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MORCEGOS INSETÍVOROS AÉREOS NEOTROPICAIS: IDENTIFICAÇÃO ACÚSTICA E PADRÕES DE ESTRUTURAÇÃO DE ASSEMBLEIAS

Dissertação apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Mestre em Biologia Animal.

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“*A mi madre*”

Agradecimentos

Desde o início e até o final um sentimento só, gratidão. Porque os sonhos se realizam, porque se cresce, porque se ajuda, porque por mais que se esteja só nunca se está sozinho. Porque quando não se tem sempre há, porque quando não há se faz, porque quando não se consegue alguém ajuda. Porque quando não se espera se recebe e se dá sem esperar receber. Porque quando se cai pode-se levantar e quando se acaba pode começar, porque muda e se transforma. Porque se aprende e se ensina, porque se sofre e se desfruta. Mas sobretudo pela família; pelos amigos de lá e de cá, pelas quatis (sim são fêmeas), pelas bolsas, pelos mestres e co-mestres também de lá e de cá, pela Amora, gratidão.

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"Morcego pescador"
IX/2016
Xilogravura: A.A.A

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Resumo: Os morcegos, ordem Chiroptera, são ecologicamente o grupo mais diverso dos mamíferos e após Rodentia ocupam o segundo lugar em diversidade taxonômica. Devido à sua dramática radiação ecológica e evolutiva, ocupam virtualmente todos os níveis tróficos. No Neotrópico ocorrem nove famílias de quirópteros, das quais oito (excluíndo Phyllostomidae) incluem quase exclusivamente espécies insetívoras que dependem principalmente da ecolocalização para a navegação e aquisição de alimento. A gravação e posterior análise de chamados de ecolocalização emitidos durante a navegação é uma alternativa ou técnica complementar para o estudo deste grupo de morcegos; este método permite identificar muitas espécies com base na estrutura e frequência dos chamados de ecolocalização, otimizando o estudo de associações espécie-habitat dentro das assembleias de morcegos insetívoros. No segundo capítulo desta dissertação intitulado *Who's calling? Acoustic identification of Brazilian bats* é apresentada uma revisão dos estudos relacionados com descrições e identificações acústicas de espécies de morcegos neotropicais que ocorrem no Brasil. No total incluiram-se 47 publicações provenientes de 17 países, para além de dados não-publicados. Das 93 espécies de morcegos não filostomídeos, 65 foram descritas acusticamente, as restantes 28 careceram de informações acústicas. A utilização de monitoramentos acústicos pode ser uma ferramenta fundamental para expandir o nosso conhecimento dos morcegos no Brasil. No terceiro capítulo intitulado *Spatiotemporal patterns of insectivorous bat activity in the Brazilian Cerrado: landscape and microclimate effects* utilizou-se esta técnica para avaliar os padrões espaço-temporais de diversidade e atividade de morcegos insetívoros numa paisagem heterogênea no Cerrado. Os nossos resultados, em concordância com estudos prévios, mostraram que a composição e configuração, em especial a extensão de fitofisionomias bem conservadas, foram fatores importantes para a seleção de hábitat pelos morcegos insetívoros assim como as condições de umidade relativa do ar, particularmente nos meses mais secos. As respostas dos morcegos ante tais fatores variaram com a escala de análise, o grupo funcional e em alguns casos a variação foi espécie-específica. São necessários mais estudos para elucidar como as espécies respondem aos câmbios de origem humana na paisagem e suas possíveis associações com as mudanças climáticas no Cerrado.

Palavras chave: bioacústica, Cerrado, Chiroptera

Abstract: Bats, order Chiroptera, are ecologically the most diverse group of mammals and after Rodentia; they are second in taxonomic diversity. Due to their dramatic ecological and evolutionary radiation, they virtually occupy all trophic levels. There are nine families of bats in the Neotropics of which eight (excluding Phyllostomidae) are almost exclusively insectivorous depending mainly on echolocation to navigate and to acquire food. Recording and posterior analysis of echolocation calls emitted while foraging, is an alternative or complementary technique for the study of this group of bats; this method allows the identification of many species based on the structure and frequency of their calls. It optimizes the study of habitat-species associations within the insectivorous bat assemblage. The second chapter of this dissertation, entitled *Who's calling? Acoustic identification of Brazilian bats* a review of acoustic description and identification studies of Neotropical bats occurring in Brazil is presented. Fourth nine publications from 17 countries were included in this revision, as well as non-published data. From 93 species of non-phyllostomid bats, 65 were acoustically described while for 28 there is no acoustic information. The use acoustic monitoring could be a fundamental tool for expanding our knowledge of bats in Brazil. In the second chapter entitled *Spatiotemporal patterns of insectivorous bat activity in the Brazilian Cerrado: landscape and microclimate effects*, such technique was used to evaluate the spatio-temporal patterns of diversity and activity of aerial insectivorous bats in a heterogeneous landscape in the Cerrado. Our results were consistent with those of previous studies, showing that composition and configuration, and especially extensiveness of well-preserved phytophysiognomies, are fundamental factors in habitat selection by bats, as well as air relative humidity conditions, particularly in dryer months. Bat responses are scale-dependent, vary with the functional group and in some cases are species-specific. More studies are necessary to elucidate how species respond to landscape human induced modifications and their possible associations with climatic changes in the Cerrado biome.

Key words: bioacoustics, Cerrado, Chiroptera

Capítulo 1. Introdução geral

Morcegos insetívoros neotropicais: estrutura de comunidades

Os morcegos, ordem Chiroptera, são ecologicamente o grupo mais diverso dos mamíferos (Patterson *et al.* 2003); com cerca de 1300 espécies atualmente descritas ocupam, após Rodentia, o segundo lugar em diversidade taxonômica (Wilson & Reeder 2005). Devido à sua dramática radiação ecológica e evolutiva, os morcegos ocupam virtualmente todos os níveis tróficos (Medellín *et al*. 2000). A sua capacidade de vôo, assim como adaptações morfológicas e sensoriais permitiram-lhes o acesso a uma ampla variedade de habitats e recursos (Kalko 1997).

Na região Neotropical co-existem nove famílias de quirópteros: Emballonuridae, Furipteridae, Molossidae, Mormoopidae, Natalidae, Noctilionidae, Phyllostomidae, Thyropteridae e Vespertilionidae. Todas as famílias são compostas exclusivamente por espécies insetívoras, à exceção de Phyllostomidae que inclui, para além de insetívoros, espécies frugívoras, nectarívoras, onívoras, carnívoras e sanguinívoras, e de Noctilionidae que inclui uma espécie quase exclusivamente piscívora. As espécies insetívoras dependem principalmente da ecolocalização para a navegação e aquisição de alimento, sendo que a ecolocalização é a capacidade de detectar a localização de objetos através do eco resultante da emissão de sinais acústicos de alta frequência (ultrassônicos) após atingirem esses objetos.

Embora altamente flexíveis na utilização do habitat, assim como em seus modos de forrageio, os morcegos insetívoros necessitam de adaptações especiais na forma das asas e nos chamados de ecolocalização para o uso diferencial do espaço dentro dos elementos estruturais de um determinado habitat (Schnitzler & Kalko 1998, Kalko *et al*. 2008, Denzinger & Schnitzler 2013). Estes fatores permitem estruturar os morcegos de uma comunidade em grupos funcionais ou guildas, o que facilita a identificação e a compreensão de padrões e fatores subjacentes à organização das comunidades (Denzinger & Schnitzler 2013). Assim, uma guilda ou grupo funcional compreende as espécies que vivem em condições ecológicas similares, usam habitats de forrageio semelhantes, e compartilham adaptações em sistemas sensoriais e motores (Schnitzler & Kalko 2001). O hábitat de forrageio das espécies está determinado pelos recursos e condições que encontram quando procuram por alimento e, no caso dos morcegos tem sido classificado em espaço aberto, espaço de borda e espaço fechado (Fig. 1) (Fenton 1990, Schnitzler & Kalko 1998, 2001, Denzinger & Schnitzler 2013).

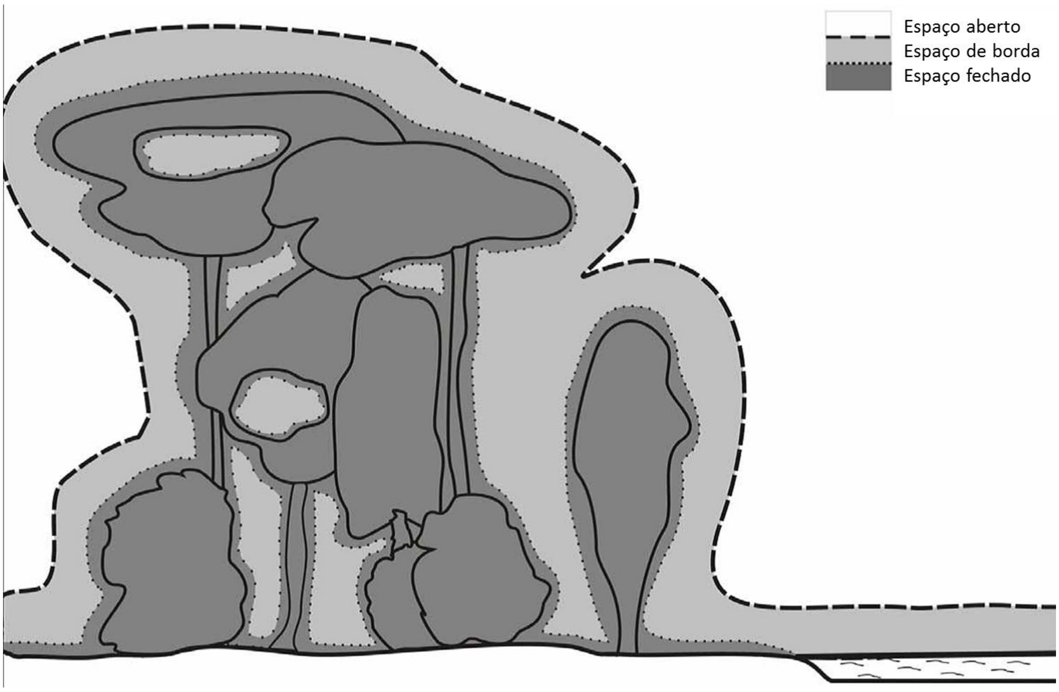

Fig.1 Classificação do habitat de forrageio de morcegos de acordo com o uso diferencial do espaço. O uso é determinado pelo comportamento de ecolocalização e seus limites são espécie-específicos. Adaptado de Denzinger & Schnitzler (2013).

Potencialidades da bioacústica para o estudo de morcegos insetívoros neotropicais

A maioria dos estudos com morcegos realizados no Neotrópico tem usado métodos tradicionais de amostragem, tais como redes de neblina ou armadilhas de harpa que capturam principalmente espécies da família Phyllostomidae, subestimando os morcegos insetívoros que possuem chamados de ecolocalização especializados e são capazes de facilmente detectar e evitar as redes ou voar por acima das mesmas (Kalko & Handley 2001, MacSwiney *et al*. 2008, Marques *et al*. 2015). Como resultado, a distribuição, padrões locais de atividade, assim como associações de micro-habitat de muitas espécies de morcegos neotropicais pertencentes às guildas de espaço aberto e espaço de borda – quase exclusivamente insetívoras – são desconhecidos (Jung & Kalko 2011).

A análise de chamados de morcegos emitidos durante a navegação ou forrageamento, gravados através de detectores de ultrassons, é uma alternativa ou técnica complementar para o estudo deste grupo de morcegos; esta metodologia permite identificar muitas espécies com base na estrutura e frequência dos chamados de ecolocalização, otimizando o estudo de associações espécie-habitat dentro das assembleias de morcegos insetívoros (Kalko *et al.* 2008). Tais assembleias podem estar constituídas por varias espécies, que diferem nas estratégias de caça e, por associação, diferem na morfologia, ecolocalização e tipo de vôo, revelando padrões na partição dos recursos (Ciechanowski *et al.* 2008). Estas características são adaptações para o forrageio em diversos ambientes (Schnitzler *et al.* 2003). Tal como já referido, espécies que procuram alimento em locais semelhantes, usando estratégias de caça semelhantes e compartilhando adaptações morfológicas classificam-se em grupos funcionais (guildas) (Schnitzler & Kalko 1998, 2001, Denzinger & Schnitzler 2013). No caso das espécies de morcegos insetívoros neotropicais, estas são classificadas de acordo com as seguintes características nos chamados de ecolocalização (Fig. 2):

i) Morcegos que forrageiam em espaços abertos: seu sistema de ecolocalização permite detectar presas a longa distância, usam sinais de busca de banda estreita, ligeiramente modulada, longa duração (8-25 ms), frequências abaixo de 30 kHz e intervalos de pulso longos (500-1000 ms) (Kalko & Schnitzler 1998). Na fase de aproximação à presa a duração dos pulsos e intervalo de pulso são reduzidos e a largura de banda aumenta à medida que a distância com a presa diminui. A sequência é finalizada com um grupo terminal de duas partes (*feeding-buzz* I e II), no qual há ainda uma maior redução na duração dos pulsos e intervalo entre pulsos. Nesta guilda incluem-se espécies das famílias Emballonuridae e Molossidae.

ii) Morcegos que forrageiam em espaços de borda: utilizam sinais de procura mistos contendo uma modulação de banda estreita levemente modulada, frequências entre 30 e 60 kHz, precedidas e/ou seguidas dum componente de banda larga e frequência modulada descendente. Os sinais têm uma duração intermédia (3-10 ms). Durante a fase de aproximação, a largura de banda dos sinais aumenta e diminui a sua duração. Finaliza com um grupo terminal de duas partes (*feeding-buzz* I e II). As espécies deste grupo funcional incluem espécies das famílias Emballonuridae, Molossidae, Mormoopidae e Vespertilionidae.

iii) Morcegos que forrageiam em espaços fechados: os sinais de ecolocalização são formados por elementos de frequência constante de em torno de 60 kHz e elementos de freqüência modulada (FM-CF). A duração dos sinais de procura varia entre 15-35 ms. A fase de aproximação finaliza com um grupo terminal característico, em que o componente de freqüência constante é mantido mesmo nos sinais mais curtos. Neste grupo funcional se inclui o complexo de espécies *Pteronotus parnellii*.

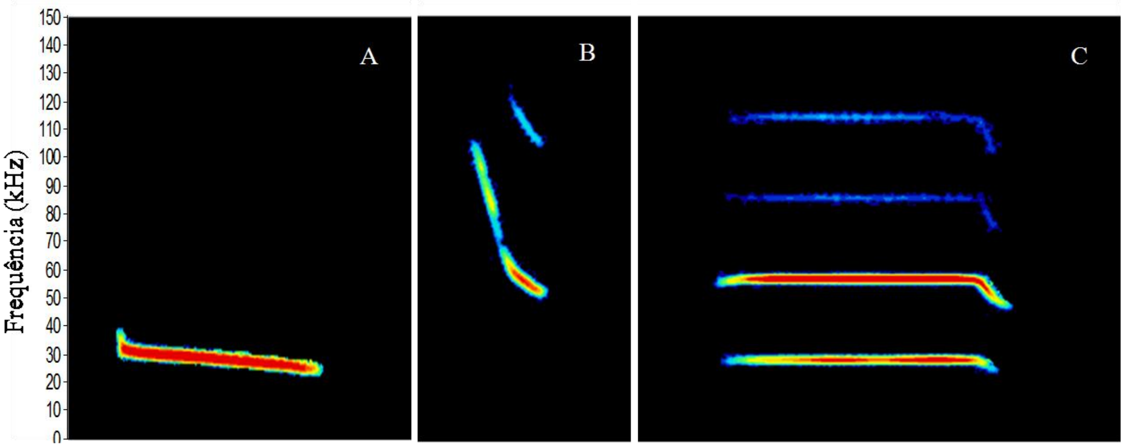

Fig. 2 Exemplos de espectrogramas de chamados de ecolocalização de morcegos que forrageiam em A) espaços abertos (*Cynomops planirostris*); B) espaços de borda (*Myotis nigricans*); e C) espaços fechados (*Pteronotus cf. parnellii*). A escala temporal não é a mesma nas três figuras.

O monitoramento acústico é, há várias décadas, comumente utilizado na Europa e América do Norte (McSwiney *et al.* 2008), essencialmente devido ao fato de, na região temperada, apenas ocorrerem espécies insetívoras que de outra forma seriam dificilmente detectadas nos seus habitats de forrageio. Em países neotropicais seu uso relacionou-se primeiramente na descrição de chamados de ecolocalização de algumas espécies (O'Farrell & Miller 1999, Ochoa *et al.* 2000, Rydell *et al.* 2002, Jung *et al.* 2007, Pio *et al.* 2010), mas nos últimos anos, o uso sistemático tem começado a ser implementado em estudos com foco mais ecológico (e.g. Jung & Kalko 2011, Barataud *et al.* 2013, Heer *et al.* 2015, Hintze *et al.* 2016, Marques *et al*. 2016).

Concluindo, a utilização desta técnica amplia e possibilita uma melhoria no nosso entendimento sobre as assembleias de morcegos insetívoros neotropicais permitindo estudar diversos aspectos da sua ecologia como uso de habitat, variação espaço-temporal na atividade, diferenciação de nicho, comportamento de forrageio e distribuição das espécies (Vaughan *et al*. 1997, Arlettaz *et al*. 2001, Ibáñez *et al*. 2003, Thoisy *et al* 2014).

O Cerrado e seus morcegos

O Cerrado é um dos ‘hotspots’ para a conservação da biodiversidade mundial e é o segundo maior bioma brasileiro, sendo superado em área apenas pela Amazônia (Klink & Machado 2005). É um mosaico contínuo de ecossistemas incluindo savanas, campos e matas de galeria (Eiten, 1972). Em paralelo, o Cerrado alberga 20% da produção agrícola brasileira, sendo que cerca da metade dos 2 milhões de km² originalmente ocupados pelo bioma foram transformados em pastagens plantadas, culturas anuais e outros tipos de uso humano (Klink & Machado 2005).

No Cerrado ocorrem mais de 100 espécies de morcegos (Aguiar *et al*. 2016), sendo o grupo de mamíferos com maior riqueza no bioma (Marinho-Filho et al. 2002). Pese a sua diversidade e importância ecológica o conhecimento atual dos quirópteros deste bioma é insuficiente, sendo que apenas 6% da área tem sido minimamente amostrada (Bernard *et al.* 2011). Nos últimos anos foram realizados vários estudos sobre a composição de espécies, riqueza e abundância de morcegos em áreas perturbadas e em unidades de conservação, em diversos estados incluindo Mato Grosso (e.g. Ferreira *et al*. 2010, Sousa *et al*. 2013, Shapiro & Bordignon 2014), Goiás (e.g. Pina *et al*. 2013), Minas Gerais (e.g. Loureiro & Gregorin 2015), Distrito Federal (e.g. Aguiar & Antonini 2008), Tocantins (e.g Gregorin *et al*. 2011, Ramos Pereira & Aguiar, submetido), Goiás (e.g. Zortéa & Ahlo 2008) e São Paulo (e.g. Muylaert *et al*. 2014). Embora os esforços amostrais tenham vindo a aumentar, a amostragem apresenta um viés para a detecção de Phyllostomidae já que estes estudos, com exceção de Ramos Pereira & Aguiar (submetido) têm utilizado quase exclusivamente redes de neblina como método principal de captura. Portanto, se faz necessária a inclusão de monitoramento acústico como ferramenta complementar ao inventariamento de espécies, assim como a possibilidade de ampliar o estudo de diversos aspectos da biologia e ecologia dos morcegos que geralmente não são capturadas, mas passíveis de detectar e gravar acusticamente.

Justificativa e estrutura da dissertação

O conhecimento acústico dos morcegos neotropicais vem-se incrementando nos últimos anos (e.g. Jung & Kalko 2007, Barataud *et al*. 2013, Jung *et al*. 2014) e, com a expansão do uso de gravadores de ultrassons para pesquisas ecológicas assim como para avaliações ambientais, faz-se necessário recompilar e esclarecer as informações acústicas existentes, avaliando as espécies descritas assim como os locais e métodos de gravação, com o propósito de determinar lacunas de conhecimento sobre que espécies e regiões carecem de informações acústicas. Neste sentido, o segundo capítulo desta dissertação apresenta uma revisão dos estudos relacionados com descrições e identificações acústicas de espécies de morcegos neotropicais que ocorrem no Brasil. Este trabalho, intitulado *Who's calling? Acoustic identification of Brazilian bats* é apresentado no formato de artigo e foi já submetido ao periódico *Mammal Review* (Anexo 1). Aqui são apresentadas as principais características utilizadas para a descrição dos chamados de ecolocalização das famílias Emballonuridae, Furipteridae, Molossidae, Mormoopidae, Natalidae, Noctilionidae, Vespertilionidae e Thyropteridae, e sua eficiência na distinção de espécies, assim como uma análise da variação regional nos chamados de acordo com a localidade de gravação. Este trabalho inclui como material suplementar uma chave de identificação acústica (desenvolvida majoritariamente pelo segundo autor do artigo – Frederico Hintze de Oliveira) incluindo espécies das famílias previamente mencionadas assim como de algumas espécies de Phyllostomidae possíveis de detecção acústica.

A crescente expansão da população humana assim como das áreas destinadas à produção agrícola e pecuária ameaçam a preservação de muitos ecossistemas naturais na região Neotropical. Como tal, se faz prioritária a integração da biodiversidade e dos sistemas produtivos em estratégias de conservação. Neste sentido, e particularmente em ecossistemas agrícolas no Brasil, o estudo de morcegos insetívoros através do uso de detectores de ultrassons não só é relevante como prioritário (Aguiar & Antonini 2008, García-Morales *et al*. 2013). Este grupo de quirópteros é responsável por serviços ecossistêmicos essenciais como o controle de populações de insetos, incluindo insetos praga, com relevante impacto econômico (Kalka *et al*. 2008, Kunz *et al*. 2011). Além disso, os padrões de ocorrência (e não-ocorrência) de espécies podem indicar como as perturbações humanas afetam a fauna local (García-Morales *et al*. 2013). Assim, o terceiro capítulo desta dissertação, igualmente apresentado no formato de artigo, apresenta um estudo sobre a variação espaço-temporal na riqueza e atividade de morcegos insetívoros no Cerrado. Este artigo, intitulado *Spatiotemporal patterns of insectivorous bat activity in the Brazilian Cerrado: landscape and microclimate effects*, encontra-se em elaboração para submissão ao periódico *Oecologia*. A região foco do estudo foi Mambaí, Goiás, na fronteira entre este estado, Bahia e Minas Gerais. Esta região forma parte da Área de Proteção Ambiental das Nascentes do Rio Vermelho alberga o Parque Municipal do Pequi e encontra-se próxima do Parque Estadual de Terra Ronca. Considera-se parte duma das áreas de Cerrado melhor preservadas, porém altamente ameaçada pelas expansões de áreas destinadas a plantações, criação de gado, e queimadas de origem humana. Isso é evidenciado na área divisória com o estado da Bahia, onde a paisagem natural do Cerrado foi drasticamente modificada em plantações, principalmente de soja, ao longo de centenas de quilômetros no eixo sul-norte no limite oeste deste estado. Esta região é assim, a paisagem heterogênea ideal para a avaliação dos efeitos da perturbação antrópica sobre os morcegos insetívoros numa região que ainda conserva seu potencial biológico natural.

Objetivos

O objetivo geral desta dissertação foi analisar como alguns fatores espaciais e bioclimáticos afetaram riqueza, composição e atividade dos morcegos insetívoros aéreos neotropicais no Cerrado.

Especificamente foram avaliadas as seguintes hipóteses e predições:

i) A atividade e composição das espécies de morcegos insetívoros aéreos variarão entre áreas com distintos usos e configurações da paisagem. Esperamos que os morcegos das guildas aberta, fechada e de borda, preferencialmente forragem em ambientes abertos, fechados e heterogêneos, respectivamente.

ii) A atividade das espécies de morcegos insetívoros aéreos variará ao longo da noite com as variações microclimáticas, sendo que as alterações de umidade afetarão principalmente as espécies de menor tamanho corporal. Dado que a disponibilidade de água em áreas semi-áridas é mais limitante para a fauna que a variação na temperatura, esperamos uma maior atividade em noites mais úmidas, especialmente na estação seca

Como objetivo complementar realizou-se uma revisão bibliográfica sobre o conhecimento acústico atual das chamadas de ecolocalização de morcegos insetívoros neotropicais com ocorrência no Brasil, pois tal informação é de fundamental importância para garantir uma identificação o mais correta possível das espécies detectadas.

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Capítulo 2. Who's calling? Acoustic identification of Brazilian bats

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Abstract

1. In Brazil most inventories have been mostly made using mist-net sampling and roost search; so, the knowledge of Brazilian bat fauna is biased towards the Phyllostomidae. Reliable data on bat echolocation calls is fundamental to improve the knowledge on the distribution patterns and foraging ecology of the remaining eight bat families present in the country.

2. 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 of knowledge both in terms of species and regions sampled; and iv) point out which species are acoustically recognizable in a reliable way. Finally we present a dichotomous key to support the acoustic identification of non-phyllostomids in Brazil.

3. We compiled publications on echolocation calls of Neotropical bat species occurring in Brazil and summarized qualitative and quantitative information of acoustic parameters used on call descriptions.

4. Information on echolocation calls was retrieved from 47 publications and acquired in 17 countries. Of 93 non-phyllostomid bat species occurring or potentially occurring in Brazil, 65 have been acoustically described but for 28 we found no published information on their acoustic profiles.

5. The use of bioacoustics can be a fundamental tool to expand the knowledge on Brazilian bats and improve their conservation.

Key-words: Bat bioacoustics, Chiroptera, echolocation calls, insectivorous bats, Neotropical bats

Running head: Echolocation calls of non-phyllostomid bat species of Brazil

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. 1997). 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, with more than 180 species (Nogueira et al. 2014, Fisher et al. 2015). However, inventories of bat fauna in Brazil have been mostly made using mist-net sampling and roost search (e.g.; Willig 1985, Sampaio et al. 2003, Bernard et al. 2011), potentially leaving behind many species of difficult capture, or roosting in unknown or inaccessible sites (e.g. Rydell et al. 2002, Kunz & Parsons 2009). Most knowledge on distribution and ecology of Brazilian bats is within the Phyllostomidae which comprises 92 species (Nogueira et al. 2014) and are much more easily captured using mist-nets than the members of the remaining eight families occurring in the country – Emballonuridae, Furipteridae, Molossidae, Mormoopidae, Natalidae, Noctilionidae, Thyropteridae and

Vespertilionidae (Kalko & Handley 2001). Indeed, there is a significant lack of knowledge on the ecology and distribution of non-phyllostomid bats in Brazil (Cunto & Bernard 2014). Phyllostomids are known to use a combination of clues to explore the environment, including echolocation, olfaction and vision, while species of the remaining families use almost exclusively echolocation to navigate and find prey (Kalko & Schnitzler 1998, Schnitzler et al. 2003). 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 & 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 & Handley 2001, Marques et al. 2015). Due to the lack of bioacoustics studies in Brazil (but see Lopez-Baucells et al. 2016) the bat fauna inventories are certainly sub represented (e.g. Bernard et al. 2011) and biased (e.g. Cunto & Bernard 2014).

In temperate regions the use of ultrasound detectors to assess bat diversity has a few decades and is widespread (e.g. Ahlén & Baagoe 1999, Kunz & Parsons 2009). Curiously, although Neotropical bats have been the object of acoustics studies since the mid-1960s (see Grinnell et al. 2016), only recently researchers started to systematically use bioacoustics as a monitoring tool in the region (e.g. Jung & Kalko 2011, Marques et al. 2015). Still, these studies have been restricted to a few localities in some countries (see Supplementary Material S1).

Recently, there has been an increase in the description of bat ultrasound calls, with larger datasets and important additions to the knowledge of families other than the Phyllostomidae (Jung et al. 2007, 2014; Barataud et al. 2013). Call descriptions for at least 38 non-phyllostomid bats are available (e.g. Jung et al. 2007, Barataud et al. 2013, Jung et al. 2014), but a close comparison with the Brazilian species list (Nogueira et al. 2014) indicates that echolocation calls of ca. 60 species of non-phyllostomids remains to be described.

Reliable data on bat echolocation calls is 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. in press) especially for impact assessments of wind farms (Valença & Bernard 2015). Moreover, acoustic monitoring can be very useful in the study of spatial-temporal activity and habitat use, niche differentiation, foraging behaviour, species distribution and even the signalization of cryptic diversity (e.g. Jones & Parijs 1993, Arlettaz et al. 2001, Greif & Siemers 2010, Marques et al. 2015, Hintze et al. 2016a, b). Therefore, considering the high bat species richness in Brazil, the need for the use of bioacoustics, and the lack of a systematized data bank on the echolocation calls of Brazilian bats, here we present a revision work aiming 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 of 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 dichotomous key to support 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 in Brazil (Reis et al. 2013, Nogueira et al. 2014, Pol et al. 2016), and for a few other species, which while never registered, also potentially occur in this country as suggested by 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, and considered works in English, Portuguese, French and Spanish (official languages in Latin America). We summarized quantitative (frequency and time parameters) and qualitative information (type and structure) of search calls of species (parameter selection varied per family according to the relevance for identification purposes). For some species we also included unpublished acoustic information from our own recordings.

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 amount 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 S1). 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 and North America (14, 14 and eight publications, respectively), 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 *S. leptura*. We did not find any acoustic information for *Diclidurus isabella*, *P. leucoptera* and *P. pallidoptera*. For some species information on echolocation calls was given as a complex including *D. 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 & Kalko (2011) and Jung et al. (2007), 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 a 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 Figure 1). Sometimes, but rarely, *Diclidurus*, *Saccopteryx* and *Rhynchonycteris* can produce calls with FME on the fundamental harmonic. With the exception of *Rhynchonycteris naso*, pulses are usually narrowband. Genera *Cormura*, *Diclidurus* and *Saccopteryx* present frequency alternation but one of the pulses may be omitted at some circumstances. The other genera produce monotone frequency calls. Peak frequency, direction of call modulation and presence of alternation are important parameters for species identification (O´Farrell & Miller 1999, Jung et al. 2007, Barataud et al. 2013; see Appendix S2 for further details).

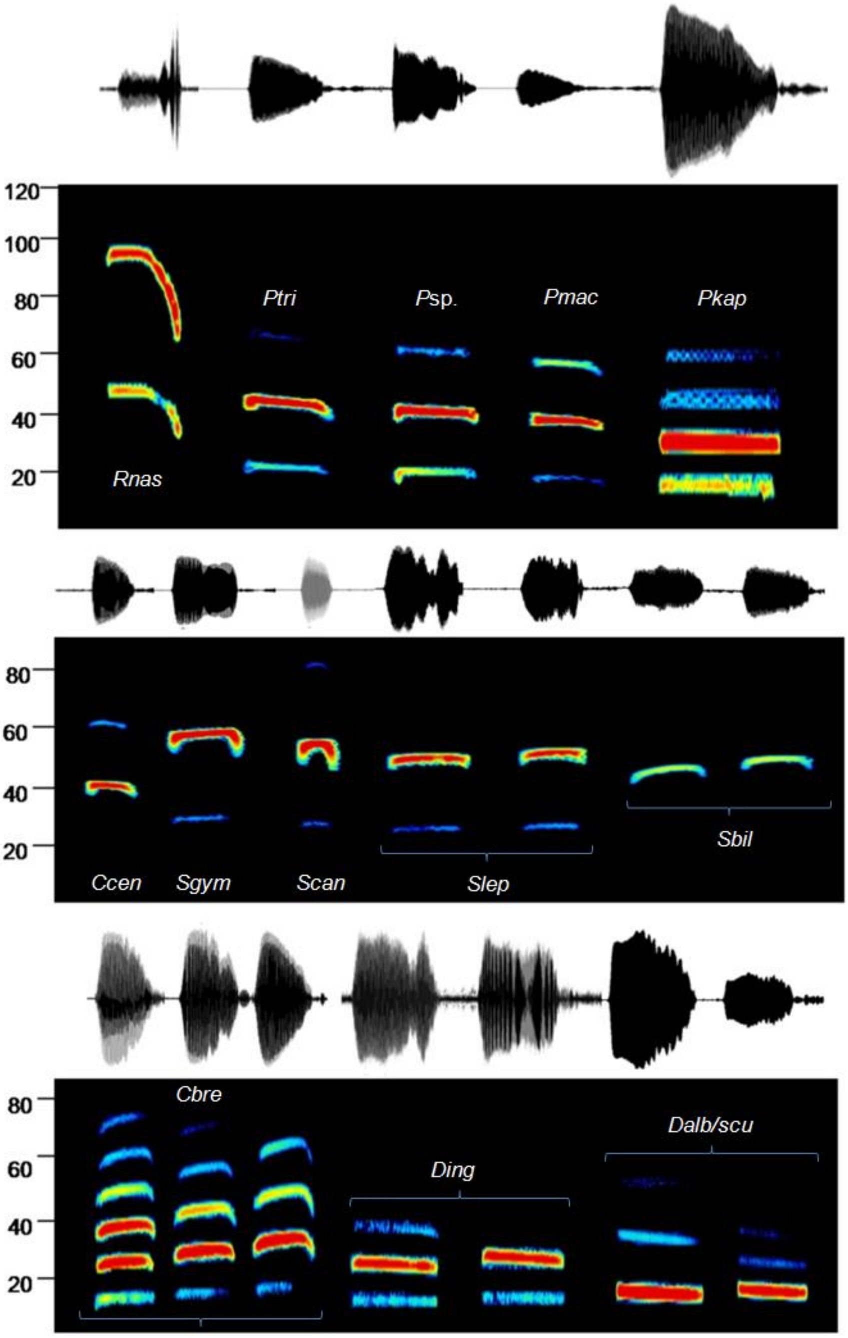

Figure 1. Echolocation calls for species of the Emballonuridae known to occur, or potentially occurring, in Brazil. Call duration and pulse intervals are not scaled. Rnas: *Rhynchonycteris naso*; Ptri: *Peropteryx trinitatis*; Psp: *Peropteryx* sp.; Pmac: *Peropteryx macrotis*; Pkap: *Peropteryx kappleri*; 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*.

Furipteridae

Furipterus horrens is found from Costa Rica to Peru, the Guianas, Brazil and Trinidad (Koopman 1993, 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 Figure 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 as can be seen in Figure 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 inflexion point (Appendix S1).

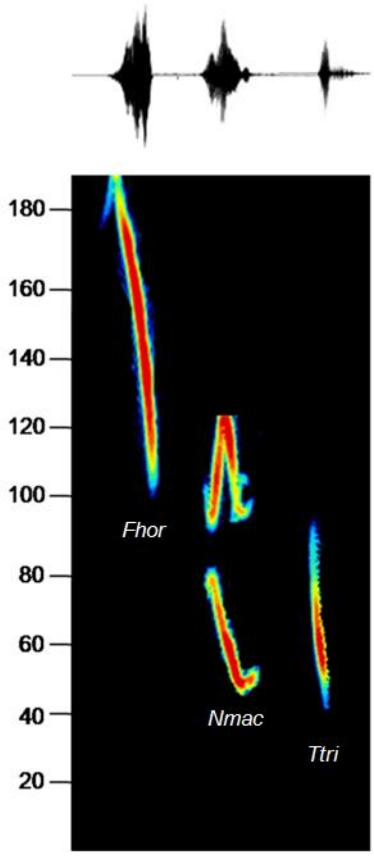

Figure 2. Echolocation calls for species of the Furipteridae, Natalidae and Thyropteridae known to occur, or potentially occurring, in Brazil. Call duration and pulse intervals are not scaled. Fhor: *Furipterus horrens*; Nmac: *Natalus macrourus*; Ttri: *Tyroptera tricolor*.

Natalidae

Natalus macrourus is the only species of this family reported to occur in Brazil (Tejedor & Davalos 2016). Even if widely distributed in the country (Rocha et al. 2013), there is no published acoustic information for this species. Besides, *N. tumidirostris* occurs north of the Amazon River (Garbino & 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 Figure 2) may give some insight on the acoustic profile of *N. macrourus*.

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 S2 and Figure 2).

Thyropteridae

The genus *Thyroptera* occurs from Mexico to south Brazil (Wilson & Reeder 2005; Passos et al. 2010). 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 *T. discifera* (from French Guiana) (Table 2 and Figure 2). Knowledge on the echolocation calls of the remaining species (*T. devivoi*, *T. lavali* and the recent described *T. 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 (<4ms) (Appendix S2).

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 Figure 3). Only one publication including molossids was found for the warm temperate South American region and two for the Caribbean Islands.

Molossus molossus, *M. 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*, *E.delticus*, *E.hansae*, *E.maurus*, *E. patagonicus*, *E. trumbulli*, *Molossus aztecus*, *M. pretiosus* and *Nyctinomops aurispinosus*. If we follow Moras et al. (2016), *C. paranus* described by Barataud et al. (2013) could relate to *C. 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*, *E. nanus* (Bartlett et al. 2013) and *E. patagonicus* (Bernardi et al. 2009) as single species. Also, we considered *Molossus barnesi* as a synonym of *M. coibensis* (Catzeflis et al. 2016).

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.

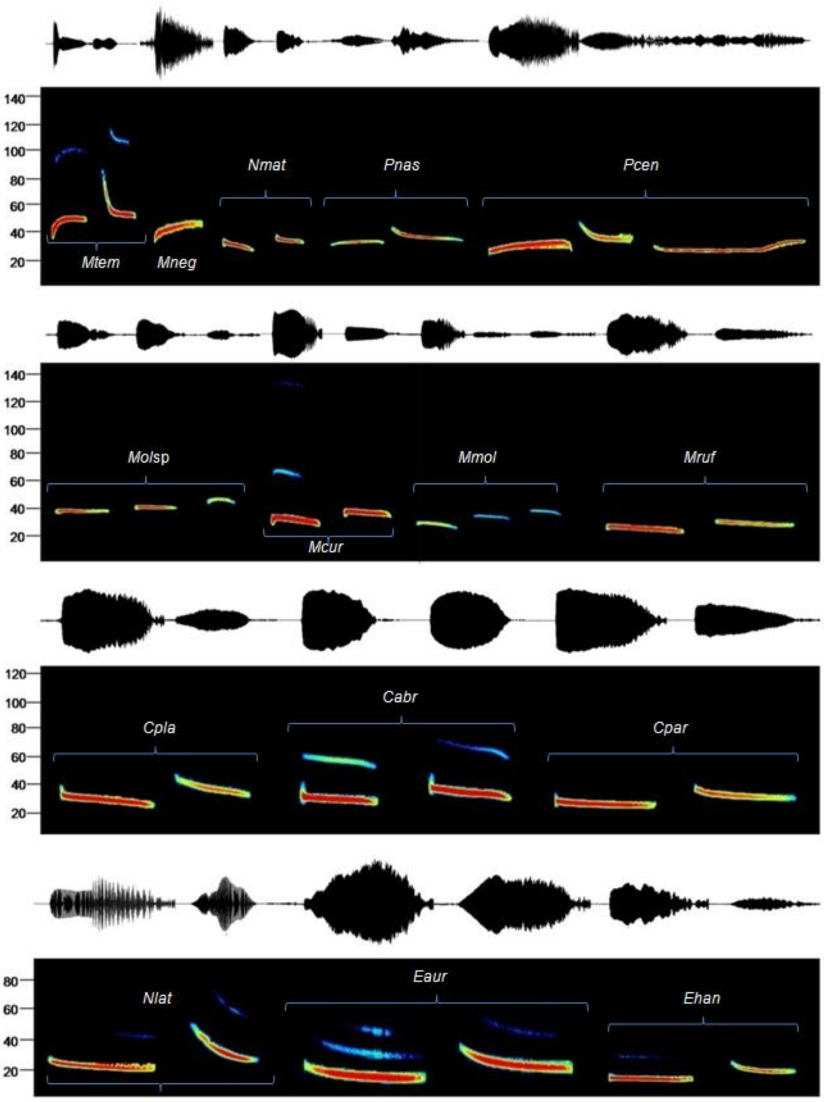

Figure 3. Echolocation calls for species of Molossidae known to occur, or potentially occurring, in Brazil. Call duration and pulse intervals are not scaled. Mtem: *Molossops temminckii*; Mneg: *Molossops neglectus*; Nmat: *Neoplatymops mattogrossensis*; Pnas: *Promops nasutus*; Pcen: *Promops centralis*; 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*.

Mormoopidae

Acoustic information of the species known to occur in Brazil was retrieved from 19 publications (Table 4 and Figure 4). *Pteronotus* cf. *parnellii* was the most studied species (21 publications). However, recent studies (Clare et al. 2013, Thoisy et al. 2014) had show that *P. parnellii* is very likely to be a complex of species, which will require further examination of the calls belonging to this taxa. 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 (>20ms) (O´Farrell & Miller 1999; Figure 4, Appendix S2).

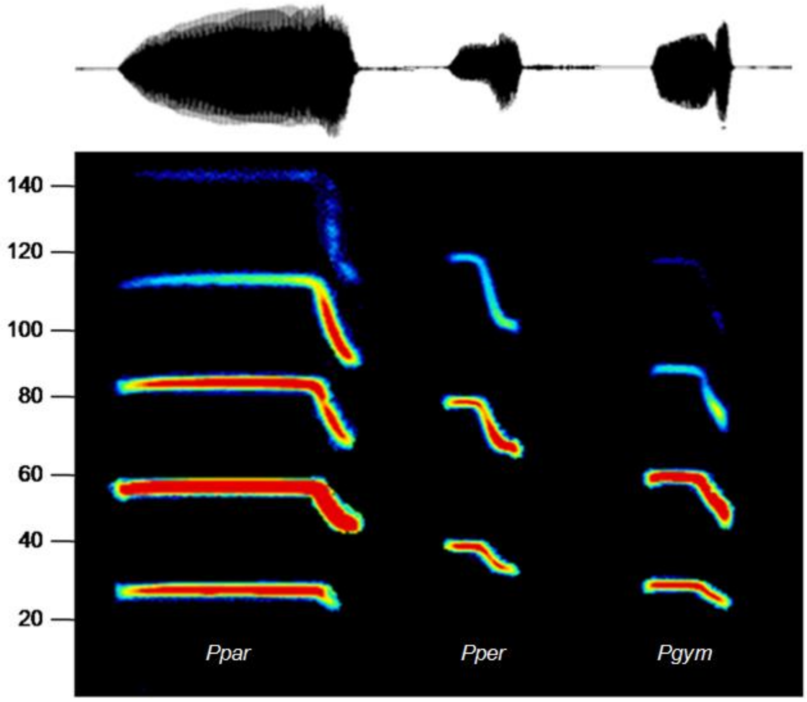

Figure 4. Echolocation calls for species of Mormoopidae known to occur, or potentially occurring, in Brazil. Call duration and pulse intervals are not scaled. Ppar: *Pteronotus* cf. *parnellii*; Pper: *Pteronotus personatus*; Pgym: *Pteronotus gymnonotus*.

Noctilionidae

The two species of this family, *Noctilio albiventris* and *N. leporinus* are widely distributed, occurring from southern Mexico to southern South America (Barquez et al. 2015 a, b); 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 Figure 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 (Figure 5; Appendix S2).

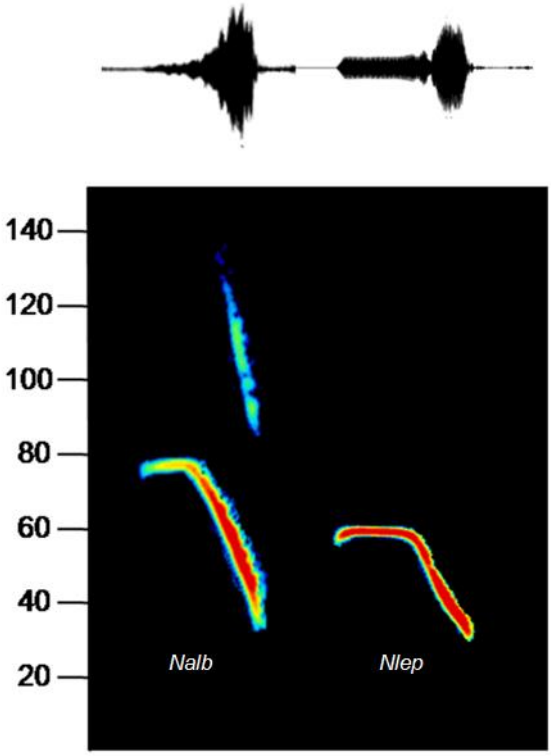

Figure 5. Echolocation calls for species of Noctilionidae known to occur, or potentially occurring, in Brazil. Call duration and pulse intervals are not scaled. Nalb: *Noctilio albiventris*; Nlep: *Noctilio leporinus*.

Vespertilionidae

Acoustic information of 19 species was compiled from 24 references (Table 6 and Figure 6). We were not able to retrieve any acoustic information on *Eptesicus andinus*, *E. taddeii*, *Histiotus alienus*, *Lasiurus ebenus*, *L. salinae*, *Myotis dinellii*, *M. izecksohni* and *M. simus*. For *L. castaneus* there is some information but as a complex with *L. egregius* (López-Baucells et al. 2016). Here we present information on echolocation calls of *Histiotus diaphanopterus*, (Eder Barbier pers. comm.) a species recently described for Brazil (Feijó et al. 2015) and included information for *M. 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 S2).

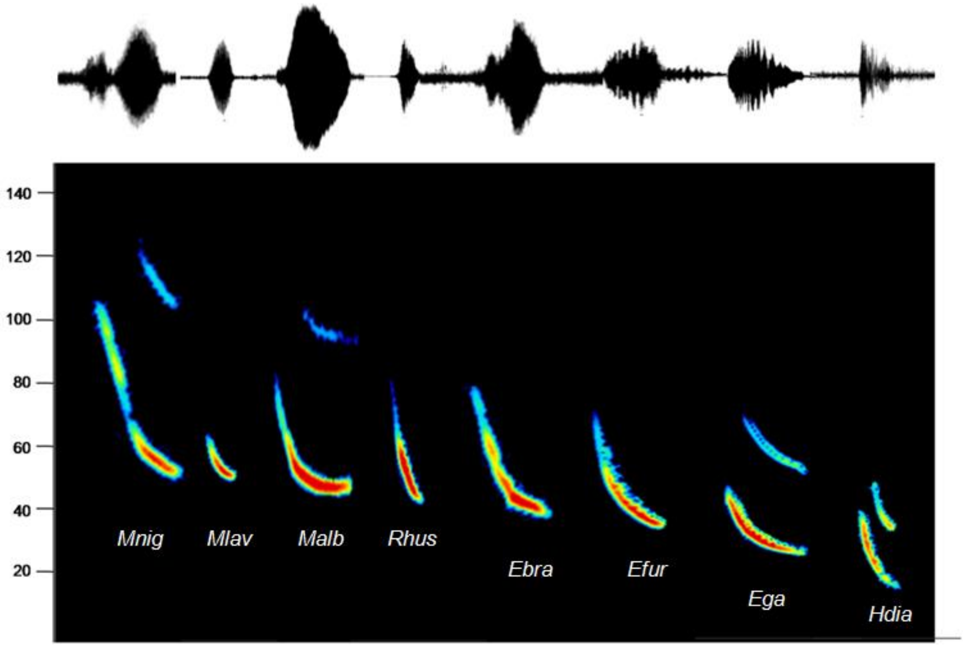

Figure 6. Echolocation calls for species of Vespertilionidae known to occur, or potentially occurring, in Brazil. Call duration and pulse intervals are not scaled. Mnig: *Myotis nigricans*; Mlav: *Myotis lavali*; Malb: *Myotis albescens*; Rhus: *Rhogeessa hussoni*; Ebra: *Eptesicus brasiliensis*; Efur: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

Acoustic identification key

Based on the data we compiled for previously presented eight families and our own data, we provide a dichotomous key supporting the acoustic identification of Brazilian bats is presented in Appendix S2.

Regional variation in echolocation calls

Considering that most acoustic information was retrieved from studies made outside Brazil, it is important to access if identifications of some species could be affected by regional variation of their echolocation calls (e.g. Jiang & Feng 2015). Therefore, we compared the parameters from calls obtained in Brazil with calls from other regions, in order to test possible regional differences. For the majority of the species we were only able to evaluate the regional variation in FME, the most commonly used acoustic parameter and, 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 regional variation in FME within some of the best-studied families and species. We found great acoustic variability in 10 bat species: *R. naso*, *S. bilineata*, *S. leptura*, *F. horrens*, *M. rufus*, *L. blossevillii*, *L. cinereus*, *L. ega*, *M. nigricans* and *M. riparius* (see Tables 1-6). For example, *L. blossevillii* showed a significant variation in FME across North, Central and South America and *M. riparius* FME ranged from 55 kHz to 66.56 kHz solely in South America (Table 6). Also, *M. rufus* showed highest 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 highly variability on echolocation calls related to flying environment. Finally, though we only retrieved two studies for North America regarding *L. cinereus*, they showed clear differences in the FME recorded for the species (20.11; 35.47 kHz),which perhaps could be related to different recording conditions (hand release recording or degree of vegetation clutter).

The review of Jiang & Feng (2015) revealed that geographic variation of bat echolocation calls is not uncommon, averaging 5 to 10 kHz differences in peak frequency; and differences above 10 kHz in FME within the same species are due to morphological differences among subspecies across large spatial scales. Also, they suggest that geographic variation in echolocation pulses of bats may be caused by genetic and cultural drift, and ecological, sexual and social selection. 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 2005). However, several studies (e.g. Appleton et al. 2004, Furman et al. 2010) demonstrated that *M. schreibersii* was a complex of several species distributed across Africa, Europe, Asia, and Oceania. 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 & Patterson 2013). 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*, *S. leptura*, *F. horrens*, *M. rufus*, *L. blossevillii*, *L. cinereus*, *L. ega*, *M. nigricans* and *M. riparius*) make them priority candidates for investigating if the geographical variation we found in this work is real, 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 67 species of non-phyllostomid bats occurring in Brazil. Still, for at least other 26 species of non-phyllostomid bats occurring in country there are no information on their echolocation calls. Indeed, some of these species are potentially very rare and difficult to capture, or were recently described (e.g. *Myotis lavali*, *M. izecksohni* – Moratelli et al. 2011). Although the gaps on the acoustic knowledge of several species are a fact, in this review we showed that some other species are relatively easy to be identified acoustically. *Promops centralis* is one of those cases; due to its ecology and foraging behaviour, 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 & Taddei 2000, Fischer et al. 2015). Using acoustic surveys in five Brazilian states it was possible to extend *P. centralis* distribution in more than 3 000 000 km^2 to the east (Hintze et al. submitted), demonstrating that acoustic monitoring can help to greatly improve our knowledge on the ecology, behaviour and distribution of poorly known Brazilian bat taxa.

Bioacoustics can be used to explore cryptic diversity in bats (e.g. Jones & Parijs 1993, Thoisy et al. 2014, Hintze et al. 2016a) and there is a great potential for this use in Brazil. In the Neotropics, two similar cases are drawing attention to 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. (2016a) hints for a new *Saccopteryx* species vocalizing with lower frequencies (39-42 kHz) than *Saccopteryx 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, captures will be necessary for the confirmation and morphological description of a new species. So, although great progress in the recording and analysis of bat echolocation calls, we can not ignore the need to collect vouchers (Ceríaco et al. 2016).

Acoustic monitoring produces huge amount of data, which results in a slow process of manual identification. But, while there have been some improvement in automated 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 & Voigt 2016). Neglecting the possibility of regional variation in the echolocation calls of the species and the potential for cryptic bat diversity (e.g. Thoisy et al. 2014, Hintze et al. 2016a), and passively accepting potentially inaccurate and incorrect automated identifications (Hintze et al. submitted) may lead to deficient species data records and consequently inefficient bat conservation (Russo & Voigt 2016).

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 adopts 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. In French Guiana, high-flying bats were mist-netted above a river where they drank. They were then released in the early morning in a clearing that allows following and observing the animal to assign a certain acoustic feature to the flight behaviour and conditions. Naturally, for ethical questions, as this technique requires animals to be maintained captive all night long, pregnant or lactating females must not be used for this protocol.

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, second, we will not be able to use automated acoustic identification programs until comprehensive databases of Neotropical bat calls are available. The use of bioacoustics can be a fundamental tool to expand the knowledge on the patterns of bat diversity in Brazil and the Neotropical region as a whole, and contribute to their conservation. We hope this review to contribute to the spark for the sustained growth of the bat bioacoustics in Brazil.

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Supporting Information

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).

Appendix S2. Illustrated identification key to the calls of Brazilian bats.

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Tables

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.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 in Appendix S1.

IUCN	Species	Region	Call type	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	CD (ms)	PI (ms)	SI
LC	*Centronycteris maximiliani (?)*	SA-Tr	mono			40.6					3
						41.5	38.1	41.6	5.2	154.8	17
	Centronycteris maximiliani/centralis	SA-Tr	single			~40					25
LC	*Centronycteris centralis*	NA-Tr					39.29	41.63	6.98		8
		CA-Tr				41.3			5.9	119	20, 21
						43.5					44
LC	*Cormura brevirostris*	CA-Tr	low			25.2			8.2	119	20, 21
			middle			28.1			8.2	100	
			high			31.4			8.6	107	
						25 28 31					44
		SA-Tr	low			26					3
			middle			29.4					
			high			32.3					
				29.39	30.11	31.36	29.01	32.52	11.97		38
			low			~25					25
			middle			~28					
			high			~30					
LC	*Cyttarop salecto*	CA-Tr				35.9			9.8	154/265	20, 21
		SA-Tr	mono			35.4					3
		SA-Tr	single			~35					25
LC	*Diclidurus albus*	CA-Tr	low			23.5			9.4/9.6	162/317	20, 21
			middle			25.8			9.7	249	
DD	*Diclidurus ingens*	SA-Tr	low			19.6					3
			high			21.8					
			low			~19					25
			high			~22					
LC	*Diclidurus isabella*										
LC	*Diclidurus scuttatus/albus*	SA-Tr	low			26.5					3
			high			30.6					
			low			26					25
			high			30					

Table1. (cont.)

IUCN	spp	Region	Call type	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	CD (ms)	PI (ms)	SI
LC	*Peropteryx kappleri*	CA-Tr				31.6			9.6	170/280	20, 21
		SA-Tr	mono			31.3					3
			single			~29-33					25
LC	*Peropteryx leucoptera*										
LC	*Peropteryx macrotis*	NA-Tr-Ar-Wt		41.71	37.56	41.61	37.54	41.87	7.3		47
		NA-Tr-Ar				38-40	33.1-36.7		5-9		40
		NA-Tr					35.56	38.81	6.14		8
						39.6	39.1	40	8.8	152	28
		CA-Tr				38.9			9.3	139/215	20, 21
		SA-Tr	mono			38.4					3
			single			~37-39					25
				38.15	36.33	39.58	36	40.16	7.29		38
			mono			39.2 ± 0.7	37.2 ± 1.1	39.5 ± 0.9	8.2 ± 2.3	193.2 ± 123.3	°
NA	*Peropteryx pallidoptera*										
LC	*Peropteryx trinitatis*	SA-Tr	mono			43.9					3
			single			~42-44					25
			mono			43.5 ± 0.8	40.4 ± 1.1	43.8 ± 0.7	5.9 ± 1.1	98.3 ± 21.8	°
NA	*Peropteryx* sp.	SA-Tr	mono			41.4 ± 0.5	38.8 ± 0.8	41.6 ± 0.6	7.1 ± 1.4	112.3 ± 24.4	°
LC	*Rhynchonycteris naso*	NA-Tr-Ar-Wt		98.25	81.84	95.79	81.84	98.71	4.38		47
		CA-Tr					40.2	47.2	6.7	60.8	29
						98.2			4.8	58	21
		SA-Tr	mono			95.6					3
			mono			89.6 ± 0.5	88.1 ± 0.6	91.0 ± 1.0	5.6 ± 0.3	74.5 ± 50.0	°
				93.65	77	87.34	77	87.34	5.89		38
		CI-Tr	a			51.3	42.2	52.2	5.3	29.3	35
			b			100	74.8	101.3	5.9	25.9	

Table 1. (cont.)

IUCN	Species	Region	Call type	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	CD (ms)	PI (ms)	SI
LC	*Saccopteryx bilineata*	NA-Tr-Ar-Wt		45.38	45.78	47.29	44.1	48.55	7.4		47
		NA-Tr	low			44.5	43.7	45	9.2	181.1	28
			high			46.8	46	47.2	8.8	180.3	
							44.24	47.41			23
		CA-Tr	a				44.5	46.6	6.7	55.8	29
			b				46.6	48.6	6.6	82.5	
							45.1	47	6.1		30
			low			44.5			7.5	73	20, 21
			middle			46.8			7.6	105	
						45 48					44
			alternating			45			8.26	60.9	37
						48			8.22	88	
			monotonous			48			6.43	93	
		SA-Tr	low			42.1					3
			high			44.1					
				43.73	43.89	46.46	43.41	46.81	7.22		38
			low			45	41.3	46.3	8.3	75.3	17
			high			47.9	45	49.3	8.6	53.5	
			low			~42					25
			high			~45					
		CI-Tr				42	32.8	43.9	5.2	56.2	35
LC	*Saccopteryx canescens*	SA-Tr	mono			52.5					3
						53.2 ± 0.6	32.8	43.9	5.2	56.2	°
	Saccopteryx canescens/gymnura	SA-Tr	single			~54					25
DD	*Saccopteryx gymnura*	SA-Tr	mono			53.9					3
						57.0 ± 0.6	53.6 ± 1.1	58.1 ± 0.5	5.5 ± 0.6	88.2 ± 24.8	
LC	*Saccopteryx leptura*	NA-Tr-Ar-Wt		48.35	47.69	50.58	46.66	51.27	6.78		47
		CA-Tr	low			51.3			7.2	68	20, 21
			middle			54.6			6.8	90	
						52.5 55.5					44
		SA-Tr	low			47.4					3
			high			49.8					
				51.47	52.5	53.31	51.16	54.52	6.76		38
		SA-Tr	low			~48					25
			high			~55					
			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	42.9	53.3	4.9	66.7	35

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.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 in Appendix S1.

IUCN	Species	Region	Call type	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
LC	*Furipterus horrens*	SA-Tr	I			161.3	128.6	190.5	61.9	3.7		11
			II			158.4	122.8	191.2	68.4	2.6	13.1	
			II			157.2	135.1	191.3	56.2	2.3	15	
						152				3.8		3
						130-170						25
		SA-Wt					120	150		<1		12
NT	*Natalus macrourus*											
LC	*Natalus tumidirostris*	SA-Tr	H1			120.2			77.4	3.5		3
DD	*Thyroptera devivoi*											
LC	*Thyroptera discifera*	SA-Tr	FH			53				2.9		3
			H1			112.5				2.5		
DD	*Thyroptera lavali*											
LC	*Thyroptera tricolor*	NA-Tr-Ar-Wt		66.38	43.5	53.09	43.5	66.38	22.88	2.76		47
		SA-Tr		123.26	91.95	103.12	91.95	123.26	31.31	1.1		38
			H1			51				3.2		3
NA	*Thyroptera wynneae*											

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.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 in Appendix S1.

IUCN	Species	Region	Call type	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
LC	*Cynomops abrasus*	SA-Tr	low			22.3				12.5		3
			middle			30				10.2		
	Cynomops greenhalli/abrasus	SA-Tr	low		~17							25
			high		~21							
LC	*Cynomops greenhalli*	CA-Tr				21-24						20
		CA_SA-Tr	low	25.2	17.4				7.8	15.9	297.1	22
			high	29	21.1				7.9	14.8	190.3	
	Cynomops mastivus											
NA	*Cynomops milleri*											
DD	*Cynomops paranus*	SA-Tr	low			26.5				15.5		3
			middle			31.6				13.9		
	Cynomops paranus/planirostris	SA-Tr	low		~21							25
			high		~24							
LC	*Cynomops planirostris*	CA-Tr				25-28						20
		CA_SA-Tr	low	28.8	21.1				7.6	16.1	236.4	22
			high	32.9	24.3				8.7	15.9	165.1	
		SA-Tr	low			27.8				13.6		3
			middle			33.9				10		
LC	*Eumops auripendulus*	CA_SA-Tr	low	32.4	18.2				14.3	20.3	269.4	22
			high	35.8	21.9				13.8	19.3	215.9	
		SA-Tr	low			18.7				21.8		3
			middle			23.3				19.5		
			high			26.7				18.4		
LC	*Eumops bonariensis*											
	Eumops nanus	CA_SA-Tr	low	27.9	25.2				2.8	5.6	294.6	22
LC	*Eumops dabbenei*	CA_SA-Tr	low	21.3	13.7				7.6	28.3	379.9	22
			high	24.6	15.8				8.9	25.6	332.7	
LC	*Eumops delticus*											
LC	*Eumops glaucinus*	CA_SA-Tr	low	27.4	19				8.4	16.2	321.1	22
			high	29.3	20.3				8.9	16.7	270.9	
LC	*Eumops hansae*	SA-Tr	low	19.1	13.7	17			5.5	18.4	517.4	°
			high	29.9	18.3	22.8			11.7	13.3	370.9	
DD	*Eumops maurus*											
LC	*Eumops patagonicus*											
LC	*Eumops perotis*	NA-Wt-Sn				13.2	9.4	19.8		15.4		18
		NA-Wt				7.4	6.8	8.2		57.9	1369	1
		SA-Tr	low			10.3 ± 0.6	8.3 ± 0.2	12.3 ± 0.8	4.1 ± 0.8	18.2 ± 7.5	742.9 ± 182.6	°
			high			12.4 ± 0.7	10.2 ± 1.3	14.9 ± 0.8	4.7 ± 1.3	21.3 ± 4.6	491.5 ± 372.6	
LC	*Eumop strumbulli*											
	E. auripendulus/glaucinus/ dabbenei/hansae/maurus	SA-Tr	low		~18	<30						25
			high		~22							

Table3. (cont.)

IUCN	Species	Region	Call type	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
DD	*Molossops neglectus*	CA_SA-Tr	low	32.5	44.3				11.8	10.5	107.2	22
			high	38.3	46.9				8.5	9.4	107	
			high II	56.2	48.9				7.3	6.1	62.2	
		SA-Tr	low		~44							25
			high		~46							
LC	*Molossops temminckii*	CA_SA-Tr	low	42.8	54.2				11.4	8.3	79.3	22
			high	45.5	54.8				9.3	7.6	82.9	
			high II	75.9	55.4				20.5	7.2	55.2	
		SA-Tr		40.4	50.4	50.4 narrow/ 45.1 broad			10.3	7.8	97	15
						51.3	44.06	52.92	8.86	3.99	61.76	31
						52.99	40.08	66.3	26.21	2.05	47.48	
						51.91	47.36	53.56	6.2	3.45	96.27	
						55.7	44.26	68.01	23.75	1.9	46.9	
						50.95	45.59	52.51	6.92	5.01	149.55	
						54.2	46.74	64.5	17.75	2.47	84.87	
						49.38	43.98	51.74	7.76	4.11	118.63	
						45.62	43.31	58.82	16.51	3.23	99.66	
			low		~54							25
			high		~55							
			low (type I)			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)			54.7 ± 0.9	52.7 ± 0.6	85.0 ± 7.1	32.2 ± 7.6	8.2 ± 0.4	48.3 ± 4.4	
LC	*Neoplatymops mattogrossensis*	CA_SA-Tr	low	32.6	28.2				4.3	12.2	160.9	22
			high	36.9	33.6				3.4	11.9	105.1	
		SA-Tr	Low			32.3 ± 1.3	27.7 ± 0.9	34.3 ± 0.9		6.5 ± 0.8	10.0 ± 0.9	°
			High II			35.8 ± 1.8	34.1 ± 1.5	37.9 ± 1.7		3.9 ± 0.5	10.0 ± 1.0	

Table 3. (cont.)

IUCN	Species	Region	Call type	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
LC	*Molossus aztecus*											
LC	*Molossus barnesi*	SA-Tr	low			32.4				12.8		3
			middle			34.9				11.5		
	Molossus coibensis	CA-Tr	I	35.4	29.8				5.6	0.4	76.2	13
			II	39.7	35				4.7	0.3	153.8	
LC	*Molossus currentium*	CA-Tr				28/30/33						20
		CA_SA-Tr	low	29.7	24.4				4.3	13.9	205.8	22
			middle	32.9	28.2				4.4	14.1	134.9	
			high	34.5	30.3				3.2	14.4	126.4	
LC	*Molossus molossus*	NA-Tr-Ar-Wt		37.45	34.95	38.38	34.71	38.93	4.22	8.72		47
		NA-Tr					33.65	38.55		9.54		8
		CA-Tr					30.3	33.9		9.3		30
						35/39/42						20
			I	39.1	34.4				4.7	0.6	75.4	13
			II	42.8	39.1				3.8	0.6	117.6	
		CA_SA-Tr	low	35.6	33.5				2.2	10.4	143.1	22
			middle	39.1	36.8				2.2	10.2	109.2	
			high	42.8	39.8				3	10.4	82.8	
		SA-Tr	low			37.5				10.5		3
			middle			41.4				10		
			high			44.3				8.6		
				37.59	35.8	38.16	35.59	38.78	3.17	12.01		38
			1			42.445	31.601	45.743		5.7		7
			2			42.376	32.201	45.934		6.2		
			3			42.69	30.507	43.283		5.2		
			low			~33-35						25
			middle			~35-40						
			high			~40-45						
			low			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			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	22.7	50.3		4.8	40.7	35
		CI-Tr	A	36.5	32.5	35.2			9.8	153.5		4
			B	44.4	38.7	41.6			9.3	92.8		
LC	*Molossus pretiosus*											

Table 3. (cont.)

IUCN	Species	Region	Call type	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
LC	*Molossus rufus*	NA-Tr	low			29.4	28.1	29.9		13.2	263.4	28
			high			33	32	33.6		13.4	344.6	
							28.8	33.61				23
							25.16	29.7		11.08		8
		NA-Tr-Ar-Wt		31.48	29.05	31.89	28.79	32.28	3.49	9.73		47
		CA-Tr					27.2	30.8		11.6		30
						25						20
						< 35						2
		CA_SA-Tr	low	26.3	24.7				1.6	12.7	409	22
			high	27.8	25.7				2	12.9	343.7	
		SA-Tr	low			26.5				17.3		3
			middle			30.7				15.3		
			high			35.2				16.2		
				27.44	24.76	26.13	24.45	27.69	3.16	13		38
			low			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			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	37.26	41.41	4.15			41
	Molossus sinaloe/currentium/rufus	SA-Tr	low			25-30						25
			middle			30-35						
			high			35-40						
			low			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	

Table 3. (cont.)

IUCN	Species	Region	Call type	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
LC	*Nyctinomops aurispinosus*											
LC	*Nyctinomops laticaudatus*	NA-Tr				26.4	25.1	29.7		12.5	189.5	28
							17.67	19.15		14.49		8
		NA-Tr-Ar-Wt		41.03	17.97	25.68	17.96	41.03	23.07	4.85		47
		CA-Tr				24-26						20
		CA_SA-Tr	low	26.7	23.6				2.4	12.5	393.7	22
			middle	28.7	24.2				4.6	12.3	292.9	
			high	32.4	24.9				7.5	12.7	213.6	
LC	*Nyctinomops macrotis*	NA-Wt				12	11.3	13		18.6	1203	1
		NA-Tr-Ar-Wt		28.59	13.79	22.346	13.79	28.66	14.86	7.92		47
		CA_SA-Tr	low	28.8	16.7				12	13.3	284.7	22
LC	*Tadarida brasiliensis*	NA-Wt				24.5	22.7	27	4.3	12.8		14
		NA-Wt-Sn				28	24.1	32.3		11.5		18
		NA-Wt				24.8			2.73	14.2		36
						24.1			5	12.3		
						25			2.49	13.6		
						27.5	26.3	30.3		13.7	239.7	1
		NA-Tr					27.32	34.04		8.69		8
				37.7	24.4	28.1				8.3	109	32
		NA-Tr-Ar-Wt		46.81	26.09	32.61	26.09	46.83	20.74	7.2		47
		CA_SA-Tr	low	27.6	24.4				3.2	3.7	273.1	22
	N. laticaudatus/T. brasiliensis	SA-Tr	low		~18	<30						25
			high		~22							

Table 3. (cont.)

IUCN	Species	Region	Call type	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
LC	*Promops centralis*	NA-Tr-Ar-Wt		22.89	26.94	26.03	22.82	27.76	4.94	47.66		47
		CA-Tr				28/32						20
		CA_SA-Tr	low	25.8	28				2.2	17.8	276.9	22
			high II	35.7	30.4				8.1	17.1	158.9	
		SA-Tr	middle			35.4				14.1		3
			low			29.3				21.2		
			low		~28							25
			high		~30							
				24.79	29.12	29.65	24.38	30.36	5.8	53.63		38
			low			29.8	26.5	31.8	5.4	23.9	253	16
			low (HDC)			28.5	24.4	31.8	7.4	103.7	99.5	
			high			35.4	33.1	43.8	10.7	15.2	71.1	
LC	*Promops nasutus*	CA_SA-Tr	low	32.7	34.7				2	11.6	209.5	22
			high II	47	37.8				9.2	8.3	105.7	
		SA-Tr	low		~34							25
			high		~37							
			low			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			38.6 ± 1.6	34.5 ± 2.1	43.9 ± 1.6	9.4 ± 0.5	19.6 ± 1.1	94.5 ± 10.7	

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.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 in Appendix S1.

IUCN	Species	Region	Call type	SF (kHz)	EF (kHz)	CF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	DC (%)	SI
LC	*Pteronotus davyi*	NA-Tr		71.5	59.4		73.3				6.4	64.8		32
							69.1	68.1	69.6		6.8	66.8		28
							73.6			16.2	4.9			43
								59.64	72.96		5.92			8
						58.88		57.44	69.23					23
		NA-Tr-Ar					59-60/70-71				6-8			40
							60.3/69.8				8.2		17.1	
							58.5/69.5				6.9		6.7	
							60.1/69.0				8.3		8.1	
							59.0/68.9				6.6		8.3	
							60.1/71.1				6.7		8	
							57.6/67.7				7.6		5.5	
		NA-Tr-Ar-Wt		69.75	58.36	59.82	66.78	58.32	71.24	12.92	5.84			47
		CA-Tr						58	68.1		5.5	62.2		29
							68.0/58.0				6.6	70.8	10.1	19
		SA-Tr		71.5										3
		CI-Tr	FH	59.9	70.70		70.50			15.50	5.2	55.2		4
			FH	38	22		34.1				2.8	15		46
			H2	70.3	51		67				4.6	41		
LC	*Pteronotus gymnonotus*	NA-Tr-Ar-Wt		54.99	45.81	46.86	51.34	45.81	55.51	9.7	5.33			47
		CA-Tr					55.00							44
							55.00							20
		SA-Tr					54.80							3
				~55 (cf)										25
			H2	~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	°
LC	*Pteronotus personatus*	Na-Tr		82.2	67.6		81.4				5.7	55.1		32
							80.1/65.9				7.1	53.9		27
							80.1	74.1	80.9		7.1	53.9		28
							85.1			15.1	4.8			43
								66.75	83.72		4.4			8
		NA-Tr-Ar-Wt		82.83	64.12	65.94	70.53	64.12	82.88	18.76	5.71			47
		CA-TR						68	83		5.7	48.3		29
							73							20
		SA-Tr					74.1							3
				~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	°

Table 4. (cont.)

IUCN	Species	Region	Call type	SF (kHz)	EF (kHz)	CF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	DC (%)	SI
LC	*Pteronotus mesoamericanus* group1	NA-Tr		61.3	55.7		63.1				27.8	64.8		32
(?)							65-66				c. 25		>20	40
							67.1	62.8			22.4		40.3	
							66.4	65			23.6		38.5	
							66.1	63.9			25.6		40.2	
							65	63.1			25		40	
							64.9	59.9			23.1		45.3	
							64.5	64.2	64.6		25.8	48		28
							64.9			10.7	19.7			43
								54.93	64.73		24.42			8
						63.05		55.61	62.71					23
		NA-Tr-Ar-Wt		61.93	52.87	64.51	63.61	52.86	64.97	12.1	21.21			47
		CA-Tr						54.5	63.5		30.4	61.9		29
			62 kHz				62.1							9
							60							20
	Pteronotus cf *parnellii* group2	SA-TR	59 kHz				58.4							3
							59.2							45
			60 kHz				~60							25
		CI-Tr	59 kHz				58.9							9
				60.6	48.05		60	59.61	60.23	0.62	21.23			26
							58.2	46.3	60.2		21	25		35
			FH	28	23		31.2				14.5	38		46
			H2	56.2	46.8		61.3				22	56		
	Pteronotus cf *parnellii* group 3-4	SA-TR	53 kHz				52.66							3
							53.4							45
			53-54 kHz				53.6							9
			55 kHz				~55							25
							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	°
	Pteronotus cf *parnellii*	SA-TR		54.2	87.8		93	54.2	93.8	39.6	117.55			38

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.SF: start frequency; EF: end frequency; FME: frequency of maximum energy; LF: lowest frequency; HF: highest frequency; CD: call duration; PI: pulse interval; BB: broad band; NB: narrow band; SI: reference number in Appendix S1.

IUCN	Species	Region	Call type	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	DC (%)	SI
LC	*Noctilio albiventris*	CA-Tr				70							44
						70							20
		SA-Tr		66.34	44.83	52.47 (fm)	44.83	67.51	22.68	9.99			38
			BB			69.7			33.6			29.5	3
			NB			71			16			67.4	
				68-76									25
				~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	°
LC	*Noctilio leporinus*	CA-Tr				56							44
						65							20
		NA-Tr-Ar-Wt		50.79	23.55	31.03	23.52	50.96	27.43	8.41			47
		NA-Tr					29.63	57.14		13.95			8
		SA-Tr	BB			57.6			33.6			24.5	3
			NB			57.6			13			70.2	
				50.66	27.63	34.61 (fm)	27.61	50.68	23.07	12.72			38
				53-61									25
				~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	BB	54.4	22.6	39.3			32	11.8	65.3		4
			NB	53.8	38.6	52.2			15.6	10.7	98.3		

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 speciesSF: 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 in Appendix S1.

IUCN	Species	Region	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
LC	*Eptesicus andinus*										
LC	*Eptesicus brasiliensis*	NA-Tr-Ar-Wt	55.83	33.3	37.12	32.93	55.83	22.89	7.8		47
		SA-Tr	70.43	34.34	44.61	34.33	70.48	36.15	3.5		38
			58.0 ± 8.5	40.0 ± 0.6	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	30.5	71.5		3	74.4	35
	Eptesicus brasiliensis/chiriquinus	SA-Tr		25-39							25
LC	*Eptesicus chiriquinus*	SA-Tr			32			30	7.6		3
DD	*Eptesicus diminutus*	SA-Wt			66.37	40.45	82.89	42.43	1.8	50.78	41
LC	*Eptesicus furinalis*	NA-Tr			37.6	36.4	40.4		7.1	175.8	28
						32.78	64.02				23
		NA-Tr-Ar			36-41						40
					36.5	33.1			9.4		
					35.8	34.2			8.9		
					37	35.1			8.7		
					36.7	33.2			10.9		
					41.4	37.1			7.7		
					36.7	32.2			4.6		
		NA-Tr-Ar-Wt	56.34	37.4	39.77	37.05	56.34	19.29	6.91		47
		CA-Tr				37.5	52.6		5.5		30
		SA-Tr			41.6			36.1	6		3
				35-45							25
			63.0 ± 9.1	36.2 ± 0.6	38.7 ± 1.5	36.2 ± 0.6	63.0 ± 9.1	26.9 ± 8.9	6.1 ± 0.5	139.2 ± 79.8	°
NA	*Eptesicus taddeii*										

Table 6. (cont.)

IUCN	spp	Region	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
LC	*Lasiurus blossevillii*	NA-Ar-Wt							>8		34
		NA-Wt-Sn			41.6	38.8	54.6		10.7		18
		NA-Tr				46.84	62.67				23
						43.58	62.89		6.11		8
		NA-Tr-Ar-Wt	89.58	39.49	53.75	39.49	90.03	50.54	3.29		47
		CA-Tr			46						20
		SA-Tr			45.5			14.3	12.3		3
			70.92	35.96	38.77	35.85	70.92	35.07	6.17		38
				40-45							25
DD	*Lasiurus castaneus*										
	Lasiurus castaneus/egregius	SA-Tr		25-35							25
LC	*Lasiurus cinereus*	NA-Wt-Sn			29.81	26.15/27.78	34.74/45.46		7.38		5
					27.88	25.51/27.02	32.04/41.69		7.69		
					26.21	23.86/25.26	29.57/37.77		9.63		
					26.8	24.17/25.79	32.28/43.56		10.27		
					20.11	18.30/19.35	21.93/27.73		18.3		
					27.43	24.72/26.19	30.98/39.61		8.92		
					29.24	25.90/27.93	32.60/42.36		5.46		
		NA-Ar				21.9	30.8		8.2		30
						22	40.8		6.2		
		NA-Wt-Sn			20.8	19.7	26		11		18
		NA-Tr-Ar-Wt	57.23	26.81	35.47	26.79	57.24	30.45	4.25		47
DD	*Lasiurus ebenus*										
LC	*Lasiurus ega*	NA-Tr-Ar			31				c. 10		40
					31.3	27.3			9.4		
					31.2	26.6			10.2		
					30.7	27.6			9.6		
					29.8	27.6			10.8		
					38	34			5.5		
		NA-Tr			32.2	31.1	34.9		8.7	149.4	28
						35.49	43.97				23
		NA-Tr-Ar-Wt	61.13	37.45	55.2	37.45	61.13	23.68	2.93		47
		CA-Tr				32	43		6.6		30
					32						44
					32						20
		SA-Tr		25-35							25
DD	*Lasiurus egregius*	SA-Tr	45.4	27.3	30.2				4.8		24
NA	*Lasiurus salinae*										

Table 6. (cont.)

IUCN	spp	Region	SF (kHz)	EF (kHz)	FME (kHz)	LF (kHz)	HF (kHz)	BW (kHz)	CD (ms)	PI (ms)	SI
DD	*Histiotus alienus*										
NA	*Histiotus diaphanopterus*	SA-Tr	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	6
NT	*Histiotus laephotis*	SA-Ar	38.2 ± 2.6	26.3 ± 1.8	30.4 ± 3.7				1.3 ± 0.4	94.0 ± 55.9	33
LC	*Histiotus montanus*	SA-Ar	46.4 ± 4.6	25.5 ± 2.2	32.1 ± 2.2				3.6 ± 2.6	144.5 ± 74.7	33
		SA-Ar	53.77 ± 0.97	29.62 ± 0.25	35.4 ± 0.4	31.3 ± 0.3	44.6 ± 0.9		3.34 ± 0.08	136.12 ± 8.03	39
DD	*Histiotus velatus*	SA-Wt				15	25		5-8		12
LC	*Myotis albescens*	CA-Tr			42						44
					52						20
				43-46							10
		SA-Tr	92.69	51.4	64	51.38	92.71	41.33	2.45		38
		CA-Tr	69.6 ± 9.2	46.9 ± 0.9	49.9 ± 1.6	46.9 ± 0.9	69.6 ± 9.2	22.7 ± 9.2	4.6 ± 0.9	66.6 ± 12.1	°
LC	*Myotis dinellii*										
NA	*Myotis izecksohni*										
NA	*Myotis lavali*	SA-Tr	67.3 ± 6.6	49.4 ± 1.1	52.0 ± 1.9	49.4 ± 1.1	67.3 ± 6.6	17.9 ± 6.7	4.4 ± 1.2	82.9 ± 26.0	°
LC	*Myotis levis*	SA-Wt			65.65	46	80.84	34.84	1.5	77.2	41
LC	*Myotis nigricans*	CA-Tr	61.5	50.9	54.2				7.2	106	42
			95.4	51.6	55				4.3	67.6	
					55						44
					55						20
				48-55							10
		SA-Tr			53.7			28.5	4.3		3
			76.86	38.56	48.25	38.53	76.9	38.37	3.41		38
				45-50							25
			67.1 ± 3.8	52.9 ± 1.1	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	51.3	125		2.2	24	35
LC	*Myotis riparius*	CA-Tr		58-60							10
					> 56						2
		SA-Tr			58.1			40.7	5		3
					55			37.4	5.2		3
			102.71	61.6	66.56	61.57	102.8	41.16	4.38		38
				>55							25
		SA-Wt				50	58		4-5		12
NT	*Myotis ruber*	SA-Wt				58	65		5		12
DD	*Myotis simus*										
DD	*Rhogeessa hussoni*	SA-Tr	59.8 ± 2.5	41.5 ± 0.8	48.2 ± 4.7	41.5 ± 0.8	59.8 ± 2.5	18.3 ± 2.5	3.6 ± 0.2	89.3 ± 7.3	°
LC	*Rhogeessa io*	CI-Tr			52.4	39.6	99.6		2.8	38.4	35
		SA-Tr		40-45							25

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).

Reference*	Region[a]	Recording site	Recording system[b]
Ávila-Flores & Fenton 2005	NA-Wt	Mexico-DF	TE
Bader et al. 2015	CA-Tr	Panama	RT
Barataud et al. 2013	SA-Tr	French Guiana	TE/RT
Barataud et al. 2015	CI-Tr	West Indies-Guadeloupe	TE
Eder Barbier pers. comm.[+]	SA-Tr	Brazil-Pernambuco	RT
Barclay et al. 1999	NA-Wt-Co	Canada	?
Borloti et al. 2014	SA-Tr	Brazil-Espírito Santo	TE
Briones-Salas et al. 2013	NA-Tr	Mexico-Oaxaca	ZC
Clare et al. 2013	CA-Tr/SA-TR/CI-Tr	Belize, Costa Rica/Guyana/Trinidad	RT
Estrada-Villegas et al. 2012	CA-Tr	Panama	RT
Falcão et al. 2015	SA-Tr	French Guiana/Brazil-Bahia	RT
Fenton et al. 1999	SA-Wt	Brazil-São Paulo	ZC
Gager et al. 2016	CA-Tr	Panama	RT
Gillam et al. 2010	NA-Wt	USA-Texas	RT
Guillén-Servent& Ibáñez 2007	SA-Tr	Venezuela	TE
Hintze et al. (submitted)	SA-Tr	Brazil	RT
Hintze et al. 2016	SA-Tr	Brazil-Pernambuco	RT
Szewczak et al. 2011	NA-Wt-Co	USA	?
Ibáñez et al. 1999	CA-Tr	Panama	TE
Jung &Kalko 2011	CA-Tr	Panama-Costa Rica	TE/RT
Jung et al. 2007	CA-Tr	Panama-Costa Rica	TE/RT
Jung et al. 2014	CA_SA-Tr	Costa Rica, Panama, Venezuela, Bolivia, Brazil	TE/RT
Kraker-Castañeda et al. 2013	NA-Tr	Mexico-Oaxaca	ZC
López-Baucells et al. 2014	SA-Tr	Brazil	RT
López-Baucells et al. 2016	SA-Tr	Brazil	RT?
Macías et al. 2006	CI-Tr	Cuba	RT
MacSwiney et al. 2006	Na-Tr	Mexico-Yucatan	TE
MacSwiney et al. 2008	NA-Tr	Mexico-Yucatan	TE
O'Farrell & Miller 1997	CA-Tr	Belize	ZC
O'Farrell et al. 1999	CA-Tr/NA-Ar	Belize/USA-Arizona	ZC
Oliveira 2015	SA-Tr	Brazil-Brasilia	RT
Orozco-Lugo et al. 2013	NA-Tr	Mexico-Morelos	TE
Ossa et al. 2015	SA-Ar	Chile	TE
Pierson et al. 2006	NA-Ar-Wt	USA-California	ZC/TE
Pio et al. 2010	CI-Tr	Trinidad	TE
Ratcliffe et al. 2004	NA-Wt	Mexico-DF	TE
Ratcliffe et al. 2011	CA-Tr	Panama	RT
Rivera-Parra &Burneo 2013	SA-Tr	Ecuador	TE
Rodríguez-San Pedro &Simonetti 2013	SA-Ar	Chile	TE
Rydell et al. 2002	NA-Tr-Ar	Mexico-Yucatan	FD/TE
Santos 2014	SA-Wt	Brazil-Parana	TE
Siemers et al. 2001	CA-Tr	Panama	TE
Smotherman&Guillén-Servent 2008	NA-Tr	Mexico-Veracruz	RT
Surlykke&Kalko 2008	CA-Tr	Panama	RT
Thoisy et al. 2014	SA-TR	French Guiana, Brazil-Amapá	TE/RT
Vaughan et al. 2004	CI-Tr	Puerto Rico	TE
Zamora-Gutierrez et al. 2016	NA-Tr-Ar-Wt	Mexico	TE/RT
Our recordings	SA-Tr	Brazil-Rio Grande do Norte/Pernambuco/Bahia/Tocantins	RT

[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.

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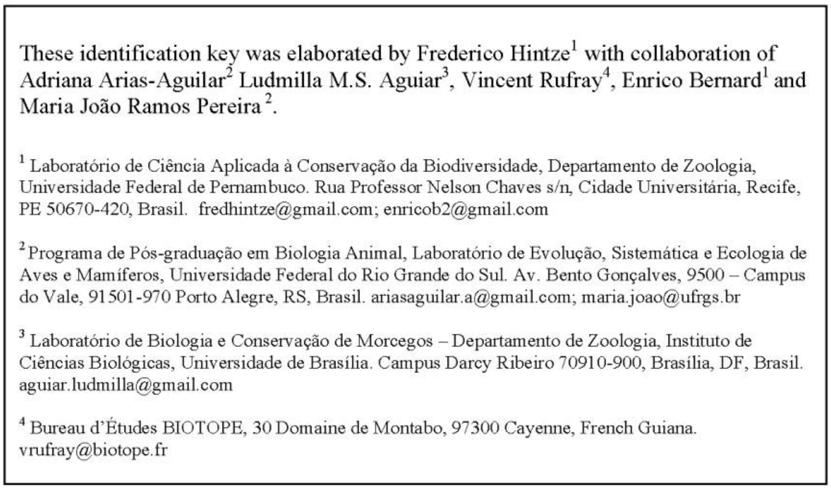
Appendix S2. Illustrated identification key to the calls of Brazilian Bats



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).

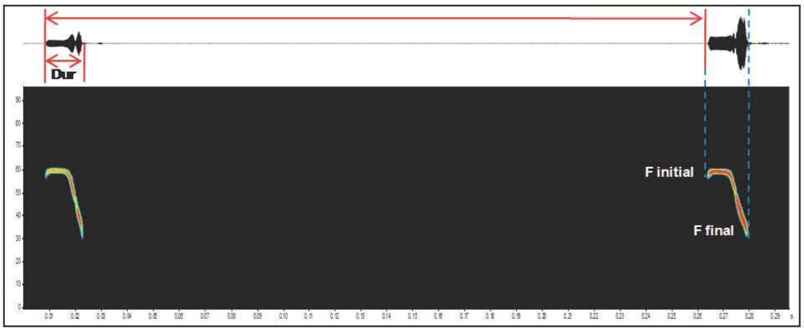


Figure N1 – Oscillogram [above, time (X) vs. amplitude (Y)] and spectrogram [below, time (X) vs. frequency (Y) vs. energy (color scale)] of two echolocation calls.

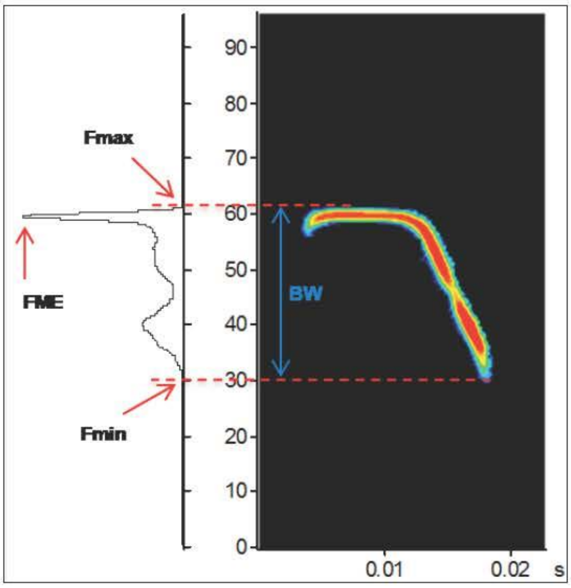


Figure N2 – Spectrogram [at right, time (X) vs. frequency (Y) vs. energy (color scale)] and power spectrum (at left, frequency (X) vs. energy (Y)] of an echolocation call.

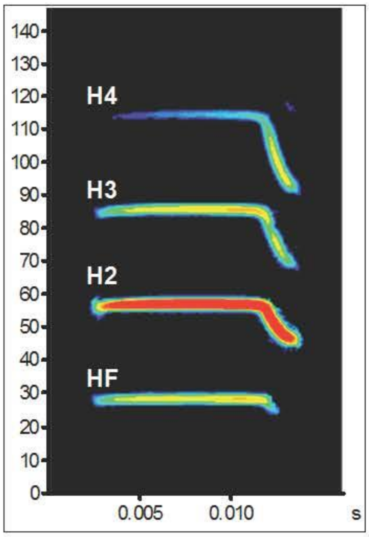


Figure N3 – Spectrogram showing four harmonics of an echolocation call. FME is on the H2.

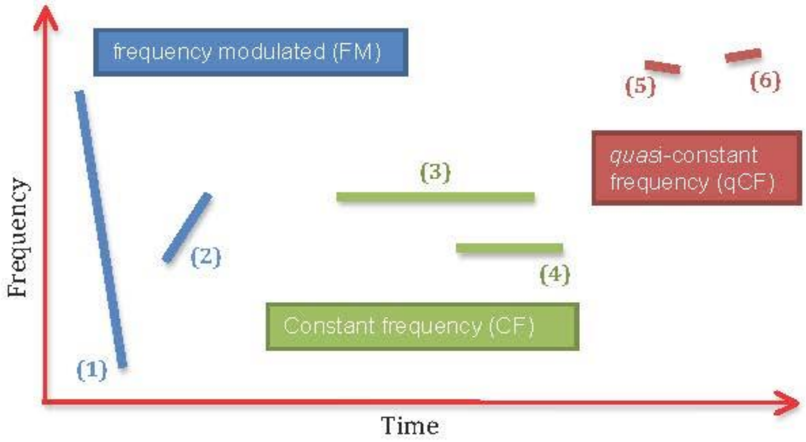


Figure N4 – Schematic representation of a spectrogram, with some basic structures of a calling.

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

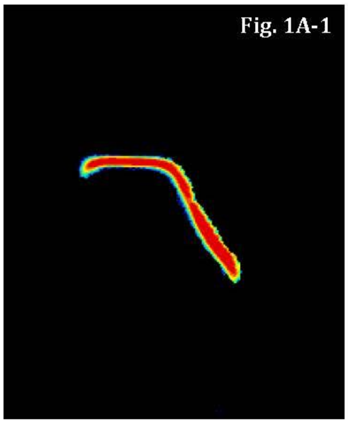


Fig. 1A-1

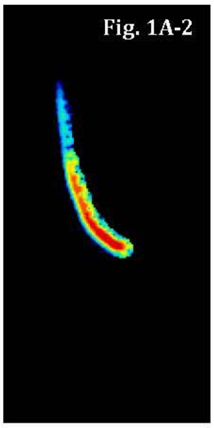


Fig. 1A-2

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

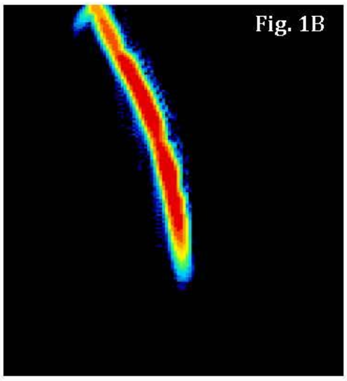


Fig. 1B

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

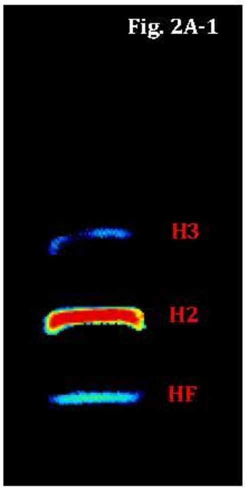


Fig. 2A-1

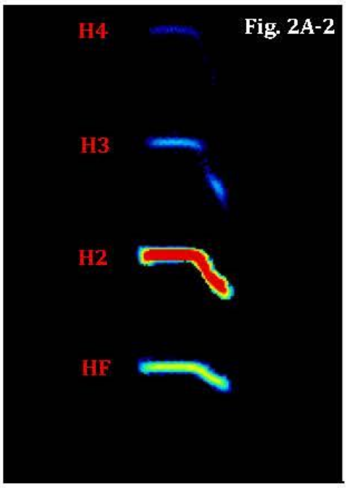


Fig. 2A-2

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

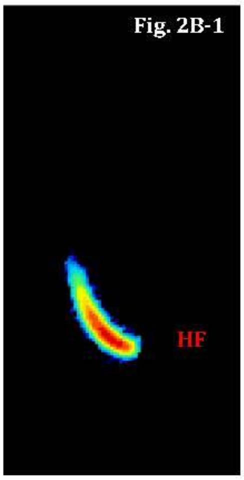


Fig. 2B-1

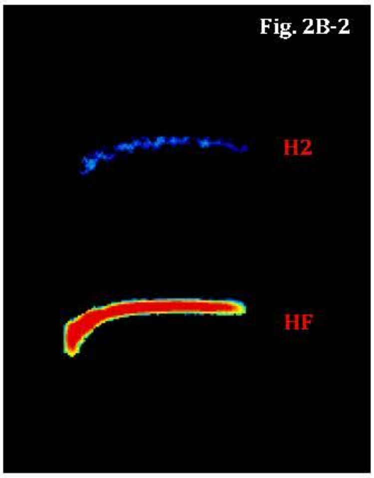


Fig. 2B-2

3.

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

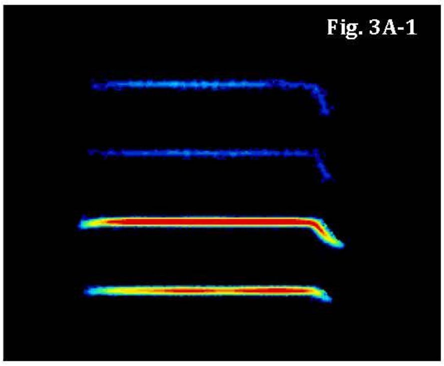


Fig. 3A-1

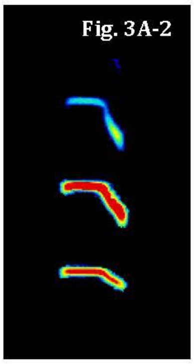


Fig. 3A-2

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

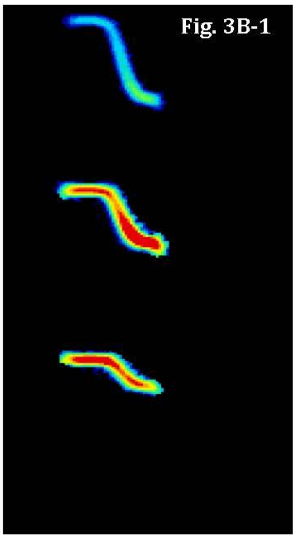


Fig. 3B-1

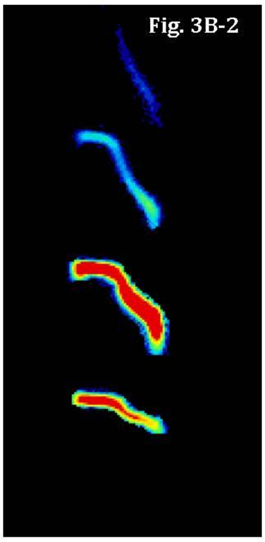


Fig. 3B-2

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

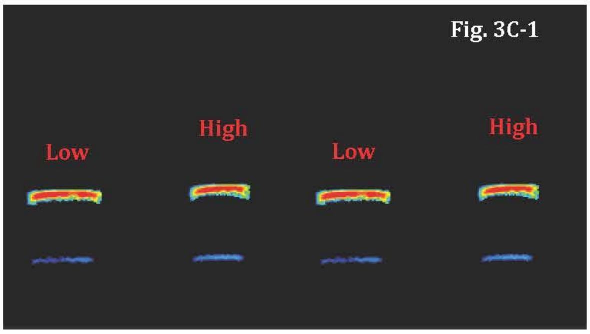


Fig. 3C-1

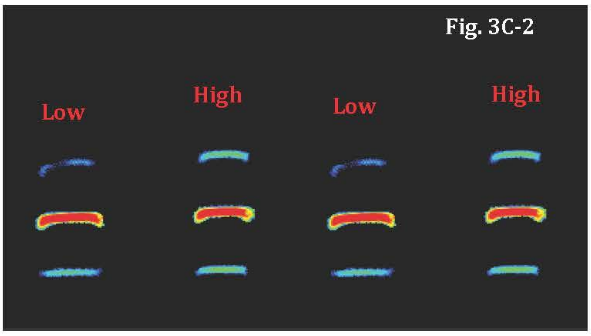


Fig. 3C-2

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

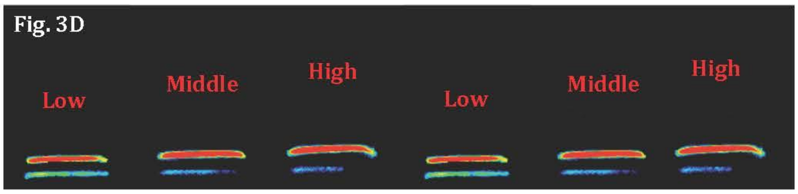


Fig. 3D

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

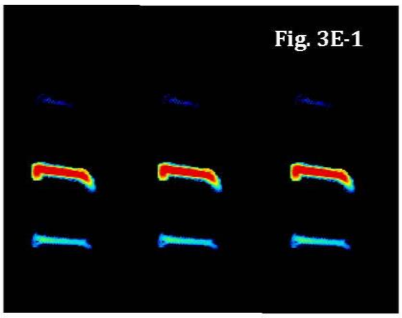


Fig. 3E-1

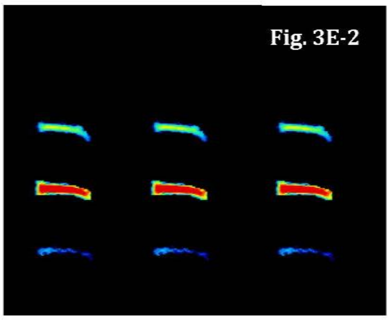


Fig. 3E-2

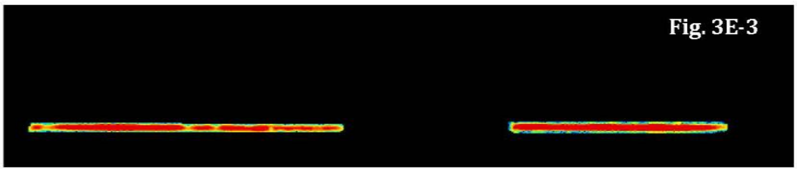


Fig. 3E-3

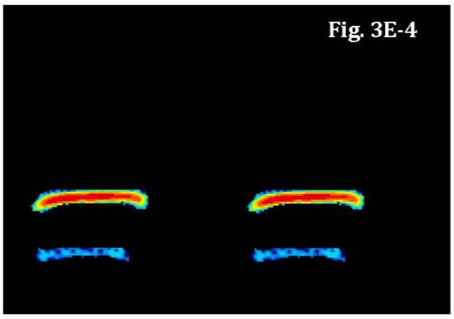
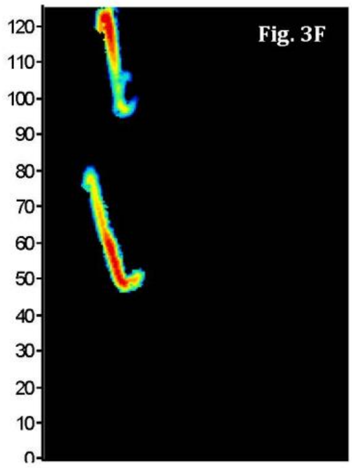


Fig. 3E-4

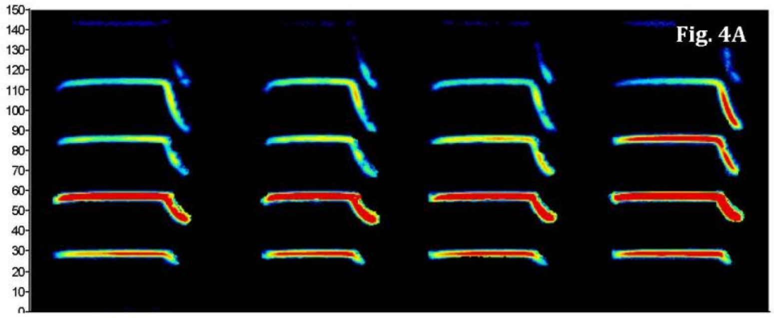
f) stFM with a very short qCF termination, FME >100 kHz (Fig. 3F)..*Natalus* **spp.**



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*

Fig. 4B

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*

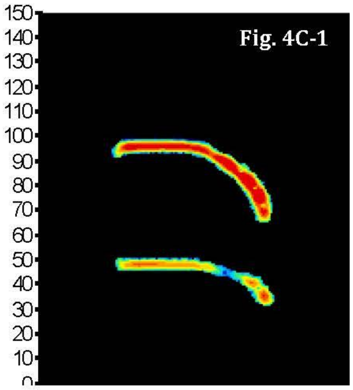


Fig. 4C-1

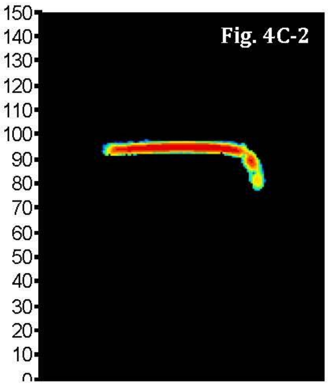


Fig. 4C-2

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***

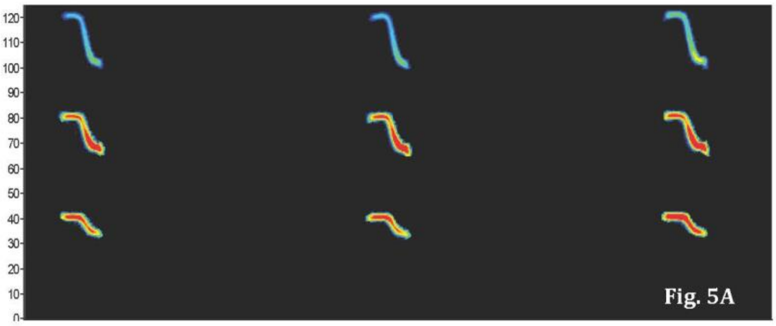


Fig. 5A

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

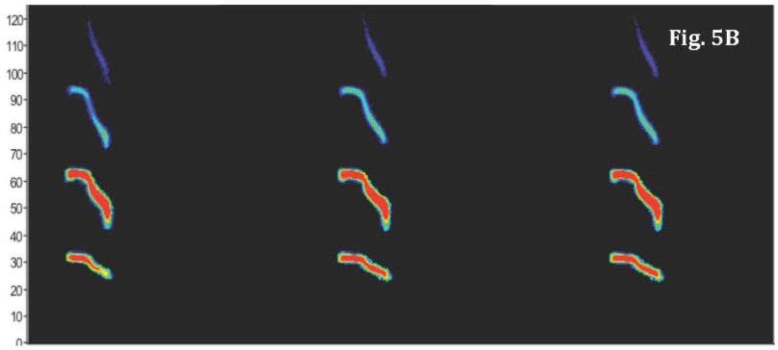


Fig. 5B

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***

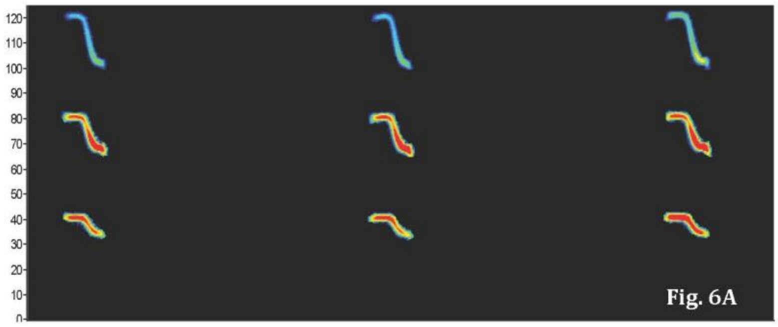


Fig. 6A

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***

Fig. 7A-1

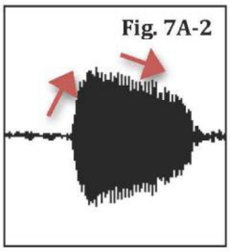


Fig. 7A-2

b) qCF component of the call with a slight upward modulation (Fig. 7B-1), $FME_1 \approx 38$ kHz e $FME_2 \approx 42$ 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”**

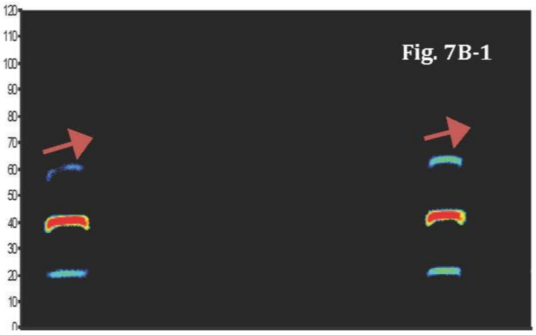


Fig. 7B-1

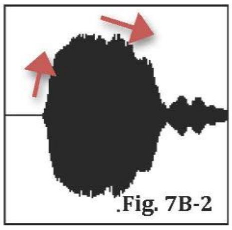


Fig. 7B-2

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***

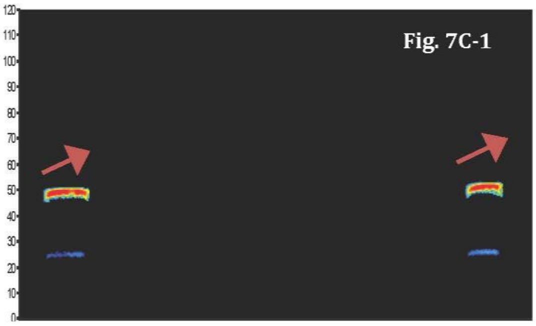


Fig. 7C-1

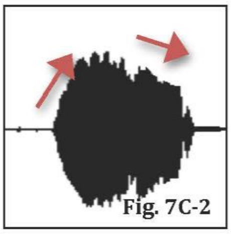


Fig. 7C-2

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

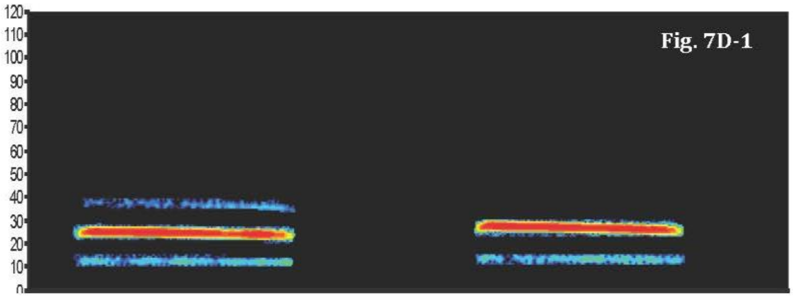


Fig. 7D-1

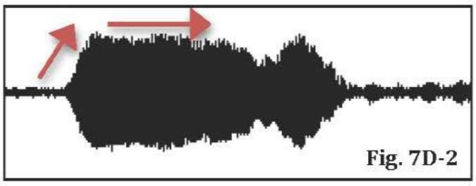


Fig. 7D-2

8. ***Diclidurus* sp.**

a) FME$_1$ ≈ 29 kHz and FME$_2$ ≈ 31 kHz..................................***Diclidurus scutatus***

b) FME$_1$ ≈ 27 kHz and FME$_2$ ≈ 31 kHz....................***Diclidurus scutatus/D. albus***

c) FME$_1$ ≈ 23 kHz and FME$_2$ ≈ 26 kHz.......................................***Diclidurus albus***

d) FME$_1$ ≈ 19 kHz and FME$_2$ ≈ 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***

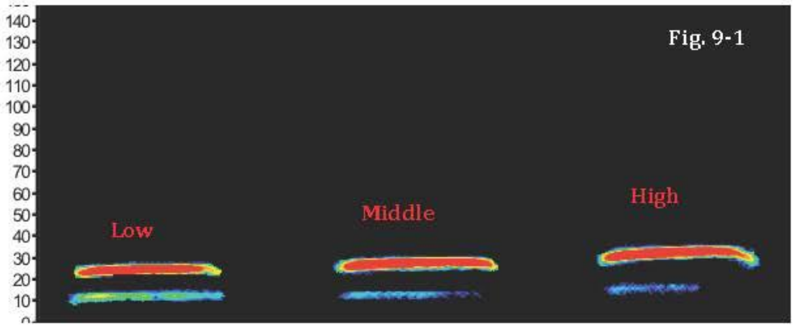


Fig. 9-1

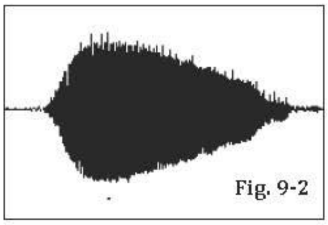


Fig. 9-2

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

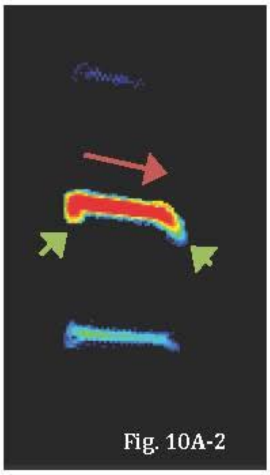


Fig. 10A-2

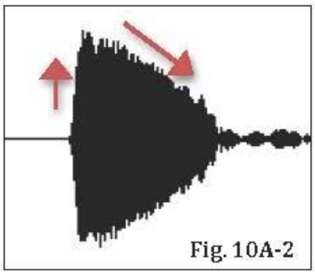


Fig. 10A-2

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***

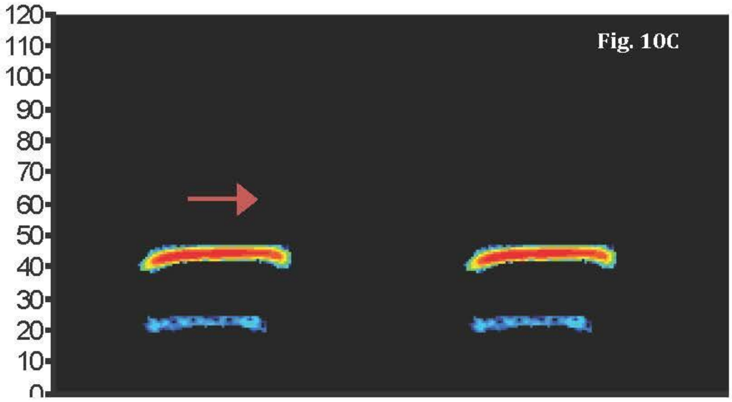


Fig. 10C

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***


Fig. 10D

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***

Fig. 10E

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

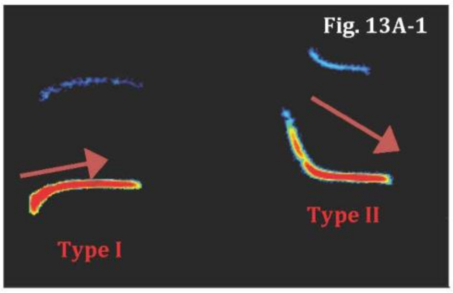


Fig. 13A-1

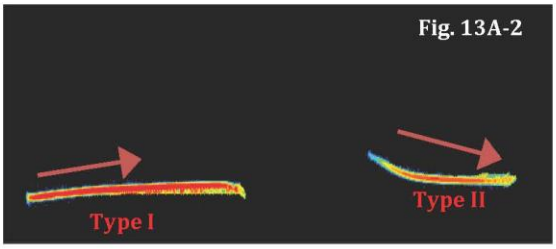


Fig. 13A-2

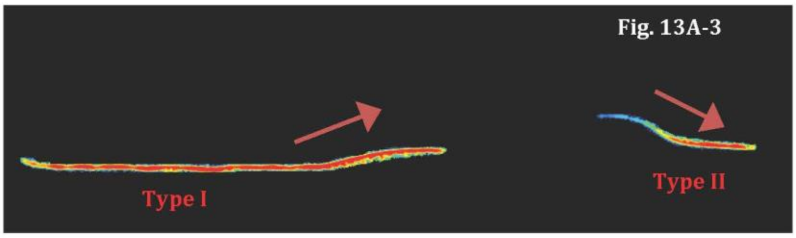
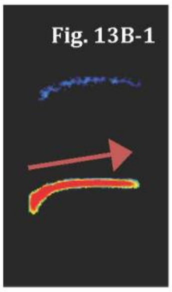
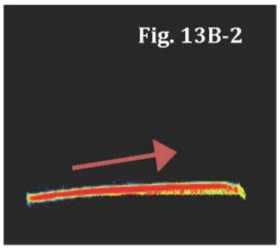
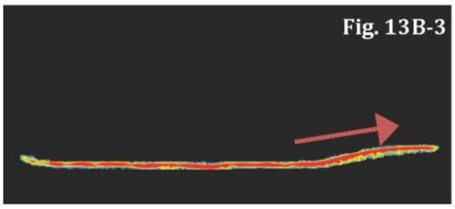


Fig. 13A-3

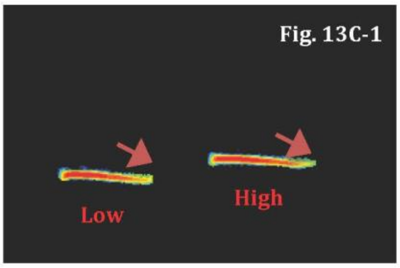
b) Calls with FM$_u$/qCF$_u$ structure without alternation (Fig. 13B-1; Fig. 13B-2; Fig. 13B-3)……………………………………………………………………......17

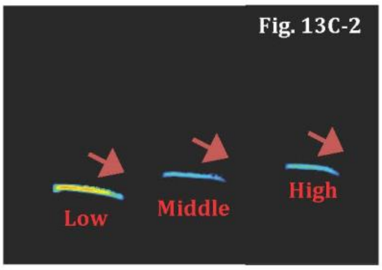






c) Irregular alternation in frequency of two (Fig. 13C-1) or three calls (Fig. 13C-2); call structure (FM$_u$)-qCF$_d$, with short BW (<10 kHz)...............................18





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


Fig. 13D

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

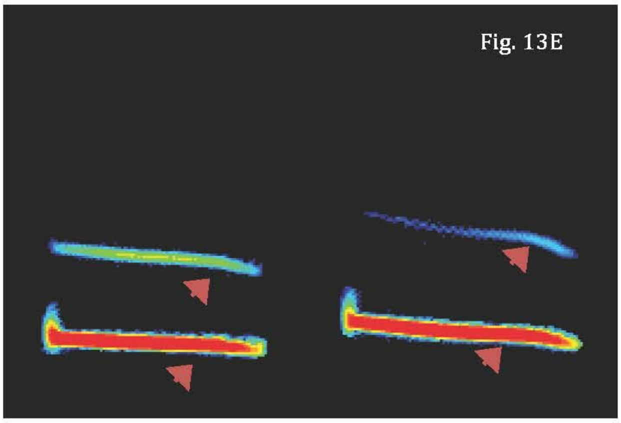


Fig. 13E

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

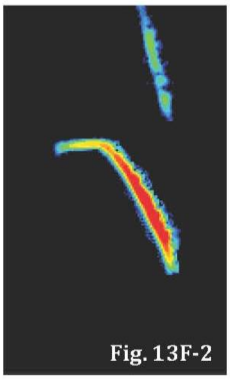


Fig. 13F-2

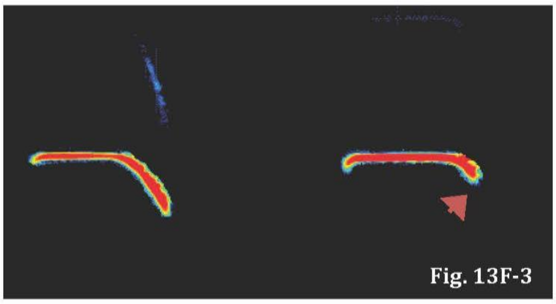


Fig. 13F-3

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


Fig. 13H-1

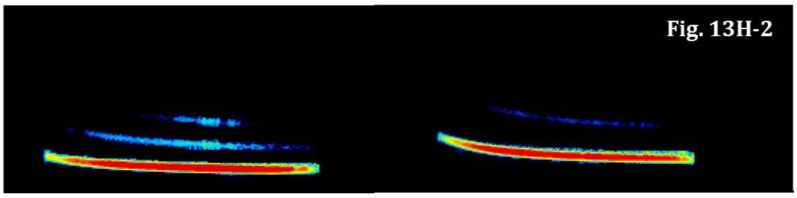


Fig. 13H-2

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

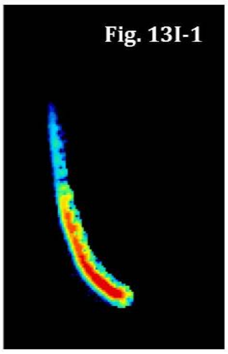


Fig. 13I-1

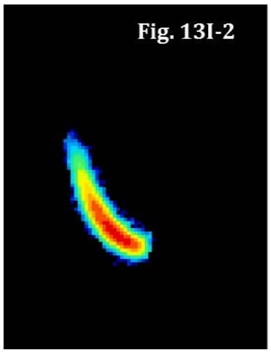


Fig. 13I-2

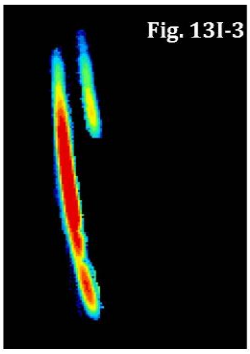


Fig. 13I-3

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

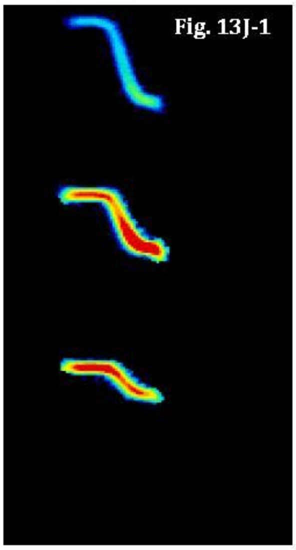


Fig. 13J-1

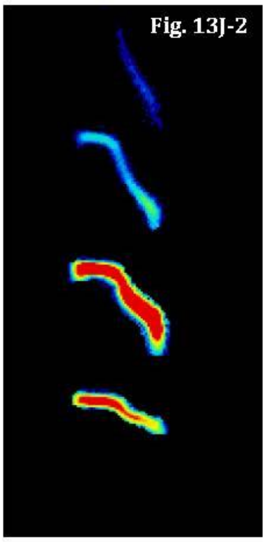


Fig. 13J-2

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***

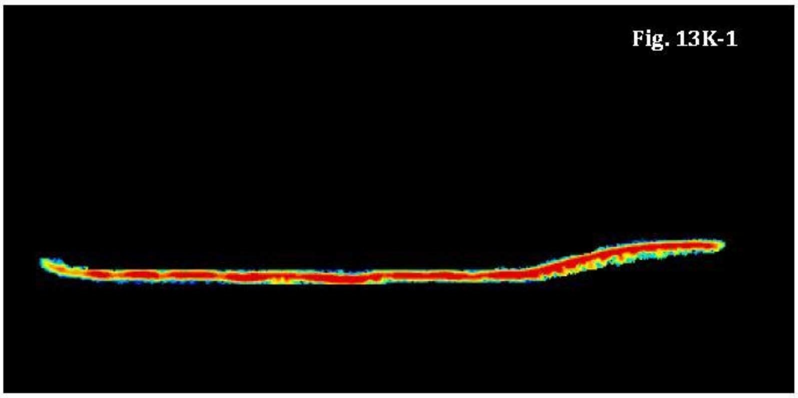


Fig. 13K-1

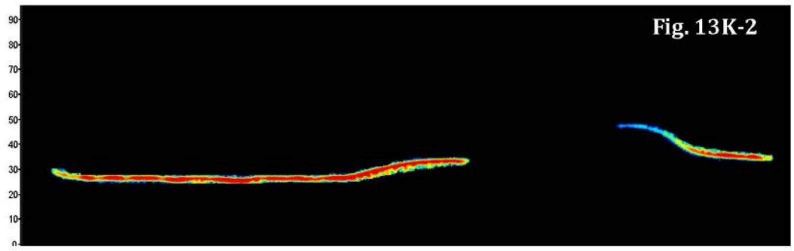


Fig. 13K-2

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***

Fig. 15A-1

Fig. 15A-2

b) <u>Call type I</u>: $F_{INITIAL}$ between 25 and 27 kHz and F_{END} between 28 and 30 kHz; FME between 25 and 31 kHz; Call duration > 15ms; <u>Call type II</u>: $F_{INITIAL}$ 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***

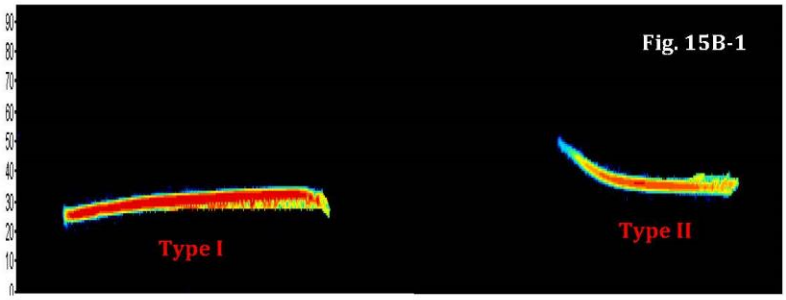


Fig. 15B-1

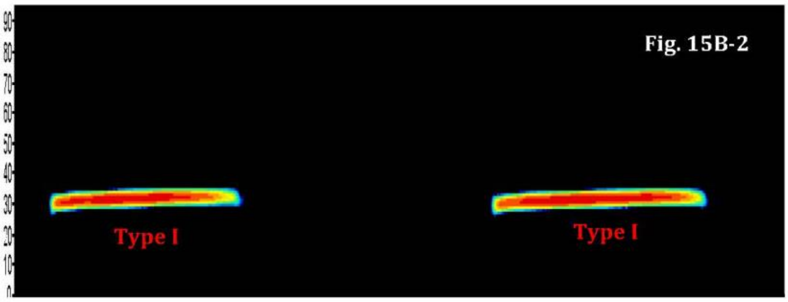
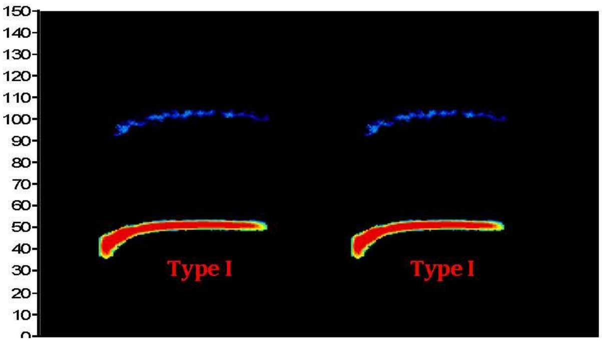


Fig. 15B-2

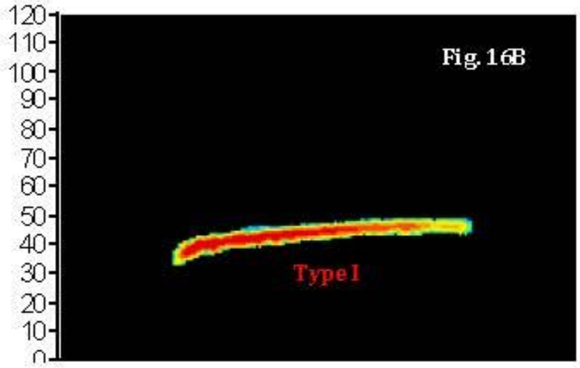
c) High duty-cycle echolocation (Duty cycle >25%); <u>Call type I</u>: prominent CF component and upward modulation (see Fig. 13K-1); call duration >20 ms; $F_{INITIAL}$ between 22 and 27 kHz and F_{END} between 27 and 33 kHz; FME between 24 and 30 kHz averaging 28 kHz. <u>Call type II</u>: $F_{INITIAL}$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

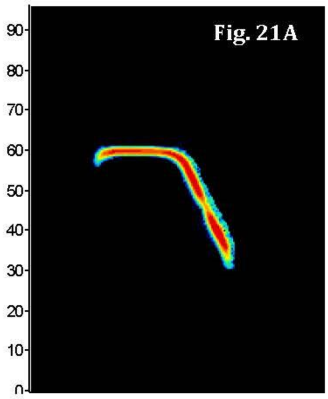
b) Call type I: $F_{INITIAL}$ between 24 e 27 kHz and F_{END} between 14 e 21 kHz; $FME_1 \approx 21$kHz. Call type II: $F_{INITIAL}$ between 29 and 31 kHz and F_{END} between 17 and 26 kHz; $FME_2 \approx 24$ kHz, it might omit this type of call……………………..***Cynomops greenhalli***

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***

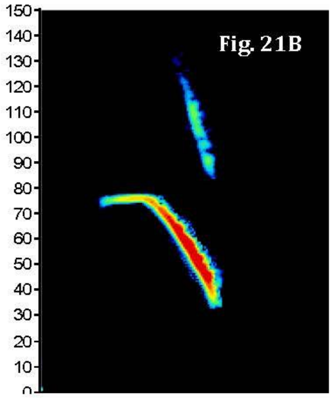
d) Call type I: $F_{INITIAL} \approx 28$ kHz and $F_{END} \approx 23$ kHz; $FME_1 \approx 27$ kHz. Call type II: $F_{INITIAL} \approx 32$ kHz and $F_{END} \approx 28$ kHz; $FME_1 \approx 31$ kHz; it might omit this type of call..***Cynomops paranus***

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 $\leq$ 2 kHz, $FME_1 \approx$ 25 kHz; $FME_2 \approx$ 28 kHz, and $FME_3 \approx$ 32 kHz..***Molossus rufus***

b) BW between 2 and 10 kHz; $FME_1 \approx$ 24 kHz and $FME_2 \approx$ 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***

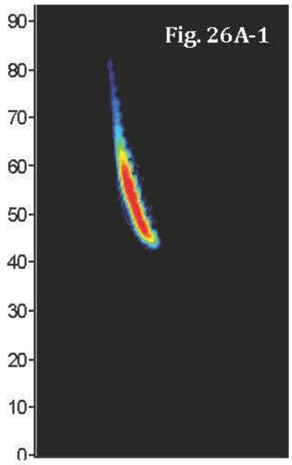


Fig. 26A-1

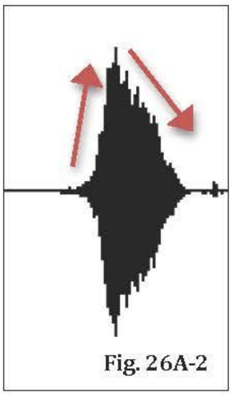


Fig. 26A-2

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*

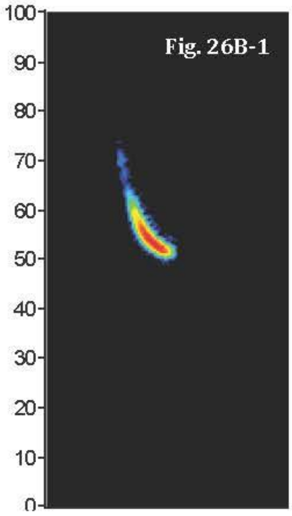


Fig. 26B-1

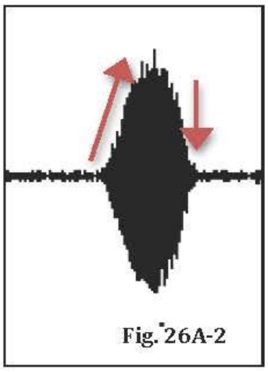


Fig. 26A-2

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*

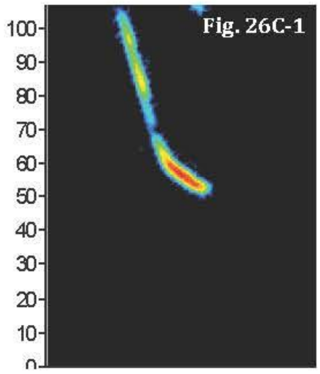


Fig. 26C-1

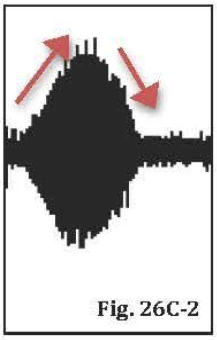


Fig. 26C-2

d) F_{MIN} ≈ 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} ≈ 58kHz; 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***

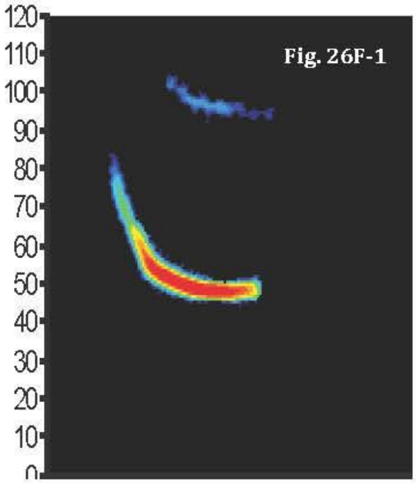


Fig. 26F-1

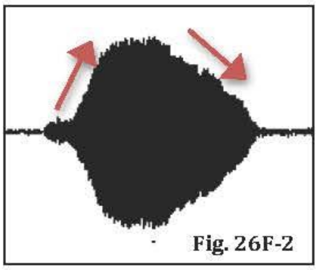


Fig. 26F-2

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

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

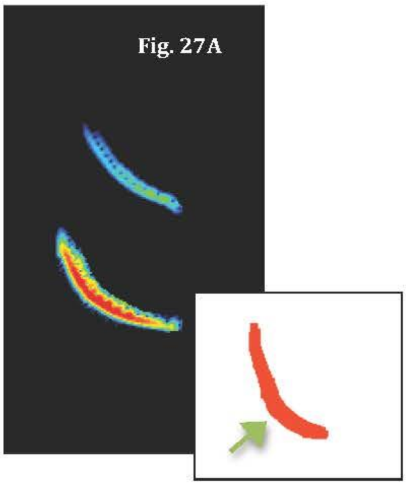


Fig. 27A

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

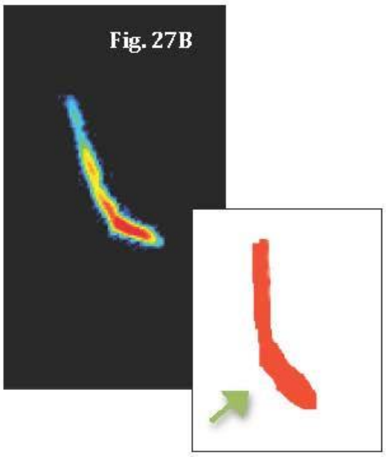


Fig. 27B

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***

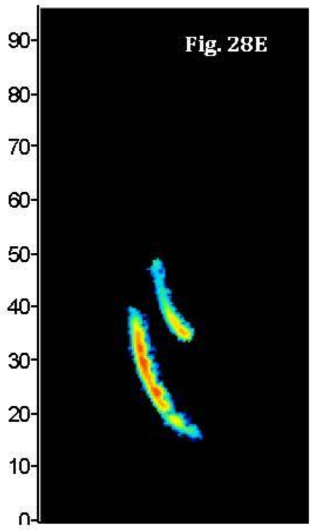


Fig. 28E

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.**

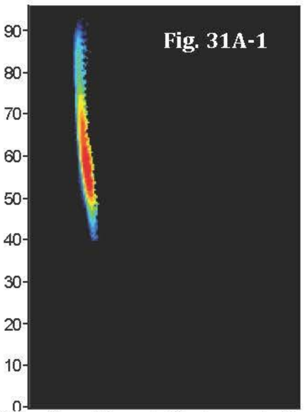


Fig. 31A-1

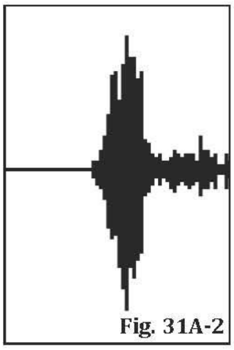


Fig. 31A-2

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***

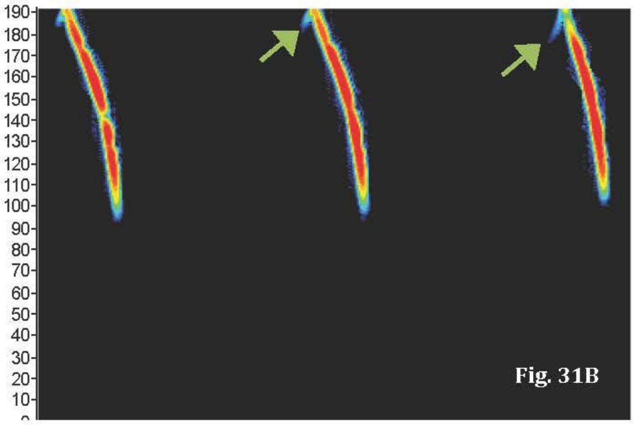


Fig. 31B

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***

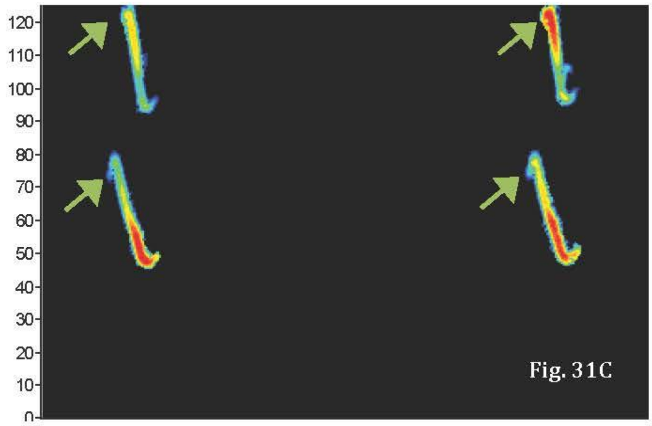


Fig. 31C

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**

Capítulo 3. Spatiotemporal patterns of insectivorous bat activity in the Brazilian Cerrado: landscape and microclimate effects.

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A ser submetido a *Oecologia*

Abstract

Aerial insectivorous bats have important ecological and economic roles. They are susceptible to landscape modifications, so are an ideal model taxon for evaluating responses to habitat changes. We aimed to understand which factors affect bat species richness and activity in the Cerrado biome in an area under noteworthy anthropogenic pressure. We hypothesize that bat responses in terms of richness and activity will vary among areas with landscape composition and configuration, and that these responses are guild-specific; bat activity should also vary according to nightly changes in microclimate, with more drastic variation in small-sized bats. We sampled bats acoustically, while simultaneously sampling microclimatic conditions. We assessed the relationship between species richness, bat activity, activity of guild and different body-sized species with landscape and climatic features at different spatial scales. Despite some tolerance to habitat changes, species richness and activity were positively associated with the presence and extensiveness of well-preserved environments, and this was a general pattern across guilds. Nightly activity patterns were species-specific and not necessarily associated with body size. Water availability had a positive effect on bat activity, and this was most evident during the drier months. Our results suggest that bats are sensitive to spatial and temporal variation in landscape and climatic conditions and that larger pristine patches of different natural physiognomies. Water related environments seem to be fundamental for bat conservation in this biome.

Key words: Chiroptera, habitat heterogeneity, microclimatic variation, semi-arid environments, vereda

Introduction

The Cerrado is one of the world's biodiversity hotspots, until recently its importance was unappreciated (Myers et al. 2000, Klink & Machado 2005). Even though it is considered the richest tropical savanna in the world in terms of flora, over 50% of its original area was already been cleared or transformed for human uses (Klink & Machado 2005, MMA 2011). The current rate of landscape transformation threatens to significantly impact and change sites which are still lacking information on many species (Bernard et al. 2012); therefore, the acquisition of scientific knowledge on the Cerrado fauna, including composition, natural history, geographic distribution and assemblage structure is fundamental for the definition of effective conservation strategies (Carmignotto et al. 2014).

Bats are an ideal model taxon for evaluating responses to habitat changes – they are ecologically diverse and highly vagile, with the potential to move over extensive areas of altered and fragmented landscapes (Meyer & Kalko 2008). Additionally, they are important in terms of their ecological and economic roles (Bernard & Fenton 2007, Jones et al. 2009). Still, it may be assumed that, because of their dispersal abilities, bats are potentially less vulnerable than other mammals to extensive deforestation and fragmentation of their habitats in the tropics (Estrada & Coates-Estrada 2012). However, if bats are strongly affected by land-use changes, important ecological processes in which they are involved will also be affected, compromising dynamics and regeneration of natural areas (Bernard & Fenton 2007). There are about 178 species of bats in Brazil, of which ca. 101 species can be found in the Cerrado (Nogueira et al. 2014). Despite its great diversity and ecological importance, the current knowledge about the Cerrado bat fauna is still insufficient and only 6 % of its area has been minimally sampled for this group (Ferreira et al. 2010, Bernard et al. 2011). Studies have particularly been focused on the Phyllostomidae due to the use of standard mist-net protocols (Zortéa & Ahlo 2008, Ferreira et al. 2010, Gregorin et al. 2011, Pina et al. 2013, Sousa et al. 2013, Muylaert et al. 2014, Shapiro & Bordignon 2014, Loureiro & Gregorin 2015). However, relying solely on mist-nets is inadequate for a comprehensive assessment of the whole bat community, leaving aside a whole assemblage of aerial insectivorous bats belonging to the remaining eight families of the

Chiroptera – Emballonuridae, Furipteridae, Molossidae, Mormoopidae, Natalidae, Noctilionidae, Thyropteridae, Vespertilionidae , present in the Neotropical region (Kalko & Handley 2001, Meyer & Kalko 2008, Estrada et al. 2010), which may represent between 30-50% of the species in those communities (Kalko et al. 2008). This guild has been systematically undersampled in studies on Neotropical communities because the sophisticated echolocation skills of these bats allows them to detect and avoid mist nets, and thus evade captures using this technique (Kalko et al. 2008, Bader et al. 2015). As such, acoustic monitoring techniques are essential to efficiently detect Neotropical aerial insectivores and, subsequently, to assess their patterns of habitat use and distribution across the landscape (Estrada et al. 2010, Barboza-Marquez et al. 2013). Moreover, determining the timing and location of activity levels is important for an understanding of bat ecology and behavior, with immediate implications for the management and conservation of this group (Hayes 1997, Adams et al. 2015). In this context, experimental and sampling designs should account for temporal variation, to avoid apparent dissimilarities or similarities among areas that could be solely an artifact of temporal variation. Studies on spatiotemporal patterns of insectivorous bat activity should thus be encouraged in Brazil, especially in less known ecosystems, in particular those under strong human pressure, where the persistence of insectivorous bats is of interest to sustainable landscape management that considers the integration of biodiversity and productive systems (Aguiar & Antonini 2008, Jones et al. 2009, Jung et al. 2012). With this in mind, knowing that the Cerrado is responsible for 20% of the Brazilian agricultural production and uses 78.5 million ha of land (Aguiar & Antonini, 2008), it is clear that the maintenance of its biodiversity depends largely on the knowledge and conservation of the species that inhabit natural vegetal remnants within anthropogenically modified areas (Ferreira et al. 2010).

Here, our aim was to understand how bat species composition and activity in the Cerrado are affected by landscape composition, configuration, and nightly climatic variation in an area under significant anthropogenic pressure. We hypothesize that insectivorous bat species composition and activity will vary among areas with distinct land cover and landscape configuration. Specifically, we expect open-, narrow-, and edge-space foraging bats to preferably hunt in more open, cluttered and heterogeneous environments, respectively. Also, we hypothesize bat activity to vary according to nightly changes in microclimate, and for changes in temperature and humidity to impact more the activity of smaller-bodied bats; also, because water availability in semi-arid areas is more limiting to wildlife than temperature variation, we expect overall higher bat activity in more humid nights, especially in the dry season.

Methods

Study area

The Cerrado is the second largest Brazilian biome with an extension of over two million square kilometers. It is located between 5° to 20° S and 45° to 60° W. It is composed by a mosaic of vegetation as a result of the diversity of soils, topography and climates (da Silva et al. 2008). Its phytophysiognomies include forest, savanna and grasslands (campos) (Riveiro & Walter 2008). The Cerrado is characterized by a wet tropical weather with a savanna subtype, with dry winter and maximum rain during the summer (da Silva et al. 2008). Mean annual values of rainfall and temperature vary between 1300-1600 mm and 20.1°C, respectively (Riveiro & Walter 2008). In general, the biome presents two well-defined seasons: a rainy one between September-October until March-April, and a dry season that begins in April-May extending until September-October.

The focal area of the study was the region of the Mambaí municipality near the border of Goiás, Minas Gerais and Bahia states (Fig.1). The area is rather unique because it is rather well preserved on its west side (state of Goiás), but the natural Cerrado cover has been almost completely destroyed by intensive plantations (e.g. soya) on its east side (state of Bahia). It encompasses some conservation units, including municipal, state and natural parks.

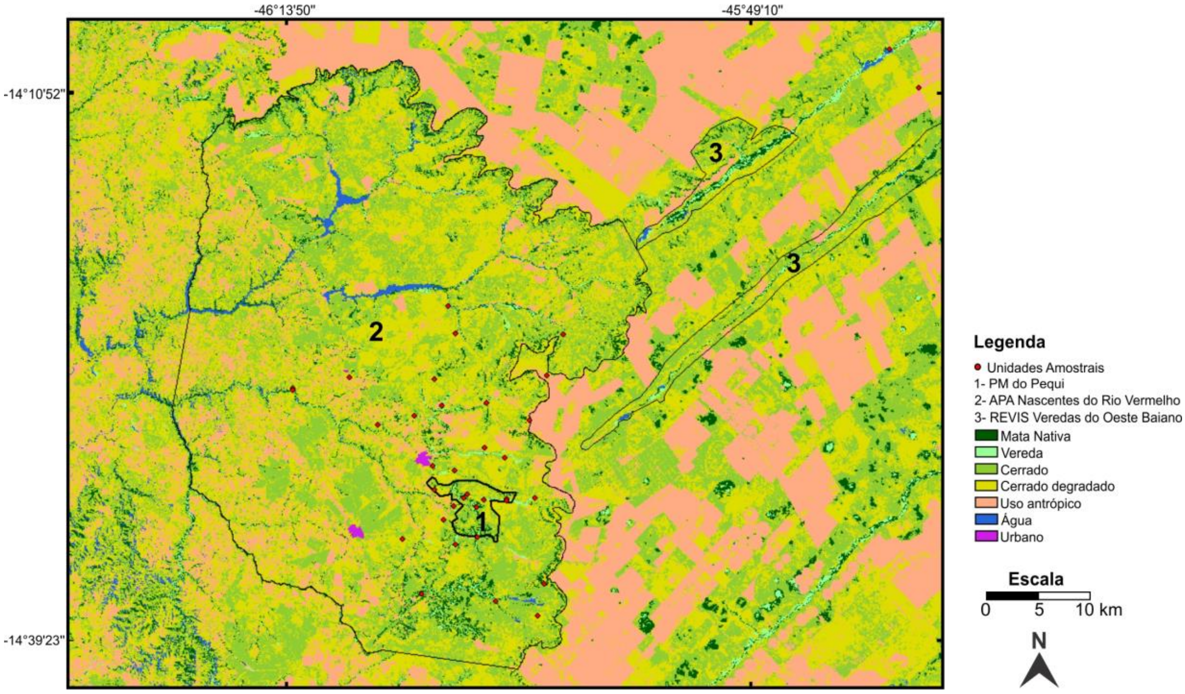

Fig. 3 Study area in Mambaí, GO, main land use characterization and sampling sites.

Bat sampling, identification and analysis

Two sampling periods of approximately 15 days each were conducted for acoustic monitoring in July 2015 and May 2016. Thirty one sites including distinct configuration and composition of Cerrado phytophysiognomies (e.g. cerrado sensu stricto, gallery forest, vereda) were sampled – 19 in July 2015 and 25 in May 2016 (of which 12 were replicates of the previous sampling season), for at least one night between sunset and the following six hours (three sites were sampled for two-nights in a row).

Bat acoustic surveys started immediately after sunset and were finished 6 hours later. Sound recordings were used to assess species presence and foraging activity at each site. Recordings were made in real time (sampling rate: 300 kHz, 16 bit) with a Petterson-D500x bat detector (Pettersson Electronic AG, Uppsala, Sweden).

Recordings were analyzed in Avisoft SASLAB Pro 5.2.09 (Raimund Specht, Avisoft, Berlin, Germany). Call parameters were gathered from existing literature and from a personal library call of South American bats (unpublished data), and calls were identified to the highest taxonomic level possible; unidentified but distinct species were classified into sonotypes.

Species were included into three guilds according to their eco-morphological characteristics (Denzinger & Schnitzler 2013, Kalko et al. 2008, Marques et al. 2015): i) open-space foragers: *Diclidurus ingens*, *Peropteryx kappleri*, *P. macrotis*, *P. leucoptera*, *P. palidoptera*, *P. trinitatis*, *Cynomops* sp., *Eumops* sp., *Nyctinomops* sp., *Molossus* sp., *M. rufus*, *M. currentium*, *M. molossus*, *Promops centralis*, *P. nasutus* and *Tadarida brasiliensis*,; ii) edge-space foragers: *Saccopteryx leptura*, *Molossops temminckii*, *Pteronotus gymnonotus*, *Natalus* sp., *Eptesicus brasiliensis*, *E. chiriquinus*, *E. furinalis*, *Lasiurus* sp., *L. ega*, *L. egregius*, *Myotis* sp., *M. albescens*, *M. nigricans*, *M. riparius* and *Rhogeessa* sp.; and iii) narrow-space foragers: *Pteronotus* cf. *parnellii*.

Bat relative foraging activity (number of bat passes per 30-min) and relative feeding activity (number of terminal phases per 30-min) were quantified for total bat activity and for each one of the three guilds.

Landscape and climate characterization

We created a map of vegetation and land-use by the interpretation and classification of LANDSAT 8 satellite images, which have resulted in the identification of seven classes in the sampling area: cerrado sensu stricto (well preserved), degraded cerrado, water, vereda, gallery forest, landscape with anthropogenic use and urban settlements. Additionally, buffers with a radius of 500 and 1000 m were generated around sampling points to quantified landscape and class metrics for each scale. All GIS routines were performed in Idrisi Selva (Clark Labs) and landscape and class metrics were calculated in Fragstat software (McGarigal et al. 2002).Then, 11 metrics considered of biological importance on previous literature were selected (Mendes et al. 2015, Chambers et al. 2016). Landscape metrics included edge density (ed: sum of the lengths of all edge segments in the landscape, divided by the total landscape area); class metrics included patch density (pd: number of patches of the corresponding patch type divided by total landscape area) of water, vereda and forest, edge density (ed: sum of the lengths of all edge segments involving the corresponding patch type, divided by the total landscape area) of water and degraded cerrado, and percentage of the landscape (pland: how much of the landscape is comprised of a particular patch type) occupied by water, cerrado sensu stricto, degraded cerrado, forest and vereda. Metrics for the cover type urban and anthropogenic use were excluded due to their low percentage on the sampling points.

Microclimatic information was obtained with air temperature/humidity sensors with a resolution of 0.3 °C and 3 %, respectively (Sensirion SHT11, Alphatech, São Paulo, SP, Brazil), coupled to data loggers in each sampling point. The sensor was placed next to the bat detector and took measurements at 1-min intervals during the bat-recording period.

Statistical analysis

Spatial variation in activity and species richness

All statistical analyses were performed with software R, version 3.3.2 (R Core Team 2016), using the hier.part (Walsh & MacNally 2013), lm4 (Bates et al. 2015), vegan, AICcmodavg (Mazerolle 2016) packages.

Richness and activity were modeled using generalized linear models (GLM) with Poisson error distribution using landscape and class metrics as predictors. GLM is flexible, least susceptible to over-fitting than other methods (Guisan & Zimmermann 2000) and able to incorporate response variables that are not normally distributed. We used the Akaike Information Criterion (AIC) and the second-order AIC (AICc) to rank the models, comparing the null model with those with increasing number of predictor variables.

Previously to the building of the models, to avoid collinearity among the predictor variables, a HPA - Hierarchical Partitioning Analysis (Chevan & Sutherland 1991, McNally 1996) was applied to evaluate the independent contribution of the 11 chosen landscapes variables at the 500m and 1000m buffers to the variation in richness, total bat activity, and open, edge- and narrow-space foragers activity. Beyond nine explanatory variables HPA performed in the hier.part package creates an inconsistency due to the fact that the entering order of the variables affects their final ranking (Olea et al. 2010). To avoid this inconsistency, and as suggested by those authors, 100 repetitions of the analysis were ran using different entering orders of the explanatory variables. The explanatory variables were then ranked and the four landscape variables that presented the highest independent contribution towards the variation of each of the response variables were selected to enter the GLM.

Temporal and climatic variation in activity

Variation in total and each guild foraging activity, and activity of small- (*Molossops temminckii* and *Myotis nigricans*) and large-sized (*Eumops* sp. – echolocation call frequencies below 16 kHz – and *Eptesicus furinalis*) species was modeled in response to nightly changes in climate also using GLM with Poisson error distribution. The chosen predictor variables were: i) air relative humidity (mean values at 30 min intervals); sampling period: July and May; and time interval (6 hours of sampling per night divided into 12 intervals of 30 min). As humidity and temperature were highly correlated (r^2 >0.5) only humidity was used as predictor in the models because, as stated above, this variable is expected to be more relevant biologically than temperature in semi-arid areas.

Results

Richness and general activity patterns

Total richness

We recorded a total of 5077 bat passes – in 282 hours of recording –, of which 2810 bat passes were recorded in May (150 recording hours) and 2267 bat passes recorded in July (132 recording hours) and 242 feeding buzzes (121/May, 121/July), from five families (Table 1), and identified 20 species: *Diclidurus ingens*, *Peropteryx kappleri*, *P. macrotis, P. trinitatis*, *Saccopteryx leptura*; *Molossus* cf. *rufus*, *Molossus* cf. *currentium*, *Molossus molussus*, *Molossops temminckii*, *Promops centralis*, *P. nasutus*, *Tadarida brasiliensis*, *Pteronotus gymnonotus, Pteronotus*.cf. *parnellii* (frequency of maximum energy: 56 kHz); *Eptesicus brasiliensis*, *E. chiriquinus*, *E. furinalis*, *Myotis* cf. *albescens*, *M. nigricans* and *M.* cf. *riparius*; three complexes: *Peropteryx palidoptera/leucoptera*, *Eumops/Cynomops /Nyctinomops*, and *Lasiurus ega/egregious*; six sonotypes at genus level: *Molossus* sp. sonotype 1 and 2, *Natalus* sp., *Lasiurus* sp., *Myotis* sp. and *Rhogessa* sp.; and two sonotypes at family level Molossidae sonotype 1 and Vespertilionidae sonotype 1. The richest sites, with 11-15 bat species, were characterized by presenting, in average, the highest percentage covers of cerrado sensu stricto (Table 1).

Table 1. Richness of species and their associated average value of vegetation cover at scales of 500m and 1000m. In parentheses are showed minimum and maximum values. pland.cer: percentage of the landscape occupied by pristine Cerrado; pd.ver: patch density of vereda; pland.ver: percentage of the landscape occupied by vereda. *p<0.05

Richness	pland.cer_500	pd.ver_500	pland.ver_1000*
2-5spp	25.6 (0.5-41.2)	3.0 (0-13.9)	1.89 (0-7.95)
6-10spp	28.08 (7.3-49.7)	5.79 (0-18.12)	3.39 (0-14.26)
11-15spp	40.62 (11.79-62.61)	6.17 (1.39-15.33)	5.55 (0.79-11.47)

Open-space foragers

We recorded a total of 3294 bat passes (1879/May, 1415/July) and 98 feeding buzzes (48/May, 50/July) in the open-space foraging guild. The complex *Eumops/Cynomops/Nyctinomops* was recorded at all sites and represented ca. 80% the activity of this guild. Almost 40% of the entire activity of this species complex was registered at one site, and particularly in July. The same site was important for the activity of *Peropteryx trinitatis* and *P. macrotis*, which accounted for 9% and 6% of the activity of the guild, respectively. This sampling site was located in a deep but large valley, crossed by a river. *P. trinitatis* and *P. macrotis* were registered across the entire study area. With the exception of *Molossus molossus* (recorded at 14 sites) and *Promops nasutus* (recorded at eight sites), the remaining species of the guild were registered in less than four locations.

Edge-space foragers

We recorded a total of 1686 passes (879/May, 807/July) and 136 feeding buzzes (69/May, 67/July) of the edge-space foraging guild. *M. temminckii* represented 30% of the total of bat passes of the guild and was recorded at 26 sites; *E. furinalis* represented another 30% of the activity in this guild, with 62% of the passes recorded at one single sampling occasion in May at a site characterized by by presence of a temporary pond and largely covered by vereda and cerrado sensu stricto; the complex *L. ega/egregious* represented 13% of the activity of the edge-space foraging guild and was recorded at only two sites, with more than 90% of its activity recorded in July at one single site; this site was characterized by 60%-55% cover of cerrado sensu stricto and 15%-10% gallery forest at the 500m and 1000m scales, respectively; *M. nigricans* accounted for 12% of the activity of the guild and was much more ubiquitous, with records at 20 sites; *Rhoggessa* sp. accounted for 6% of the guild activity. Each of the remaining 11 species in this guild was recorded in less than five sampling points.

Narrow-space foragers

This guild was represented by one single species – *Pteronotus* cf. *parnellii*. We recorded 97 bat passes (52/May, 45/July) and eight feeding buzzes (4/May, 4/July). While this species was registered practically across the entire study region, the activity at the majority of the sampled sites was low, except for one site that accounted more than 20% of their total activity. This site was characterized by high percentage of vereda and cerrado sensu stricto at both spatial scales.

Relation between total richness and landscape predictors

The relationship between richness and landscape variables at the 500m scale was better explained by the model including a marginally non-significant positive association with the percentage of the landscape cover by cerrado sensu stricto (z=1.83, p=0.07) and patch density of vereda (z=0.93, p=0.35) (Table 2). At the 1000m scale, the best model included a positive association with vereda percentage cover (z= 2.69, p<0.01; Table 2).

Relation between bat activity and landscape

The summaries of all the adjusted models relating total and guild activity with landscape and sampling season are presented in Table 1. Overall bat activity was lower in May when measured at the 500m scale (z=3.16, p<0.01) and higher in this month when measured at the 1000m scale (z=-2.28, p=0.02). At the 500m scale total bat activity was positively associated with edge (z=2.39, p<0.01) and percentage of the landscape occupied by vereda (z=10.10, p=0.02), while at the scale of 1000m it was negatively associated with forest patch density (z=-21.89, p<0.01). Feeding activity at the 500m scale was positively associated with edge (z=3.68, p<0.01) and percentage of the landscape occupied by forest (z=2.06, p=0.04), while at the 1000m scale it was negatively associated with patch density of vereda (z=-3.39, p<0.01).

As for the open-space foragers, activity was significantly lower in May, and this was only significant when measured at the 1000m scale (z=-2.01, p=0.04). No seasonal significant changes in feeding activity were detected. At the scale of 500m, we found a positive association between foraging activity and edge (z=22.62, p<0.01); percentage of the landscape occupied by vereda was also included in our best model but was not significant (z=1.47, p=0.1). Nevertheless, feeding activity was significantly and positively associated with vereda cover (z=1.97, p=0.05). At the scale of 1000m the association was also positive with edge (z=15.39, p<0.01), but negatively associated with patch density of forest (z=-28.17, p<0.01). Feeding activity of open-space foragers was positively related to the percentage of the landscape occupied by vereda (z=2.77, p<0.01), and degraded cerrado (z=2.27, p=0.02).

As occurred with open-space foragers, the activity of edge-space foragers was significantly lower in May, but this was only significant when measured at the 1000m scale (z=-7.79, p<0.01). At the scale of 500m, edge-space foragers activity was negatively associated with edge (z=-3.11; p<0.01), edge of degraded cerrado (z=-11.0; p<0.01) and patch density of vereda (z=-15.32; p<0.01). At the scale of 1000m, edge-space foragers activity was negatively associated with patch density of cerrado sensu stricto (z=-25.52;p<0.01) and positively associated with land cover by degraded cerrado (z=10.88, p<0.01). Edge-space foragers feeding activity was negatively associated with patch density of vereda (z=-2.88, p<0.01).

At the 500m and 1000m scales we found a positive association between the activity of narrow-space foragers and the percentage of the landscape occupied by vereda (500m: z=2.13; p=0.03; 1000m: z=2.51; 0.01). Due to the low number of feeding buzzes in this guild no model was adjusted for this variable.

Table 2.

Summary of the GLM explaining bat richness and activity at the 500m and 1000m spatial scales. ed: edge density, pland: percentage of the landscape occupied by class, pd: patch density, deg: degraded cerrado, cer: cerrado sensu stricto, for: forest, ver: vereda, wat: water, samp: sampling period. *p <0.05

Dependent variables	Model GLM (500 m)	AICc (500m)	ΔAIC (500m)	Model GLM (1000 m)	AICc (1000m)	ΔAIC (1000m)
Species richness	pd.ver+pland.cer	167.85	0.00	pland.ver*+ed.wat	195.10	0.00
	pd.ver	168.74	0.89	pland.ver*	195.71	0.61
	ed+pd.ver+pland.cer	170.47	2.62	pland.ver*+ed.wat+pd.cer	195.87	0.77
	ed+pd.ver	171.16	3.31	pland.ver*+pd.cer	196.32	1.22
Total bat activity	ed*+pland.ver*+samp*	5481.42	0.00	pd.for*+samp*	6002.97	0.00
	pland.ver*+samp*	5484.59	3.17	pd.for*+pland.cer+samp*	6004.08	1.11
	pland.ver*+ed*	5488.82	7.40	pd.for*	6017.99	15.02
	pland.ver*	5491.14	9.72	pd.for*+pland.cer	6018.62	15.64
Total feeding activity	ed*+pland.for*	372.21	0.00	pd.ver*+samp*	459.05	0.00
	ed*+pland.for*+ed.cer	374.52	2.32	pd.ver*+pland.deg+samp*	461.28	2.23
	pland.for*	384.54	12.34	pd.ver*	461.88	2.83
	pland.for*+pd.cer	386.88	14.67	pd.ver*+pland.deg	462.92	4.87
Open-space guild activity	pland.ver+ed*+samp*	4523.01	0.00	ed*+ pd.for*+samp*	4891.60	0.00
	pland.ver+ed*	4525.12	2.11	pd.for*+ed*	4893.17	1.58
	samp*+ed*	5067.63	544.63	pd.for*+samp	5136.57	244.98
	ed*	5069.83	546.83	pd.for*	5137.59	245.99
Open-space guild feeding activity	pland.ver*	317.55	0.00	pland.ver*+pland.deg*+samp	349.86	0.00
	pland.ver*+pd.ver	317.59	0.03	pland.ver*+pland.deg*	350.18	0.32
	pland.ver*+pd.ver+samp	318.57	1.01	pland.ver*	352.04	2.18
	pland.ver*+samp	318.65	1.09	pland.ver*+samp	352.71	2.85
Edge-space guild activity	ed*+pd.ver*+ed.deg*	1643.59	0.00	pd.cer*+pland.deg*+samp*	2504.87	0.00
	pd.ver*+ed.deg*	1650.76	7.17	pd.cer*+pland.deg*	2563.32	58.45
	pd.ver+ed*	1880.36	236.76	pd.cer*+samp*	2621.51	116.64
	pd.ver*	2391.04	747.45	pd.cer*	2641.28	136.41
Edge- space guild feeding activity	pland.wat+pland.for	266.42	0.00	pd.ver*	293.84	0.00
	pland.for+pland.cer+pland.wat	267.93	1.51	pd.ver*+samp	293.86	0.02
	pland.for	269.23	2.81	pd.ver*+pd.for	294.18	0.34
	pland.for+pland.cer	271.21	4.80	pd.ver*+pd.for+samp	294.55	0.71
Narrow-space guild activity	pland.ver*	255.07	0.00	pland.ver*	289.31	0.00
	pland.ver*+pd.cer	255.22	0.15	pland.ver+pland.deg	289.41	0.10
	pland.ver*+samp	256.89	1.82	pland.ver*+samp	291.33	2.02
	pland.ver*+samp+pd.	257.39	2.32	pland.ver+pland.deg+samp	291.78	21.19

Influence of microclimate in bat activity

The best model explaining total bat activity, edge-space guild activity and the activity of small- and large-bodied bats included as explanatory variables humidity, time interval and the interaction between humidity and the sampling season. More specifically, total bat activity and edge-space guild activity decreased along the night (t=-4.55; p<0.01; t= -7.41, p<0.01) as expected, but were positively related with humidity in May (t=2.73, p<0.01; t= 2.48, p=0.01). In open space foragers there was a marginally non-significant relation of their activity with humidity in May (t= 1.87, p= 0.06).

In small-bodied species, *M. temminckii* activity decreased along the night (t= - 3.28, p<0.01). A posterior analysis of the data showed that more than 97% of the total activity of this species was registered during the first hour of the night. The activity of *M. nigricans* was overall negatively associated with humidity (t=-3.65, p<0.01), but positively associated with this variable in May (t=4.93, p<0.01).

In large-bodied species, the activity of *E. furinalis* also significantly decreased along the night (t=-5.53, p<0.01), and while the species showed an overall negative association with humidity (t=-2.28, p=0.02), its activity increased in more humid environments in May (t=5.55, p<0.01).

Table 3. Summary of the GLM explaining total bat activity, narrow-, edge-, and open-space bat foraging activity, small-bodied species (*Molossops temminckii* and *Myotis nigricans*) and large-bodied species (*Eptesicus furinalis* and *Eumops* sp.) activity, using humidity, time interval and sampling period as predictor variables. Model 1: global model (all variables); Model 2: Interaction of humidity with sampling period; Model 3: only humidity.

Dependent variables	Model GLM	AICc	ΔAIC
Total bat activity	1	10603.57	0.00
	2	11163.23	559.65
	3	11322.00	718.43
	Null	11611.32	1007.74
Edge-space foragers activity	1	5355.06	0.00
	2	6338.93	983.87
	3	6391.04	1035.98
	Null	6431.38	1076.32
Narrow-space foragers activity	3	620.53	0.00
	1	621.37	0.84
	Null	624.04	2.02
	2	624.04	3.51
Open-space foragers activity	1	8800.32	0.00
	2	8857.92	57.60
	3	8966.68	166.37
	Null	9227.28	426.96
Molossops temminckii activity	1	1389.89	0.00
	2	2718.59	1328.69
	3	2729.30	1339.41
	Null	3020.77	1630.88
Myotis nigricans activity	1	1032.38	0.00
	2	1036.24	3.86
	3	1119.81	87.43
	Null	3106.16	2073.78
Eptesicus furinalis	1	2325.59	0.00
	2	2648.55	322.95
	3	3047.61	722.02
	Null	3154.83	829.24
Eumops sp.	1	5663.85	0.00
	2	5698.62	34.77
	3	5793.82	129.97
	Null	5905.14	241.29

Discussion

Bat richness is dependent on well-preserved environments

Activity, species richness and composition of aerial insectivorous bats were influenced by climatic and landscape factors that work at different spatial and temporal scales. Aerial insectivorous bats seem to be able to adapt, up to a certain extent, to human-altered environments but the tolerance level to disturbance is species-specific (Jung & Kalko 2010). Despite some tolerance to habitat changes, species richness seems to be determined by the presence and extensiveness of well-preserved areas of cerrado sensu stricto and vereda. This conclusion is supported by the results of other studies in the Neotropics which demonstrated that some species, even with wide distribution ranges, are exclusively recorded at well-conserved sites due to their dependence on adequate foraging areas (Jung & Kalko 2010, Estrada-Villegas et al. 2012). In fact, in our study, sites with more than 40% covered by unmodified cerrado accounted for the highest number of species (at the 500m scale).

Size matters: patch area, not patch quantity, promotes bat activity

Heterogeneity of the landscape including pristine environments but also human-altered habitats, has been previously reported as an important factor for occupancy and activity of aerial insectivorous bats (Estrada-Villegas et al. 2010, Bader et al. 2015, Chambers et al. 2016). Our results partially support this conclusion as the response in activity varied between guilds. For *Pteronotus* cf. *parnellii*, the only narrow-space forager in our sampling, activity was strongly associated with areas covered by vereda. The wing morphology of this species allows flexible and adaptable flight, so that it may exploit different habitats (Marinello & Bernard 2014); nonetheless, as in our study, Jung & Kalko (2010) in Panama also found this species almost exclusively at well-preserved forest sites, even though other environments, including some with different levels of anthropogenic change, were available (at the time of their study the species was identified as *P.* cf. *parnellii*, but presently, in Central America, it is recognized as a different species – *P. mesoamericanu*s). It is very likely for this species to select cluttered environments as foraging sites potentially harboring higher prey availability (de Oliveira et al. 2015).

We found that edge density was an important predictor of total bat activity and of open-space foraging guild activity, at both scales. Similar results were found by Chambers et al. (2016) where edge density was a dominant configuration metric in predicting bat capture rates and occurrence in several species. Interestingly, the activity of edge-space foragers decreased with total edge density and patch density of vereda but responded positively to the percentage of landscape occupied by degraded cerrado. Similarly, Bader et al. (2015) found that some species of this guild rather forage in open spaces than in mature forests, and are able to use habitats resulting from deforestation, such as pastures. At the 1000m scale, we found a negative response of bat activity to forest and vereda fragmentation, contrasting with other studies where forest fragmentation did not negatively affect forest-associated aerial insectivores (Estrada-Villegas et al. 2010, Chambers et al. 2016).

As a metric of configuration, patch density brings information about the fragmentation level of an area, but it conveys no information about the size and spatial distribution of the patches. It has been suggested that habitat area is more influential than habitat fragmentation (Fahrig 1997); this is partly supported by our results as species and guild activity was, in many cases, generally positively related to percentage cover of unmodified habitats, but negatively related to the number of patches of those same habitats. So, as other vertebrates, some bat species may avoid crossing open or degraded areas in a matrix that includes discontinuous patches of favorable habitats. Indeed, Chambers et al. (2016) found that, specifically for bats, landscape configuration may be as important as composition. So, even if prey availability is a key factor for bats to choose their foraging grounds, structural environment characteristics appear to have primacy in their selection of habitat as they define if bats are willing or physically capable of crossing or hunting within that specific area (Armitage et al. 2012). Estrada-Villegas et al. (2010), in Panama, found that even small fragments of forest are important for bats, especially in a matrix of degraded land. It seems that, in our case, the bat assemblage still has options to choose among less fragmented habitats of great quality (in terms of roosting and foraging resources).

Nightly activity patterns are species-specific and not necessarily associated with body size.

Bat activity patterns may vary within nights, among nights within seasons, among seasons, and between sites in response to a variety of exogenous and endogenous factors (e.g. abundance of insects, air temperature, relative humidity, metabolic water balance, interspecific competition)

(Hayes 1997). It is unknown if foraging tactics may cause any species-specific differences in sensitivity for temporal dynamics and spatial variation of resources (Ciechanowski et al. 2008). Our results revealed for example, that the nightly variation in the activity of edge-space foragers was much more accentuated than that of open-space foragers, with most of the activity during the first hours of the night. It has been suggested that for many bat species, especially those foraging in open and edge space, food abundance is a fundamental factor influencing their activity, so they concentrate their foraging activities in the first hours after sunset to take advantage of higher prey abundance at that time (Wang et al. 2010, Luo et al. 2013). In our study this may be so for edge-space foragers, but we found no evidence for a similar pattern in open-space foragers. Nonetheless, our results may be somewhat biased by those species with higher number of bat passes within each guild.

Responses in the activity of bats with different body sizes were species-specific. For many species of bats, nightly activity presents a bimodal distribution with an activity peak shortly after sunset and a second, smaller peak just before sunrise, probably reflecting a period of initial foraging and drinking after emerging from day roosts, reduced activity during the middle of the night when bats are at night roosts, and a final bout of foraging and commuting towards the day roosts (Hayes 1997). Due to logistic constraints we only sampled half the night so, even if bat activity presented this bimodal pattern, we were only able to detect the first peak after sunset in *M. temminckii* and, to a lesser extent, also in *E. furinalis*. On the other hand, *M. nigricans* presented highly variable levels of activity along the night while the nightly activity of large *Eumops* sp. apparently stayed constant. Reasons for this variability may be related to changes in the abundance of insects, meteorological conditions, social factors, energetic needs, among others (Hayes 1997). For example, large-bodied open-space foragers, such as large *Eumops* species, that capture their prey in flight (away from the ground, vertical obstacles, or water surfaces) tend to feed on much scarcer, dispersed, and spatio-temporally varying food resources (Ciechanowski et al. 2008) and, for that reason, may need to hunt for longer continuous periods of time.

Humidity matters, mostly when it’s dry

Fire is a common and natural event in the Cerrado biome and an important factor determining structure, form and function of its vegetal communities and phytophysiognomies (Hoffman & Moreira 2002, Miranda, Bustamente & Miranda 2002, Simon et al. 2009). During the rainy season and transition dry-rainy season there is a high number of forest fires caused by lightning that are often restricted to small patches and are rapidly extinguished by rain; contrasting during the dry season most forest fires are caused by humans and tend to be severe, burning extensive areas (Ramos-Neto & Pivello 2000, Medeiros & Fiedler 2004, Fiedler et al. 2006). In addition to low humidity conditions other factors, such vegetation type, may favor the spread of fires (Freire et al. 2002). In the last 10 years there has been an increase in the number and the severity of fires at the beginning of the dry season (around May), with maximum intensity occurring during September-October (INPE).

Our sampling period was relatively short and the two sampled months were part of the same season (July 2015 and May 2016, mid and beginning of the dry season, respectively), so we did not expect significant differences in environmental conditions, and consequently, nor in patterns of bat activity. Nonetheless, between our sampling months, specifically in October 2015, almost the entire Mambaí region was burnt by an extensive fire. This event, and the following low precipitation levels, probably explains the positive relation between bat activity and humidity in May, when most of the region was under a serious drought. A detailed analysis of our data showed that the highest richness (15 bat species), and higher activity in May, was found at one site characterized by the presence of a temporary pond. Still, it clearly demonstrates the importance of water resources for bats in semi-arid environments. Indeed, in xeric environments, sources of water typically concentrate high levels of bat activity and exert a major structuring force on the bat assemblages in the region (Rainho & Palmeirim 2011, Adams & Thibault 2014). Our data also supports the idea that when some resources are available only in some habitat patches, all species using the same space, time, or similar spectrum of prey in that region will face similar impacts from weather, food availability, and vegetation dynamics (Ciechanowski et al. 2008). It should be noted that within the Cerrado biome the alternation of periods of water excess and deficit normally favors the occurrence of seasonal grasslands, particularly near headwaters, like veredas, which play a key role in watershed protection, and may include palm groves of *Mauritia flexuosa* (buriti-palm) (Oliveira-Filho & Ratter 2002); this may be one of the reasons why this physiognomy was so important for overall bat activity in the two sampled scales.

Conclusions and implications for conservation

Insectivorous bat richness and activity are affected by habitat type and weather conditions, and also, as expected, by how human activities impact the landscape. Our data supports the idea that several small patches of pristine phytophisiognomies may not be enough for bat conservation, as bat richness and activity seem to be dependent on the extent of well-preserved habitats in the Cerrado.

Our understanding of how spatial and temporal variation affects richness and activity of bats depends on how we interpret their responses to different composition and configuration of the landscape and to weather conditions, at different scales of analysis. These scales of analysis are highly subjective, even if based on information on the home-ranges of some species, so they may not represented how bats perceive the landscape and microclimate.

Still, as in previous studies, we found that landscape composition and configuration are more important for site selection by bats at broader scales, while weather conditions impose a greater pressure locally (Chambers et al. 2016, Mendes et al. 2015). Ability of bats to exploit an environment depends on their eco-morphological adaptations (Kalko et al. 2008) and our results seem to support this idea, as species from a certain guild usually responded similarly to the same variables; nevertheless, there are some species-specific responses. Further work is certainly necessary to better elucidate how different species respond to human-induced changes in the landscape and the associated modifications in the climatic patterns in the Cerrado.

While bats in this biome have co-evolved with often dramatic fluctuations in relative humidity and temperature both daily and seasonally, extreme events such as human-induced fires of great dimension may result in observable responses in bat assemblages, modifying patterns of species coexistence and guild-specific activity patterns. The dependence on a few patches of favorable habitats or water sources for foreseeable longer periods may result in increased competition between species that usually do not compete for space, foraging or drinking resources, with unpredictable impacts on population dynamics. For this reason, we emphasize the urgency of preserving larger pristine patches of different natural physiognomies in the Cerrado, ever more threatened by intensive agricultural schemes and uncontrolled fires (Ribeiro & Walter 2008). The fundamental role of the vereda physiognomy in the hydrological cycle within the biome should not be neglected, as it has reflexes in the maintenance of the Cerrado biota, acting as roosting, foraging and reproduction site for many terrestrial and aquatic animal species (Carvalho 1991).

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Considerações finais

Os morcegos insetívoros aéreos são um grupo diverso dentro de Chiroptera não só em termos de riqueza de espécies, mas também na sua capacidade de adaptação. Esta diversidade se expressa na morfologia, nas distintas estratégias de ecolocalização e comportamentos de forrageio e nos distintos habitats em que se encontram. Na região Neotropical, as principais ameaças que este grupo de quirópteros enfrenta são degradação e perda de habitat e alterações climáticas ocasionadas majoritariamente por atividades humanas. Diante destas circunstâncias a riqueza e atividade dos morcegos numa área determinada, respondem parcialmente, à variação espacial e temporal da paisagem. Particularmente no Cerrado, e na área de nosso estudo, a ocorrência e uso pelas espécies diferiram em relação à configuração espacial dos distintos elementos da paisagem da região, sendo que locais heterogêneos com alta porcentagem de áreas cobertas com vegetação natural bem conservada abrigaram a maior diversidade e atividade de espécies. Por outro lado, os padrões de variação temporal na atividade de morcegos insetívoros sugerem que as condições ambientais, em particular a umidade relativa, afetam de forma diferencial a atividade das guildas, tendo efeitos espécie-específicos.

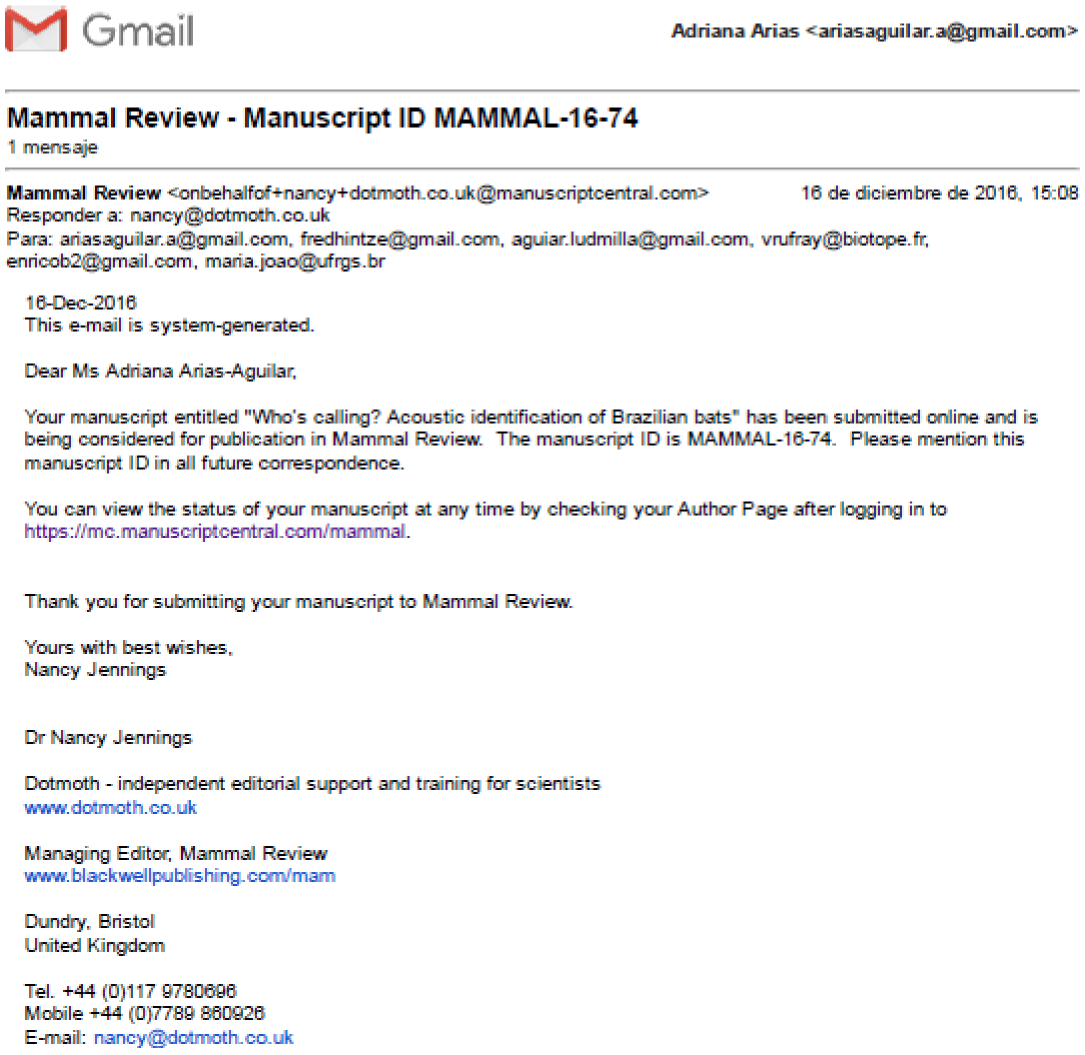
Concluímos que o arranjo espacial e o nível de conservação das manchas de habitat naturais do Cerrado têm evidente influência sobre a diversidade e a atividade das espécies em multi-escala, sendo que a composição e configuração dos diversos elementos estruturais determinam, em parte, as condições microclimáticas ante as quais a atividade das espécies varia a uma escala mais local. A principal variação nas condições de umidade no Cerrado acontece estacionalmente. Na época seca os incêndios de origem humana, pela sua grande intensidade e extensão acentuam as condições de deficiência hídrica que afetam a atividade dos morcegos. Assim, habitats com recursos temporários de água e alimento como as veredas, tornam-se fundamentais para a persistência dos morcegos insetívoros aéreos.

Esperamos que a informação recopilada na revisão inclusa no segundo capítulo desta dissertação seja o primeiro passo para elucidar as causas da variação regional entre os morcegos insetívoros neotropicais, e que, fundamentalmente ajude a melhorar a qualidade das identificações dos morcegos desta região através de seus chamados de ecolocalização.

Concluímos que a utilização de monitoramentos acústicos para avaliar os padrões de diversidade e atividade de morcegos insetívoros no Cerrado mostrou ser determinante e eficaz, sublinhando assim a sua relevância para melhorar o nosso conhecimento das comunidades de morcegos no Neotrópico. Com certeza, há ainda muito por saber sobre os morcegos insetívoros do Cerrado, do Brasil e da região Neotropical em geral, sendo que o nosso acelerado ritmo de crescimento e, em especial, os nossos hábitos de consumo ameaçam destruir os habitats naturais e a persistência de muitas dessas espécies. Conhecer a distribuição dessas espécies e diversos aspectos da sua ecologia como uso de habitat, variação espaço-temporal na atividade, diferenciação de nicho, e comportamento de forrageio, é um dos passos para contribuir para a sua conservação.

Anexos

Anexo 1. Recibo de submissão do artigo *Who's calling? Acoustic identification of Brazilian bats* ao periódico Mammal Review



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