± 1.2	40.7 ± 16.5	35
			A	Qcf (concave/ convex)/fm	36.5 ± 2.9	32.5 ± 3.8	35.2 ± 3.9			4.2 ± 2.2	9.8 ± 2.5	153.5 ± 386.1	4
			B	Qcf or fm	44.4 ± 7.1	38.7 ± 4.2	41.6 ± 4.6			5.8 ± 5.8	9.3 ± 2.6	92.8 ± 37.6	
Molpre	LC												
Molruf	LC	NA-Tr	Low				29.4 ± 1.9	28.1 ± 2.5	29.9 ± 1.8		13.2 ± 3.3	263.4 ± 82.5	28
			High				33.0 ± 1.5	32.0 ± 1.7	33.6 ± 1.7		13.4 ± 3.6	344.6 ± 131.9	
								28.8	33.61				23
								25.16 ± 4.05	29.7 ± 3.74		11.08 ± 3.55		8

Table 3 (continued)

Species	IUCN	Region	Call type	Structure	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
		NA-Tr-Ar-WT			31.48 ± 3.95 (12.55)	29.05 ± 2.94 (10.12)	31.89 ± 3.91 (12.26)	28.79 ± 2.88 (10)	32.28 ± 3.82 (11.83)	3.49 ± 2.32 (66.48)	9.73 ± 4.24 (43.58)		47
		CA-Tr						27.2 ± 4.43	30.8 ± 4.29		11.6 ± 3.68		30
				Qcf (down)			25						20
							< 35						2
		CA_SA-Tr	Low	Qcf down	26.3 ± 0.4	24.7 ± 0.6				1.6 ± 0.6	12.7 ± 0.7	409 ± 116.3	22
			High	Qcf down	27.8 ± 0.4	25.7 ± 0.5				2 ± 0.5	12.9 ± 1.2	343.7 ± 131.0	
		SA-Tr	Low	Qcf			26.5 (24.4–30.7)				17.3 (8.6–20.8)		3
			Middle	Qcf			30.7 (29.4–33.7)				15.3 (9.1–17.7)		
			High	Qcf (steep fm)			35.2 (34.3–38.2)				16.2 (10.4–24.2)		
					27.44 (26.35–28.53)	24.76 (24.08–25.59)	26.13 (25.36–26.98)	24.45 (23.90–25.19)	27.69 (26.86–28.73)	3.16 (2.74–3.57)	13.0 (11.88–14.27)		38
			Low	Qcf down or qcf convex			24.7 ± 1.1	20.2 ± 1.3	27.2 ± 0.8	7.0 ± 1.2	16.4 ± 1.0	259.5 ± 114.6	°
			Middle				28.5 ± 0.9	24.0 ± 2.9	30.5 ± 1.1	6.5 ± 2.6	16.4 ± 1.5	148.7 ± 54.2	
			High	Qcf or fm-qcf down			32.7 ± 0.7	28.7 ± 0.2	42.0 ± 0.4	13.3 ± 0.2	23.0 ± 1.3	83.8 ± 7.3	
		SA-WT					40.44 ± 5.09	37.26 ± 4.84	41.41 ± 5.16	4.15 ± 1.62	3.6 ± 1.2		41
Molsin/cur/ruf		SA-Tr	Low	Fm up convex qcf down			25–30						25
			Middle				30–35						
			High				35–40						
			Low	Qcf down or qcf convex			29.5 ± 1.1	26.0 ± 1.4	30.4 ± 0.8	4.4 ± 1.0	7.6 ± 1.3	121.4 ± 3.1	°
			Middle				33.3 ± 0.5	31.3 ± 0.8	34.4 ± 0.2	3.1 ± 0.8	7.4 ± 0.3	91.5 ± 14.5	
			High				35.7 ± 0.7	32.4 ± 0.8	36.1 ± 0.4	3.7 ± 0.7	6.6 ± 0.6	94.9 ± 9.8	
Nycaur	LC												
Nyclat	LC	NA-Tr					26.4 ± 2.5	25.1 ± 2.0	29.7 ± 3.1		12.5 ± 2.1	189.5 ± 19.5	28
								17.67 ± 0.67	19.15 ± 0.85		14.49 ± 1.50		8
		NA-Tr-Ar-WT			41.03 ± 4.19 (10.21)	17.97 ± 3.95 (21.98)	25.68 ± 3.35 (13.05)	17.96 ± 3.95 (21.99)	41.03 ± 4.19 (10.21)	23.07 ± 3.91 (16.95)	4.85 ± 1.40 (28.87)		47
		CA-Tr		(Fm) qcf down			24–26						20
		CA_SA-Tr	Low		26.7 ± 1.3	23.6 ± 0.9				2.4 ± 0.9	12.5 ± 1.4	393.7 ± 116.7	22
			Middle		28.7 ± 1.1	24.2 ± 0.9				4.6 ± 1.6	12.3 ± 1.2	292.9 ± 82.3	
			High		32.4 ± 1.3	24.9 ± 1.2				7.5 ± 2.0	12.7 ± 2.9	213.6 ± 59.6	
Nycmac	LC	NA-WT					12 (12.8)	11.3 (11.3)	13 (16.2)		18.6 (23.5)	1203 (75.9)	1
		NA-Tr-Ar-WT			28.59 ± 4.52 (15.81)	13.79 ± 4.26 (30.90)	22.34 ± 2.76 (12.35)	13.79 ± 4.26 (30.89)	28.66 ± 4.48 (15.63)	14.86 ± 3.38 (22.75)	7.92 ± 1.40 (17.68)		47
		CA_SA-Tr	Low	(Fm) qcf down	28.8	16.7				12	13.3	284.7	22
Procen	LC	NA-Tr-Ar-WT			22.89 ± 1.38 (6.03)	26.94 ± 1.45 (5.38)	26.03 ± 1.33 (5.11)	22.82 ± 1.32 (5.78)	27.76 ± 1.06 (3.82)	4.94 ± 1.40 (28.34)	47.66 ± 24.30 (50.99)		47
		NA-Ar		Fm up	23.0 ± 0.72	25.6 ± 0.47	24.7 ± 0.57			2.7 ± 0.56	20.6 ± 3.90		16
		CA-Tr		Fm up qcf/ fm down qcf			28/32						20
		CA_SA-Tr	Low	Fm up qcf	25.8 ± 0.8	28 ± 0.7				2.2 ± 0.7	17.8 ± 3.3	276.9 ± 91.2	22
			High II	Fm down qcf	35.7 ± 6.5	30.4 ± 1.1				8.1 ± 0.7	17.1 ± 7.8	158.9 ± 88.8	
		SA-Tr	Middle	Qcf concave			35.4 (33.7–36.7)				14.1 (13.2–14.8)		3
			Low	Qcf up			29.3 (26.3–32.3)				21.2 (17.4–35)		
			Low	Convex qcf up		~28							25
			High	concave qcf down		~30							
					24.79 (23.16–29.05)	29.12 (27.1–30.40)	29.65 (28.19–30.03)	24.38 (23.12–25.68)	30.36 (29.40–32.52)	5.8 (4.71–6.98)	53.63 (26.24–75.91)		38
Pronas	LC	CA_SA-Tr	Low	Fm up qcf	32.7 ± 1.3	34.7 ± 1.3				2 ± 0.5	11.6 ± 0.6	209.5 ± 21.9	22
			High II	Fm down qcf	47 ± 0.0	37.8 ± 0.0				9.2 ± 0.0	8.3 ± 0.0	105.7 ± 0.0	
		SA-Tr	Low	Convex qcf up		~34							25
			High	concave qcf down		~37							
			Low	Qcf up			34.1 ± 1.2	32.6 ± 1.3	35.8 ± 1.6	3.2 ± 1.4	14.3 ± 2.9	227.4 ± 121.0	°
			High	Fm-qcf down			38.6 ± 1.6	34.5 ± 2.1	43.9 ± 1.6	9.4 ± 0.5	19.6 ± 1.1	94.5 ± 10.7	
Tadbra	LC	NA-WT-Sn					28	24.1	32.3		11.5		18
		NA-WT					24.5 ± 1.6	22.7 ± 1.5	27 ± 3.0	4.3 ± 2.4	12.8 ± 1.1		14
							24.8 (23.9–25.2)			2.73 (1.68–3.13)	14.2 (13.8–16.0)		36
							24.1 (22.8–25.4)			5.0 (3.06–5.59)	12.3 (12.1–14.5)		

Table 3 (continued)

Species	IUCN	Region	Call type	Structure	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
							25.0 (24.9–26.8)			2.49 (1.52–2.92)	13.6 (13.2–15.0)		
							27.5 (13.8)	26.3 (13.6)	30.3 (17.5)		13.7 (16.2)	239.7(38.3)	1
		NA-Tr						27.32 ± 0.97	34.04 ± 3.16		8.69 ± 2.72		8
					37.7 ± 0.01	24.4 ± 0.06	28.1 ± 0.01				8.3 ± 0.03	109	32
		NA-Tr-Ar-WT			46.81 ± 5.42 (11.58)	26.09 ± 2.47 (9.47)	32.61 ± 3.73 (11.44)	26.09 ± 2.47 (9.47)	46.83 ± 5.41 (11.55)	20.74 ± 5.04 (24.3)	7.20 ± 1.93 (26.81)		47
		CA_SA-Tr			27.6 ± 3.0	24.4 ± 1.3				3.2 ± 2.5	13.7 ± 1.5		22
		SA-Ar	Low	(Fm) qcf down	28.03 ± 0.59	21.05 ± 0.25	24.31 ± 0.32	22.75 ± 0.25	27.41 ± 0.50	4.65 ± 0.37	13.62 ± 0.29	273.1 ± 55.5	39
		CI-Tr		Concave qcf	26.9 ± 2.7	26.1 ± 2.0	27.3 ± 2.2			2.8 ± 1.5	12.1 ± 1.8	286.90 ± 18.92	4
		SA-Tr	Low	Concave qcf		~ 18	<30					267.7 ± 116.9	25
Nyctal Tadbra			High			~ 22							

SF start frequency, *EF* end frequency, *FME* frequency of maximum energy, *LF* lowest frequency, *HF* highest frequency, *BW* bandwidth, *CD* call duration, *PI* pulse interval, *SI* reference number and species name abbreviations in Appendix 1

Echolocation calls of molossids have FME at fundamental harmonic with long, shallow-modulated signals emitted at rather low frequencies (Jung et al. 2014). Usually, calls show irregular frequency alternation, variable amplitude, and great plasticity.

Mormoopidae

Acoustic information of the species known to occur in Brazil was retrieved from 19 publications (Table 4 and Fig. 4). *Pteronotus* cf. *parnellii* was the most studied species (21 publications). However, recent studies (Clare et al. 2013; Thoisy et al. 2014) had shown that *P. parnellii* is very likely to be a complex of species, which will require further examination of the calls belonging to these *taxa*. *Pteronotus davyi*, *Pteronotus personatus*, and *Pteronotus gymnonotus* accounted 12, 10, and five publications, respectively. To the present, *P. davyi* has not been recorded in the Brazilian territory; nevertheless, considering its wide distribution, its occurrence in neighboring regions, and knowledge on its ecology, we decided to consider it as potentially occurring in Brazil.

Echolocation calls of moormopids are very distinguishable: the calls are usually multi-harmonic and FME is in the second harmonic; calls are shaped like a "lazy-z" (*P. personatus* and *P. davyi*), though sometimes not fully evident (*P. gymnonotus*); *P.* cf. *parnellii* presents high duty cycle echolocation (> 25%) and, frequently, its pulses show a long constant frequency (CF) section (> 20 ms) (O'Farrell and Miller, 1999) (Fig. 4, Appendix 2).

Noctilionidae

The two species of this family, *Noctilio albiventris* and *Noctilio leporinus* are widely distributed, occurring from southern Mexico to southern South America (Barquez et al. 2015a, 2015b); nevertheless, acoustic information was limited to a few localities of the tropical regions of North, Central, and South America and West Indies (Table 5 and Fig. 5). Echolocation calls of this family are very characteristic showing FME in the fundamental harmonic, a qCF/FM structure with energy uniformly distributed along the pulse or at the end of the FM component; the bandwidth of the FM component is usually > 10 kHz (Fig. 5; Appendix 2).

Vespertilionidae

Acoustic information of 19 species was compiled from 24 references (Table 6 and Fig. 6).

We were not able to retrieve any acoustic information on *Eptesicus andinus*, *Eptesicus taddeii*, *Histiotus alienus*, *Lasiurus ebenus*, *Lasiurus salinae*, *Myotis dinellii*, *Myotis izecksohni*, and *Myotis simus*. For *Lasiurus castaneus*, there

is some information but as a complex with *Lasiurus egregious* (López-Baucells et al. 2016). Here we present information on echolocation calls of *Histiotus diaphanopterus* (E. Barbier personal communication, 2016), a species recently described for Brazil (Feijó et al. 2015) and included information for *Myotis lavali* and *Rhogeessa hussoni* from our own recordings.

Echolocation calls of this family show FME in the fundamental harmonic; pulse structure usually shows a broadband downward FM component and a downward qCF termination. FME and Fmin are important call parameters for species recognition (Appendix 2).

Acoustic identification key

Based on the data we compiled for previously presented eight families and our own data, we provide here a key supporting the acoustic identification of Brazilian bats (Appendix 2). This key was made using several qualitative and quantitative acoustic parameters (e.g., call structure, harmonics, call frequencies, call duration, and duty-cycle) that allow identifying 62 taxa, including two Phyllostomidae species (*Lonchorhina aurita* and *Lonchorhina inusitata*). Working with spectrograms, oscillograms, and power spectrum on bioacoustics software, this key

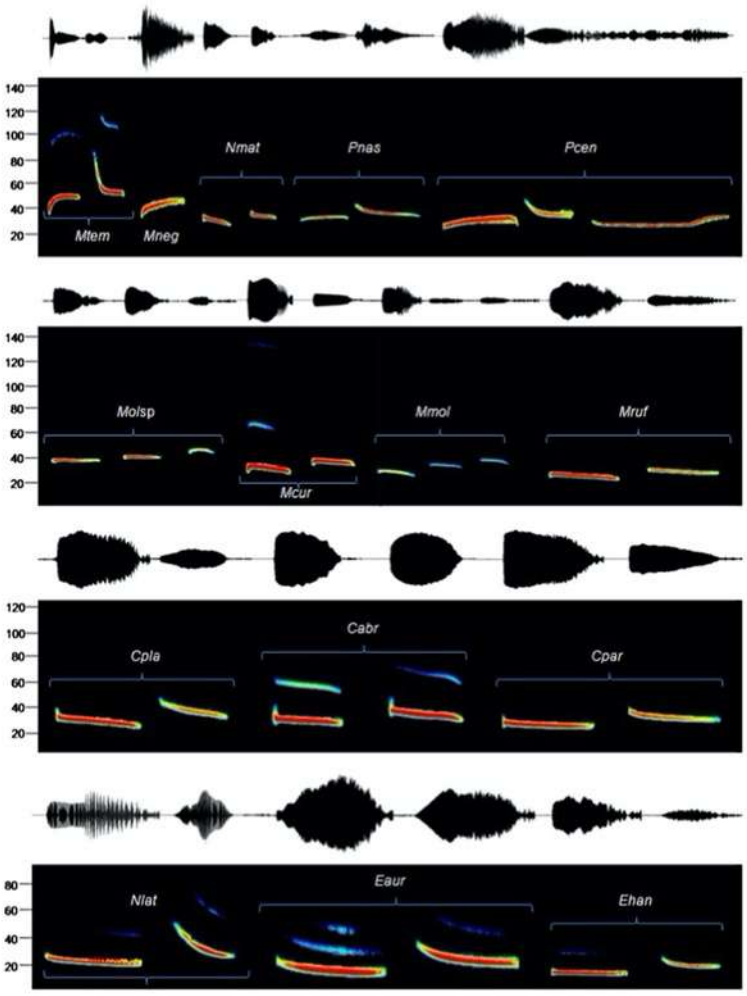

Fig. 3 Echolocation calls for species of Molossidae known to occur, or potentially occurring, in Brazil. Call duration and pulse intervals are not scaled. Mtem *Molossops temminckii*, Mneg *Molossops neglectus*, Nmat *Neoplatymops mattogrossensis*, Pnas *Promops nasutus*, Pcen *Promops centralis*, Molsp *Molossus* sp., Mcur *Molossus currentium*, Mmol *Molossus molossus*, Mruf *Molossus rufus*, Cpla *Cynomops planirostris*, Cabr *Cynomops abrasus*, Cpar *Cynomops paranus*, Nlat *Nyctinomops laticaudatus*, Eaur *Eumops auripendulus*, Ehan *Eumops hansae*

Table 4 Summary of echolocation call parameters as retrieved from the literature and our own data for species of the Mormoopidae known to occur, or potentially occurring, in Brazil, with information on region of recording and IUCN status of each species

Species	IUCN	Region	Call type	Structure	SF (kHz)	EF (kHz)	Charact. F	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	DC (%)	SI
Ptedav	LC	NA-Tr		Cf fm qcf	71.5 ± 0.05	59.4 ± 0.03		73.3 ± 0.03				6.4 ± 0.02	64.8		32
								69.1 ± 1.2	68.1 ± 1.8	69.6 ± 1.2		6.8 ± 0.9	66.8 ± 20.1		28
								73.6 ± 2.0			16.2 ± 1.8	4.9 ± 0.6			43
									59.64 ± 1.06	72.96 ± 1.32		5.92 ± 0.99			8
							58.88		57.44	69.23					23
		NA-Tr-Ar		Cf fm down cf			69.8 ± 0.7				8.2 ± 0.5			17.1	40
		NA-Tr-Ar-WT			69.75 ± 3.05 (4.37)	58.36 ± 2.05 (3.51)	59.82 ± 1.95 (3.26)	66.78 ± 5.52 (8.27)	58.32 ± 2.02 (3.46)	71.24 ± 2.52 (3.54)	12.92 ± 1.60 (12.38)	5.84 ± 1.11 (19.01)			47
		CA-Tr							58.0(0.20)	68.1(0.17)		5.5(0.13)	62.2(3.38)		29
				Cf fm down qcf				68.0 ± 0.8/58.0 ± 0.9				6.6 ± 0.7	70.8 ± 22.8	10.1 ± 2.3	19
		SA-Tr		Qcf fm down qcf	71.5 ± 0.2										3
		CI-Tr	FH	Qcf/fm/qcf	59.9 ± 1.7	70.7 ± 1.4		70.5 ± 1.7			15.5 ± 1.9	5.2 ± 1.5	55.2 ± 23.2		4
			FH		38	22		34.1				2.8	15		46
			H2		70.3 ± 1.3	51.0 ± 4.4		67.0 ± 2.2				4.6 ± 1.5	41 ± 31		
Ptegym	LC	NA-Tr-Ar-WT			54.99 ± 3.14 (5.71)	45.81 ± 2.85 (6.22)	46.86 ± 2.74 (5.85)	51.34 ± 4.87 (9.49)	45.81 ± 2.84 (6.2)	55.51 ± 3.19 (5.75)	9.70 ± 1.140 (11.75)	5.33 ± 0.82 (15.38)			47
		CA-Tr						55.00							44
				Cf fm down				55.00							20
		SA-Tr		Qcf fm down qcf				54.8 ± 0.6							3
				Cf fm down	~ 55 (cf)										25
			H2	Qcf fm down qcf	~ 60			53.1 ± 2.7	48.4 ± 1.5	60.6 ± 1.0	12.3 ± 1.7	5.3 ± 0.6	84.9 ± 53.0	7.5 ± 3.2	°
Pteper	LC	Na-Tr		Cf fm qcf	82.2 ± 0.05	67.6 ± 0.02		81.4 ± 0.05				5.7 ± 0.02	55.1		32
								80.1 ± 1.5/65.9 ± 1.6				7.1 ± 0.5	53.9 ± 10.0		27
								80.1 ± 1.5	74.1 ± 4.2	80.9 ± 1.5		7.1 ± 0.5	53.9 ± 10.0		28
								85.1 ± 1.3			15.1 ± 1.5	4.8 ± 0.09			43
									66.75 ± 1.61	83.72 ± 1.44		4.4 ± 0.57			8
		NA-Tr-Ar-WT			82.83 ± 2.68 (3.24)	64.12 ± 2.84 (4.43)	65.94 ± 3.10 (4.7)	70.53 ± 5.25 (7.44)	64.12 ± 2.84 (4.43)	82.88 ± 2.66 (3.21)	18.76 ± 3.11 (16.58)	5.71 ± 1.18 (20.67)			47
		CA-Tr							68.0 (0)	83.0 (0.21)		5.7 (0.14)	48.3 (1.50)		29
				Cf fm down				73							20
		SA-Tr		Cf fm down cf				74.1 ± 3.4							3
				Cf fm down cf	~ 68–69 (cf)										25
			H2		~ 80			68.7 ± 3.1	65.3 ± 2.4	80.0 ± 1.6	14.7 ± 1.6	5.1 ± 0.8	55.4 ± 28.0	9.4 ± 2.5	°
Ptemes G1	LC (?)	NA-Tr		Fm up cf. fm down	61.3 ± 1.8	55.7 ± 2.8		63.1 ± 1.1				27.8 ± 3.1	64.8		32
				Cf fm down				67.1 ± 0.5	62.8 ± 2.4			22.4 ± 2.1		40.3	40
								64.5 ± 1.0	64.2 ± 1.1	64.6 ± 1.1		25.8 ± 3.1	48.0 ± 21.1		28
								64.9±			10.7 ± 1.8	19.7 ± 6.2			43
									54.93 ± 1.61	64.73 ± 1.42		24.42 ± 3.7			8
							63.05		55.61	62.71					23
		NA-Tr-Ar-WT			61.93 ± 2.04 (3.29)	52.87 ± 2.20 (4.16)	64.51 ± 2.15 (3.33)	63.61 ± 3.19 (5.01)	52.86 ± 2.20 (4.16)	64.97 ± 1.27 (1.95)	12.1 ± 2.13 (17.6)	21.21 ± 4.97 (23.43)			47
		CA-Tr							54.5 (0.17)	63.5 (0)		30.4 (0.50)	61.9 (2.69)		29

Table 4 (continued)

Species	IUCN	Region	Call type	Structure	SF (kHz)	EF (kHz)	Charact. F	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	DC (%)	SI
			group 1 62 kHz					62.1 ± 1.91							9
				Cf fm down				60							20
Ptepar G2		SA-Tr	phonic type 59	Cf fm down				58.4 ± 0.7							3
			phonic type 59					59.2 ± 0.68							45
			60 kHz	Fm up cf. fm down				~ 60							25
		CI-Tr	group 2 59 kHz					58.9 ± 0.39							9
					60.6 ± 0.08	48.05 ± 0.61		60 ± 0.17	59.61 ± 0.16	60.23 ± 0.16	0.62 ± 0.05	21.23 ± 0.87			26
								58.2 ± 0.7	46.3 ± 1.9	60.2 ± 0.8		21.0 ± 5.5	25.0 ± 15.6		35
			FH		28	23		31.2				14.5	38		46
			H2		56.2 ± 3.9	46.8 ± 1.6		61.3 ± 0.8				22.0 ± 5.7	56 ± 20		
Ptepar G3–4		SA-Tr	phonic type 53	Cf fm down				52.6 ± 0.5							3
			phonic type 53					53.4 ± 0.62							45
			group 3–4 53–54 kHz					53.6 ± 0.30							9
			55 kHz	Fm up cf. fm down				~ 55							25
				(Fm up-) cf-fmd				53.9 ± 3.4	46.7 ± 2.3	57.2 ± 0.5	10.6 ± 2.4	15.8 ± 4.8	47.4 ± 37.7	31.1 ± 10.9	°
Ptepar		SA-Tr			54.2	87.8		93	54.2	93.8	39.6	117.55			38

SF start frequency, *EF* end frequency, Charact *F* characteristic frequency, *FME* frequency of maximum energy, *LF* lowest frequency, *HF* highest frequency, *BW* bandwidth, *CD* call duration, *PI* pulse interval, *DC* duty cycle, *SI* reference number and species name abbreviations in Appendix 1

allows identifying at the species level in some cases. Despite the new additions performed in this work, yet this key does not embrace all the species occurring in Brazil. We emphasize that the goal of this key is not to exclude bibliographic search but to be one more tool to aid in the acoustic identification of Brazilian bats.

Acoustic variability in echolocation calls

Considering that most of the acoustic information of the species was retrieved from outside Brazil, it is important to assess if identifications of some species could be affected by regional variation of their echolocation calls (Jiang et al. 2015) or by another sources of variation. Therefore, when available, we compared the parameters from calls obtained in Brazil with calls from other regions, in order to detect possible regional differences. For the majority of the species, we were only able to compare the regional variation in FME, the most commonly used acoustic parameter and, at least from our compilation, apparently less susceptible to biases due to recording method and technology. However, the number of individual pulses evaluated per species was highly variable across studies (from 3 to 1295), so the average values presented by the authors have variable accuracy and precision. For this reason, we only describe general patterns in acoustic variation in FME within some of the best-studied families and species. If the detected differences are due to low taxonomic resolution, biased data, or to some local adaptation (geographic variation) is still to be determined. In fact, we must underline that there may be erroneous identifications in several groups, as the taxonomic resolution of many species is still far from accomplished.

We found great acoustic variability in 10 bat species: *R. naso*, *S. bilineata*, *S. leptura*, *F. horrens*, *M. rufus*, *Lasiurus blossevillii*, *Lasiurus cinereus*, *Lasiurus ega*, *Myotis nigricans* and *Myotis riparius* (see Tables 1, 2, 3, 4, 5, and 6). For example, *L. blossevillii* showed a significant variation in FME across North, Central, and South America and *M. riparius* FME ranged from 55 to 66.56 kHz solely in South America (Table 6). Also, *M. rufus* showed higher FME values in South America; there is significant overlap in FME between *M. rufus* and *M. currentium*, which may be due to erroneous identification as one of the species or more likely, due to their high variability on echolocation calls related to the flying environment. Finally, though we only retrieved four studies for North America regarding *L. cinereus*, they showed clear differences in the FME recorded for the species (20.8; 35.47 kHz), which perhaps could be related to different recording conditions (hand release recording or degree of vegetation clutter).

The review of Jiang et al. (2015) revealed that geographic variation of bat echolocation calls is not uncommon, averaging 5 to 10 kHz differences in peak frequency. Differences above 10 kHz in FME within the same species are, according to those authors, due to morphological differences among

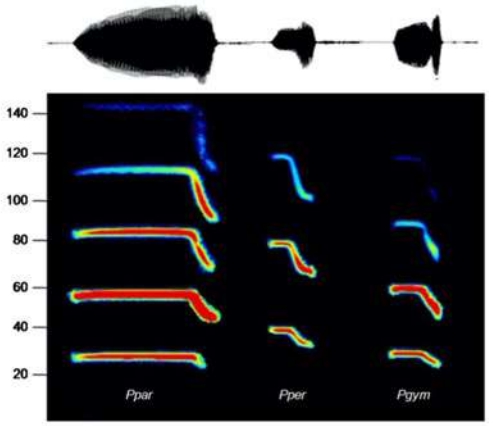

Fig. 4 Echolocation calls for species of Mormoopidae known to occur, or potentially occurring, in Brazil. Call duration and pulse intervals are not scaled. Ppar *Pteronotus* cf. *parnellii*, Pper *Pteronotus personatus*, Pgym *Pteronotus gymnonotus*

subspecies across large spatial scales. Also, they suggest that geographic variation in echolocation pulses of bats may be caused by genetic drift, cultural drift, and ecological, sexual, and social selection. Changes in echolocation pulses may thus reflect previous changes in other aspects of the phenotype (e.g., morphology) and local adaptation (changes in prey preferences), which may lead to reproductive isolation, eventually to divergence among populations of the same species, and ultimately to species subdivision.

In bats and other small-bodied mammals, species with extremely large distribution ranges have historically been split into complexes of cryptic species. The genus *Miniopterus* is an example: Until recently, *M. schreibersii* was considered to be a cosmopolitan species with a near-global distribution (Simmons et al. 2005). However, several studies, from molecular to ecological modeling (Appleton et al. 2004; Miller-Butterworth et al. 2005; Furman et al. 2010a, 2010b) demonstrated that *M. schreibersii* is a complex of several species distributed across Africa, Europe, Asia, and Oceania, with at least 18 clades occurring solely in Madagascar (Christidis et al. 2014). We hypothesize that for some Neotropical species, this is also the case. Indeed, many of the presently accepted species for this region show very large distribution ranges, and recent works have already revealed complexes of species within the same taxon [e.g., *Pteronotus parnellii* (López-Wilchis et al. 2016), genus *Sturnira* (Velazco and Patterson 2013), *Platyrhinus* (Velazco 2005), *Saccopteryx* and *Cormura* (Clare et al. 2007)]. Acoustic variation within the *P. parnellii* species complex supports this idea (Table 4). Therefore, the differences we found for some species (*R. naso*, *S. bilineata*,

Table 5 Summary of echolocation call parameters as retrieved from the literature and our own data for the two species of the Noctilionidae, with information on region of recording and IUCN status of each species

Species	IUCN	Region	Call type	Structure	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	DC (%)	SI
Nocalb	LC	CA-Tr					70							44
				Cf-fm down			70							20
		SA-Tr			66.34 (65.80–67.07)	44.83 (42–49.18)	52.47 (48.37–57.28)	44.83 (42–49.18)	67.51 (67.04–68.11)	22.68 (18.59–25.42)	9.99 (9.12–10.73)			38
			Broad band	Cf-fm down			69.7 (68–75.7)			33.6 (22–39.1)			29.5	3
			Narrow band	Cf-fm down			71 (66.7–74.7)			16 (9.7–42)			67.4	
				Cf-fm down	68–76									25
				Cf-fmd	~ 74		48.6 ± 3.9	38.9 ± 4.9	74.1 ± 1.4	35.3 ± 4.6	7.8 ± 1.1	62.7 ± 36.8	13.8 ± 7.6	°
Noclep	LC	CA-Tr					56							44
				Cf-fm down			65							20
								40.7 ± 10.54	51.2 ± 5.06		7.0 ± 3.62			30
		NA-Tr-Ar-WT			50.79 ± 5.09 (10.02)	23.55 ± 3.44 (14.61)	31.03 ± 3.45 (11.12)	23.52 ± 3.42 (14.54)	50.96 ± 5.22 (10.24)	27.43 ± 4.75 (17.32)	8.41 ± 3.44 (40.9)			47
		NA-Tr						29.63	57.14		13.95			8
		SA-Tr	Broad band	Cf-fm down			57.6 (53.4–60.6)			33.6 (22–39.1)			24.5	3
			Narrow band	Cf-fm down			57.6 (56.3–59.3)			13 (8.3–17.6)			70.2	
					50.66 (48.11–53.11)	27.63 (26.58–28.58)	34.61 (32.52–37.24)	27.61 (26.57–28.57)	50.68 (48.16–53.12)	23.07 (20.88–25.15)	12.72 (11.73–13.79)			38
				Cf fm down	53–61									25
				Cf fmd	~ 60		48.4 ± 5.4	34.1 ± 5.6	60.2 ± 0.6	26.1 ± 5.4	10.7 ± 2.4	66.9 ± 100.7	24.7 ± 10.4	°
		CI-Tr	Narrow band	Cf/fm	53.8 ± 7.7	38.6 ± 7.2	52.2 ± 7.7			15.6 ± 5.5	10.7 ± 2.0	98.3 ± 48.1		4
			Broad band	Cf/fm	54.4 ± 7.2	22.6 ± 4.9	39.3 ± 8.6			32.0 ± 5.4	11.8 ± 2.2	65.3 ± 23.7		

SF start frequency, *EF* end frequency, *FME* frequency of maximum energy, *LF* lowest frequency, *HF* highest frequency, *CD* call duration, *PI* pulse interval, *DC* duty cycle, *SI* reference number and species name abbreviations in Appendix 1

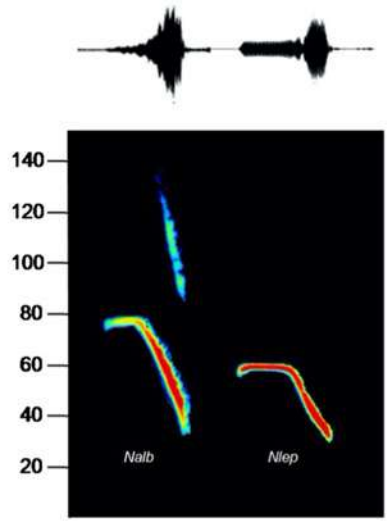

Fig. 5 Echolocation calls for species of Noctilionidae known to occur, or potentially occurring, in Brazil. Call duration and pulse intervals are not scaled. Nalb *Noctilio albiventris*, Nlep *Noctilio leporinus*

S. leptura, *F. horrens*, *M. rufus*, *L. blossevillii*, *L. cinereus*, *L. ega*, *M. nigricans* and *M. riparius*) make them priority candidates for investigating the existence of geographical variation, the actual magnitude of such variation, and ultimately to detect potential cryptic complexes of species suggested by significant acoustic variation.

Current status and perspectives

We compiled and presented detailed data for echolocation calls for nearly two-thirds of non-phyllostomid bats occurring in Brazil, including 67 species of Emballonuridae, Furipteridae, Molossidae, Mormoopidae, Natalidae, Noctilionidae, Thyropteridae, and Vespertilionidae. These species offer reliable viability for their acoustical identification (Barataud et al. 2013; this study). Even so, considering the high species richness for Brazil, for at least other 26 species of non-phyllostomid bats occurring in the country, there are neither published information on their echolocation calls nor sound files available to allow their identification. Indeed, some of these species are potentially very rare and difficult to capture or were recently described [e.g., *M. lavali*, *M. izecksohni* (Moratelli et al. 2011). Obtaining acoustical data for those 26 species should be a priority for Brazil. The refinement of the information on their calls could also support the solution of taxonomic problems, joining more resolution to molecular and/or morphological studies (e.g., Barratt et al. 1997; Thoisy et al. 2014).

Although the gaps in the acoustic knowledge of several species are a fact, here we showed that some other species are relatively easy to be identified acoustically. Due to species-specific calls, bioacoustics is widely used for several ecological and behavioral studies. This includes detailing species occurrence and distribution using acoustic monitoring schemes as a complement to mist-net sampling (e.g., Fenton et al. 1983; Ekman and de Jong 1996; Ahlén and Baag 1999). *Promops centralis* is one of those cases; due to its ecology and foraging behavior, mist-net records of this species are uncommon, however, this species has very distinctive calls allowing a fairly easy acoustic identification (Barataud et al. 2013; Jung et al. 2014). Accordingly to previous studies, in Brazil *P. centralis* was restricted to Amazonian states and to the state of Mato Grosso do Sul (Gregorin and Taddei 2000; Fischer et al. 2015). Using acoustic surveys in eight Brazilian states, it was possible to extend *P. centralis* distribution in more than 3,000,000 km^2 to the east (Hintze unplublished data), with less effort and more efficiently than using mist netting. This case is an important proof that when acoustic monitoring is effectively implemented, it will help to greatly improve our knowledge, filling the large gaps on the ecology, behavior, and distribution of poorly known Brazilian bat taxa.

Bioacoustics can be used to explore cryptic diversity in bats (Jones and Parijs 1993; Thoisy et al. 2014; Hintze et al. 2016c), and there is a great potential for this use in Brazil. A paradigmatic case in Europe was the discovery of two different sonotypes in what was thought to be colonies of *Pipistrellus pipistrellus* (45 and 55 kHz sonotypes) (Jones and Parijs 1993). This was the first clue to hypothesize the existence of two sympatric cryptic species (*P. pipistrellus* and *P. pygmaeus*) in the late 90s of the last century (Barratt et al. 1997; Jones and Barratt 1999). In the Neotropics, two similar cases are drawing attention to a new potential cryptic species complex. Thoisy et al. (2014) found *Pteronotus parnellii* individuals with different vocalizations living in sympatry (53 and 59 kHz sonotypes) both in French Guiana and northern Brazil, while Hintze et al. (2016c) hints for a new *Saccopteryx* species vocalizing with lower frequencies (39–42 kHz) than *S. bilineata* (45–48 kHz)—thus suggesting the existence of a larger species of the genus—the two potentially living in sympatry in the Atlantic Forest of northeastern Brazil. In the first case, morphological and molecular studies seem to support the presence of distinct species within the *Pteronotus parnellii* complex (Thoisy et al. 2014). In the latter study, despite the acoustic differences identified, captures will be necessary for the confirmation and morphological description of a new species (Hintze et al. 2016c).

Moreover, acoustic monitoring produces a huge amount of data, which results in a slow process of manual identification. But, while there has been some improvement in automated

Table 6 Summary of echolocation call parameters as retrieved from the literature and our own data for species of the Vespertilionidae, with information on region of recording and IUCN status of each species

Species	IUCN	Region	Structure	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
Eptand	LC											
Eptbra	LC	NA-Tr-Ar-WT		55.83 ± 11.48 (20.56)	33.30 ± 3.46 (10.40)	37.12 ± 6.07 (16.35)	32.93 ± 3.46 (10.51)	55.83 ± 11.48 (20.56)	22.89 ± 8.93 (39.01)	7.80 ± 3.77 (48.33)		47
		SA-Tr		70.43 (63.26–75.21)	34.34 (32.24–36.72)	44.61 (40.24–49.60)	34.33 (32.24–36.63)	70.48 (63.38–75.21)	36.15 (29.0–40.66)	3.5 (2.70–4.18)		38
						43.6 ± 2.7	40.0 ± 0.6	58.0 ± 8.5	17.9 ± 8.7	3.1 ± 0.4	100.1 ± 26.4	°
		CI-Tr				41.1 ± 1.3	30.5 ± 6.4	71.5 ± 14.8		3.0 ± 1.6	74.7 ± 23.3	35
Eptbra/chi		SA-Tr	Fm with qcf tail		25–39							25
Eptchi	LC	SA-Tr	Fm flat			32 ± 2.6			30 ± 11.3	7.6 ± 1.6		3
Eptdim	DD	SA-WT				66.37 ± 3.36	40.45 ± 1.59	82.89 ± 6.41	42.43 ± 6.45	1.8 ± 0.37	50.78 ± 25.42	41
Eptfur	LC	NA-Tr				37.6 ± 1.3	36.4 ± 1.4	40.4 ± 2.1		7.1 ± 1.9	175.8 ± 78.3	28
							32.78	64.02				23
		NA-Tr-Ar	Fm down. Ends with narrow-band "tail"			36.5 ± 0.4	33.1 ± 0.5			9.4 ± 0.5		40
		NA-Tr-Ar-WT		56.34 ± 8.69 (15.42)	37.40 ± 1.45 (3.88)	39.77 ± 3.55 (8.93)	37.05 ± 1.23 (3.32)	56.34 ± 8.69 (15.42)	19.29 ± 8.74 (45.31)	6.91 ± 1.72 (24.89)		47
		CA-Tr					37.5 ± 1.13	52.6 ± 8.61		5.5 ± 1.58		30
		SA-Tr	Fm flat			41.6 ± 2			36.1 ± 9.8	6 ± 1.3		3
			Fm with qcf tail		35–45							25
			Fm qcf			38.7 ± 1.5	36.2 ± 0.6	63.0 ± 9.1	26.9 ± 8.9	6.1 ± 0.5	139.2 ± 79.8	°
Epttad	NA											
Lasblo	LC	NA-Ar-WT	Low slope							>8		34
		NA-WT-Sn	U-shaped			41.6 (37–61)	38.8 (36–52)	54.6 (44–102)		10.7 (2.9–14)		18
		NA-Tr					46.84	62.67				23
							43.58 ± 1.36	62.89 ± 1.14		6.11 ± 1.67		8
		NA-Tr-Ar-WT		89.58 ± 10.56 (11.79)	39.49 ± 5.93 (15.02)	53.75 ± 10.72 (19.94)	39.49 ± 5.93 (15.02)	90.03 ± 10.66 (11.84)	50.54 ± 9.18 (18.16)	3.29 ± 1.28 (38.91)		47
		CA-Tr	Fm down qcf			46						20
		SA-Tr	Fm			45.5 ± 5.3			14.3 ± 7	12.3 ± 2.5		3
				70.92 (66.06–74.41)	35.96 (34.54–37.16)	38.77 (37.27–41.13)	35.85 (34.54–36.97)	70.92 (66.06–74.41)	35.07 (30.57–38.20)	6.17 (5.38–7.22)		38
			Fm down. Irregular and alternating sequences		40–45							25
Lascas	DD	SA-Tr	Fm down. Irregular and alternating sequences		25–35							25
Lascin	LC	NA-WT-Sn				27.43 ± 2.24	24.72 ± 1.79	39.61 ± 5.08		8.92 ± 1.45		6
						29.24 ± 2.80	25.90 ± 3.05	42.36 ± 6.31		5.46 ± 2.31		
		NA-Ar					21.9 ± 2.36	30.8 ± 7.18		8.2 ± 2.82		30
							22.0 ± 1.89	40.8 ± 7.03		6.2 ± 3.11		
		NA-WT-Sn	Pronounced or subtle U-shape			20.8	19.7	26		11		18
		NA-Tr-Ar-WT		57.23 ± 7.92 (13.84)	26.81 ± 4.39 (16.37)	35.47 ± 7.11 (20.05)	26.79 ± 4.39 (16.39)	57.24 ± 7.92 (13.84)	30.45 ± 5.12 (16.81)	4.25 ± 1.39 (32.71)		47
Lasebe	DD											
Lasegu	LC	NA-Tr-Ar	Long down-sweeps. Ends with short narrow-band "tail"			31.3 ± 1.3	27.3 ± 2.5			9.4 ± 1.2		40
		NA-Tr				32.2 ± 1.2	31.1 ± 1.4	34.9 ± 1.6		8.7 ± 2.5	149.4 ± 64.7	28
							35.49	43.97				23
		NA-Tr-Ar-WT		61.13 ± 4.50 (7.36)	37.45 ± 0.98 (2.62)	55.20 ± 5.41 (9.8)	37.45 ± 0.98 (2.62)	61.13 ± 4.50 (7.36)	23.68 ± 4.89 (20.65)	2.93 ± 0.51 (17.41)		47
		CA-Tr					32.0 ± 2.45	43.0 ± 8.64		6.6 ± 2.73		30
						32						44
			Fm down qcf			32						20
		SA-Tr	Fm down. Irregular and alternating sequences		25–35							25

Table 6 (continued)

Species	IUCN	Region	Structure	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
Lasegr	DD	SA-Tr		45.4 ± 7.1	27.3 ± 1.9	30.2 ± 3.5				4.8 ± 1.3		24
			Fm down. Irregular and alternating sequences		25–35							25
Lassal	NA											
Hisali	DD											
Hisdia	NA	SA-Tr	Fm	37.3 ± 2.6	15.3 ± 0.6	28.3 ± 4.0	15.3 ± 0.6	37.3 ± 2.6	22.0 ± 2.6	2.8 ± 1.2	113.7 ± 81.1	5
Hislae	NT	SA-Ar	Fm	38.1 ± 2.6	26.3 ± 1.8	30.3 ± 3.6				1.3 ± 0.3	89.6 ± 55.7	33
Hismon	LC	SA-Ar	Fm	46.3 ± 4.5	25.4 ± 2.1	32.0 ± 2.1				3.6 ± 2.6	147.1 ± 75.3	33
				53.77 ± 0.97	29.62 ± 0.25	35.36 ± 0.41	31.28 ± 0.31	44.62 ± 0.91		3.34 ± 0.08	136.12 ± 8.03	39
Hisvel	DD	SA-WT					15	25		5–8		12
Myoalb	LC	CA-Tr				42						44
			Fm-down qcf			52						20
			Downward steep FM-shallow modulated		43–46							10
		SA-Tr		92.69 (84.78–100.82)	51.4 (47.44–56.48)	64.00 (57.28–72.61)	51.38 (47.44–56.45)	92.71 (84.83–100.82)	41.33 (34.07–47.99)	2.45 (1.86–3.03)		38
			Fm-qcf down			80.5 ± 9.6	51.4 ± 2.4	125.9 ± 7.0	74.5 ± 7.6	2.5 ± 0.4	62.8 ± 17.2	°
Myodin	LC											
Myoize	NA											
Myolav	NA											
Myolev	LC	SA-WT				65.65 ± 3.64	46.00 ± 1.35	80.84 ± 3.28	34.84 ± 3.54	1.5 ± 0.28	77.2 ± 28.48	41
Myonig	LC	CA-Tr		61.5 ± 2.3	50.9 ± 0.6	54.2 ± 0.04				7.2 ± 0.3	106.2 ± 11.2	42
				95.4 ± 4.7	51.6 ± 1.1	55.0 ± 1.2				4.3 ± 0.5	67.6 ± 13.1	
						55.00						44
			Fm-down qcf			55						20
			Downward steep FM-shallow modulated		48–55							10
		SA-Tr	Fm flat			53.7 ± 4			28.5 ± 11.7	4.3 ± 1.2		3
			Structure	76.86 (69.10–84.63)	38.56 (36.05–43.94)	48.25 (42.67–55.79)	38.53 (36.05–43.94)	76.9 (69.18–84.63)	38.37 (30.47–43.93)	3.41 (2.54–4.11)		38
			Fm with qcf tail		45–50							25
			Fm-qcf down			55.0 ± 1.4	52.9 ± 1.1	67.1 ± 3.8	14.2 ± 4.1	3.8 ± 0.7	63.8 ± 18.4	°
		CI-Tr				66.2 ± 7.9	51.3 ± 1.3	125.0 ± 7.5		2.2 ± 0.1	24.0 ± 6.2	35
Myorip	LC	CA-Tr	Downward steep FM-shallow modulated		58–60							10
						> 56						2
		SA-Tr	Fm/qcf			58.1 ± 2.5			40.7 ± 11.8	5 ± 1.3		3
			Fm/qcf			55 ± 1.8			37.4 ± 9.5	5.2 ± 1.1		3
				102.71 (98.60–106.43)	61.6 (60.48–63.12)	66.56 (64.36–70.21)	61.57 (60.48–62.74)	102.8 (99.04–106.43)	41.16 (36.90–44.74)	4.38 (3.77–5.36)		38
			Fm with qcf tail		> 55							25
		SA-WT					50	58		4–5		12
Myorub	NT	SA-WT					58	65		5		12
Myosim	DD											
Rhohus	DD	SA-Tr	Steep fm			48.2 ± 4.7	41.5 ± 0.8	59.8 ± 2.5	18.3 ± 2.5	3.6 ± 0.2	89.3 ± 7.3	°
Rhoio	LC	SA-Tr	Fm down. Irregular and alternating sequences		40–45							25
		CI-Tr				52.4 ± 3.7	39.6 ± 3.9	99.6 ± 6.5		2.8 ± 0.6	38.4 ± 28.6	35

SF start frequency, *EF* end frequency, *FME* frequency of maximum energy, *LF* lowest frequency, *HF* highest frequency, *BW* bandwidth, *CD* call duration, *PI* pulse interval, *SI* reference number and species name abbreviations in Appendix 1

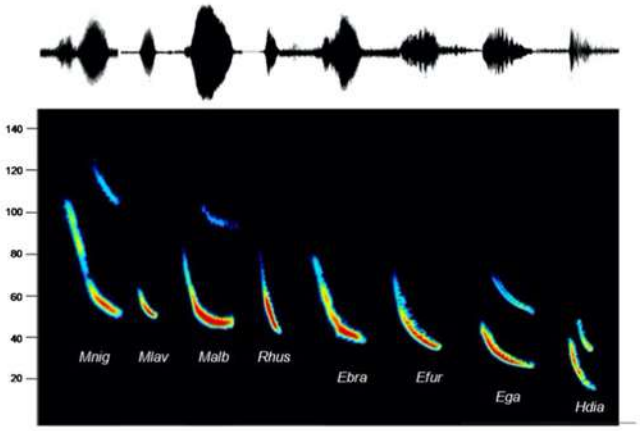

Fig. 6 Echolocation calls for species of Vespertilionidae known to occur, or potentially occurring, in Brazil. Call duration and pulse intervals are not scaled. Mnig *Myotis nigricans*, Mlav *Myotis lavali*, Malb *Myotis albescens*, Rhus *Rhogeessa hussoni*, Ebra *Eptesicus brasiliensis*, Efur *Eptesicus furinalis*, Lega *Lasiurus ega*, Hdia *Histiotus diaphanopterus*

identification tools these programs support, their identifications are usually based on limited libraries of calls and much too often in calls collected in a few restricted regions (Russo and Voigt 2016). Biologists working with bat echolocation identification should still resist the temptation of solely using automatic classifiers (Russo and Voigt 2016). Neglecting the possibility of regional variation in the echolocation calls of the species and the potential for cryptic Neotropical bat diversity (Thoisy et al. 2014; Hintze et al. 2016c), the passive acceptance of potentially inaccurate and incorrect automated identifications (Hintze et al. 2016a) may lead to deficient species data records and consequently to serious problems in bat conservation (Russo and Voigt 2016). This does not mean that we should be discouraged to develop better-automated identification tools, based on comprehensive sound databases and powerful algorithms. Nonetheless, we must accept that perhaps some species may never be distinguished because they overlap too much in call parameters; indeed, after decades of studies, recordings and analyses, the acoustic discrimination of several species of European *Myotis* remains a huge challenge for bat researchers (e.g., Barataud 2015).

Also, comparison among studies to detect geographical variation, the actual magnitude of such variation, and potential cryptic complexes of species suggested by significant acoustic variation will only be possible if recording and analytical procedures are detailed in the published information.

The construction of bat sound libraries, as Xeno-Canto for birds, is highly desirable to progress in bioacoustics. For this, it seems very important that every expert adopt a similar recording protocol. Indeed, high-flying bats (in particular molossids and some vespertilionids like *Lasiurus*) turn out recognizable during cruising or hunting flight at high altitude. In vegetation edges, or near the ground, they produce very similar sounds, which are thus difficult to identify. Consequently, the production of reference sounds for high-flying bats should respect some criteria: a rather long acoustic sequence which includes take-off, ascent towards the sky (and thus generally a swirling flight near edges) and a high cruise flight in open environment. This type of recording supplies all fundamental acoustic features of those species.

Consequences of these gaps in knowledge are straightforward. First, we will have a lot to learn and update on bat species diversity, occurrence, distribution and conservation status in the Neotropics as already exemplified by the *P. centralis* and *P.* cf. *parnellii* cases mentioned above. Second, we will not be able to use automated acoustic identification programs until comprehensive databases of Neotropical bat calls are available. Indeed, Hintze et al. (2016a) found that the accuracy level (percentage of correct identifications) of two widespread automated acoustic identification programs is quite low (below 12%) for Brazilian bats easily manually identified by bat acoustic experts. They also point out the need for those software and their classifiers to undergo much improvement and validation tests before being publicized in the market for wide use in acoustic identification of bats in Brazil. And third, as climate influences some aspects of the ecology and behavior of the species including foraging behavior and biogeography, the actual rate of climate change represents a serious and increasing threat to biodiversity (Sherwin et al. 2013), with unknown effects on the actual species distribution as well on the acoustics profiles of Brazilian bats.

We need to accept this as a great challenge for the next few years: the need to collect good acoustic data for all species and especially for those for which we have no information. This will improve our identifications and contribute to the construction of more comprehensive sound libraries for manual and automated identification, and to better understand the patterns of bat

diversity in Brazil and the Neotropical region as a whole. So, in conclusion, the use of bioacoustics can be a fundamental tool to expand the knowledge on Brazilian bats and improve their conservation. We hope that this will be the initiating spark for the sustained growth of the bat bioacoustics in Brazil.

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	Reference*	Region[a]	Recording site	Recording system[b]	Dispersion measure
1	Ávila-Flores & Fenton 2005	NA-Wt	Mexico-DF	TE	(CV)
2	Bader et al. 2015	CA-Tr	Panama	RT	None
3	Barataud et al. 2013	SA-Tr	French Guiana	TE/RT	(Min-Max) or ±SD
4	Barataud et al. 2015	CI-Tr	West Indies-Guadeloupe	TE	±SD
5	Eder Barbier pers. comm.+	SA-Tr	Brazil-Pernambuco	RT	±SD
6	Barclay et al. 1999	NA-Wt-Co	Canada	?	±SD
7	Borloti et al. 2014	SA-Tr	Brazil-Espírito Santo	TE	None
8	Briones-Salas et al. 2013	NA-Tr	Mexico-Oaxaca	ZC	±SD
9	Clare et al. 2013	CA-Tr/SA-TR/CI-Tr	Belize, Costa Rica/Guyana/Trinidad	RT	±SD
10	Estrada-Villegas et al. 2012	CA-Tr	Panama	RT	None
11	Falcão et al. 2015	SA-Tr	French Guiana/Brazil-Bahia	RT	±SD
12	Fenton et al. 1999	SA-Wt	Brazil-São Paulo	ZC	None
13	Gager et al. 2016	CA-Tr	Panama	RT	±SD
14	Gillam et al. 2010	NA-Wt	USA-Texas	RT	±SD
15	Guillén-Servent& Ibáñez 2007	SA-Tr	Venezuela	TE	±SD
16	González-Terrazas et al., 2016	NA-Ar	Mexico	RT	±SD
17	Hintze et al. 2016	SA-Tr	Brazil-Pernambuco	RT	±SD
18	Szewczak et al. 2011	NA-Wt-Co	USA	?	(Min-Max)
19	Ibáñez et al. 1999	CA-Tr	Panama	TE	±SD
20	Jung &Kalko 2011	CA-Tr	Panama-Costa Rica	TE/RT	None
21	Jung et al. 2007	CA-Tr	Panama-Costa Rica	TE/RT	±SD
22	Jung et al. 2014	CA_SA-Tr	Costa Rica, Panama, Venezuela, Bolivia, Brazil	TE/RT	±SD
23	Kraker-Castañeda et al. 2013	NA-Tr	Mexico-Oaxaca	ZC	None
24	López-Baucells et al. 2014	SA-Tr	Brazil	RT	±SD
25	López-Baucells et al. 2016	SA-Tr	Brazil	RT?	None
26	Macías et al. 2006	CI-Tr	Cuba	RT	±SD
27	MacSwiney et al. 2006	Na-Tr	Mexico-Yucatan	TE	±SD
28	MacSwiney et al. 2008	NA-Tr	Mexico-Yucatan	TE	±SD
29	O'Farrell & Miller 1997	CA-Tr	Belize	ZC	(SEM)
30	O'Farrell et al. 1999	CA-Tr/NA-Ar	Belize/USA-Arizona	ZC	±SD
31	Oliveira 2015	SA-Tr	Brazil-Brasilia	RT	±SD
32	Orozco-Lugo et al. 2013	NA-Tr	Mexico-Morelos	TE	±SD
33	Ossa et al. 2015	SA-Ar	Chile	TE	±SD
34	Pierson et al. 2006	NA-Ar-Wt	USA-California	ZC/TE	None
35	Pio et al. 2010	CI-Tr	Trinidad	TE	±SD
36	Ratcliffe et al. 2004	NA-Wt	Mexico-DF	TE	(Interquartile ranges)
37	Ratcliffe et al. 2011	CA-Tr	Panama	RT	±SE
38	Rivera-Parra &Burneo 2013	SA-Tr	Ecuador	TE	(Min-Max)
39	Rodríguez-San Pedro &Simonetti 2013	SA-Ar	Chile	TE	±SE
40	Rydell et al. 2002	NA-Tr-Ar	Mexico-Yucatan	FD/TE	±SD
41	Santos 2014	SA-Wt	Brazil-Parana	TE	±SD
42	Siemers et al. 2001	CA-Tr	Panama	TE	±SD
43	Smotherman&Guillén-Servent 2008	NA-Tr	Mexico-Veracruz	RT	±SD
44	Surlykke&Kalko 2008	CA-Tr	Panama	RT	None
45	Thoisy et al. 2014	SA-TR	French Guiana, Brazil-Amapá	TE/RT	±SD
46	Vaughan et al. 2004	CI-Tr	Puerto Rico	TE	±SD
47	Zamora-Gutierrez et al. 2016	NA-Tr-Ar-Wt	Mexico	TE/RT	±SD (CV)
°	Our recordings	SA-Tr	Brazil-Rio Grande do Norte/Pernambuco/Bahia/Tocantins	RT	±SD

Appendix S1. Supporting literature for the information on echolocation calls of the bat species potentially occurring in Brazil (includes information for 67 of the 93 species potentially occurring in the country).

[a] NA, North America; CA, Central America; SA, South America, CI, Caribbean Islands; Tr, tropical; Wt, warm temperate; Ar, arid; Co, cold.

[b] RT, real time; TE, time expansion; FD, frequency division; ZC, zero crossing.

Species name abbreviations

Table 1	
Cenmax (?)	*Centronycteris maximiliani (?)*
Cenmax/cen	*Centronycteris maximiliani/centralis*
Cencen	*Centronycteris centralis*
Corbre	*Cormura brevirostris*
Cytale	*Cyttarops alecto*
Dicalb	*Diclidurus albus*
Dicing	*Diclidurus ingens*
Dicisa	*Diclidurus isabella*
Dicscu/alb	*Diclidurus scuttatus/albus*
Perkap	*Peropteryx kappleri*
Perleu	*Peropteryx leucoptera*
Permac	*Peropteryx macrotis*
Perpal	*Peropteryx pallidoptera*
Pertri	*Peropteryx trinitatis*
Per sp.	*Peropteryx sp.*
Rhynas	*Rhynchonycteris naso*
Sacbil	*Saccopteryx bilineata*
Saccan	*Saccopteryx canescens*
Saccan/gym	*Saccopteryx canescens/gymnura*
Sacgym	*Saccopteryx gymnura*
Saclep	*Saccopteryx leptura*
Table 2	
Furhor	*Furipterus horrens*
Natmac	*Natalus macrourus*
Nattum	*Natalus tumidirostris*
Thydev	*Thyroptera devivoi*
Thydis	*Thyroptera discifera*
Thylav	*Thyroptera lavali*
Thytri	*Thyroptera tricolor*
Thywyn	*Thyroptera wynneae*
Table 3	
Cynabr	*Cynomops abrasus*
Cyngre/abr	*Cynomops greenhalli/abrasus*
Cyngre	*Cynomops greenhalli*
Cynmas	*Cynomops mastivus*
Cynmil	*Cynomops milleri*
Cynpar	*Cynomops paranus*
Cynpar/plan	*Cynomops paranus/planirostris*
Cynplan	*Cynomops planirostris*
Eumaur	*Eumops auripendulus*
Eumbon	*Eumops bonariensis*
Eumnan	*Eumops nanus*
Eumdab	*Eumops dabbenei*
Eumdel	*Eumops delticus*
Eumgla	*Eumops glaucinus*

Eumhan	*Eumops hansae*
Eummau	*Eumops maurus*
Eumpat	*Eumops patagonicus*
Eumper	*Eumops perotis*
Eumtru	*Eumops trumbulli*
Eumaur/gla/dab/han/mau	*Eumops auripendulus/glaucinus/dabbenei/hansae/maurus*
Molneg	*Molossops neglectus*
Moltem	*Molossops temminckii*
Neomat	*Neoplatymops mattogrossensis*
Molazt	*Molossus aztecus*
Molbar	*Molossus barnesi (sinonimia de coibensis)*
Molcoi	*Molossus coibensis*
Molcur	*Molossus currentium*
Molmol	*Molossus molossus*
Molpre	*Molossus pretiosus*
Molruf	*Molossus rufus*
Molsin/cur/ruf	*Molossus sinaloe/currentium/rufus*
Nycaur	*Nyctinomops aurispinosus*
Nyclat	*Nyctinomops laticaudatus*
Nycmac	*Nyctinomops macrotis*
Procen	*Promops centralis*
Pronas	*Promops nasutus*
Tadbra	*Tadarida brasiliensis*
Nyclat/Tadbra	*Nyctinomops laticaudatus/Tadarida brasiliensis*
Table 4	
Ptedav	*Pteronotus davyi*
Ptegym	*Pteronotus gymnonotus*
Pteper	*Pteronotus personatus*
***Ptemes* G1**	*Pteronotus mesoamericanus* group 1
***Ptepar* G2**	*Pteronotus* cf *parnellii* group 2
***Ptepar* G3-4**	*Pteronotus* cf *parnellii* group 3-4
Ptepar	*Pteronotus* cf *parnellii*
Table 5	
Nocalb	*Noctilio albiventris*
Noclep	*Noctilio leporinus*
Table 6	
Eptand	*Eptesicus andinus*
Eptbra	*Eptesicus brasiliensis*
Eptbra/chi	*Eptesicus brasiliensis/chiriquinus*
Eptchi	*Eptesicus chiriquinus*
Eptdim	*Eptesicus diminutus*
Eptfur	*Eptesicus furinalis*
Epttad	*Eptesicus taddeii*
Lasblo	*Lasiurus blossevillii*
Lascas	*Lasiurus castaneus*
Lascin	*Lasiurus cinereus*
Lasebe	*Lasiurus ebenus*
Lasega	*Lasiurus ega*

Lasegr	*Lasiurus egregius*
Lassal	*Lasiurus salinae*
Hisali	*Histiotus alienus*
Hisdia	*Histiotus diaphanopterus*
Hislae	*Histiotus laephotis*
Hismon	*Histiotus montanus*
Hisvel	*Histiotus velatus*
Myoalb	*Myotis albescens*
Myodin	*Myotis dinellii*
Myoize	*Myotis izecksohni*
Myolav	*Myotis lavali*
Myolev	*Myotis levis*
Myonig	*Myotis nigricans*
Myorip	*Myotis riparius*
Myorub	*Myotis ruber*
Myosim	*Myotis simus*
Rhohus	*Rhogeessa hussoni*
Rhoio	*Rhogeessa io*

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*Our recordings

Illustrated identification key to the calls of Brazilian bats

These identification key was elaborated by Frederico Hintze[1] with collaboration of Adriana Arias-Aguilar[2] Ludmilla M.S. Aguiar[3], Vincent Rufray[4], Enrico Bernard[1] and Maria João Ramos Pereira [2].

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Abbreviations:

FM – Modulated Frequency

FM_u – upward Modulated Frequency

FM_d – downward Modulated Frequency

stFM – steep FM

CF – Constant Frequency

qCF – *quasi*-Constant Frequency

qCF_u – upward *quasi*-Constant Frequency

qCF_d - downward *quasi*-Constant Frequency

FME – Frequency of Maximum Energy of the call

FME_1 – FME of call type I

FME_2 - FME of call type II

FME_3 – FME of call type III

FME_{QCF} - FME of the call's qCF component

F_{MIN} – Minimum Frequency of the call

F_{MAX} – Maximum Frequency of the call

$F_{INITIAL}$ – Initial Frequency/Start frequency of the call

F_{END} – End Frequency of the call

BW – Bandwidth of the call

Dur – Call duration

IPI – Inter-pulse Interval (interval between calls)

HF – Fundamental Harmonic (First harmonic)

H2 – Second Harmonic

H3 – Third Harmonic

H4 – Forth Harmonic

Note

This key is an adaptation of another key made for French Guiana by Barataud *et al.* (2013). A comprehensive bibliographic search was performed plus we added our own records for developing the key. Yet, this key does not contain all Brazilian bat species. And additional information, calls for reference and suggestions are welcome. Therefore, in certain cases, our identifications are restricted to the family level, to a complex of species or even referred as "unidentified". We emphasize that in order to use this key, users need a minimum training on bat bioacoustics, and further frequent bibliographic search is also necessary, so updates can be included and mistakes corrected. The main goal of this key is to be one more tool to support the acoustical identification of the Brazilian bats.

Bat echolocation calls are not to be addressed like birdcalls. In the case of bats, using the echolocation to navigate and perceive their surroundings and to catch prey, the call parameters of a species can be highly variable depending on the vegetation clutter, type of habitat and activity (e.g. Barclay et al., 1999; Schnitzler et al., 2003). For bat identification purposes, this key only considers acoustic parameters of search calls (used for navigation) and not of feeding-buzzes or social-calls (see Schnitzer & Kalko, 2001; Fenton, 2003; Schnitzler et al., 2003).
Acoustic parameters can be measured with any bioacoustics software using spectrograms, oscillograms and power spectrum. Such parameters can be extracted manually or with softwares that automatically extract the acoustic parameters of the selected calls. Time-related parameters (i.e. Duration – Dur- and Inter Pulse Interval - IPI) should be extracted using the oscillogram (see Figure N1); Initial frequency – Finitial – and Final Frequency – Ffinal – can also be extracted using a combination of oscillogram and spectrogram (Figure N1). Frequency-related parameters as Minimum Frequency – Fmin and Maximum Frequency – Fmax, should be extracted using the power spectrum or the spectrogram (the Frequency with Most Energy – FME – should be obtained only

in the power spectrum, see Figure N2). Bandwidth – BW – can be calculated as the difference between Fmax and Fmin (see Figure N2).

Beware that sometimes the echolocation calls presents harmonics (see Figure N3). The lowest harmonic is always the fundamental harmonic (HF or first harmonic – H1) and the harmonics are counted from the lowest to the highest (HF, H2, H3, etc.) (Figure N3). All harmonics are always multiples of the fundamental (i.e. if the fundamental is at 30 kHz, the second is at 60 kHz and the third at 90 kHz). The FME can be in the HF, H2 or H3, and this can be very indicative of certain *taxa*.

Call structure is also an important feature used for bat acoustics identification. The call structure can be examined in the spectrogram. Beware that, depending on the software and approach, zooming on the X-axis can distort your perception; therefore, the call structure should be examined with a maximum zoom of two calls in the spectrogram. There are two main basic call structures: frequency modulated (FM), where the frequency varies over time; and constant frequency (CF), where the frequency does not varies over time (Figure N4). The FM component can be downward (descendant - FMd) or upward (ascendant - FMu) (Figure N4, 1 and 2 respectively). Sometimes the frequency varies slightly over time – known as *quasi*-constant frequency (qCF) – and also can be downward (qCFd, descendant) or upward (qCFa, ascendant) (Figure N4, 5 and 6 respectively). Some calls are composed of several types of these basic structures (e.g. FM-qCF; CF-FMd; FMu-qCFd-FMd).

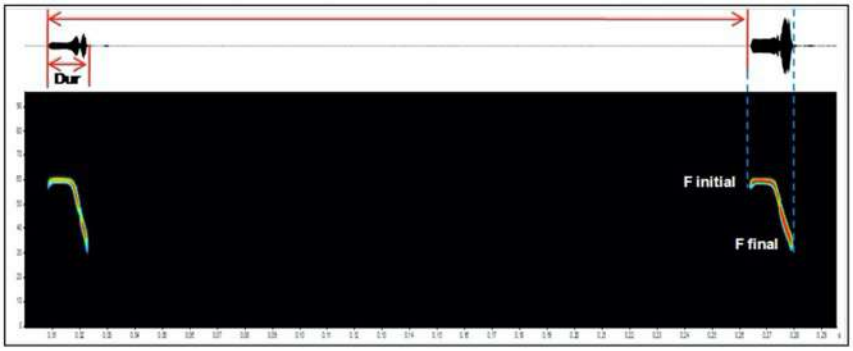


Figure N1 – Oscillogram [above, time (X) vs. amplitude (Y)] and spectrogram [below, time (X) vs. frequency (Y) vs. energy (color scale)] of two echolocation calls.

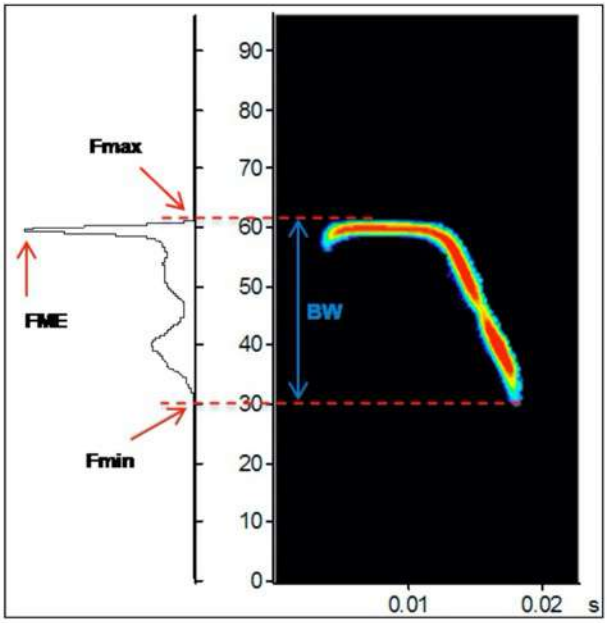


Figure N2 – Spectrogram [at right, time (X) vs. frequency (Y) vs. energy (color scale)] and power spectrum (at left, frequency (X) vs. energy (Y)] of an echolocation call.

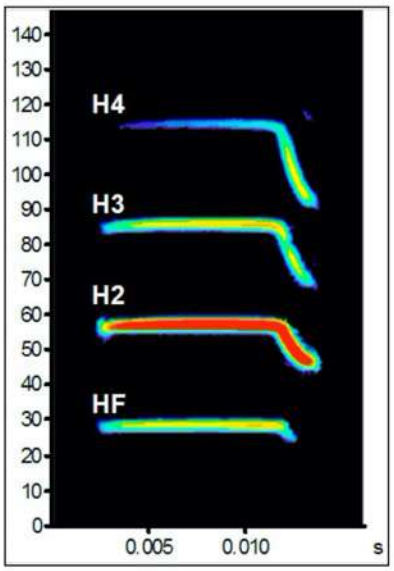


Figure N3 – Spectrogram showing four harmonics of an echolocation call. FME is on the H2.

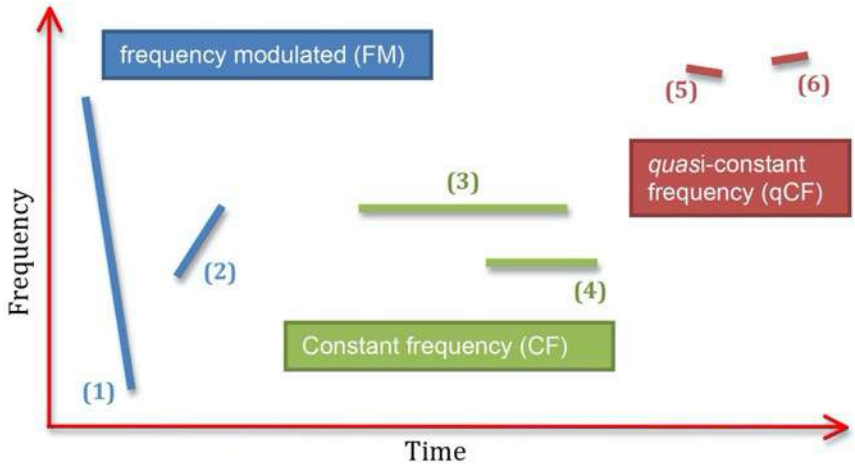


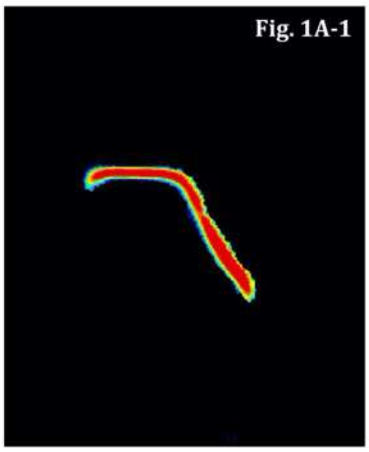
Figure N4 – Schematic representation of a spectrogram, with some basic structures of a calling.

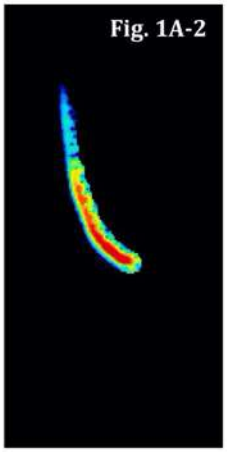
Dichotomous key

Note: Inter-pulse intervals (IPI) and duration (Dur) of the calls in the figures of this key are not scaled.

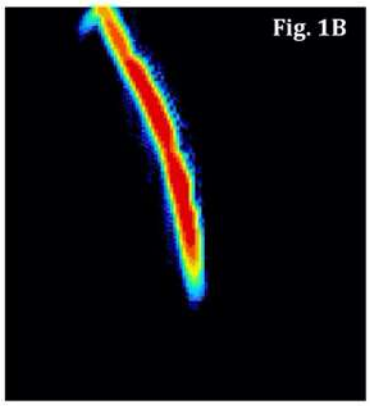
1.

a) Call structure with, at least, one CF (Fig. 1A-1) or qCF (Fig. 1A-2) component.....2



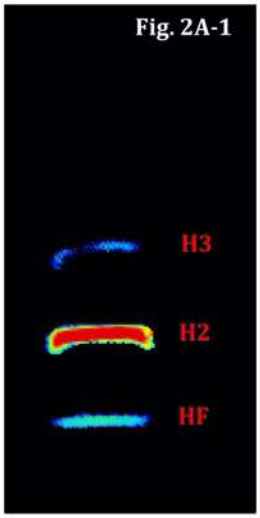


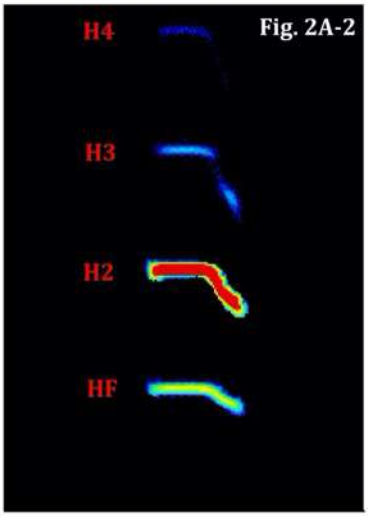
b) Call structure without any CF or qCF component (Fig. 1B).....31



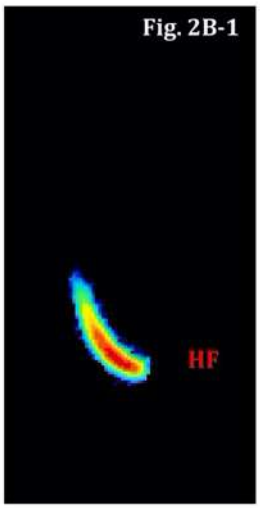
2.

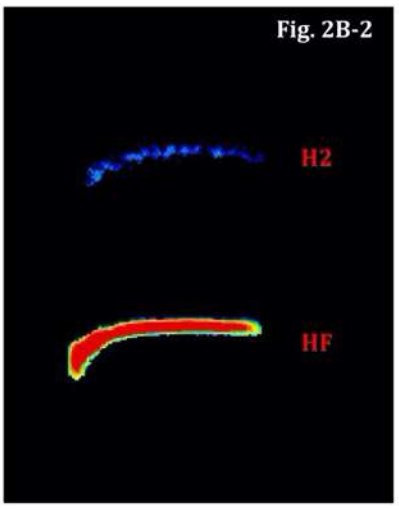
a) FME usually in a **non-fundamental** harmonic (H2 or H3) (Fig. 2A-1; Fig. 2A-2), occasionally the fundamental harmonic is not perceptible……..…..3





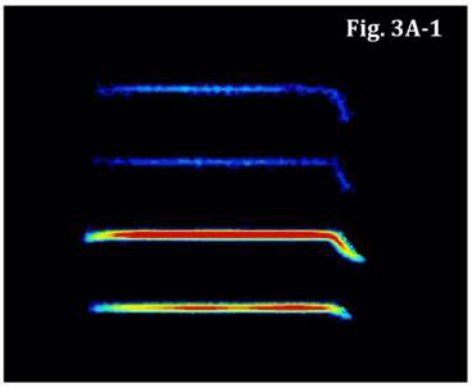
b) FME usually in the **fundamental** harmonic (HF) (Fig. 2B-1; Fig. 2B-2).....13

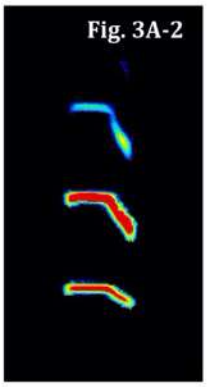




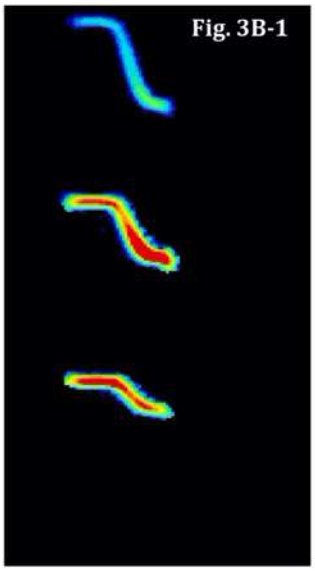
3.

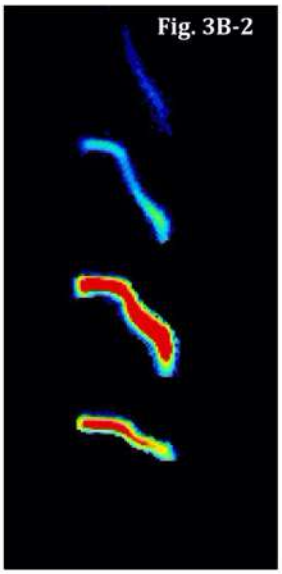
a) Call structure is (qCF)/CF/FM_d; sometimes presents multi-harmonic sequences (Fig. 3A-1; Fig. 3A-2)…….....4



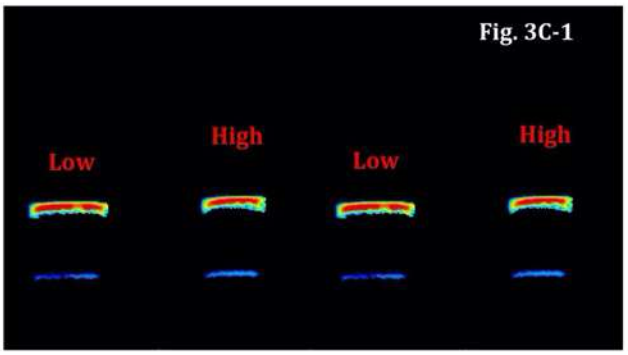


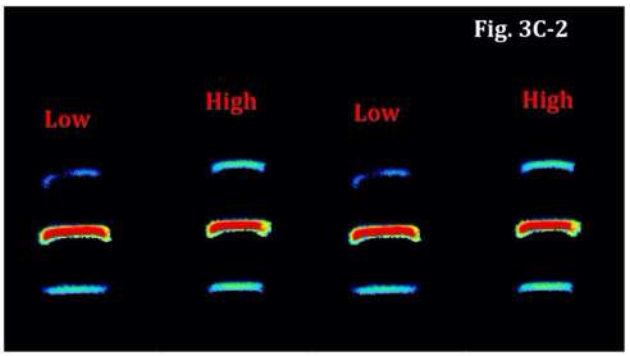
b) qCF_u/FM/qCF_d ("lazy-z") (Fig. 3B-1; Fig. 3B-2); FME usually in the H2 or equally distributed by the harmonics; sometimes presents multi-harmonic sequences.....5



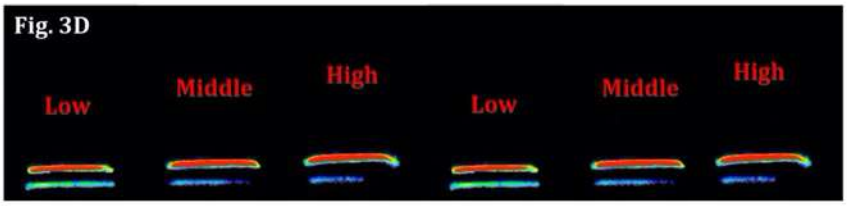


c) $FM_u/qCF_u/FM_d$; regular frequency alternations of two call types (Fig. 3C-1; Fig. 3C-2); FME in the H2.....7

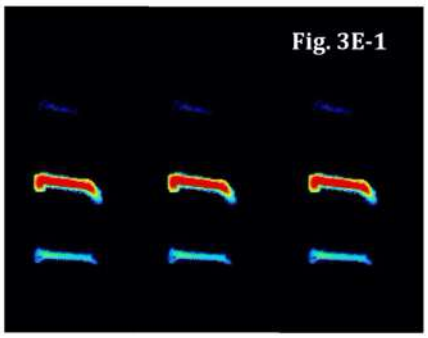


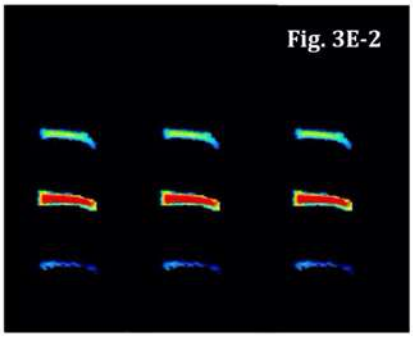


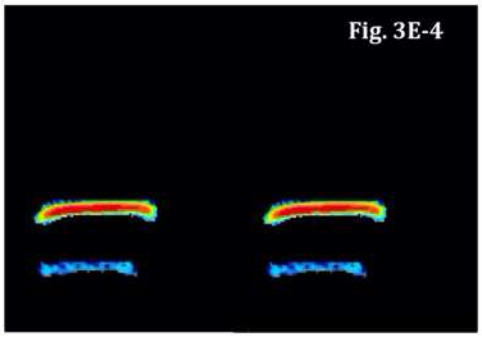
d) $(FM_u)/qCF_u/FM_d$; regular frequency alternations of three call types (Fig. 3D); FME in the H2.....9



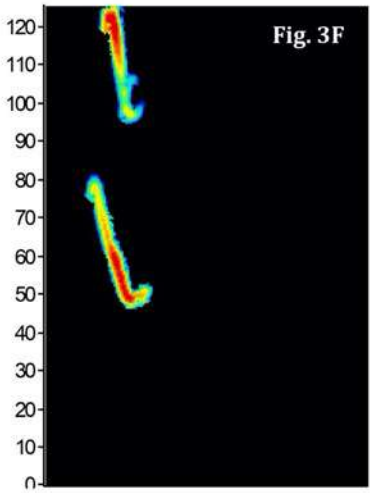
e) $FM_u/qCF_d/FM_d$ (Fig. 3E-1), qCF/FM_d (Fig. 3E-2), qCF (Fig. 3E-3) or $FM_u/qCF/FM_d$ (Fig. 3E-4) without frequency alternations; FME in the H2.....10







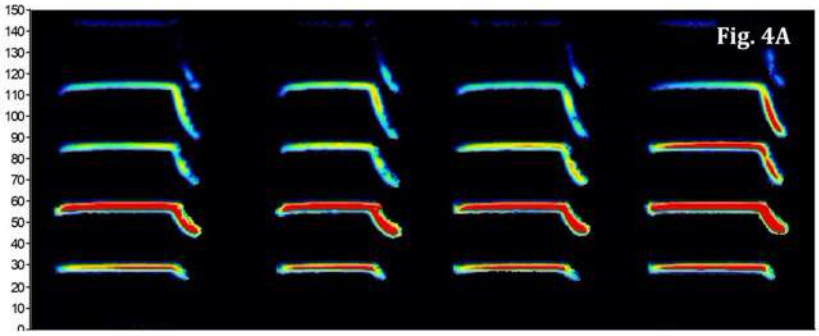
f) stFM with a very short qCF termination, FME >100 kHz (Fig. 3F).....***Natalus* spp.**



g) High duty-cycle echolocation (Duty cycle >25%); FME between 55 and 65 kHz; very prominent CF component; call duration usually greater than 20 ms (see Fig. 4A)…….....……..……..***Pteronotus* cf *parnellii***

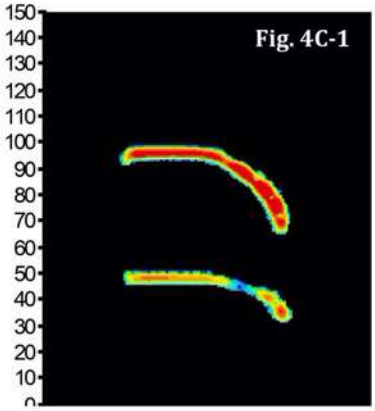
4.

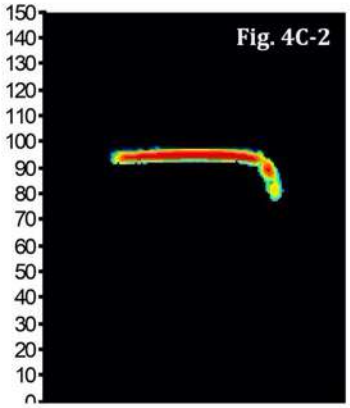
a) CF component's duration >20 ms, FME between 55 and 65 kHz, high duty-cycle echolocation (Duty cycle >25%) (Fig. 4A).....***Pteronotus* cf *parnellii***



b) FME of the initial CF component (in H2) around 60 kHz; call duration usually <10 ms (Fig. 4B).....***Pteronotus gymnonotus***

c) Call structure is usually (qCF_u)-CF-FM_d (Fig. 4C-1), but occasionally the FM component is imperceptible or absent (Fig. 4C-2); FME between 85 and 100 kHz; call duration <8 ms.....***Rhynchonycteris naso***





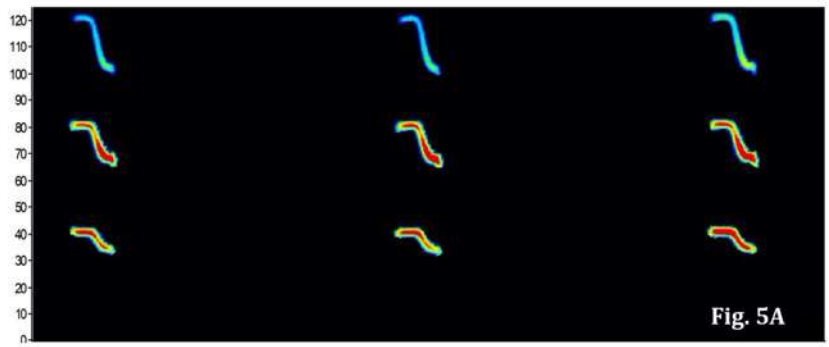
d) FME of the initial CF component between 55 and 80 kHz; FME in the H2……..…5

e) FME in the H3; FME of the initial CF component between 45 and 50 kHz; call duration between 5 and 10 ms; occasionally the FM component is imperceptible or absent……..…..***Lonchorhina aurita***

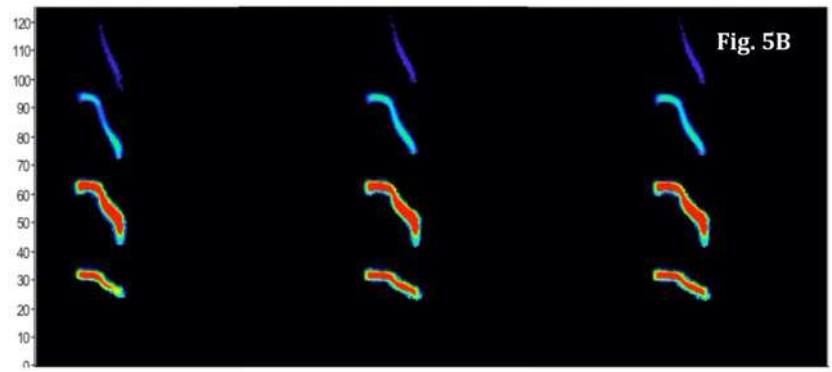
f) FME in the H3; FME of the initial CF component between 35 and 40 kHz; call duration between 4 and 8 ms; occasionally the FM component is imperceptible or absent……..……..…..***Lonchorhina inusitata***

5. ***Pteronotus*** **sp.**

a) FME of the initial CF component (in H2) >74 kHz (Fig. 5A).....***Pteronotus personatus***



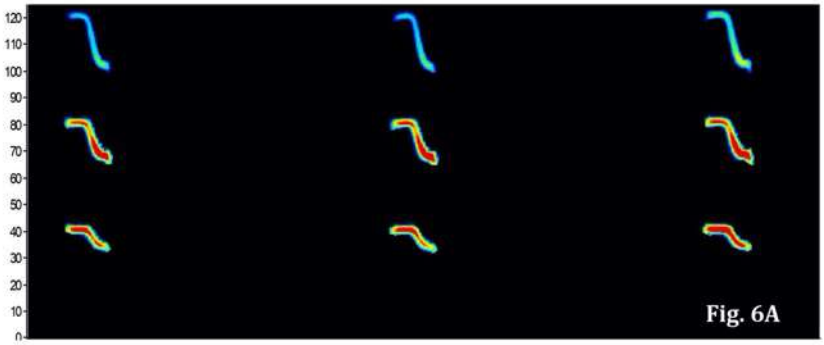
b) FME of the initial CF component (in H2) between 55 and 65 kHz (Fig. 5B).....***Pteronotus gymnonotus***



c) FME of the initial CF component (in H2) between 68 and 74 kHz.....6

6. ***Pteronotus* sp.**

a) F_{min} of the final CF component (in H2) >60 kHz (Fig. 6A)…….....***Pteronotus personatus***

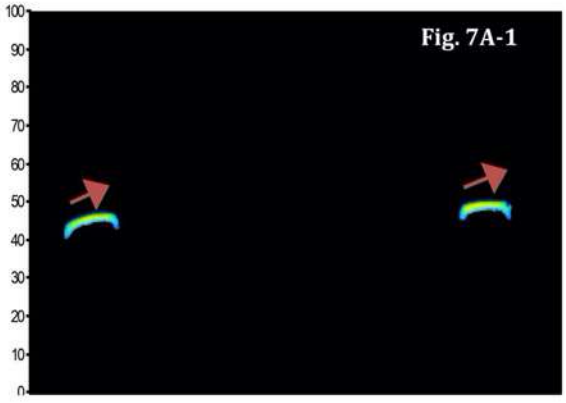


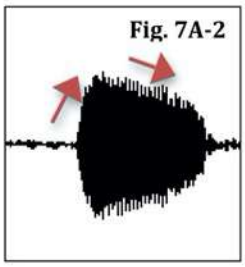
b) F_{min} of the final CF component (in H2) between 59 and 60 kHz.....***Pteronotus davyi/P. personatus***

c) F_{min} of the final CF component (in H2) <59 kHz.....***Pteronotus davyi***

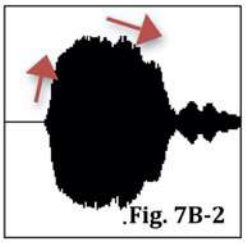
7. **Emballonuridae**

a) qCF component of the call with a slight upward modulation (Fig. 7A-1), $FME_1 \approx 44$ kHz e $FME_2 \approx 48$ kHz; usually, in the oscillogram, the maximum amplitude is at the beginning of the call, descending along the call (Fig. 7A-2).....***Saccopteryx bilineata***

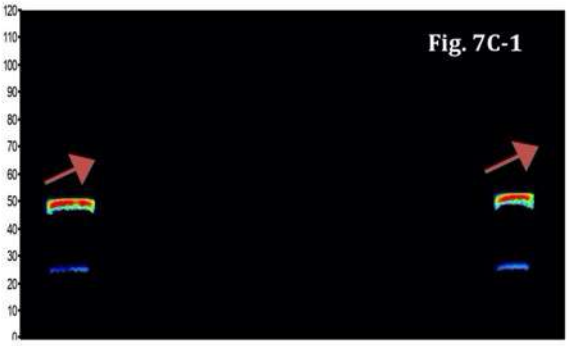


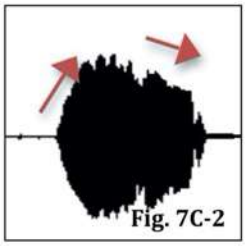


b) qCF component of the call with a slight upward modulation (Fig. 7B-1), FME_1 ≈ 38 kHz e FME_2 ≈ 42 kHz; usually, in the oscillogram, the maximum amplitude is at the beginning of the call, slightly descending along the call (Fig. 7B-2)……..…..***Saccopteryx* sp. "38-42kHz"**



c) qCF component of the call with a slight upward modulation (Fig. 7C-1), FME_1 between 47 and 49 kHz and FME_2 between 49 and 52 kHz; usually, in the oscillogram, the maximum amplitude is at the beginning of the call, descending along the call (Fig. 7C-2)…….....***Saccopteryx leptura***





d) qCF component of the call without modulation; initial and final FM components barely perceptible or absent (Fig. 7D-1); irregular Call duration and IPI; FME of the calls is always below 32 kHz; usually, in the oscillogram, the maximum amplitude is at the beginning of the call, with low variation along the call (Fig. 7D-2).....8

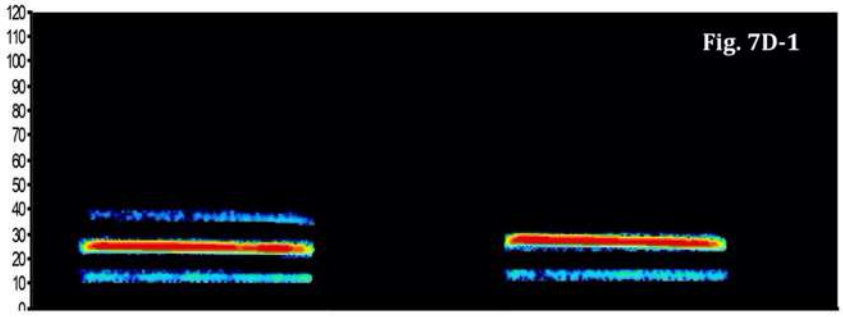


Fig. 7D-1

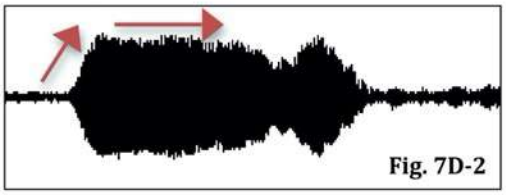


Fig. 7D-2

8. ***Diclidurus*** **sp.**

a) $FME_1 \approx 29$ kHz and $FME_2 \approx 31$ kHz.....***Diclidurus scutatus***

b) $FME_1 \approx 27$ kHz and $FME_2 \approx 31$ kHz.....***Diclidurus scutatus/D. albus***

c) $FME_1 \approx 23$ kHz and $FME_2 \approx 26$ kHz.....***Diclidurus albus***

d) $FME_1 \approx 19$ kHz and $FME_2 \approx 22$ kHz.....***Diclidurus ingens***

9. qCF component of the call with a slight upward modulation; $FME_1 \approx$ 25-26 kHz, $FME_2 \approx$ 28-29 kHz and $FME_3 \approx$ 31-32 kHz, occasionally one of the calls is not emitted (Fig. 9-1); usually, in the oscillogram, the call has a conical shape and the maximum amplitude is at the beginning of the call (Fig. 9-2).....***Cormura brevirostris***

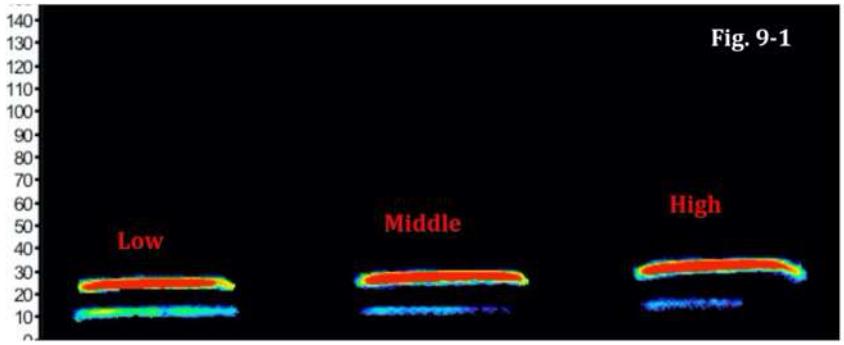


Fig. 9-1

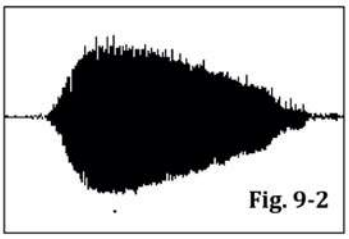


Fig. 9-2

10. Emballonuridae

a) qCF component of the calls without upward modulation (Fig. 10A-1, in red arrow) or downward (Fig. 10A-2, in red arrow); evident final FM component but initial FM component is absent (Fig. 10A-1, in green arrow) or barely perceptible (Fig. 10A-2, in green arrow), call duration typically >7 ms, very regular call duration and IPI; usually, in the oscillogram, the maximum amplitude is at the beginning of the call (Fig. 10A-3), descending sharply along the call (triangular shape).....11

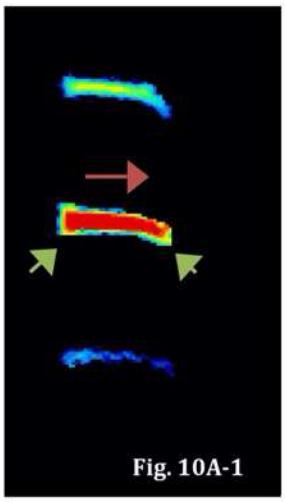


Fig. 10A-1

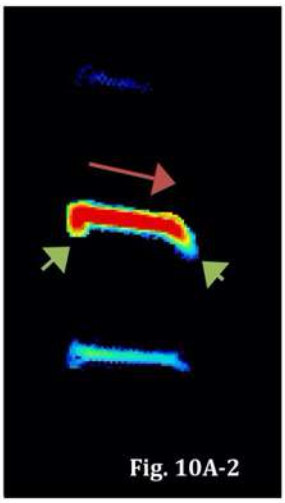


Fig. 10A-2

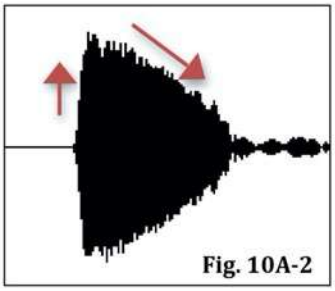
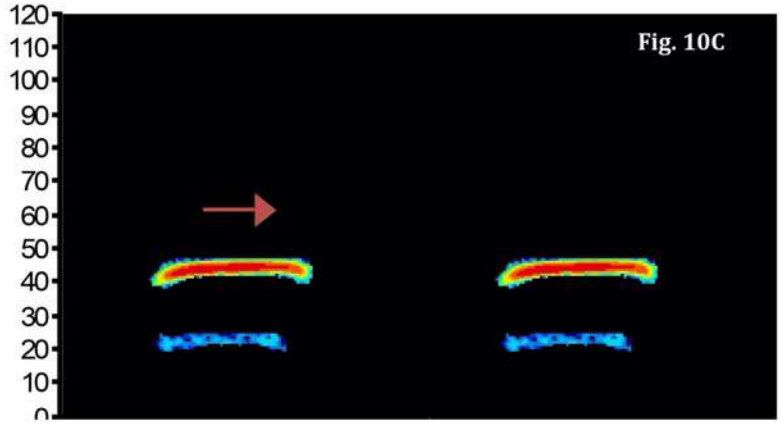


Fig. 10A-2

b) Initial and final FM components barely perceptible or absent (see Fig. 7E-1); irregular Call duration and IPI; FME of the calls is always below 32 kHz; usually, in the oscillogram, the maximum amplitude is at the beginning of the call, not varying much along the call (see Fig. 7E-2).…….....12

c) qCF component of the call without modulation (Fig. 10C); evident initial and final FM components; occasionally the final FM is barely perceptible; short call duration (<7 ms) and constant IPI; FME between 41 and 42 kHz.....***Centronycteris maximiliani***



d) qCF component of the call with an upward modulation; very evident initial and final FM components; FME around 53 kHz; highly variable call duration (between 3 and 14 ms) (Figure 10D).....***Saccopteryx canescens***

e) qCF component of the call with upward modulation; very evident initial and final FM components; FME > 54 kHz (56-58 kHz); call duration less variable (4–7 ms) than in *S. canescens* (Figure 10E)……**...*Saccopteryx gymnura***

f) qCF component of the call with upward modulation; FME around 34 and 36 kHz, call duration between 8 and 12 ms.....***Cyttarops alecto***

11. ***Peropteryx*** **sp.**

a) FME between 29 and 32 kHz.....***Peropteryx kappleri***

b) FME between 37 and 39 kHz.....***Peropteryx macrotis***

c) FME between 42 and 44 kHz.....***Peropteryx trinitatis***

d) FME between 39 and 42 kHz (?).....***Peropteryx leucoptera/P. palidoptera***?

12. ***Diclidurus*** **sp.**

a) FME ≈ 29 kHz.....***Diclidurus scutatus***

b) FME ≈ 27 kHz.....***Diclidurus scutatus/D. albus***

c) FME ≈ 23 kHz.....***Diclidurus albus***

d) FME ≈ 19 kHz.....***Diclidurus ingens***

13.

a) Irregular alternation of two types of calls with opposing modulation: one call with FM_u/qCF_u structure (Type I) and the other with FM_d/qCF_d structure (Type II) (Fig. 13A-1; Fig. 13A-2 and Fig. 13A-3).....14

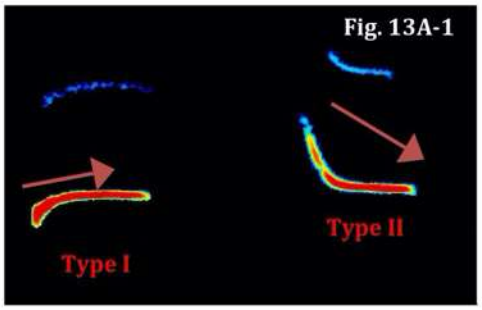


Fig. 13A-1

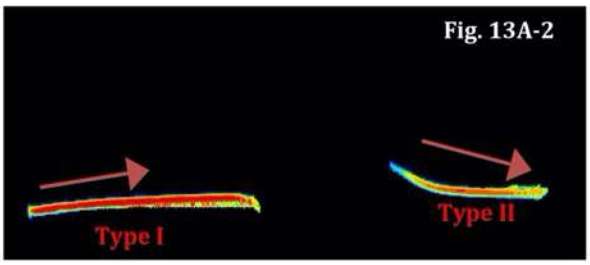


Fig. 13A-2

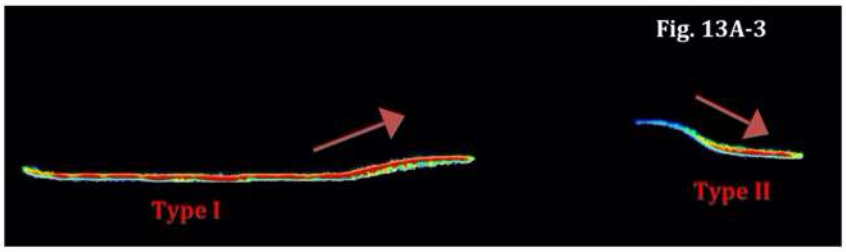
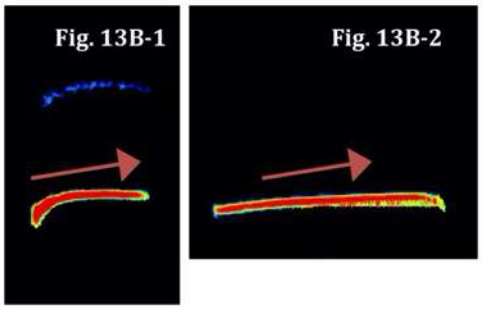
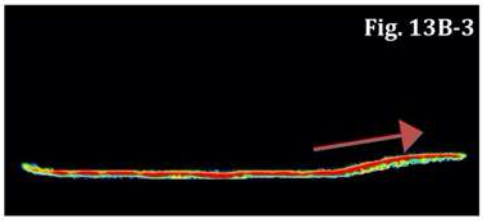


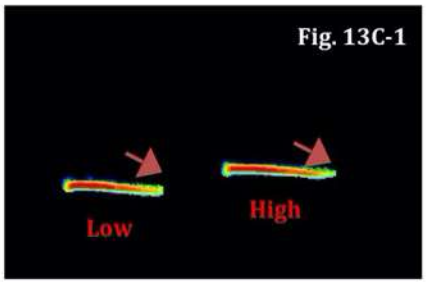
Fig. 13A-3

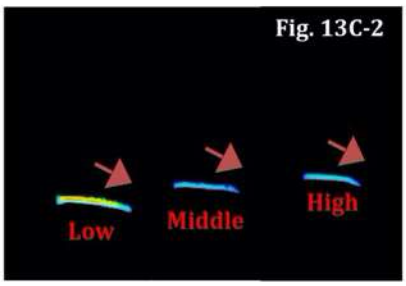
b) Calls with FM_u/qCF_u structure without alternation (Fig. 13B-1; Fig. 13B-2; Fig. 13B-3)…….....17





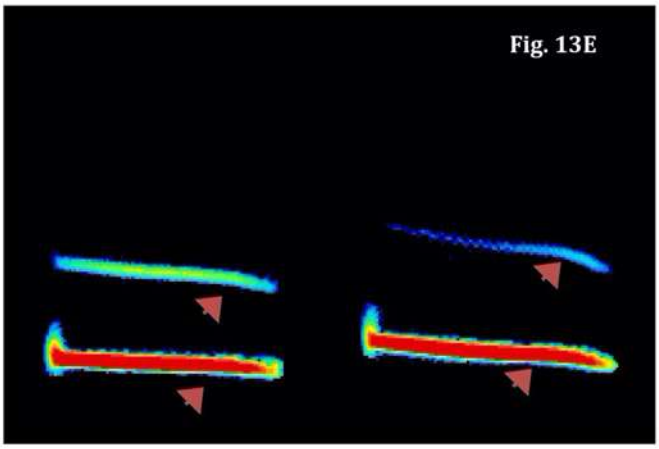
c) Irregular alternation in frequency of two (Fig. 13C-1) or three calls (Fig. 13C-2); call structure (FM_u)-qCF_d, with short BW (<10 kHz).....18





d) Alternations in frequency of two call types: the first with FM_u/qCF_d structure (Type I) and the second with FM_d/qCF (Type II) (Fig. 13D); sometimes the second pulse is omitted.....19

e) Call structure presenting a small inflexion point in the middle of the pulse, increasing the call descending modulation (red arrow, Fig. 13E); long call duration (>10 ms); calls may present alternation in frequency; call energy (amplitude) is usually distributed along the call.....20



f) qCF/FM or CF/FM call structure; FM component with a large BW (normally >10 kHz); qCF or CF component is highly variable in duration; call energy (amplitude) usually distributed along the call (Fig. 13F-1) or is in the FM component (Fig. 13F-2); sometimes alternates calls with shorter FM components (Fig. 13F-3).....21

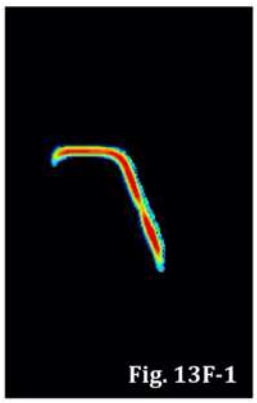


Fig. 13F-1

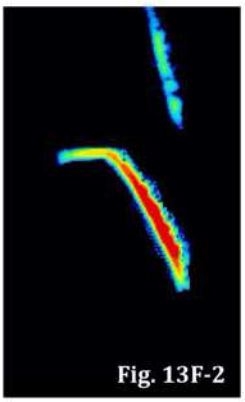


Fig. 13F-2

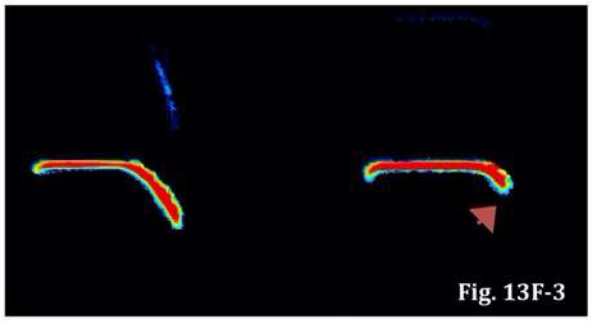
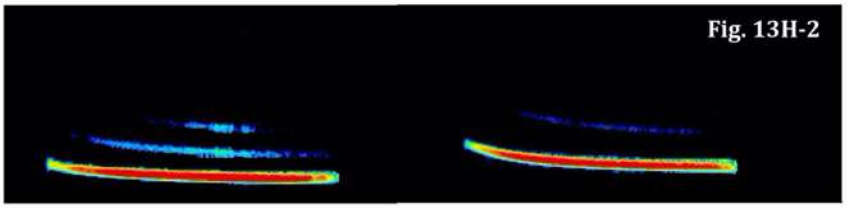


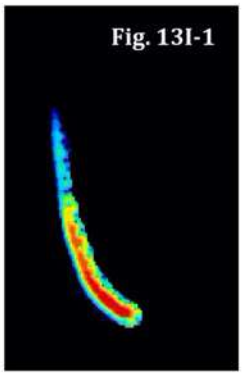
Fig. 13F-3

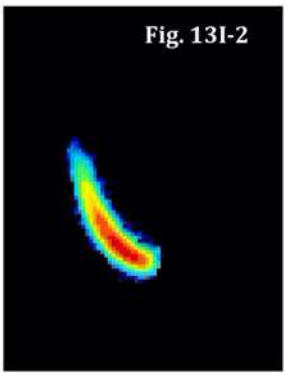
g) qCF_d call structure without frequency alternation: call duration >10 ms; very short BW (<5 kHz) and very reduced slope (<1 Hz/ms).....23

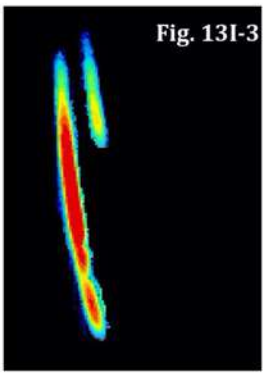
h) Long call duration (usually >12 ms); FM_d/qCF_d calls where the qCF_d component has more meaning than the FM component or only the qCF_d component is present; call amplitude is usually distributed along the call; frequency alternation is common (Figures 13H-1 and 13H-2)……..... 24



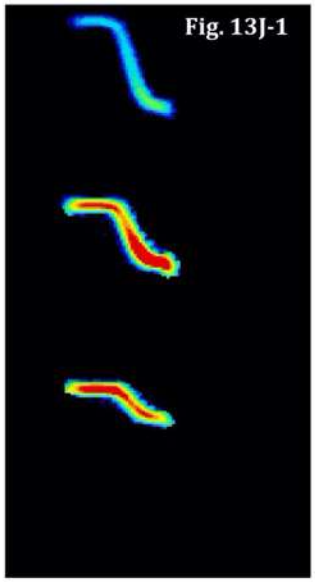
i) FM_d/qCF_d calls without frequency alternation; the FM component is prominent whereas the qCF component represents the terminal part of the call (Figs. 13I-1 and 13I-2) or is almost absent (Fig. 13I-3); FME is usually in the qCF component; when the qCF component is not present the FME location is more variable.....25

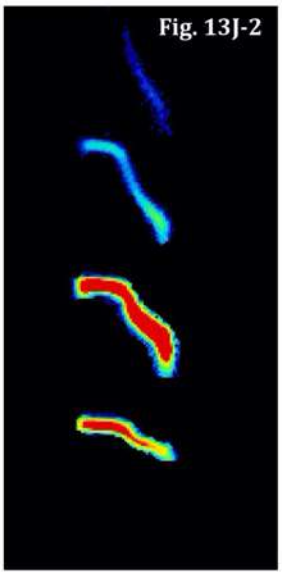




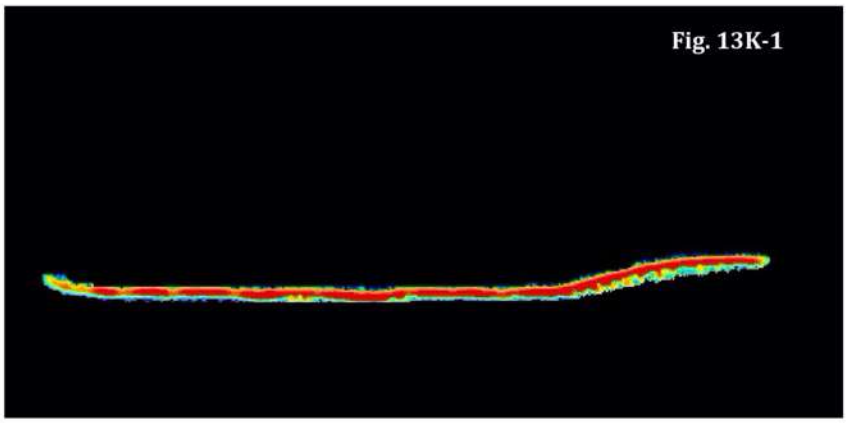


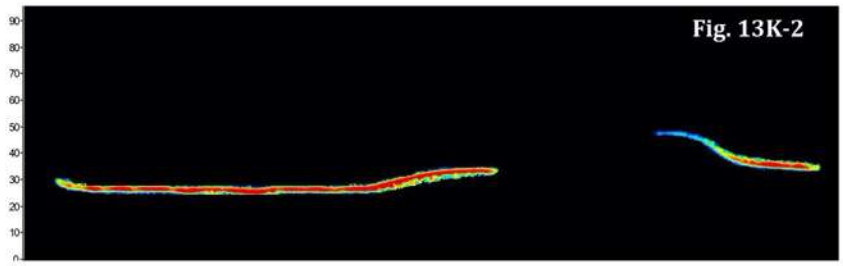
j) Call structure is $qCF_u/FM/qCF_d$ (shaped as a "lazy-z") (Figs. 13J-1 and 13J-2).....4





k) High duty-cycle echolocation (duty cycle >25%); prominent CF component and upward modulation (Fig. 13K-1); call duration >20 ms; $F_{INITIAL}$ between 22 and 27 kHz and F_{END} between 27 and 33 kHz; FME between 24 and 30 kHz averaging 28 kHz; often typical calls alternate with downward modulated calls of higher frequencies (FME between 33 and 38 kHz) (Fig. 13K-2)……..……..***Promops centralis***





14. **Molossidae**

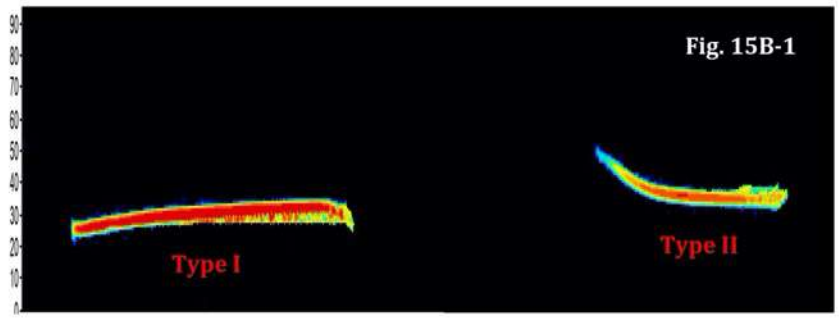
a) FME of call type I < 40 kHz.....15

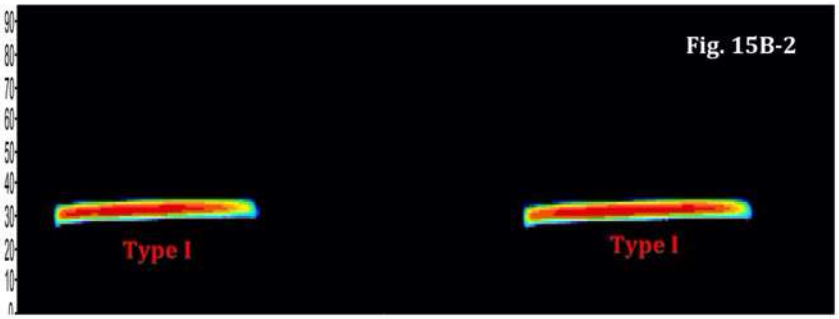
b) FME of call type I > 40 kHz.....16

15. ***Promops*** **sp.**

a) Call type I: $F_{INITIAL}$ between 32 and 35 kHz and F_{END} between 33 and 36 kHz; FME ≈ 35 kHz; Call duration < 15ms. Call type II: $F_{INITIAL}$ ≈ 47 kHz e F_{END} ≈ 38 kHz (Fig. 15A-1); this type of call may be omitted (Fig. 15A-2).....***Promops nasutus***

b) Call type I: $F_{INITIAL}$ between 25 and 27 kHz and F_{END} between 28 and 30 kHz; FME between 25 and 31 kHz; Call duration > 15ms; Call type II: $F_{INITIAL}$ between 29 and 47 kHz and F_{END} between 29 and 35 kHz, FME between 33 and 38 kHz, Call duration > 10 ms (Fig. 15B-1); this type of call may be omitted (Fig. 15B-2).....***Promops centralis***

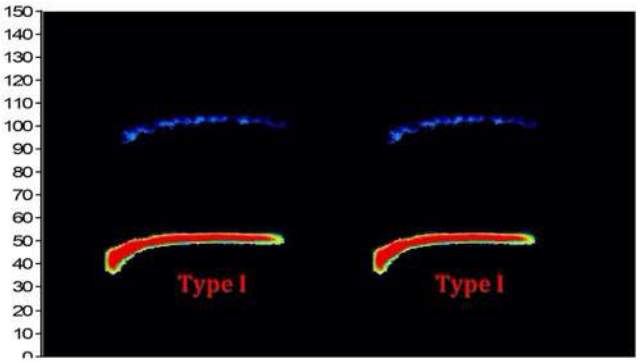




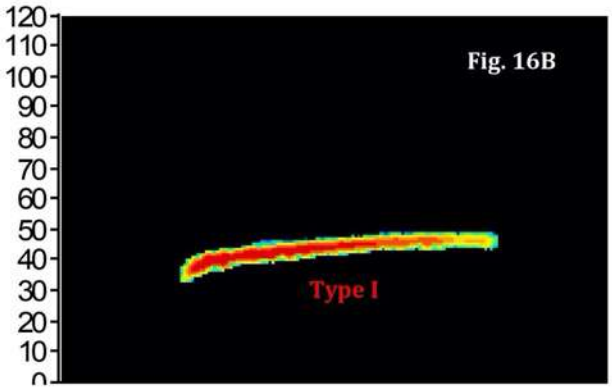
c) High duty-cycle echolocation (Duty cycle >25%); Call type I: prominent CF component and upward modulation (see Fig. 13K-1); call duration >20 ms; $F_{INITIAL}$ between 22 and 27 kHz and F_{END} between 27 and 33 kHz; FME between 24 and 30 kHz averaging 28 kHz. Call type II: $F_{INITIAL}$ between 29 and 47 kHz and F_{END} between 29 and 35 kHz, FME between 33 and 38 kHz, Call duration > 10 ms (see Fig. 13K-2); this type of call may be omitted…..…..……..***Promops centralis***

16. ***Molossops*** **sp.**

a) Call type I: $F_{INITIAL}$ between 40 and 45 kHz and F_{END} between 50 and 56 kHz or $F_{INITIAL}$ between 43 and 48 kHz and F_{END} between 53 and 56 kHz; FME between 50 and 55 kHz; Call type II: $F_{INITIAL}$ between 66 and 86 kHz and F_{END} between 54 and 57 kHz (Fig. 16A-1); it might omit type II calls (Fig. 16A-2).....***Molossops temminckii***



b) Call type I: $F_{INITIAL}$ between 30 and 36 kHz and F_{END} between 42 and 46 kHz or $F_{INITIAL}$ between 36 and 41 kHz and F_{END} between 46 and 48 kHz; FME ≈ 45 kHz; Call type II: $F_{INITIAL}$ between 50 and 60 kHz and F_{END} around 47 kHz, it might omit type II calls (Fig. 16B).....***Molossops neglectus***



17. ***Molossidae***

a) $F_{INITIAL}$ between 32 and 35 kHz and F_{END} between 33 and 36 kHz; FME ≈ 35 kHz; call duration usually < 16 ms (see Fig. 15A-2).....***Promops nasutus***

b) $F_{INITIAL}$ between 25 and 27 kHz and $F_{INITIAL}$ between 28 and 30 kHz; FME between 25 and 31 kHz; Call duration > 15 ms (see Fig. 15B-2).....***Promops centralis***

c) High duty-cycle echolocation (Duty cycle >25%); prominent CF component and upward modulation (see Fig. 13K-1); call duration >20 ms; $F_{INITIAL}$ between 22 and 27 kHz and F_{END} between 27 and 33 kHz; FME between 24 and 30 kHz averaging 28 kHz.……..…..***Promops centralis***

d) $F_{INITIAL}$ between 40 and 45 kHz and F_{END} between 53 and 56 kHz or $F_{IINITIAL}$ between 43 and 48 kHz and F_{END} between 53 and 56 kHz; FME between 50 and 55 kHz (see Fig. 16A).....***Molossops temminckii***

e) $F_{INITIAL}$ between 29 and 36 kHz and F_{END} between 42 and 46 kHz or $F_{INITIAL}$ between 36 and 41 kHz and F_{END} between 46 and 48 kHz; FME ≈ 45 kHz (see Fig. 16B).....***Molossops neglectus***

18. **Molossidae**

a) Frequency alternation of two calls or occasionally 3 calls: $FME_1 \approx 30$ kHz, $FME_2 \approx 33$ kHz and $FME_3 \approx 36$ kHz.....***Molossus currentium***

b) Frequency alternation of two calls or occasionally 3 calls: $FME_1 \approx 34$ kHz (33–35 kHz), $FME_2 \approx 39$ kHz (35–40 kHz) and $FME_3 \approx 42$ kHz.....***Molossus molossus***

c) Frequency alternation of two calls or occasionally 3 calls: $FME_1 \approx 38$ kHz (36–40 kHz), $FME_2 \approx 42$ kHz (41–43kHz) e $FME_3 \approx 45$ kHz (43–48 kHz).....***Molossus* spp.** "small size" (*M. aztecus/M. coibensis*?)

d) Frequency alternation of two calls or occasionally 3 calls: FME_1 between 24 and 25 kHz, FME_2 between 26 and 28 kHz.....22

19. Call type I: $F_{INITIAL}$ between 31 and 34 kHz and F_{END} between 27 and 30 kHz; Call type II: $F_{INITIAL}$ between 36 and 38 kHz and F_{END} between 32 and 35 kHz, it might omit this type of call; FME $\approx$ 33 kHz.....***Neoplatymops mattogrossensis***

20. ***Cynomops* sp.**

a) Call type I: $F_{INITIAL}$ between 28 and 32 kHz and F_{END} between 19 and 26 kHz; FME_1 between 25 and 29 kHz. Call type II: $F_{INITIAL}$ between 32 and 37 kHz and F_{END} between 21 and 33 kHz; FME_2 between 28 and 35 kHz; it might omit this type of call.....***Cynomops planirostris***

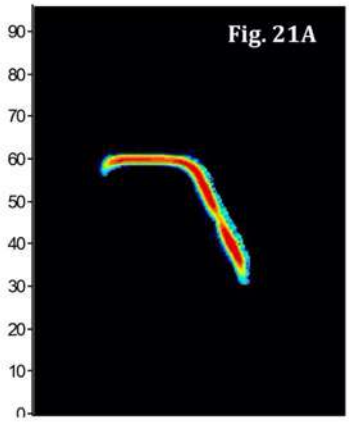
b) Call type I: $F_{INITIAL}$ between 24 e 27 kHz and F_{END} between 14 e 21 kHz; $FME_1 \approx 21$kHz. Call type II: $F_{INITIAL}$ between 29 and 31 kHz and F_{END} between 17 and 26 kHz; $FME_2 \approx 24$ kHz, it might omit this type of call.....***Cynomops greenhalli***

c) Call type I: $F_{INITIAL} \approx 27$ kHz and $F_{END} \approx 19$ kHz; $FME_1 \approx 22$ kHz. Call type II: $F_{INITIAL} \approx 32$ kHz and $F_{END} \approx 28$ kHz; $FME_1 \approx 30$ kHz; it might omit this type of call.....***Cynomops abrasus***

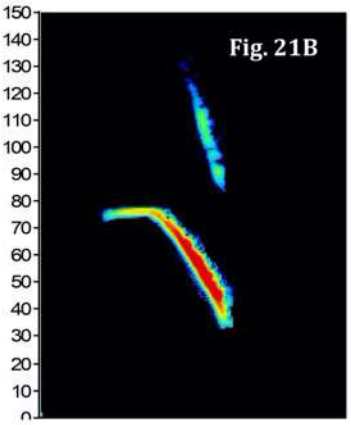
d) Call type I: $F_{INITIAL} \approx 28$ kHz and $F_{END} \approx 23$ kHz; $FME_1 \approx 27$ kHz. Call type II: $F_{INITIAL} \approx 32$ kHz and $F_{END} \approx 28$ kHz; $FME_1 \approx 31$ kHz; it might omit this type of call.....***Cynomops paranus***

21. ***Noctilio*** **sp.**

a) FME_{QCF} between 55 and 63 kHz (Fig. 21A).....***Noctilio leporinus***



b) FME_{QCF} between 67 and 76 kHz (Fig. 21B).....***Noctilio albiventris***



22. Molossidae

a) BW ≤ 2 kHz, FME_1 ≈ 25 kHz; FME_2 ≈ 28 kHz, and FME_3 ≈ 32 kHz.....***Molossus rufus***

b) BW between 2 and 10 kHz; FME_1 ≈ 24 kHz and FME_2 ≈ 26 kHz…….....***Nyctinomops laticaudatus***

23. FME ≈ 24 kHz (23-26 kHz).....***Tadarida brasiliensis***

24. **Molossidae**

a) $FME_1 \approx 24$ kHz and $FME_2 \approx 26$ kHz……..*Nyctinomops laticaudatus*

b) FME ≥ 18 kHz.....*Nyctinomops macrotis/Eumops* **sp.**

c) FME ≤ 18 kHz.....*Eumops* **sp.**

d) FME ≤ 13 kHz.....*Eumops perotis*?

25. **Vespertilionidae**

a) FME ≥ 48 kHz and call duration ≤ 7 ms.....26

b) FME between 30 and 46 kHz and call duration ≥ 5 ms.....27

c) F_{MIN} < 20 kHz.....28

26. ***Myotis*** **sp. /** ***Rhogeessa*** **sp.**

a) $F_{MIN} \approx 43$ kHz; BW >15 kHz; Call with *broadband* and steep FM structure with a small qCF termination (Fig. 26A-1) and oscillogram with triangular shape, where the maximum amplitude is near the beginning of the call (Fig. 26A-2); FME ≈ 50 kHz and call duration less than 4 ms…….....*Rhogeessa hussoni*

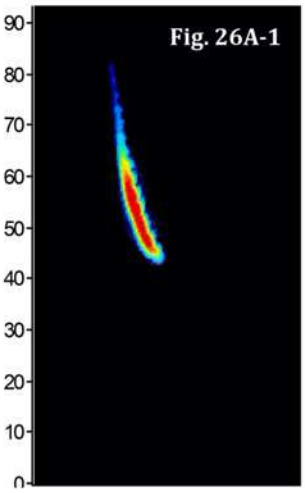


Fig. 26A-1

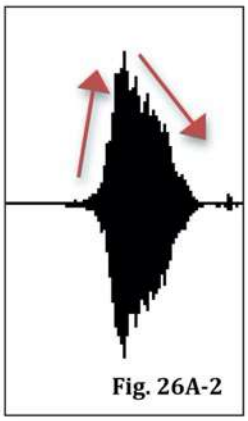


Fig. 26A-2

b) F_{MIN} between 45 and 51 kHz; Call with *broadband* FM structure with a qCF termination (Fig. 26B-1) and oscillogram with oval or triangular shape, where the maximum amplitude is in the middle or near the end of the call (Fig. 26B-2); FME between 49 and 52 kHz and call duration up to 7 ms…….....***Myotis lavali***

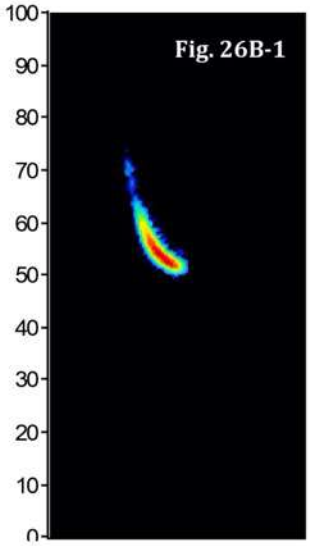


Fig. 26B-1

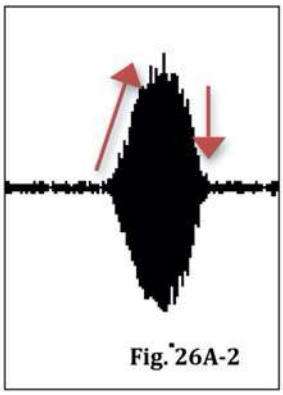
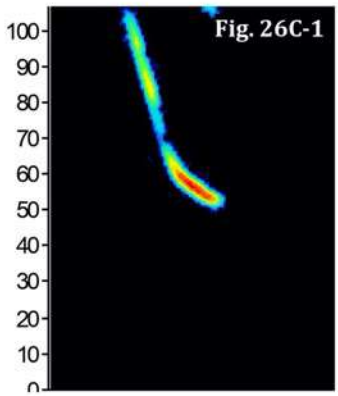
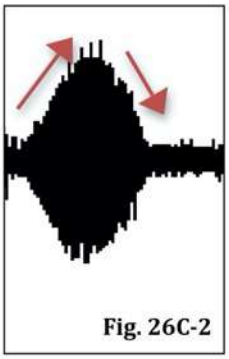


Fig. 26A-2

c) F_{MIN} between 50 and 55 kHz; Call with *broadband* FM structure with a qCF termination, the qCF component can be very evident (Fig. 26C-1) and oscillogram with oval or triangular shape, where the maximum amplitude is in the middle or near the end of the call (Fig. 26C-2); FME between 52 and 55 kHz and call duration up to 7 ms…….....***Myotis nigricans***

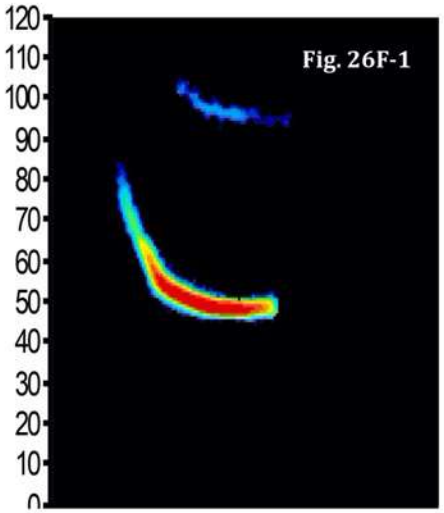


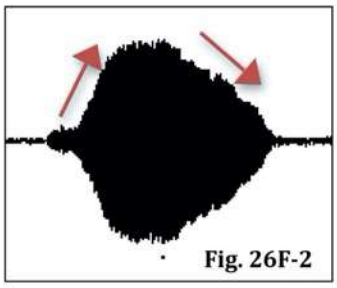


d) $F_{MIN} \approx 55$ kHz; Call with *broadband* FM structure with a qCF termination that can be very noticeable; FME ≈ 58 kHz and call duration up to 5 ms.....***Myotis riparius***

e) $F_{MIN} \approx 58$kHz; Call with *broadband* FM structure with a qCF termination; call duration up to 5 ms.....***Myotis ruber***

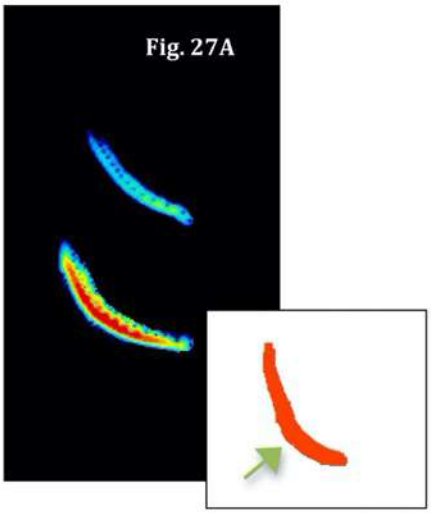
f) F_{MIN} between 44 and 48 kHz; Call with *broadband* FM structure with an evident qCF (Fig. 26F-1) and oscillogram with conical or triangular shape, where the maximum amplitude is in the middle or near the beginning of the call (Fig. 26F-2); FME ≈ 50 kHz and call duration up to 5 ms.....***Myotis albescens***



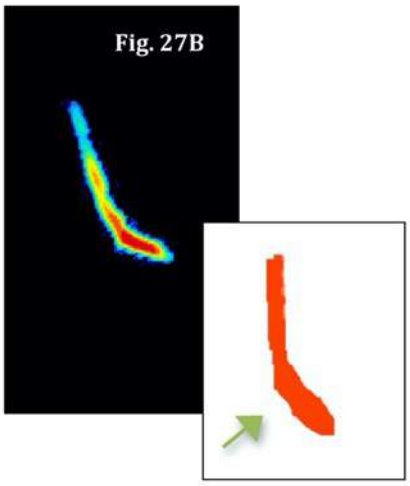


27. ***Eptesicus*** **sp. /** ***Lasiurus*** **sp.**

a) Rounded inflexion point ("inverted walking cane" type) (Fig. 27A).....29



b) Abrupt inflexion point ("hockey stick" type) (Fig. 27B).....30



28. Vespertilionidae

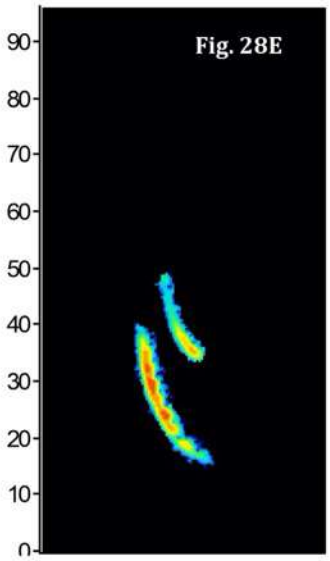
a) F_{MIN} between 20 and 26 kHz; FME ≈ 25 kHz; F_{MAX} between 28 and 35 kHz, Call duration around 10 ms; Rounded inflexion point ("inverted walking cane" type) (see Fig. 27A)..... ***Lasiurus cinereus***

b) F_{MIN} ≈ 15 kHz; F_{MAX} ≈ 25 kHz; FME (?); Call duration between 5 and 8 ms..... ***Histiotus velatus***

c) F_{MIN} between 25 and 30 kHz; F_{MAX} ≥ 45 kHz; FME ≈ 34 kHz; Call duration up to 5 ms..... ***Histiotus montanus***

d) F_{MIN} between 25 and 30 kHz; F_{MAX} < 40 kHz; FME ≈ 30 kHz; Call duration less than 3 ms..... ***Histiotus laephotis***

e) F_{MIN} ≈ 15 kHz; F_{MAX} > 30 kHz; FME ≈ 28 kHz; Call duration up to 5 ms; a second harmonic can be very evident (Fig. 28E)..... ***Histiotus diaphanopterus***



29. ***Lasiurus*** **sp.**

a) F_{MIN} ≈ 40 (40-45) kHz; FME ≈ 46 (38-45) kHz; variable call duration averaging 12 ms; it can present frequency alternation of the calls.....***Lasiurus blossevillii***

b) F_{MIN} ≈ 25 (23-30) kHz; FME ≈ 32 kHz; variable call duration between 4 and 11 ms; it can present frequency alternation of the calls.....***Lasiurus ega/L. egregius***

30. ***Eptesicus*** **sp.**

a) F_{MIN} ≈ 36 kHz; FME ≈ 39 (37-41) kHz; variable call duration between 5 and 11 ms.....***Eptesicus furinalis***

b) F_{MIN} ≈ 40 (35-40) kHz; FME ≈ 43 (42-45) kHz; variable call duration between 3 and 8 ms.....***Eptesicus brasiliensis***

c) F_{MIN} ≈ 30kHz; FME ≈ 32 (28-35) kHz; call duration ≈ 8 ms.....***Eptesicus chiriquinus***

31.

a) FME might be in the fundamental harmonic (HF) or in the second harmonic (H2). FME_{HF} between 47 and 59 kHz (Fig. 31A-1) and FME_{H2} between 100 and 115 kHz; Call duration less than 4 ms; FM calls with an explosive beginning (i.e. elevated amplitude near to the beginning of the call) (Fig. 31A-2).....***Thyroptera* sp.**

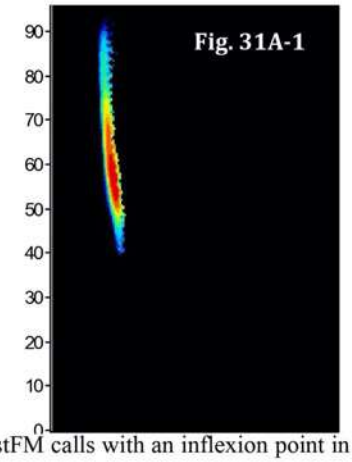


Fig. 31A-1

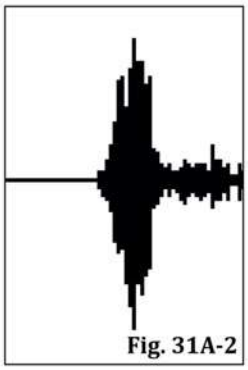


Fig. 31A-2

b) stFM calls with an inflexion point in the middle of the call (Fig. 31B), FME in the HF and is between 130 and 170 kHz. This species presents the highest frequencies of the neotropical bats. It can present a FM_u component in the beginning of the call when the call's frequency extends the limits of the detector due to an acoustic artefact (Fig. 31B, green arrow)……..*Furipterus horrens*

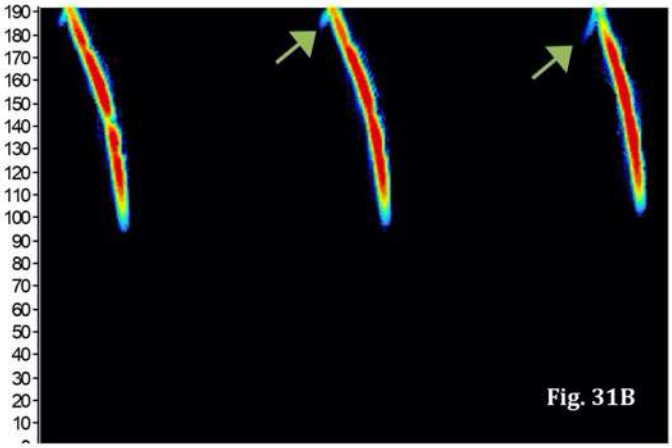


Fig. 31B

c) stFM calls; it can present a very short qCF termination; FME in the H2 (Fig. 31C); FME > 100 kHz; It can present a FM_u component in the beginning of the call when the call's frequency extends the limits of the detector due to an acoustic artefact (Fig. 31C, green arrow)…….....***Natalus macrourus***

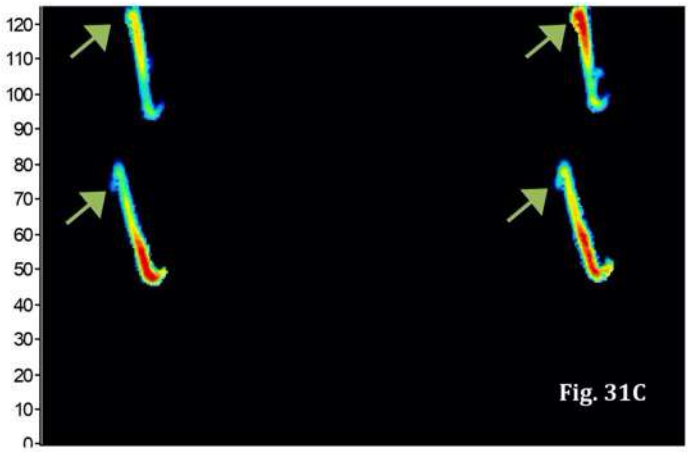


Fig. 31C

d) Multi-harmonic calls (HF, H2, H3, H4); call energy (amplitude) is shared between the harmonics in "temporal" form (i.e. FME can be present in the beginning of H2 and in the end of H3) (for more information see Barataud et al. 2013). Usually, the calls have low amplitude (whispering bats).....**Phyllostomidae**