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A URBANIZAÇÃO E OS MORCEGOS INSETÍVOROS DO CERRADO: RIQUEZA, ATIVIDADE E ECOLOCALIZAÇÃO

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RESUMO GERAL

A urbanização é uma das formas mais intensas de modificação do habitat. Recentemente, a ciência tem demonstrado que a biodiversidade urbana possui adaptações populacionais, morfológicas e genéticas. As espécies de morcegos respondem de forma espécie-específica à urbanização e podem ser excluídas, beneficiadas ou exibir neutralidades em função dessa pressão. O Cerrado é classificado como um *hotspot* de biodiversidade. No bioma existe uma grande lacuna no conhecimento básico da distribuição das espécies de morcegos insetívoros e sobre os efeitos da urbanização. Essa dissertação avalia os efeitos da urbanização em morcegos insetívoros no Cerrado. No Capítulo 1, demonstro a existência de uma grande lacuna de conhecimentos básicos sobre as espécies insetívoras. A grande maioria dos estudos sobre distribuição de morcegos no Cerrado são realizados com redes de neblina, o que favorece a captura de espécies não insetívoras. Por meio da bioacústica, foram investigadas a riqueza e a composição de espécies em habitats não urbanizados, periurbanos e urbanizados no Distrito Federal e Goiás, região central do bioma. Eu encontrei a redução da riqueza e da similaridade da composição de espécies com o aumento da urbanização, no entanto mudanças podem ser observadas quando as estações seca e chuvosa são consideradas separadamente. Durante a estação seca, a riqueza é semelhante, no entanto a composição difere entre os habitas, e na estação chuvosa encontrei alta riqueza e similaridade na composição de espécies entre os habitats. Apenas *Molossops neglectus* não havia sido registrada em zonas urbanas do Cerrado, enquanto *Molossus currentium*, *M. molossus* e *N. laticaudatus* ocorreram em todos os habitats e estações, sendo as espécies utilizadas nas análises dos capítulos 2 e 3. Por meio de pulsos de ecolocalização morcegos detectam o ambiente em sua volta. A poluição sonora pode funcionar como um fragmentador ambiental, assim como a iluminação artificial, além de demandar maior atividade cognitiva. No Cerrado, conhecimentos básicos como a descrição acústica das espécies ainda são necessários. No segundo capítulo, meu objetivo é

investigar as diferenças nos chamados das espécies *Molossus currentium*, *M. molossus* e *N. laticaudatus*. Os pulsos de *M. currentium,* e *N. laticaudatus* são emitidos mais baixos e são influenciados pelo tipo de habitat e estação, enquanto *M. molossus* é influenciado apenas pela estação. Apesar das diferenças, todos os pulsos registrados já foram descritos como parte do repertório vocal das espécies, no entanto o *duty-cycle* é reduzido quando comparados com os registros em habitats florestais. Morcegos ajustam seu período de atividade para otimizar as oportunidades, são animais que permanecem em abrigos ao longo do dia e permanecem ativos durante a noite. Fatores intrínsecos e extrínsecos das espécies determinam a disponibilidade e utilização dos abrigos, assim como o período de forrageio. Em habitats urbanos, a iluminação artificial está associada a alterações nos padrões de atividade. No terceiro capítulo, meu o objetivo é investigar diferenças nos padrões de atividade das espécies selecionadas nos diferentes habitats. Os padrões de atividade das espécies de *Molossus* é melhor explicados pelo GLMM com modelo interativo e o de *N. laticaudatus* pelo nulo. Alguns dos padrões encontrados foram similares aos descritos em habitats florestais e insulares das Américas Central e do Sul.

Palavras-chave: *Adaptação; bioacústica, biodiversidade; Chiroptera, cidades, Molossidae.*

GENERAL ABSTRACT

Urbanization is one of the most intense forms of habitat modification. Recently, science has shown that urban biodiversity has a population, morphological and genetic adaptations. Bat species respond in a species-specific way to urbanization and can be excluded, benefited or neutral in this habitat. Cerrado is a hotspot biodiversity. In Cerrado, there is a significant gap in basic knowledge of the distribution and the effects of urbanization on insectivorous bat species. This dissertation evaluates the effects of urbanization on insectivorous bats in Cerrado. In Chapter 1, I demonstrate the existence of a substantial gap in basic knowledge about insectivorous species. Most studies on bat distribution in the Cerrado are carried out with mist nets, which favors the capture of non-insectivorous species. The richness and composition of species in non-urbanized, peri-urban and urbanized habitats in the Federal District and Goiás, the central region of the biome, are investigated through bioacoustics. I found a reduction in species richness with increasing urbanization; however, changes can be observed when the dry and wet seasons are considered separately. In the dry season, the richness was similar; however, the composition differed between the habitats, and in the rainy season, high richness and similarity in species composition between the habitats were found. Only *Molossops neglectus* had not been recorded in urban areas of the Cerrado, while *Molossus currentium*, *M. molossus*, and *N. laticaudatus* occurred in all habitats and seasons, being the species used in the analyzes of chapters 2 and 3. Through ultrasound pulses bats detect the environment around them. Noise pollution and artificial lighting can act as a source of environmental fragmentation, demanding more significant cognitive activity. In the Cerrado, basic knowledge such as the acoustic description of species is still needed. In the second chapter, I investigate intraspecific differences in *M. currentium, M. molossus and N. laticaudatus* pulses. *M. currentium* and *N. laticaudatus* emit lower pulses and are influenced by habitat type and season, while *M. molossus* is influenced only by season. Despite the

differences, all recorded pulses have already been described as part of the species' vocal repertoire; however, the duty cycles are reduced when compared to the duty-cycles found in forest habitats. Animals adjust their activity period to optimize opportunities. Bats are animals that stay in shelters throughout the day and remain active at night. Intrinsic and extrinsic factors of the species determine the availability and use of shelters, and the foraging period. In urban habitats, artificial lighting is associated with changes in activity patterns. In the second chapter, the objective is to investigate possible differences in the activity patterns of the selected species in the different habitats. The activity pattern of *Molossus* species is better explained by the GLMM's interactive model and *N. laticaudatus* by the null model. Some of the patterns found are similar to those described in forest and island habitats in Central and South America.

A urbanização ocorre em muitos *hotspots* de biodiversidade (áreas com alta endemicidade vegetal e alta perda de habitat) ao redor do mundo, consistindo em uma grande fonte de mudança no uso da terra (Miller & Hobbs, 2002). Essas paisagens dominadas pelo ser humano possuem complexas interações entre variáveis sociais, econômicas, institucionais e ambientais que levam a perda de funções ecossistêmicas e da biodiversidade (Alberti, 2005). Entre as principais consequências da urbanização para a biodiversidade estão o declínio das populações de espécies ameaçadas e vulneráveis, diminuição da riqueza de espécies, altas densidades populacionais, comunidades com poucas espécies e homogeneização do habitat (Miller & Hobbs, 2002; Schoat *et al.* 2006; McKinney, 2002). Os dois principais determinantes para riqueza de espécies em ambientes urbanos são os fragmentos de habitat e a conectividade entre eles. Fragmentos com mais de 50 hectares, maior diversidade, densidade e variação na estrutura da vegetação e corpos d'água são pontos chave para maior riqueza (Beninde *et al.*, 2015). Essa biodiversidade urbana tem despertado grande interesse da ciência, pois populações urbanas demonstram maior plasticidade ecológica e comportamental, mudanças micro evolutivas quando comparadas com populações em ambiente não urbano, assim como divergências genéticas devido à interrupção do fluxo genético entre as populações urbanas e não urbanas (Luniak, 2004; Halfwerk *et al.*, 2019; Richardson *et al.*, 2020). Também ocorrem alterações morfológicas, mudanças na dinâmica populacional e na estrutura das comunidades (Schoat *et al.*, 2006; Tomassini *et al.*, 2013, Lintott *et al.*, 2014, DePasquale et al., 2020).

A urbanização geralmente está associada a efeitos negativos na assembleia de morcegos (Jung & Threlfall, 2016), devido à menor riqueza de espécies encontradas nesses ambientes (Avila-Flores & Fenton, 2005; Jung & Kalko, 2010; 2011; Coleman & Barclay, 2012; Bader *et al.*, 2015, Ramírez-Mejía *et al.*, 2019) e a alterações comportamentais em maternidades e adultos em voo livre em resposta à presença humana e predadores urbanos (Gallo *et al.*, 2017;

Ancilloto *et al.*, 2019, Geipel *et al.*, 2019). Altos índices de mortalidade estão relacionados a geradores de energia eólica, linhas de transmissão, predação por novos predadores como, por exemplo, o gato doméstico e o falcão peneireiro-vulgar (*Falco tinnunculus*) (Hayes *et al.*, 2013; Mikula *et al.*, 2013; Vlaschenko *et al.*, 2018; Tella *et al.*, 2020). A competição por abrigos com espécies exóticas como, por exemplo, o periquito *ringneck* (*Psittacula kamersi*) pode reduzir a quantidade de abrigos disponíveis (Hernández-Brito *et al.*, 2018). Por fim, a contaminação e a bioacumulação de metais pesados e de pesticidas, como por exemplo, o mercúrio e o Dicloro-Difenil-Tricloroetano (DDT), e com pesticidas, que estão associados ao comprometimento da resposta imune, do metabolismo e da reprodução (Heiker *et al.*, 2018; Souza *et al.*, 2020; Oliveira et al. 2021).

Algumas espécies de morcegos respondem positivamente à urbanização. O morcego *Myotis lucifugus* (LeConte 1831), por exemplo, se torna espécie dominante no habitat urbano e compõe grande parte da abundância da assembleia local em Alberta, Canadá (Coleman & Barclay, 2012). O *Pipistrellus kuhlii* (Kuhl, 1817) expandiu sua distribuição ao acompanhar o desenvolvimento da iluminação artificial na Europa, essa expansão foi acompanhada de mudanças na dieta e no tamanho dos indivíduos (Tomassini *et al.*, 2013). O ambiente urbano provê também uma nova diversidade de insetos e frutos para as espécies que persistem nele possam se alimentar, muitas vezes alterando a dieta e o comportamento de forrageio (Jung & Kalko, 2010; Laurindo et al., 2020).

Por fim, contrário aos exemplos anteriores, existem espécies de morcegos que permanecem neutras a urbanização, apesar dessa resposta ser mais rara (Russo & Ancilloto, 2015). Este é o caso do *Rhinolophus hipposideros* (Bechstein, 1800), que em relação a alterações morfológicas, não apresenta diferenças no comprimento do antebraço em zonas urbanas e não urbanas (Salinas-Ramos *et al.*, 2020). No México, o *Molossus rufus* (E. Geoffroy, 1805), o *Lasiurus cinereus* (Palisot de Beauvois 1796) e o *L. intermedius* possuem níveis de

atividade similar tanto em ambientes urbanos quanto intermediários e não urbanos (Rodríguez-Aguilar et al., 2017).

No Brasil, o grande endemismo vegetal e a alta taxa de antropização caracterizam o Cerrado como um *hotspot* para conservação (Myers *et al.*, 2000). O bioma possui 203,4 milhões de hectares, clima Aw na classificação de Köppen (inverno seco e verão chuvoso), temperatura média anual entre 22 – 23ºC e precipitação entre 1200 – 1800 mm (IBGE, 2004). A vegetação é caracterizada por um mosaico de gramíneas, arbustos e árvores que formam um gradiente de fitofisionomias dominadas por gramíneas até fitofisionomias dominadas por espécies arbóreas (Eiten, 1972). Até 2002, o Cerrado já havia perdido 54,9% da sua cobertura original, quando 65,9 milhões de hectares foram convertidos em agricultura e pastagens (Klink & Machado, 2005). As zonas urbanas ocupam 3 milhões de hectares no Cerrado e, entre 1970 e 2010, a população no Cerrado cresceu de 12 milhões para 30 milhões de habitantes, aproximadamente, e a taxa de urbanização de 51 para 87% no mesmo período (Klink & Machado, 2005; Campolina, 2019). Desde a década de 1990, o crescimento da população tem desacelerado com a diminuição dos fluxos de migração (Klink & Machado, 2005; Campolina, 2019). O bioma também possui espécies animais endêmicas: 113 Squamata, 102 Anura, 22 mamíferos, 16 aves (Azevedo *et al.*, 2016; Nogueira *et al.*, 2011, Gutiérrez & Marinho-Filho, 2017; Silva, 1995).

No Cerrado, os dados conhecidos até o momento indicam que a maior diversidade de morcegos está nas regiões central e norte (Silva et al., 2018). As três principais formações florestais – mata de galeria, mata ciliar e mata seca - possuem árvores de 15 a 30 metros de altura que ocupam entre 70 e 95% da área da fitofisionomia (Ribeiro & Walter, 1998). No bioma, a ocupação dos habitats por morcegos é espécie-específica e, de modo geral, existe uma correlação positiva com o tamanho dos fragmentos florestais, a densidade e a heterogeneidade destes fragmentos (dos Santos *et al.*, 2016; Muylaert *et al.*, 2016). A distribuição dos animais pode ser explicada tanto por variáveis locais como, por exemplo, altura da copa, número de

árvores e número de lianas do fragmento, quanto por variáveis da paisagem como a quantidade de vegetação nativa e o número de fragmentos naturais (Mendes *et al.*, 2017). Os fragmentos florestais também estão associados ao maior número de interações morcego-planta dos morcegos nectarívoros e frugívoros presentes no bioma e aos abrigos diurnos das demais espécies (Aguirre *et al.*, 2003; Oliveira *et al.*, 2019).

Levantamentos de fauna básicos para conhecer a riqueza e distribuição de espécies de Chiroptera no Brasil demandam urgência, pois 61% do território não possui registros de morcegos e a região norte do Cerrado é uma das regiões prioritárias para a condução de estudos do tipo no país (Aguiar *et al.*, 2020). Essa porção norte do bioma e a porção central, potencialmente, têm a maior riqueza de espécies e são as mesmas áreas onde atualmente ocorrem a maior expansão agrícola no Cerrado (Silva *et al.*, 2018). Existe uma tendência da diminuição da riqueza das espécies com o aumento da perturbação antrópica nas fitofisionomias do Cerrado (Pereira *et al*, 2018). A remoção da vegetação nativa causada pela atividade agropecuária, principalmente das fitofisionomias florestais, afeta negativamente a assembleia de morcegos e pode levar a perda de serviços ecossistêmicos e da recuperação de áreas degradadas (Oliveira *et al.*, 2017, 2019). As mudanças climáticas também apresentam uma ameaça a diversidade de morcegos no Cerrado. Sob um cenário de aumento entre 0,9 e 2,0ºC, 36 espécies devem restringir sua distribuição a apenas 20% da distribuição atual e cinco espécies devem ser localmente extintas (Aguiar *et al.*, 2016). Entretanto, estes estudos não avaliaram o efeito do aumento da urbanização na assembleia de morcegos, na atividade e tampouco em aspectos da ecolocalização. Portanto, meus objetivos são primeiro, no Capítulo 1, avaliar a riqueza e composição de espécies de morcegos insetívoros por meio do monitoramento acústico no gradiente não urbano – periurbano – urbano e possíveis diferenças entre as estações seca e chuvosa. No Capítulo 2, avalio diferenças nos parâmetros tonais e temporais dos pulsos de ecolocalização e o *duty-cycle* de três espécies da família Molossidae:

Molossus currentium, *M. molossus* e *Nyctinomops laticaudatus* ao longo do gradiente de urbanização e durante as estações, pois essas foram as espécies presentes em todos os habitats e estações no capítulo 1, e no capítulo 3 avalio diferenças no padrão de atividade temporal das mesmas espécies ao longo do gradiente de urbanização e entre as estações.

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CAPÍTULO 1

A VARIAÇÃO DA RIQUEZA E COMPOSIÇÃO DE ESPÉCIES MORCEGOS INSETÍVOROS EM UM GRADIENTE DE URBANIZAÇÃO

Variation of insectivorous bats species richness and composition along an urbanization gradient

ABSTRACT

Bat species richness and composition are threatened by urbanization. In this study, our aimed was to assess bat species richness and composition along an urbanization gradient at different seasons in Cerrado. We used acoustic data from seven areas for a 12 h period (18:00–06:00), employing 7 or 8 recorders per area. The results showed that 26 species belonging to Vespertilionidae, Molossidae, Emballonuridae, Thyropteridae, and Mormoopidae families were observed, among which, 24 were observed in non-urban habitats, 21 in peri-urban habitats, and 16 in urban areas. There was a decrease in species richness in urban habitat and a decrease in species composition similarity with increasing urbanization. There was no difference in species richness between the habitats during the dry season, but species composition was considerably different. Additionally, there was a high similarity in richness and composition between non-urban and peri-urban habitats during the rainy season. In general, the bats favored habitats with low levels of urbanization. Insectivorous bats in urban habitats might be in an ecological trap, a process common in habitats under intense modifications and common to bats. Overall, the findings of this study contribute to the understanding of the impact of urbanization on bats in Neotropical ecosystems.

Key Words: Biodiversity, Brazil, Cerrado, Chiroptera, cities, mammals, Neotropical, savannas.

RESUMO

A riqueza e composição de espécies de morcegos são ameaçadas pela urbanização. Nesse estudo, nosso objetivo foi avaliar a riqueza e composição de espécies de morcegos ao longo de um gradiente de urbanização em diferentes estações do ano no Cerrado. Usamos

dados acústicos de sete áreas por um período de 12 h (18:00–06:00), empregando 7 ou 8 gravadores por área. Foram registradas 26 espécies pertencentes às famílias Vespertilionidae, Molossidae, Emballonuridae, Thyropteridae e Mormoopidae, das quais 24 foram observadas em habitats não urbanos, 21 em habitats periurbanos e 16 em áreas urbanas. Houve uma diminuição na riqueza de espécies no habitat urbano e uma diminuição na similaridade da composição de espécies com o aumento da urbanização. Não houve diferença na riqueza de espécies entre os habitats durante a estação seca, mas a composição de espécies foi consideravelmente diferente. Além disso, houve uma alta similaridade na riqueza e composição entre os habitats não urbanos e periurbanos durante a estação chuvosa. Em geral, os morcegos favoreceram habitats com baixos níveis de urbanização. Morcegos insetívoros em habitats urbanos podem estar em armadilha ecológica, processo comum em habitats sob intensas modificações e comum aos morcegos. De modo geral, os achados deste estudo contribuem para a compreensão do impacto da urbanização sobre os morcegos em ecossistemas neotropicais.

Palavras-chave: Biodiversidade, Brasil, Cerrado, Chiroptera, cidades, mamíferos, Neotropical, savanas.

<div align="center">INTRODUCTION</div>

In cities, intermediate and high levels of urbanization negatively affect bat habitats (Jung and Threlfall, 2016). Studies in Canada (Coleman and Barclay, 2011), Mexico (Ávila-Flores and Fenton, 2005), Panama (Jung and Kalko, 2010, 2011), and Australia (Hourigan et al. 2010; Threlfall et al. 2012; Luck et al. 2013) have shown that bat species richness is lower in urban habitats than in natural habitats. However, sometimes suburbs tend to have the highest species richness in urban-rural gradients (Threlfall et al., 2011). The bat population's primary limiting factors in urban areas include low shelter availability, poor adaptability to available feed and survival in the fragmented and poorly connected landscape, noise

pollution, and water availability (Russo and Ancilloto, 2015). These factors are related to bats' temporal activity patterns and echolocation characteristics. These changes in habitat occupation are species-specific and have no phylogenetic or functional effects (Jung & Threlfall, 2016). Edge, open-space, and trawling bats tend to tolerate urbanization, and the local extinction of species can be predicted by their flexibility in shelter use, foraging behavior, and morphology (Jung and Threlfall, 2018).

The human population is projected to increase by 115.4 million in the Neotropical region by 2050, which could considerably impact on bat species. Currently, 81.2% of 664.5 million Neotropical inhabitants live in urban areas, which is expected to increase to 87.8% in 2050 (UN, 2018). This region has a remarkable diversity of bat species (IUCN, 2021). Brazil occupies the second position for Chiroptera species richness, although it is considered a subsampled country for this group (Bernard et al. 2011). Among the 181 species that occur in Brazil, 118 are found in the Cerrado biome hotspot (Aguiar et al. 2016; Garbino et al. 2020), distributed in eight families, with 70 of them being insectivorous (Aguiar et al., 2016). However, studies on bat assemblages in the Cerrado native vegetation and agriculture areas using mist net usually record 15–25 species and communities dominated by non-insectivorous Phyllostomidae, which can represent up to 90% of species richness, and more than 90% of abundance (Falcão et al. 2003; Gonçalves and Gregorin, 2004; Lima et al. 2016). The richness and abundance of these species may respond to the seasonality and heterogeneity of the habitat, increasing during the rainy season and with higher heterogenity (Zortéa et al. 2008; Mass et al. 2015; Lima et al. 2016).

Furthermore, insectivorous bat species comprise open-space and edge foragers. Open-space foragers capture insects while flying away from obstacles, and edge foragers capture insects while fllying at forest edges, clearings, and above waterways (Schnitzler and Kalko, 2001; Denzinger and Schnitzler, 2013). For example, Molossidae species forage above forest

canopy (Pedro and Taddei, 1997). Despite constituting 61% of the Chiroptera species richness in the Cerrado region (Aguiar et al. 2016), 90% of studies in the Neotropical region are performed without any method that favors data collection on insectivorous species (Cunto and Bernard, 2012).

Although studies on bats in urban areas in the Cerrado region are limited, museum surveys and mist-net studies have identified similar results to those in native vegetation and agriculture areas: non-insectivorous Phyllostomidae species as the dominant species in urban areas, with few insectivorous bat species (Perini et al. 2003; Bruno et al. 2003; Ferreira et al. 2010). Recently, acoustic monitoring confirmed the high species richness of insectivorous bats in urban areas in the Cerrado, identifyng more than 20 species belonging to the families Molossidae, Vespertilionidae, Emballonuridae, Mormoorpidae, and Noctilionidae (Reis 2019). Moreover, 84 species have been identified in Brazilian cities, the most common of which were insectivores (51 species; Nunes et al. 2017). In cities, these bats can feed on Coleoptera, Lepidoptera, Homoptera, and Hemiptera, which some species are considered agricultural pests and vectors of diseases like St. Louis encephalitis and other arboviral infections (Aguiar and Antonini 2008, Aguiar et al. 2021).

In the Cerrado region, insects such as Coleoptera, Diptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, and Trichoptera tend to respond to seasonality, with increased abundance during October and November, peaking in November (Aranda et al. 2021). This period coincides with an increase in temperature and the beginning of rainy season (Silva et al. 2011). Since these insects are the primary prey of insectivorous bats, these bats may respond to seasonality, leading to differences in species richness and abundance at different seasons. However, no studies have evaluated these patterns, indicating a significant gap in our knowledge of insectivorous bats in the Cerrado region. Moreover, studies have yet to assess urbanization and seasonality's effect on bat species richness and composition.

Thus, we hypothesized bat species richness would decrease with the increasing urbanization of the study area due to ecological limitations, and that urbanization will probably favor bats belonging to the Molossidae, Emballonuridae, and Vespertilionidae families. These families are adaptable to the urban environment due to the ability to move in the fragmented landscape and the flexibility of feeding behavior, which allows them to feed on insects concentrated around artificial light and concentrate the activity of foraging in the early hours of the night (Ávila-Flores and Fenton, 2005; Jung & Kalko, 2010; Bader et al. 2015). Additionally, we hypothesized that the bat species richness from these habitats would be influenced by seasonal variations, including dry and rainy seasons; therefore, this study aimed to evaluate the species richness of insectivorous bats along a non-urban-urban gradient in the Cerrado region across different seasons.

MATERIALS AND METHODS

Study Area

This study was conducted in two parks in the state of Goiás (GO) and five parks in Federal District (FD) within the Cerrado biome (Fig. 1). Cerrado vegetation is a mosaic of grasslands, savanna and forests phytophysiognomies and these vegetation types are defined by the proportion of grasses, bushes and trees (Eiten, 1972). The two parks in GO were Chapada dos Veadeiros National Park (CVNP; 14° 10' S, 47° 30' W) and Terra Ronca State Park (TRSP; 13°29' S, 46°23' W; Fig. 2), and the five parks in the FD were Brasília National Park (BNP; 15° 38' S 48° 1' W), Ecological Station of Águas Emendadas (ESAE; 15° 33' S, 47° 36' W), Brasília Botanical Garden Ecological Station (BBGES; 15º 88' S, 47º 85' W), Ezechias Heringer Ecological Park (EHEP; 15º 83' S, 47º 95' W), and the Águas Claras Ecological Park (ACEP; 15º 83' S, 48º 02' W; Fig. 3). CNVP has a tropical wet and dry (Aw) climate, according to the Köppen classification, with a maximum altitude of 1670 m, an average annual temperature between 19°C and 22°C, and an average annual precipitation

between 1600 mm and 1800 mm (Cardoso et al., 2014). TRSP also has an Aw climate, with a mean annual temperature of 24–25°C and a mean annual rainfall of 1000–1200 mm (Cardoso et al., 2014). The FD (576,078.4 ha, population of 3,055,149 inhabitants; IBGE, 2010) has an average annual precipitation of 1400–1600 mm and an average temperature of 20–21°C (Cardoso et al. 2014).

Parks were classified as non-urban, peri-urban, and urban, using the 2019 Cerrado Land Use Map (30 × 30 m resolution) from the NGO Mapbiomas (Souza et al. 2020). We obtained the shapefiles from the Brazilian Conservation Units of the Ministry of the Environment (MMA) and the DF conservation units at the Brasília Environmental Institute (IBRAM). Areas in the map were reclassified as Cerrado, agriculture, urban habitat, and water, using the 'sf' (Pebesma, 2018), 'raster' (Hijmans, 2021), 'tmap' (Tennekes, 2018), 'dplyr' (Wickham et al., 2021a), and 'stars' (Pesbema, 2021) packages in R software (v. 4.0.5; R Core Team, 2021), with a 3 km buffer around the parks. Urban areas were considered as the central areas of the cities, and peri-urban areas as intermediate regions at the interface of urban areas, rural areas and natural vegetation (Clergeau et al. 2001). We created three classes to classify the parks using the percentage of the urban land cover area of the buffer zones: non-urban parks: urban habitat corresponds to < 10% of the buffer zone; peri-urban parks: the urban habitat corresponds to 11–50% of the buffer zone; and urban parks: the urban habitat corresponds to an area > 51% of the buffer zone (Table 1).

Non-urban habitat — CVNP, TRST, and ESAE have several forests, savannah, and grasslands phytophysiognomies from the Cerrado (Felfili et al. 2007; MMA/ICMBio, 2009; Teixeira et al. 2017). There are 118 species of mammals in CNVP, of which 9 are endemic and 35.6% of these species are bats. Among bats, 20 species are insectivorous (MMA/ICMBio, 2009). In TRSP, 43 species of insectivorous bats belonging to the families

Molossidae, Emballonuridae, Vespertilionidae, Mormoopidae, Noctilionidae and Thyropteridae have already been recorded (Rodrigues, 2019).

Peri-urban habitat — BNP has 11 Cerrado phytophysiognomies, Cerrado *stricto sensu* is the predominant formation (46.39% of the area), and lake Santa Maria occupies 755 ha (Farias et al. 2008). BBGES have forest, savanna, and grassland phytophysiognomies (Moreira, 2000; Nobrega et al. 2001; Arruda, 2018).

Urban habitat — ACEP has typical Cerrado formations, such as gallery forest, Cerrado *strictu sensu*, and grasslands (Munhoz and Amaral, 2007). 21 species of insectivorous bats from the families Emballonuridae, Molossidae and Vespertillionidae were recorded inside the park (Reis, 2019). EHEP has seasonal humid fields, dirty field, Cerrado *stricto sensu*, gallery forest and marsh and 495 plant species distributed in 286 genera and 95 families (Nogueira et al. 2002). Some of these species are exotic to the Cerrado (Chacon et al. 2014). Inside the park, 20 species of insectivorous bats distributed in the families Emballonuridae, Molossidae and Vespertilionidae and insects of the orders Coleoptera, Diptera, Hemiptera, Hymenoptera and Orthoptera have already been recorded (Reis, 2019).

Data Collection

We obtained the data from the Laboratory of Biology and Conservation of Bats, Department of Zoology, Institute of Biological Sciences, University of Brasília. In each park, we selected seven or eight recorders, totaling 15 recorders per habitat/season, in exception the non-urban habitat in dry season where we selected 14 recorders. All records obtained were done in non-urban habitats with Songmeter (Wildlife Acoustics) recorders and in urbanized habitats with Audiomoth (LABmaker) recorders, and all of them were positioned 3m above the ground in an open area, configured to record from 18:00 to 6:00 of the following day, remaining active for three minutes in 15-minute cycles overnight, and at a sampling rate of

384 kHz and. The recordings in the CVNP took place in dry season (September/2014), in the TRSP in rainy season (February/2014), in ESAE, BBGES, BNP, EHEP and ACEP parks the recordings took place in dry season (August/2017 and September/2018) and in rainy season (February/2018 and 2019. Generally, sampling for the first 4 h of one night is sufficient to capture 90% of the species richness of insectivorous bats in Neotropical habitats, and extra sampling effort will not significantly increase the number of novel species identified (López-Baucells et al. 2021).

Species Identification

Bat pulses were extracted using 'bioacoustics' package using as reference the default values provided for pulse extraction from Canadian insectivorous bats (Marchal et al. 2021) in the R software (v. 4.0.5; R Core Team, 2021). The package generates automatically spectrograms and measures the following quantitative parameters: Maximum Energy Frequency (FME), Maximum Frequency (FMAX), Minimum Frequency (FMIN), Bandwidth (BW = FMAX-FMIN), Initial Frequency (FINITIAL), Final Frequency (FEND), Pulse Duration (D or t). In addition, we calculated Inter-pulse Interval (IPI) manually by subtracting the end time of the previous pulse from the start time of the next pulse. We also used the 'dplyr' (v. 1.0.6; Whickham et al. 2021a), 'tools' (v. 4.0.5; R Core Team, 2021), and 'tidyr' (v. 1.3.3; Wickham et al. 2021b) packages for data manipulation during pulse extraction and in the subsequent analyses.

We defined a pass as a sequence of three or more pulses with an IPI of less than 1 s. When the pass consisted of more than 3 pulses, we selected three sequential pulses for identification based on qualitative parameters (pulse type: FM, CF or qCF; pulse modulation: upwards or downwards) inferred from spectrograms and based on the quantitative parameters. For standardization, we considered only the first 2 IPIs. Therefore, an identified pass was

considered a record of a species. Species identification was performed by comparing the parameters with those provided by Arias-Aguilar et al. (2018).

Statistical Analyses

We performed a Quadratic Discriminant Analysis with the quantitative parameters to evaluate species/sonotypes' identification confidence for species with more than eight registers (number of passes should be at least the same number of quantitative parameters) (Tharwat, 2016) with 'MASS' package (Venables and Ripley, 2002) For validation we used a ten-fold cross validations using 80% of data set for training and 20% for testing. To evaluate richness differences among habitats, we performed a bicaudal randomization test with 100 randomizations at 'rich' package (Rossi, 2011) with the cumulative value over all samples, and alfa=0.05, and species accumulation curves with random method (sites added in random order) with 10,000 permutations at 'vegan' package (Okansen et al. 2020). To evaluate composition, we calculated a similarity matrix based on Jaccard index for all pairs of habitats, and a PERMANOVA with 10,000 permutations at 'vegan'. To evaluate differences among habitats, we did pairwise comparisons with 10,000 permutations with 'pairwiseAdonis' package (Arbizu, 2017). To evaluate the effect of seasons on species richness and composition, we separated the data by season and repeated the tests. We conducted all statistical analyses in R software (v. 4.0.3; R Core Team, 2021).

RESULTS

Bat Activity

The total observation time in each habitat/station was 2,160 min, except in the non-urban habitat, where the observation time totaled 2,016 min in the dry season. We registered 198 passes in the dry season and 402 in the rainy season in the non-urban habitat, 382 and 892

passes in the peri-urban habitat, and 856 and 615 passes in the urban habitats, respectively. A total of 3,345 passes were registered during this study.

Species Richness

We identified 26 insectivorous bat species/sonotypes belonging to the families Vespertilionidae (11), Molossidae (10), Emballunoridae (3), Mormoorpidae (1), and Thyropteridae (1) (Table 2). Global accuracy for species/sonotypes with more than eight passes was 0.753 (*Kappa = 0.7218, p < 0.001*) and varied between 0.5 for *Eumops sp.*, *Myotis ruber*, and *Molossus rufus*, and 1.0 for *Eptesicus furinalis* (Supplementary Data S1). We identified 24 species/sonotypes distributed across all prementioned families in the non-urban habitats, among which 17 were observed in the dry and 21 in the rainy season. Additionally, we identified 21 species/sonotypes belonging to Vespertilionidae, Molossidae, and Thyropteridae in the peri-urban habitat, among which 15 were observed in the dry and 6 in the rainy season. In the urban habitats, we identified 16 species/sonotypes belonging to the families Vespertilionidae, Molossidae, Emballonuridae, and Thyropteridae, among which 13 were recorded during the dry and 12 during the rainy season.

The annual species accumulation curves of the non-urban and urban habitats were steeper than that of the peri-urban habitats; however, the species accumulation curve tended to plateau after the first 6h of sampling, indicating stability in species accumulation. During the dry season, the curve tended to be more stable for the urban habitat than for the other habitats, and the curves tended to plateau after the first 6h of sampling. In the rainy season, the curves for peri-urban and urban habitats tended to plateau after the first 6 h of sampling, whereas non-urban habitats remained steep (Fig. 4).

Furthermore, the permutation test indicated no significant difference in species richness between non-urban and peri-urban habitats annually (*q0.025 = -5, q 0.975 = 4, p = 0.188, q = quartiles*). However, there were significant differences in species richness between

non-urban and urban habitats ($q0.025 = -6$, $q0.975 = 6$, $p = 0.009$), and between peri-urban and urban habitats ($q0.025 = -3.5$, $q0.975 = 3.5$, $p = 0.019$). There were no significant differences in species richness between non-urban and peri-urban habitats ($q0.025 = -6$, $q0.975 = 5.5$, $p = 0.356$), between non-urban and urban habitats ($q0.025 = -5, 5$, $q0.975 = 6$, $p = 0.217$), and between peri-urban and urban habitats ($q0.025 = -4$, $q0.975 = 5$, $p = 0.287$) during the dry season. During the rainy season, species richness was not computed between the non-urban and peri-urban habitats, as both had the same richness. However, these two habitats differed significantly in species richness relative to the urban habitat ($q0.025 = -8$, $q0.975 = 8$, $p = 0.009$).

Species composition

We found *Lasiurus ega* and *Pteronotus cf. parnellii* observed exclusively during the dry season, and *Peropteryx trinitatis* during the rainy season in non-urban habitat; moreover, *Saccopteryx leptura* was exclusive to this habitat both during the rainy and dry season. *Eptesicus furinalis*, *Lasiurus cinereus*, *Myotis albescens*, *Myotis riparius*, *Myotis ruber*, and *Molossops neglectus* were observed in the peri-urban habitats. *Eptesicus brasiliensis*, *Myotis lavali*, *Myotis nigricans*, *Rhogeessa hussoni*, the sonotype *Eumops sp.*, *Molossops temminckii*, *Molossus rufus*, *Nyctinomops macrotis*, *Promops nasutus,* and *Thyroptera sp.* were observed in all three habitats, but not in all seasons. *Molossus currentium*, *Molossus molossus*, sonotype *Molossus spp.*, and *Nyctinomops laticaudatus* were observed in all habitats and seasons. *M. albescens*, *R. hussoni*, *Eumops sp.*, *M. neglectus*, *N. macrotis*, and *P. nasutus* were observed only during the rainy season in the non-urban habitats. *Eptesicus chiriquinus* was observed in peri-urban and urban habitats but only co-occurred during the rainy season. The species recorded in the dry season formed a subset of the rainy season, with *E. furinalis*, *L. cinereus*, *Eumops sp.*, *M. neglectus*, and *M. rufus* being recorded only during the rainy season. The sonotype *Saccopteryx sp. "38 –*

42 kHz'' was identified only once during the rainy season in the urban habitat. *E. brasiliensis*, *M. lavali*, *M. nigricans*, and *Thyroptera sp*. were identified only in the dry season, and *M. temminckii* during the rainy season (Table 2; Supplementary Data S1).

Annually, the Jaccard similarity index indicated high similarity between non-urban and peri-urban habitats (*0.80*), followed by peri-urban and urban habitats (*0.68*), and non-urban and urban habitats (*0.54*). During the dry season, the species similarities between non-urban and peri-urban habitats, peri-urban and urban habitats, and non-urban and urban habitats, were *0.52*, *0.65*, and *0.43,* respectively. Additionally, during the rainy season the similarities between non-urban and peri-urban habitats, peri-urban and urban habitats*,* and non-urban and urban habitats were *0.83*, *0.50*, and *0.43,* respectively.

Similarly, PERMANOVA indicated a weak effect of habitat on species composition ($R^2_2 = 0.17, perm = 10,000, P < 0.001$). Pairwise comparisons revealed significant differences in species composition across all habitat pairs (non-urban × peri-urban: $R^2_1 = 0.04, perm=10,000, P=0.013$; non-urban × urban: $R^2_1 = 0.16, perm = 10,000, P = 0.001$; peri-urban × urban: $R^2_1 = 0.13, perm = 10,000, P = 0.001$). During the dry season, there were significant differences in species composition between habitats ($R^2_2 = 0.20, perm = 10,000, P < 0.001$), and pairwise comparisons revealed that these differences occurred between all pairs (non-urban × peri-urban: $R^2_1 = 0.07, perm = 10,000, P = 0.02$; non-urban × urban: $R^2_1 = 0.24, perm = 10,000, P = 0.001$; peri-urban × urban: $R^2_1 = 0.15, perm = 10,000, P = 0.001$). During the rainy season, significant differences in species composition were found between habitats ($R^2_2 = 0.20, perm = 10,000, P < 0.001$), and pairwise comparisons revealed no significant differences between non-urban and peri-urban habitats ($R^2_1 = 0.04, perm = 10,000, P = 0.291$), but significant differences were found between non-urban and urban habitats ($R^2_1 = 0.12, perm = 10,000, P = 0.001$) and between peri-urban and urban habitats ($R^2_1 = 0.16, perm = 10,000, P = 0.001$).

Contrary to our hypothesis, the findings of the present study showed was no decrease in species richness along non-urban-urban gradient, actually it occurred only from peri-urban to urban habitat. A previous finding indicated that land-use intensification is associated with a reduction of bat species richness, but when acoustic monitoring data was separated from mist-net data these relationships became weaker (Pereira et al. 2018). The present study results showed that differences in land-use around the non-urban and peri-urban habitats were not associated with a decrease in the insectivorous bat species richness, which was consistent with previous studies on intermediate habitats in Sydney, Australia (Threlfall et al., 2011). It could be attributed to the higher productivity in intermediate habitats than vegetated habitats or lower human density in intermediate habitats than urban habitats, species characteristics, and habitat characteristics, which favors open-space foragers (Threlfall et al., 2011, 2012). A previous study showed that there was a decrease in species richness in urban habitats in tropical forest areas of Panama when compared with non-urban habitats in villages (Jung and Kalko, 2010), and similar results were obtained in Mexico (Ávila-Flores and Fenton, 2005).

Analysis of the bat species composition inhabiting different habitats showed that the species formed subsets along the non-urban-urban gradient. Species inhabiting the peri-urban habitats formed a subset of those observed in the non-urban habitats, except for *E. chiriquinus*, and species in the urban habitats formed a subset of those inhabiting the peri-urban habitats, except for *Saccopteryx sp. "38–42 kHz,"* in line with the findings of Jung and Kalko (2010). Differences in species composition between non-urban and peri-urban habitats could be due to the absence or presence of *E. chiriquinus* and Emballonuridae species. However, *E. chiriquinus* has recently been observed in fragmented habitats in Brazil (Gregorin and Loureiro, 2011; Zortéa et al, 2013, Loureiro and Gregorin, 2015). *P. trinitatis* was recorded in urban parks in the DF and protected areas next to these urban areas

(Ramalho, 2019; Reis, 2019). *Saccopteryx leptura* was found in forest fragments in the urban areas of Amazonas, Rio de Janeiro, and Paraíba states, and in protected areas next to urban areas in the FD (Militão, 2017; Nunes et al. 2017). Differences in species richness and composition between peri-urban and urban habitats could be attributed to the absence of some Vespertilionidae and Molossidae species in the urban habitats, and the absence of some Mormoopidae species in the peri-urban habitats. However, *E. furinalis*, *L. cinereus*, *L. ega*, *M. albescens*, *M. riparius*, *M. ruber*, *M. neglectus*, and *P. parnellii* have been recorded in Brazilian urban habitats (Militão, 2017; Nunes et al. 2017, Ramalho, 2019, Reis 2019).

Among the 16 species observed in the urban habitats, *P. parnellii* and *Thyroptera sp.* were members of the Emballonuridae, Vespertilionidae, and Molossidae families. Therefore, it is impossible to conclude that urbanization favored these families, thus disproving our hypothesis. There was an uneven reduction in the species richness of these families with increasing urbanization. Changes in habitat use by bats tend to be species-specific and have no phylogenetic or functional influence (Jung and Threlfall, 2016). In addition to decreased in species richness in the Cerrado, intensification of land use change is also associated with the loss of functional and phylogenetic diversity (Pereira et al. 2018). The Vespertilionidae absence in the urban habitats indicates that urbanization did not favor this family members in the Cerrado. However, forest habitats this families due to echolocation pulses characteristics (Denzinger and Schnitzler, 2013) and morphological characteristics, possibly enabling them to move between habitats (Bader et al., 2015) and to micro-foraging habitats (Jung and Kalko, 2010, 2011).

Furthermore, the present study findings supported our hypotheses that seasonal variations influence both bat species richness and composition. The insectivorous bats species richness and composition seasonality found here could be attributed to primary prey life cycles. For instance, the population of the insects belonging to the orders Coleoptera,

Lepidoptera, and Hemiptera, which are the primary preys of insectivorous bats (Aguiar and Antonini 2008, Aguiar et al. 2021) peaks in the rainy season in both natural and urbanized habitats in the Cerrado (Silva et al. 2011; Aranda et al. 2011). Additionally, *E. furinalis* and *M. nigricans* may have an 80% overlap in diet and no variation throughout the year in the Cerrado (Aguiar and Antonini, 2008). Hence, a greater abundance of resources could lead to less competition between these insectivorous bats and be one of the reasons for the high similarity in species richness and composition between non-urban and peri-urban habitats during the rainy season and the decrease in the composition similarity during the dry season. Generally, non-urban habitats are more productive than urban habitats (Jung and Threlfall, 2016). Moreover, seasonality can influence shelter patterns and habitat occupancy, reproduction, diet, and species richness and abundance, among insectivorous bats. For instance, seasonality affects the shelter of *Tadarida brasiliensis* in urban areas (Scales et al. 2007). *Eptesicus nilssoni* is found in forested and agricultural areas during the summer. In spring and autumn, this specie is found near artificial lighting environments (Rydell, 1991). For cave-dwelling insectivores, shelters away from foraging areas, insect biomass, and higher rainfall can restrict the reproductive period to the most fertile periods, whereas tree-dwelling insectivores reproduce throughout the year (Nurul-Ain et al. 2017).

Regarding Mormoopidae, prey availability is a major determining factor, leading to seasonal variation in species richness and composition, with a higher prey population during the rainy season (Salinas-Ramos et al., 2015). In Amazonia, the richness of animalivorous Phyllostomidae is dependent on seasons, and the abundance is dependent on landscape configuration and composition during the dry and rainy seasons, respectively, with obvious and observed species-specific responses (Klingbeil and Wilig, 2010). In addition to biological and ecological factors, other urbanization-related changes, such as artificial lighting, fragmented landscapes, and greater exposure to predators, can also influence the occurrence

of bats (Russo and Ancilloto, 2015). Therefore, several biological, ecological, and anthropogenic variables can be examined to predict the insectivorous bats' species richness.

Additionally, urban habitats might be an ecological trap for insectivorous bat populations in the Cerrado region. Ecological traps are poor habitats that were previously perceived as suitable habitat, probably leading to the extinction of the present population (Schlaepfer et al. 2002). The occurrence and existence of ecological traps are common in landscapes undergoing intense modifications (Battin, 2004). Despite high population densities and supply of resources, bats in urban habitats are subject to a greater risk of opportunistic predation, exposure to diseases, noise and pollution, and increased resource competition, stress, and mortality (Russo and Ancilloto, 2015). For example, *Myotis lucifugus* is more abundant in urban habitats on North American prairies; however, these individuals also have lower body condition, lower reproductive rates, and lower production of juveniles (Coleman and Barclay, 2012). Additionally, although *Pteropus poliocephalus* tend to favor urban habitats due to a higher supply of resources, they also suffer high mortality rates from high-voltage networks (Tella et al. 2020).

Overall, the findings of this study demonstrate the importance of bioacoustics as a tool for sampling Neotropical insectivorous bats. This technique was more efficient in identifying insectivorous bats species than the mist net technique used by Oliveira et al. (2017). Also, 4h of sampling was not enough to reach 90% of the species richness, contrary to what was indicated by López-Baucells et al. (2021) for Neotropical habitats. In Cerrado, at least the first 6h needs to be sampled. Moreover, the results of this study are in line with previous findings of high species richness of insectivorous bats in urban areas of the Cerrado region (Stutz et al. 2004; Pacheco et al. 2010; Shapiro et al. 2013), emphasizing the importance of urban parks in maintaining bat diversity in cities.

ACKNOWLEDGMENTS

Supplementary data S1. Species/sonotypes Quadratic Driscriminant Analysis predicted values and accuracy. *Eptesicus brasiliensis* (ebra); *E. furinalis* (efur); *Myotis nigricans* (mnig), *M. riparius* (mrip); *M. ruber* (mrub); *Rhogeessa hussoni* (rhus); *Eumops sp.* (esp); *Molossops temminckii* (mtem); *Molossus currentium* (mcur); *M. molossus* (mmol); *M. rufus* (mruf); *Molossus spp.* (mspp); *Nyctinomops laticaudatus* (nlat); *Promops nasutus* (pnas); and *Thyroptera sp.* (Thy).

Classified as	True Group ebra	efur	mlav	mnig	mrip	mrub	rhus	esp	mtem	mcur	mmol	mruf	mssp	nlat	nmac	pnas	Thy
ebra	88	0	3	0	0	0	2	0	0	0	23	0	1	0	0	0	1
efur	0	8	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
esp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
mcur	0	0	0	0	0	0	0	0	0	68	36	0	1	0	0	6	0
mlav	3	0	26	2	0	0	2	0	0	0	0	0	1	0	0	0	3
mmol	3	0	0	0	0	0	0	0	0	1	86	0	1	0	0	2	0
mnig	0	0	13	54	1	0	0	0	0	0	0	0	0	0	0	0	2
mrip	0	0	0	1	5	3	0	0	1	0	0	0	0	0	0	0	3
mrub	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
mruf	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
mssp	3	0	4	0	0	0	0	0	0	0	0	0	28	0	1	0	0
mtem	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0
nlat	0	0	0	0	0	0	0	0	0	0	0	2	0	29	1	0	0

nmac	0	0	0	0	0	0	0	2	0	0	0	0	0	0	64	0	0
pnas	0	0	0	0	0	0	0	0	0	6	6	0	0	0	0	7	0
rhus	2	0	4	0	0	0	4	0	0	0	0	0	0	0	0	0	2
Thy	1	0	1	0	0	3	0	0	0	1	0	0	0	1	0	0	5
Total	100	8	51	58	6	6	8	2	23	77	152	2	32	30	68	15	18
Sensitivity	0.88	1.00	0.51	0.93	0.83	0.00	0.50	0.00	0.96	0.88	0.57	0.00	0.88	0.97	0.94	0.47	0.28
Specificity	0.95	1.00	0.98	0.97	0.99	1.00	0.99	1.00	1.00	0.93	0.99	1.00	0.99	1.00	1.00	0.98	0.99
Pos Pred Value	0.75	0.80	0.70	0.77	0.38	0.00	0.33	NaN	1.00	0.61	0.92	0.00	0.78	0.91	0.97	0.37	0.42
Neg Pred Value	0.98	1.00	0.96	0.99	1.00	0.99	0.99	1.00	1.00	0.98	0.88	1.00	0.99	1.00	0.99	0.99	0.98
Prevalence	0.15	0.01	0.08	0.09	0.01	0.01	0.01	0.00	0.04	0.12	0.23	0.00	0.05	0.05	0.10	0.02	0.03
Detection Rate	0.13	0.01	0.04	0.08	0.01	0.00	0.01	0.00	0.03	0.10	0.13	0.00	0.04	0.04	0.10	0.01	0.01
Detection Prevalence	0.18	0.02	0.06	0.11	0.02	0.00	0.02	0.00	0.03	0.17	0.14	0.00	0.05	0.05	0.10	0.03	0.02
Balanced Accuracy	0.91	1.00	0.75	0.95	0.91	0.50	0.74	0.50	0.98	0.90	0.78	0.50	0.93	0.98	0.97	0.72	0.63

Supplementary Data S2 — Call parameters from the echolocation pulses emitted by insectivorous bats in Cerrado. Harmonic (H) with maximum energy; Pulse structure (Pulse Str): pulse type: frequency modulated (FM), constant frequency (CF) or quasi-constant frequency (qCF); modulation: upwards (up) or downwards (d); Maximum Energy Frequency (FME), Maximum Frequency (FMAX), Minimum Frequency (FMIN), Bandwidth (BW), Initial Frequency (FINITIAL), Final Frequency (FEND), Pulse Duration (D).

Specie	H	Pulse Str	FME (Hz)	FMAX (Hz)	FMIN (Hz)	BW (Hz)	FINITIAL (Hz)	FEND (Hz)	D (ms)	IPI (ms)
Vespertilionidae										
Eptesicus brasiliensis	H1	FM-qCFd	43241.83±517	51016.5±207	40568.39±1814.28	10448.12±7403.81	50804.86±8451.51	40965.73±1806.28	2.34±0.54	196.94±117.17
Eptesicus chiriquinus	H1	FM-qCFd	35231.47±1229.99	41602.51±3845.35	33410.56±1611.55	8191.94±3266.92	41224.43±3891.16	33779.19±1524.27	1.9±0.38	426.93±168.72
Eptesicus furinalis	H1	FM-qCFd	35403.46±1218	39771.16±1836.42	33825.29±1090.89	5945.87±1668.66	39478.7±1980.48	34204.33±1193.06	2.14±0.29	289.22±156.02
Lasiurus cinereus	H1	FM-qCFd	25646.8±2640.68	31890.59±5546.04	23752.68±2890.19	8137.9±6736.69	28460.39±2511.83	25631.42±2617.46	2.26±0.13	329.06±151.26
Lasiurus ega	H1	FM-qCFd	33944.69	41411.76	32652.87	8758.89	41411.76	32652.87	1.69	436.38
Myotis albescens	H1	FM-qCFd	47830.32±944.39	67187.05±11644.63	45323.51±2365.31	21863.54±12826.55	67078.12±11848.25	45570.83±2563.45	2.53±0.67	135.13±76.4
Myotis lavali	H1	FM-qCFd	49361.93±2420.67	62845.9±8880.58	46385.65±2527.55	16460.25±8682.97	62774.42±8955.51	46670.64±2573.6	2.19±0.46	201.11±127.16
Myotis nigricans	H1	FM-qCFd	54134.07±1429.32	68194.41±6227.87	51488.87±1315.86	16705.54±6209.71	68165.33±6256.71	51771.52±1451.91	2.01±0.29	190.6±140.36
Myotis riparius	H1	FM-qCFd	57549.38±1509.52	71116.46±7706.33	54759.92±1935.76	16356.55±7971.18	71088.43±7731.23	55185.19±1922.09	1.88±0.23	232.27±128.93
Myotis ruber	H1	FM-qCFd	59603.67±2465.5	71834.69±11227.77	56916.76±2083.5	14917.93±10987.46	71745.81±11298.3	57309.95±2210.13	1.98±0.37	192.61±108.55
Rhogeessa hussoni	H1	FM-qCFd	48656.06±2272.41	64768.58±8045.37	43585.88±1696.25	21182.7±7440.54	64716.2±8091.67	43744.22±1666.54	2.15±0.33	168.32±73.88
Molossidae										
Eumops sp.	H1	qCFd	17679.78±270.68	18245.57±786.82	17242.77±188.64	1002.8±664.08	17774.91±712.84	17619.01±435.37	4.38±1.96	490.88±271.15

Species									
Molossops neglectus	H1	qCFup	52648.25±2943.61	54273.37±2943.61	50806.75±3968.83	3466.62±1491.43	52247.23±4625.75	52781.95±2434.4	6.21±7.44	231.69±123.55
Molossops temminckii	H1	qCFup	47985.48±2773.03	50259.64±3408.32	44118.19±2917.02	6141.45±1829.94	44531.84±3822.26	49534.03±2839.35	2.55±1.03	217.84±128.71
Molossus currentium	H1	qCFd	30766.11±813.97	32199.37±813.97	28976.29±985.8	3223.09±873.34	31078.08±1247.11	29692.57±1021.45	4.83±2.1	258.85±134.73
	H1	qCFd	33759.46±1046.95	34812.82±1046.95	32242.4±1272.2	2570.42±747.63	33574.72±1207.58	32972.63±1359.74	4.89±1.66	284.46±153.89
	H1	qCFd	35866±647.05	36838.68±647.05	34253.82±703.88	2584.86±573.62	35462.26±1011.6	34998.01±724.69	5.04±1.49	275.82±126.48
Molossus molossus	H1	qCFd	34523.76±719.98	35821.19±719.98	33466.68±572.3	2354.51±787.96	34416.36±1050.63	34280.66±529.26	3.77±1.44	319.97±172.34
	H1	qCFd	37238.25±1435.65	38310.8±1435.65	35683.63±1381.23	2627.17±619.12	36899.06±1638.77	36416.26±1347.8	4.94±1.32	224.87±133.91
	H1	qCFd	41773.6±2330.11	43480.56±2330.11	40241.27±944.9	3239.29±1885.05	42465.08±1920.61	40931.28±2049.16	4.17±1.74	204.5±108.45
Molossus rufus	H1	qCFd	24337.11±1742.59	25317.32±1612.98	23254.85±1601.61	2062.47±387.08	24300.03±1653.09	24211.47±1678.28	3.24±0.82	376.34±154.03
Molossus spp.	H1	qCFd	48425.42±2987.61	50406.49±3372.4	46697.45±3144.48	3709.04±1817.39	49707.5±3515.99	47632.76±3352.88	2.92±1.03	197.22±121.16
Nytcinomops laticaudatus	H1	qCFd	23945.33±1317.52	25705.2±1293.17	22371.89±1111.2	3333.31±821.66	24810.81±1372.02	22954.52±1223.17	4.82±1.97	424.15±183.4
Nyctinomops macrotis	H1	qCFd	18987.11±2135.12	20067.85±2375.06	17946.62±1978.14	2121.23±841.51	19263.97±2336.53	18791.94±2118.54	6.06±2.82	428.58±193.35
Promops nasutus	H1	qCFup	34722.55±1677.62	35630.46±1733.83	32909.55±1731.8	2720.91±948.03	33470.24±1865.37	34293.35±1632.29	4.6±1.4	273.83±133.11
Emballonuridae									
Peropteryx triniatis	H2	qCF-FMd	42274.63±689.53	43011.97±712.93	40696.39±903.84	2315.58±467.44	41357.91±721.09	41626.75±1050.63	6.94±0.72	254.43±146.52

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Table 1.1 Study areas in Goiás and FD classified according to the land use buffer in a 3 km around them in 2019. Buffer composition is divided into Cerrado (native vegetation), agriculture, urban habitat and water.

Habitat	Non-urban						Peri-urban				Urban			
Park	CVNP		TRSP		EEAE		BNP		BBGES		EHEP		ACEP	
Park area (ha)	255137.9		40615.15		9203.13		42697.74		4581.45		350		115.29	
Buffer composition	Area (ha)	%	Area (ha)	%	Area (ha)	%	Area (ha)	%	Area (ha)		Area (ha)	%	Area (ha)	%
Cerrado	108885	0.80	17203.10	0.53	6835.59	0.39	17458.40	0.41	6007.77	0.50	1045.26	0.18	432.45	0.09
Agriculture	34494.8	0.20	15134.70	0.47	9081.54	0.52	19430.60	0.46	2671.29	0.22	606.96	0.10	438.75	0.10
Urban	418.23	0.00	4.86	0.00	1475.01	0.08	5384.61	0.13	2956.59	0.25	4237.83	0.72	3687.93	0.81
Water	35.73	0.00	0.54	0.00	9.36	0.00	54.18	0.00	402.30	0.03	5.40	0.00	0	0.00
Total	143834	1	32343.1	1	17401.5	1	42327.70	1	12038	1	5895.45	1	4559.13	1

Table 2.2. Number of passes (N) from the registered species in each habitat from the urbanization gradient across Cerrado in dry and rainy seasons.

Habitat type		Non-urban		Peri-urban		Urban	
Season		Dry	Rainy	Dry	Rainy	Dry	Rainy
Family	Species	N	N	N	N	N	N
Vespertilionidae	*Eptesicus brasiliensis*	7	18	125	196	155	-
	Eptesicus chiriquinus	-	-	-	6	-	1
	Eptesicus furinalis	1	1	-	39	-	-
	Lasiurus cinereus	2	-	-	2	-	-
	Lasiurus ega	1	-	-	-	-	-
	Myotis albescens	-	1	2	1	-	-
	Myotis lavali	20	56	55	92	36	-
	Myotis nigricans	20	38	39	192	1	-
	Myotis riparius	14	7	1	12	-	-
	Myotis ruber	12	15	1	6	-	-
	Rhogeessa hussoni	-	1	27	6	5	1
Molossidae	*Eumops sp.*	-	1	-	1	2	6
	Molossops neglectus	-	2	-	2	-	-
	Molossops temminckii	15	24	27	45	-	7
	Molossus currentium	18	13	32	65	155	102
	Molossus molossus	3	128	22	55	396	161
	Molossus rufus	1	4	-	6	1	1
	Molossus spp.	7	33	14	85	15	6
	Nyctinomops laticaudatus	51	38	7	25	7	22
	Nyctinomops macrotis	-	5	3	15	36	284
	Promops nasutus	-	2	3	22	29	23
Emballonuridae	*Peropteryx triniatis*	-	7	-	-	-	-
	Saccopteryx leptura	1	1	-	-	-	-
	Saccopteryx sp. "38-42kHz"	-	-	-	-	-	1
Mormoopidae	*Pteronotus cf. parnellii*	1	-	-	-	-	-
Thyropteridae	*Thyroptera sp.*	24	7	24	19	18	-
Species richness		17	21	15	21	13	12
Total Species Richness			24		21		16
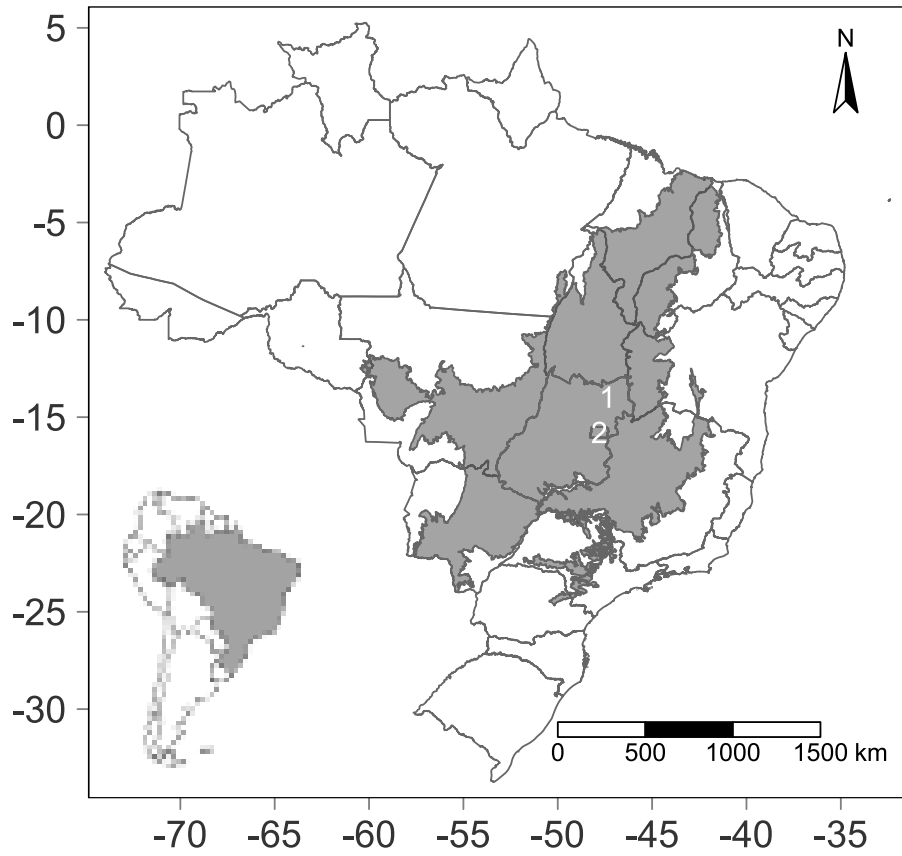
Figure 1.1. Map showing the Cerrado biome in Brazil and the studied protected areas in

Goiás state (1) and the Federal District (2), and Brazil's location in South America.
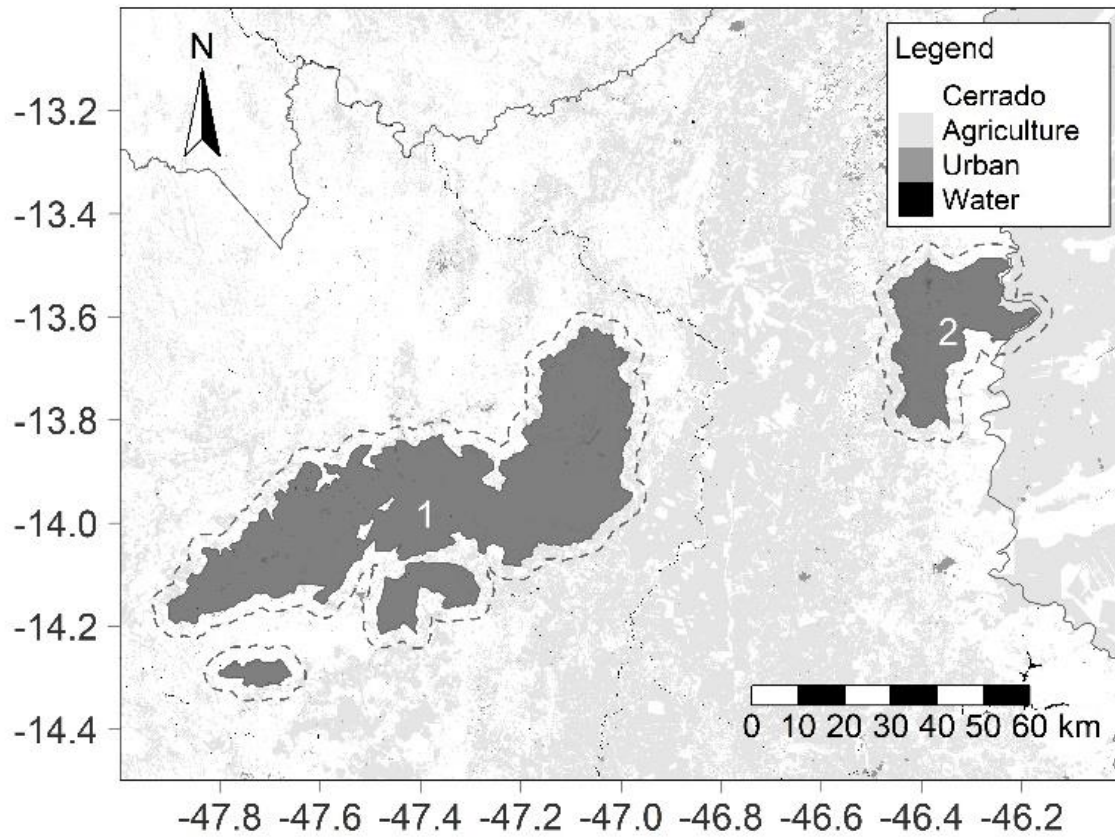
Figure 1.2. Map showing the studied areas in Goiás State (1:Chapada dos Veadeiros National Park; 2: Terra Ronca StatePark) with the 3km buffer (dotted lines).
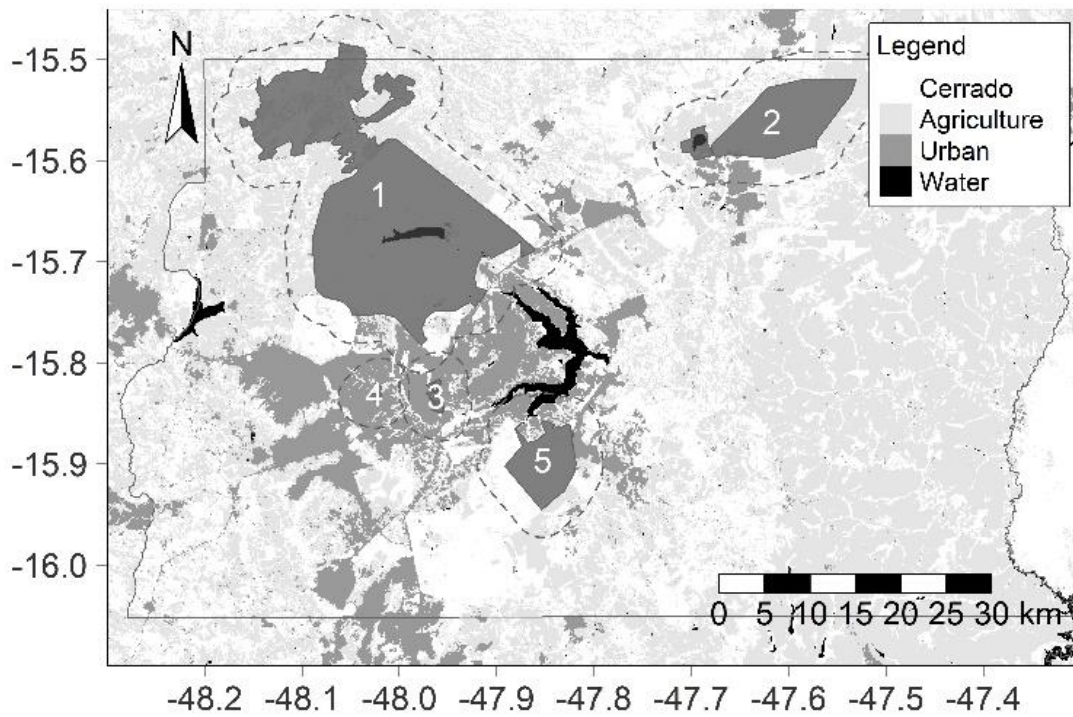
Figure 1.3. Map showing the studied areas in the Federal District (1: Brasilia National Parl; 2: Ecological Station of Aguas Emendadas; 3: Ezachias Heringer Ecological Park; 4: Aguas Claras Ecological Park, and 5: Brasilia Botanical Garden Ecological Station) with the 3 km buffer (dotted lines).
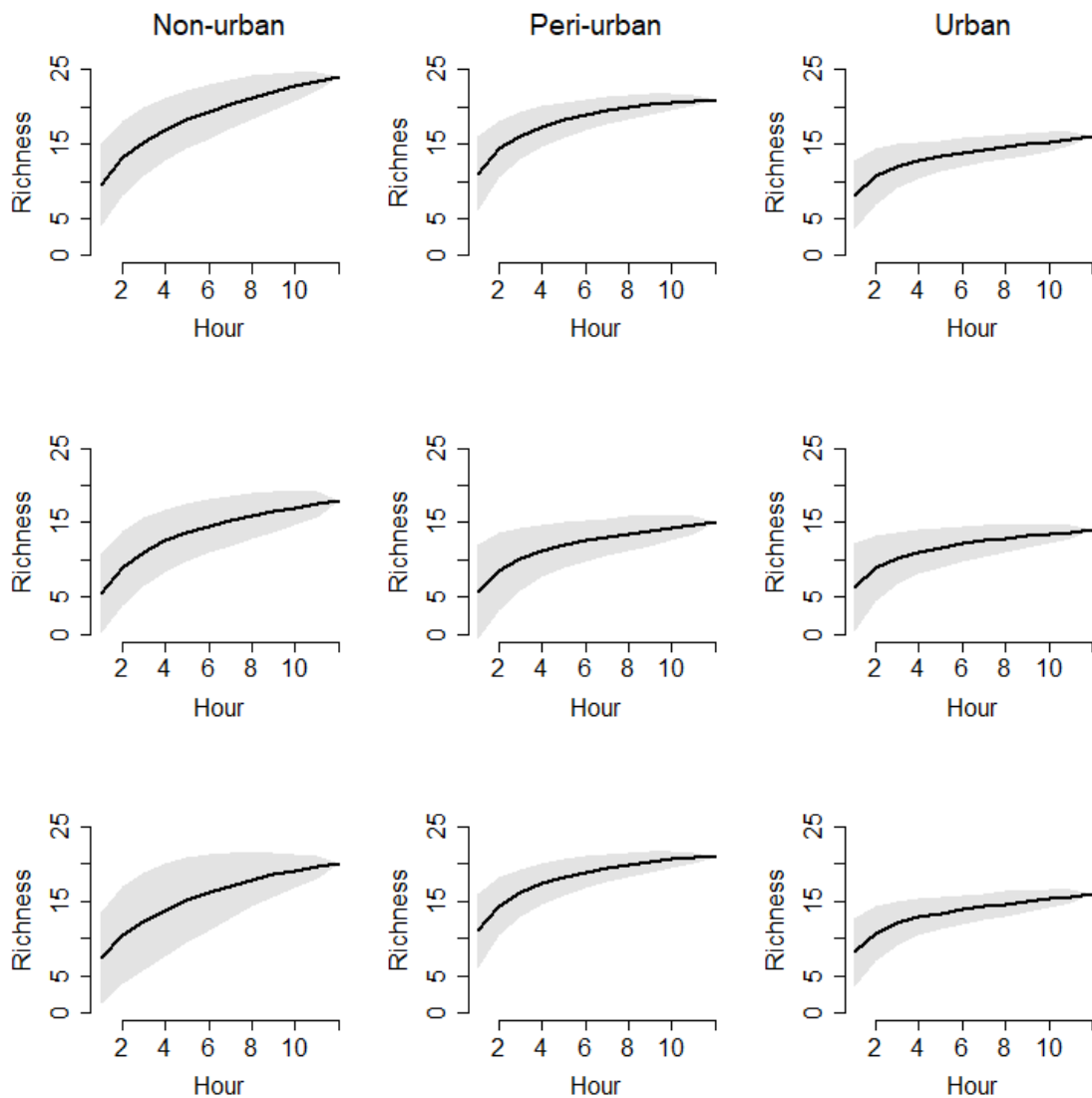
Figure 1.4. Species accumulation curves of sampling hours, starting 18:00 and following the next 12 hours, from non-urban, peri-urban and urban habitats all year and separated in dry and rainy season in Cerrado and confidence intervals (grey).

CAPÍTULO 2

ECOLOCALIZAÇÃO DE MOLOSSIDAE EM UM GRADIENTE URBANO
NO CERRADO

Esse capítulo será submetido a Acta Chiroperologica e está formatado de acordo com o periódico.

Molossidae echolocation across an urban gradient in Cerrado

ABSTRACT

Echolocation in bats is a form of spatial orientation that is also adapted for foraging, consisting of the emission of pulses at ultrasound frequencies allowing the detection, characterization, and identification of the landscape and prey. Through these pulses, it is possible to characterize species. In urban areas, noise pollution can lead to a decreased fitness of the species since constant noise masks its prey and predators, and unpredictable noise considered danger can lead to local evasion of bats. In these habitats, bats need to adapt to avoid acoustic masking and reduce impacts on foraging efficiency and/or evasion. One way to adapt is to change the tonal and temporal aspects of the pulses. Our objective was to evaluate whether there are intraspecific differences in the echolocation pulses of *Molossus currentium*, *M. molossus,* and *Nyctinomops laticaudatus* under the hypothesis that *N. laticaudatus* is affected by the habitat and the species of Molossus are not and that the species present differences in the parameters associated with the seasonality. Thus, we took the average for three selected pulses from each pass of the following parameters: Frequency of Maximum Energy (FME), Maximum Frequency (F_{MAX}), Minimum Frequency (F_{MIN}), Bandwidth (BW = F_{MAX}-F_{MIN}), Initial Frequency ($F_{INITIAL}$), End Frequency (F_{END}), Pulse Duration (D), Inter-Pulse Interval (IPI), and the Duty-Cycle (DC). We performed a 2-way ANOVA on ranks which indicated that *M. currentium* emits higher pulses, less modulated, and with a higher DC value in urbanized than in non-urban habitats, *M. molossus* emitted pulses with higher frequency and longer duration in rainy season, and *N. laticaudatus* significant differences in pulses were find to all parameters. Despite changes in the pulses between habitats, all the pulses described here are part of the vocal repertoire of these species, corroborating the wide plasticity they present.

Keywords: Adaptation, bioacoustics, Chiroptera, city, pulse, vocalization.

INTRODUCTION

Bats use echolocation as a navigation mechanism, the accepted hypotheses indicate that echolocation was primarily a form of spatial orientation and later was adapted to predation (Schnitzler et al. 2003). Echolocation is the emission of ultra-frequency sound signals and the use of the returning echo to detect, characterize and identify the environment

(Schnitzler and Kalko, 2001). The Duty-Cycle (DC; ratio between signal and period, here as the ratio between the pulse duration and the sum of pulse duration and inter-pulse interval) allows to separate the species of Chiroptera in High Duty-Cycle (HDC), these species separate the pulse and the returning echo through the frequency and are limited to the families Rhinolophidae, Hipposisderidae and *Pteronotus parnellii* species complex (Mormoopidae), and Low Duty-Cycle (LDC), which are the other species that echolocate and separate the pulses and the returning echo in time, to avoid acoustic masking due to simultaneous emission of the pulse and the returning echo (Fenton et al. 2012). Two main types of pulses are emitted: Narrowband pulses, characterized by little variation in the emitted frequency and are divided into Constant Frequency (CF) and Quasi-constant Frequency (QCF), and broadband, which are called Frequency-Modulated (FM). Narrowband pulses are used for detection and characterization, while broadband pulses are used for prey characterization and identification (Schnitzler and Kalko, 2001).

Echolocation pulses have species-specific characteristics and are related to variation in body size, habitat, and behavior (Barclay et al. 1999). In addition, bats can change pulse characters such as frequency of maximum energy and duration to reduce the effects that temperature and humidity have on sound, a phenomenon known as atmospheric attenuation (Chavierri and Quirós, 2017). Despite these changes, it's possible to identify species through the parameters Frequency of Maximum Energy (FME), Maximum Frequency (F_{MAX}), Minimum Frequency (F_{MIN}), Bandwidth (BW = F_{MAX}-F_{MIN}), Initial Frequency ($F_{INITIAL}$), End Frequency (F_{END}), Pulse Duration (D) and Inter-Pulse Interval (IPI) (Fenton, 2003; Menon et al. 2018, Arias-Aguilar et al, 2018). These parameters are extracted from echolocation spectrograms obtained in acoustic monitoring using ultra-frequency recorders (Barclay et al. 1999). This method, known as acoustics sampling, also allows the evaluation of temporal and spatial activity patterns, allowing the identification of more discreet animals, which emit fewer vocalizations, and of some carnivores and frugivores that use echolocation to identify small vertebrates and fruits of animals which they feed (Brigham and Fenton, 1986; Arlettaz et al. 2001; Hintze et al. 2016; Fenton et al. 1987; Frick, 2013; Estrada et al. 2004). In the Neotropics, open-space and edge-eating insectivorous bats emit narrowband pulses with little modulation and varying up to 60 kHz (Schnitzler and Kalko, 2001; Denzinger and Schnitzler, 2013). In this case, acoustics sampling is the most recommended method for sampling, allowing the sample to have more species per night and more species in general, especially for open-space foragers (O'Farrell and Gannon, 1999; Silva, 2017).

Bats can distinguish natural sounds from sounds of anthropic origin (Geipel et al. 2019). Human sounds are not limited to urban areas and the noise of planes and highways, for example, can reach natural areas (Lynch et al. 2011), with negative consequences on the acoustic landscape and the behavior of birds, frogs, and mammals, especially species that depend on sound to forage (Barber et al. 2010, Bunkley et al. 2015). In urban habitats, noise pollution affects bats emergence period and foraging periods, and habitats (Russo and Ancilloto, 2015). This interference can happen through chronic and frequent noises that interfere with the ability to detect prey and predators due to acoustic masking, intermittent and unpredictable sounds that can be perceived as threats and increase the stress of individuals (Francis and Barber, 2013; Luo et al. 2015) or attention deficit in foraging activity due to reduced cognitive activity that was previously directed to this task (Luo et al. 2015). Consequently, there may be reduced fitness of individuals (Francis and Barber, 2015), decreased foraging efficiency (Siemers and Schaub, 2011), evasion, or reduced activity of bats in habitats with anthropogenic noise, even without acoustic masking. (Finch et al. 2020; Li et al. 2020; Domer et al. 2021).

When they persist in urban habitats and with constant noise, some echolocation characteristics may favor the occupation of these habitats, such as lower frequency of echolocation pulses for bats from Asia, Australia and North America and longer pulse duration for bats from Australia, and South America (Jung and Threlfall, 2018). *T. brasiliensis* (Molossidae), for example, increases pulse duration by 0.90 ms and decreases bandwidth by 600 Hz (Bunkley et al. 2015). The number of pulses emitted may be reduced in car traffic noise conditions, but the duration of the pulse sequence remains the same (Song et al. 2019). The same can occur with social calls that become less complex and monosyllable sequences (Jiang et al. 2015). And in situations of acoustic masking by urban noise, *Trachops chirrhosus* uses its vision to capture other prey cues in addition to the emission of vocalizations by its prey (frogs) (Gomes et al. 2016).

In this study, our aim is to evaluate whether there are intraspecific differences in the echolocation pulses of *Molossus currentium*, *Molossus molossus*, and *Nyctinomops laticaudatus* comparing the calls recorded in non-urban, peri-urban and urban habitats in the dry and rainy seasons in the Cerrado. We will test the hypotheses (a) *N. laticaudatus*, by emitting pulses with a lower frequency, would present differences in tonal and temporal parameters and duty-cycle related to the habitat, while *M. currentium* and *M. molossus* have calls with greater frequency and would not be affected by the habitat and (b) The three species would present intraspecific tonal and temporal differences in pulses related to seasonality and

different duty-cycles. We hope that, as *T. brasiliensis* was observed by Bunkley et al. (2015) altering tonal and temporal aspects of its echolocation pulses in habitats with persistent noise, in Cerrado *N. laticaudatus* would emit different pulses in urbanized habitats, as these are associated with greater noise pollution (Lynch et al. 2011). Both species have QCF downward calls and FME around 24 kHz (Arias-Aguilar et al. 2018). We also expected species would have differences in echolocation pulses associated with seasonality, as *M. molossus* itself and *Molossops temminckii* (Molossidae) were observed emitting different pulses under different temperature and humidity conditions on the border between Brazil and Uruguay (Chaverri and Quirós, 2017; Oliveira et al. 2018).

MATERIALS AND METHODS

Study area

Urban habitats are central areas in cities and peri-urban areas are areas at the interface of urban, rural, and natural vegetation (Clergeau et al. 2001). For this study, we selected seven parks within the Cerrado biome and previously classified them into non-urban (<10% urban habitat), peri-urban (11 – 50% urban habitat), and urban (>50% urban habitat) habitats based on land use in a 3 km buffer around the parks. We used the Cerrado land use map (30x30 m resolution) from the NGO Mapbiomas (Souza et al. 2020) to create the buffers and shapefiles of the parks obtained from the Ministry of the Environment and the Instituto Brasília Ambiental. We performed the reclassification of the map in Cerrado, agriculture, urban, and water was in R software (v. 4.0.5; R. Core Team, 2021) with the help of 'sf' (Pebesma, 2018), 'raster' (Hijmans, 2021), 'tmap' (Tennekes, 2018), 'dplyr' (Wickham et al., 2021a), and 'stars' (Pesbema, 2021) packages.

Non-urban habitat. – We classified two parks in the state of Goiás: Chapada dos Veadeiros National Park (CVNP; 14° 10' S, 47° 30' W) and Terra Ronca State Park (TRSP; 13°29' S, 46°23' W). These parks have 255,137.9 hectares (ha) and 40,615.15 ha and the buffers have 143,834 ha and 32,343.1 ha, respectively. In both, 0% were classified as urban habitat. The local climate is Aw (tropical with a dry season in winter) in Köppen classification, CVNP has a maximum altitude of 1670 m, average annual temperature between 19ºC and 22ºC, and average annual precipitation between 1600 mm and 1800 mm, TRSP has an average annual temperature between 24 – 25ºC and average annual rainfall between 1000 – 1200 mm (Cardoso et al. 2014). We selected one more park, but this one in the Federal District (FD): Águas Emendadas Ecological Station (ESAE; 15° 33' S, 47° 36' W), this park

has 9,203.74 ha and a buffer of 17,401.50 ha, of which 8% of the area is classified as urban area. The FD has an average annual temperature between 1400 – 1600 mm and an average annual temperature between 20 – 21 ºC (Cardoso et al. 2014). In these parks, it is possible to find cerrado phytophysiognomies of forest, savanna, and grassland types (Felfili et al. 2007; MMA/ICMBio, 2009).

Peri-urban and urban parks were all selected in FD and are under the same climate conditions as ESAE.

Peri-urban habitat. – Brasilia National Park (BNP; 15° 38' S 48° 1' W) has 42,697.74 ha and a buffer of 42,327.72 ha, of which 13% is classified as urban habitat, and the Brasilia Botanical Garden Ecological Station (BBGES; 15º 88' S, 47º 85' W) has 4,581.45 ha, and a buffer of 12,038 ha, of which 25% is classified as urban habitat. Inside BNP, the predominant Cerrado phytophysiognomy is Cerrado *stricto sensu*, not excluding other forest, savanna, and grassland formations, as well as in the BBGES (Moreira, 2000; Nobrega et al. 2001; Farias et al. 2008; Arruda, 2018).

Urban habitat. –Águas Claras Ecological Park (ACEP; 15º 83' S, 48º 02' W) has 115.29 ha and a buffer of 4559.13 ha, of which 72% of the area is classified as urban habitat, and the Ezachias Heringer Ecological Park (EHEP; 15º 83' S, 47º 95' W) has 350 ha and a buffer of 5,895.45 ha, of which 72% of the area is classified as an urban habitat. In the parks, it is possible to find typical Cerrado formations, such as gallery forest, Cerrado *stricto sensu*, and grassland formations (Nogueira et al. 2002; Munhoz and Amaral, 2007).

Data collection

We obtained the data from the Laboratory of Biology and Conservation of Bats, Department of Zoology, Institute of Biological Sciences, University of Brasília. In each park, we selected seven or eight recorders, totaling 15 recorders per habitat/season, in exception the non-urban habitat in dry season where we selected 14 recorders. All records obtained were done in non-urban habitats with Songmeter (Wildlife Acoustics) recorders and in urbanized habitats with Audiomoth (LABmaker) recorders, and all of them were positioned 3m above the ground in an open area, set to record between 18:00 and 6:00 of the following day, with a sampling rate of 384 kHz and remained active for three minutes in 15-minute cycles overnight. In contrasting Neotropical habitats, one night of sampling is enough to detect differences in habitat selection differences in insectivorous bats (López-Baucells et al. 2021). The recordings in the CVNP took place in dry season (September/2014), in the TRSP

in rainy season (February/2014), in ESAE, BBGES, BNP, EHEP and ACEP parks the recordings took place in dry season (August/2017 and September/2018) and in rainy season (February/2018 and 2019. The total sampling effort for non-urban habitat in dry season was 2.016 min and in all other habitat/season was 2,160 min.

Bat pulses

Molossus currentium, *M. molossus* and *N. laticaudatus* emit pulses of the qCFd type with small bandwidth (BW < 10 kHz) and irregular pulse alternation. *Molossus currentium* emits pulses classified as types 1, 2 and 3, characterized by FME of 30 kHz, 33 kHz and 36 kHz, respectively. *Molossus molossus* emits pulses of types 1, 2 and 3, characterized by FME of 34 kHz, 39 kHz and 42 kHz, respectively. *Nyctinomops laticaudatus* emits type 1 and type 2 pulses, characterized by FME of 24 kHz and 26 kHz, respectively (Arias-Aguilar et al. 2018). For *M. currentium*, the three types of pulses were detected in all habitats and seasons, therefore we used all records (n = 385). For *M. molossus*, only type 2 was recorded in all habitats and seasons, therefore we used only type 2 pulses (n= 380 passes). Type 1 pulses (n=28 passes) were not detected in the peri-urban habitat and type 3 pulses (n=350 passes) were not recorded in the dry season of the non-urban habitat. For *N. laticaudatus*, we recorded only type 1 pulses in all habitats and seasons (n = 150).

Parameters measurement

We extracted pulses in R software (v. 4.0.5; R Core Team, 2021) with 'bioacoustics' package (Marchal et al. 2021). We separated pulses and exported to an Excel table for later identification with 'dplyr' (v. 1.0.6; Whickham et al. 2021a), 'tools' (v. 4.0.5; R Core Team, 2020) and 'tidyr' packages (v. 1.3.3; Wickham et al. 2021b. In this work, we define a bat pass as a sequence of three or more pulses with an interval of less than 1 second between pulses. When the pass consisted of more than three pulses, we used only three sequential pulses for species identification based on qualitative parameters (FM, CF or qCF; modulation upwards or downwards) and eight quantitative parameters, six tonal and two temporals, following Marchal et al. (2021) and Arias-Aguilar et al. (2018) definitions: FME is the frequency of maximum energy in pulse, F_{MAX} is the highest pulse frequency, F_{MIN} is the lowest pulse frequency, BW is the difference between F_{MAX} and F_{MIN}, $F_{INITIAL}$ is the frequency at the beginning of the pulse, F_{END} is the final pulse frequency, D is the pulse duration, IPI is the interval between the end of the current pulse and the beginning of the next pulse. Finally, species identification was performed following Arias-Aguilar et al (2018). The duty cycle was defined as D/(D+IPI), which means the pulse duration divided by the period (Fenton et al. 2012), based on the mean of the D and the first two IPIs of each pass.

Statistical analyzes

To analyze the data, we used the mean of each parameter in each pass. For each parameter and the duty-cycle, we performed a 2-way ANOVA with the data transformed into ranks (MacFarland and Yates, 2016), as the assumption of normality of the data was not obtained with the transformations in log and square root. We use each parameter and the duty-cycle as the dependent variable and the habitat, season and the habitat x season interaction as independent variables with the aov function of the 'stats' package (R Core Team, 2021). In the same package, we performed *post hoc* comparisons of the Tukey test with the TukeyHSD function with the ranked data.

RESULTS

M. currentium

We found significant differences in pulses for habitat and habitat x season interaction for the following parameters: FME, F_{MAX}, F_{MIN}, BW, $F_{INITIAL}$ and F_{END} and habitat effect in D and in DC (Table 3.1). *Post-hoc* comparisons performed with the Tukey test revealed that the differences in habitat are between non-urban habitat and urbanized habitats, in urbanized habitats the species emitted pulses with higher frequencies and with lower bandwidth (Tables 3.2 and 3.3). We found a similar result of higher pulses and with lower bandwidth in the habitat x season interaction, where most of the significant differences were between the non-urban habitat in the dry and rainy seasons with the urbanized habitats also in the two seasons (Tables 3.2 and 3.3). Pulses were emitted different in the peri-urban habitat in dry season with rainy season and with the urban habitat in dry and rainy seasons in the parameters FME, F_{MAX}, F_{MIN}, $F_{INITIAL}$ and F_{END} (Table 3.2). In this situation, the pulses emitted in the peri-urban habitat in the dry season have higher frequencies than in the other habitats (Table 3.3). In addition to higher pulses with lower bandwidth, the pulses also have a longer duration in urbanized habitats than in non-urban habitats, but with the same IPI (Tables 3.1 and 3.2). As the IPI did not show significant differences, the DC increased in urbanized habitats in relation to non-urban (Tables 3.2 and 3.3).

M. molossus

Significant differences occurred in pulses emitted between the seasons (Table 3.4). The pulses were emitted with higher FME and F_{MAX} during the rainy season, but with lower $F_{INITIAL}$. There was also an increase in the rainy season in IPI, which resulted in a lower DC (Tables 3.4 and 3.5).

N. laticaudatus

FME and the F_{MIN} had significant differences in the interaction, however the Tukey test did not indicate in which pairs of interactions the differences were. The F_{MAX} was higher in dry season and we found differences between the seasons in the non-urban habitat (and the non-urban habitat in dry season with the urban in dry season and the peri-urban in rainy season. BW was higher in dry season and we observed differences between the seasons in the non-urban habitat and between the non-urban in the rainy season and the peri-urban in the dry season (Tables 3.6, 3.7 and 3.8). $F_{INITIAL}$ had differences in habitat and season, ANOVA and Tukey's test revealed that pulses are emitted higher in non-urban than in urban habitats, in dry season, in dry season in the non-urban habitat versus rainy season and the two seasons in the urban habitat (Tables 3.6, 3.7 and 3.8). F_{END} differed among habitats and Tukey's test indicated it was higher in non-urban than in peri-urban habitat. D had differences in habitat, where it was lower in peri-urban habitat than in non-urban and urban habitat, the IPI was different between habitats, where it was higher in the non-urban than in the urban and differences in the season, where it was higher in rainy season (Tables 3.6 and 3.8). As a result, DC was higher in urban than in non-urban and peri-urban habitats (Tables 3.6 and 3.8).

DISCUSSION

To date, there are no studies on the influence of noise pollution during the emergency period and foraging sites of insectivorous bats in the Brazilian Cerrado. Also, there are no studies on variations in the parameters of the echolocation calls of bats within the biome. Public libraries and large bioacoustics databases are virtually non-existent for the entire Neotropical region, and studies evaluating species distribution, assemblage compositions, and regional variations in calls are rare (Silva et al. 2018; Arias-Aguilar et al, 2018). In Cerrado urban parks noise pollution is associated with the exclusion of bird species and changes in the frequencies emitted in songs (Perillo et al. 2017; Machado et al, 2017; Tolentino et al. 2018). A biophony study carried out around a mining company in the Atlantic Forest demonstrated that noise pollution led to the exclusion of one bat species. However, the study did not identify the species and focused on other taxa (Duarte et al. 2015). In Brazil, studies on the impacts of noise pollution on the behavior and distribution of animals also focus on fish, anurans, primates, and insects (Duarte et al. 2011; 2015; Caorsi et al. 2017; Passos et al. 2020; Leduc et al. 2021).

Partially corroborating our hypothesis, (a) the echolocation pulses of *N. laticaudatus* were affected by the habitat and *M. molossus* were not, however *M. currentium* was also

affected by the habitat, and corroborating our hypothesis, and (b) all species were affected by the season in some of their pulses parameters. *M. currentium* emits pulses at intermediate frequencies between *M. molossus* and *N. laticaudatus* and was the species that presented the greatest number of changes in pulse parameters. There was a clear dominance of type 1 pulses in non-urban habitat and type 2 pulses in urbanized habitats, which can be observed by the means. To date, only two studies Panama describe these species calls and both have sampled a variety of habitats, but have not analyzed the existence of variation in the calls between habitat types. First, *M. currentium* emmits qCFd pulses with FME of 28 kHz, 30 kHz, and 33 kHz (Jung and Kalko 2011). These pulses have the same structure observed in the Cerrado. In the second study, the specie emits three types of pulses with $F_{INIITIAL}$ 30 kHz, 33 kHz or 35 kHz, FEND 24 kHz, 28 kHz, or 30 kHz, BW 4.3 kHz or 3.2 kHz, D 14 ms, IPI 205 ms, 135 ms or 126 ms and DC 7.5%, 12.3% or 12.8% (Jung et al. 2014). Concerning the Cerrado, the two highest pulses have $F_{INITIAL}$ similar to those observed in urbanized habitats but are characterized by lower F_{END} and higher BW, which results in greater modulation. The duration is almost three times longer than the duration observed in the urban habitat (5.1 ms), however, the IPI is lower than all those observed in the Cerrado, as a consequence of this the higher duty cycles. The highest recorded DC is 3.16% in the Cerrado while in Panama the lowest is 7.5%.

Molossus molossus is known for the plasticity that it can emit its pulses, it can emit three types of pulses in the search phase alternating between them (Mora et al. 2004, Borloti et al. 2014). In Havana, Cuba, in the urban habitat, the highest pulses have FME 39.65 kHz, F_{MAX} 40.53 kHz, and F_{MIN} of 37.29 kHz, BW 3.22 Hz and D 11.42 ms (Mora et al. 2004). These pulses are similar type 2 pulses, but in Cerrado habitats type 2 are emitted with lower FME, $F_{MAX,}$ and F_{MIN}. The BW is only not higher than in the non-urban habitat in the dry season. The duration is twice the duration found in the Cerrado. In Espírito Santo, *M. molossus* emits three types of pulses with FME 42 kHz, F_{MAX} 46 kHz, F_{MIN} 31 kHz, and D 5.7 ms (Borloti et al. 2014), however, these animals were not in free flight and this condition may have influenced the recorded pulses. When recorded in free flight, Molossidae pulses show greater variability than when recorded during release (Loureiro et al. 2020). In this study, the season was the only factor that influenced aspects of *M. molossus* pulses. This species can use the plasticity that emits the pulses in closed habitats or to compensate for atmospheric attenuation. In the first situation, Pio et al. (2010) observed that *M. molossus* issued calls with more pronounced FM characteristics with FME 47.0 kHz, F_{MAX} 50.3 kHz, F_{MIN} 22.7 ± 2.6 kHz, D 4.8 ms, and IPI 40.7 ms. The second situation was observed in

Uruguay, where the pulses have little modulation in frequency, FME 39 kHz and D of 4.4 ms. In this habitat, in conditions of low temperature and high humidity the FME is reduced and in conditions of low temperature and humidity the duration increased (Chavierri and Quirós, 2017). In Peru, *M. molossu*s emits all three types of pulses. Type 2 pulses have FME 36.79 kHz, $F_{INITIAL}$ 37.83 kHz, F_{END} 34.57 kHz, BW 3.26 kHz, D 10.82 ms, and IPI 253.18 ms. With the exception of duration, the other tonal and temporal parameters are similar to those found in the Cerrado. In Panama, *M. molossus* was recorded with FME 35 kHz, 39 kHz, and 42 kHz (Jung and Kalko 2011). Also in Panama, *M. molossus* emits type 1, 2 and 3 pulses. Type 2 have $F_{INITIAL}$ 39.16, F_{END} 36.86 kHz, BW 2.2 kHz, D 10.2 ms, IPI 109.2 kHz and DC 10.9 %. Regarding tonal aspects, only BW is similar to Cerrado, while in temporal aspects D is double that observed in Cerrado and IPI is reduced, once again the consequence is a longer DC.

Like *M. currentium*, aspects of echolocation of *N. laticaudatus* are poorly understood. So far, in Panama it emits pulses with $F_{INIITIAL}$ 26.7 kHz, 28.7 kHz, or 32.4 kHz. The lowest pulses have F_{END} 23.6 kHz, BW 2.4 kHz, D 12.5 ms, IPI 393.7 ms, and DC 3.6 % (Jung and Kalko, 2011; Jung et al. 2014). In Peru, *N. laticaudatus* emits pulses with ascending FM beginning and qCFd ending, FME 23.16 kHz, $F_{INITIAL}$ 24.45 kHz, F_{END} 21.69 kHz, BW 2.77 kHz, D 13.78 ms, and IPI 441.81 ms (Mena et al. 2021). Once again, the tonal aspects have similar characteristics to the pulses in the Cerrado, especially in the urban habitat, but the temporal aspects differ due to the increase in the duration of the pulses, and consequently, an increase in the duty cycle occurs.

Despite emitting the three types of pulses, the FME of *M. currentium* was around 31 – 34 kHz, values close to what Arias-Aguilar et al. (2018) named types 1 and 2, indicating that these are the most used pulses in the study area. These FME values are close to *M. molossus* type 1 pulses (Arias-Aguilar et al. 2018) and were the least recorded and discarded pulses from the analyses. Molossidae can emit alternating frequency pulses to avoid interference with other individuals foraging in the same area (Ulanovsky et al. 2004). This could explain the preference of *M. molossus* for emitting pulses that Arias-Aguilar et al. (2018) named types 2 and 3. The design of pulses of the genus Molossus is the result of local adaptations and evolutionary convergence (Loureiro et al. 2020).

New world Molossidae species typically emit pulses of long duration and low bandwidth, which are associated with foraging in open space. The alternation of the FME is another character of the family, which reveals high plasticity in the calls (Jung et al. 2014). Open space foragers are favored in urbanized habitats (Jung and Threlfall, 2018) and the

plasticity of the pulses may offer an additional advantage for these species, as the ability to deal with noise pollution is described as the last limiting factor by Russo and Ancilloto (2015) for urban occupation by bats. However, the species studied did not present pulses with characters not previously recorded in the literature, but rather greater use of part of their vocal repertoire. Therefore, possibly these species are minimally affected by urban noise and noise pollution in Cerrado.

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Table 2.1. 2-Way ANOVA performed on ranks for *Molossus currentium* echolocation pulses.

Parameter	Response	Df	Sum Sq	Mean Sq	F value	Pr(>F)
FME	habitat	2	476579	238289	22.06	**0.000**
	season	1	25391	25391	2.351	0.126
	habitat:season	2	159580	79790	7.387	**0.001**
	Residuals	379	4093971	10802		
	habitat	2	271317	135659	11.932	**0.000**
F_{MAX}	season	1	18644	18644	1.64	0.201
	habitat:season	2	156469	78234	6.881	**0.001**
	Residuals	379	4309090	11370		
	habitat	2	483433	241717	22.43	**0.000**
F_{MIN}	season	1	23699	23699	2.199	0.139
	habitat:season	2	164046	82023	7.611	**0.001**
	Residuals	379	4084341	10777		
	habitat	2	482776	241388	21.863	**0.000**
BW	season	1	13218	13218	1.197	0.275
	habitat:season	2	74923	37461	3.393	**0.035**
	Residuals	379	4184603	11041		
	habitat	2	170876	85438	7.37	**0.001**
$F_{INITIAL}$	season	1	33584	33584	2.897	0.090
	habitat:season	2	157731	78865	6.803	**0.001**
	Residuals	379	4393330	11592		
	habitat	2	457466	228733	21.134	**0.000**
F_{END}	season	1	25435	25435	2.35	0.126
	habitat:season	2	170733	85366	7.888	**0.000**
	Residuals	379	4101887	10823		
	habitat	2	91.6	45.78	17.642	**0.000**
D	season	1	3.3	3.26	1.255	0.263
	habitat:season	2	9	4.49	1.729	0.179
	Residuals	379	983.4	2.59		
	habitat	2	12023	6011	0.483	0.617
IPI	season	1	11271	11271	0.906	0.342
	habitat:season	2	19134	9567	0.769	0.464
	Residuals	379	4713092	12436		
	habitat	2	194228	97114	8.127	**0.000**
DC	season	1	313	313	0.026	0.872
	habitat:season	2	32369	16185	1.355	0.259
	Residuals	379	4528609	11949		

Table 2.2. *Post-hoc* Tukey comparisons for habitat and interaction habitat x season for *Molossus currentium* echolocation pulses performed on ranks. (ns = not significant in ANOVA).

		FME	F_{MAX}	F_{MIN}	BW	$F_{INITIAL}$	F_{END}	D	IPI	DC
Habitat	Non-urban x Peri-urban	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	**0.000**	ns	**0.000**
	Non-urban x Urban	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	**0.000**	ns	**0.001**
	Peri-urban x Urban	0.904	0.762	0.922	0.563	0.732	0.773	0.967	ns	0.746
Interaction	Non-urban dry x Non-urban rainy	0.549	0.725	0.388	0.324	0.747	0.350	ns	ns	ns
	Non-urban dry x Peri-urban dry	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	ns	ns	ns
	Non-urban dry x Urban dry	**0.000**	**0.000**	**0.000**	**0.000**	**0.004**	**0.000**	ns	ns	ns
	Non-urban dry x Peri-urban rainy	**0.000**	**0.008**	**0.000**	**0.000**	0.087	**0.000**	ns	ns	ns
	Non-urban dry x Urban rainy	**0.000**	**0.000**	**0.000**	**0.000**	**0.010**	**0.000**	ns	ns	ns
	Non-urban rainy x Peri-urban dry	**0.000**	**0.004**	**0.000**	0.050	**0.022**	**0.000**	ns	ns	ns
	Non-urban rainy x Urban dry	**0.028**	0.339	**0.041**	**0.029**	0.723	0.074	ns	ns	ns
	Non-urban rainy x Peri-urban rainy	0.260	0.759	0.329	0.382	0.983	0.393	ns	ns	ns
	Non-urban rainy x Urban rainy	**0.044**	0.333	0.068	0.119	0.810	0.121	ns	ns	ns
	Peri-urban dry x Peri-urban rainy	**0.003**	**0.004**	**0.003**	0.574	**0.002**	**0.003**	ns	ns	ns
	Peri-urban dry x Urban dry	**0.032**	**0.019**	**0.044**	1.000	**0.017**	**0.023**	ns	ns	ns
	Peri-urban dry x Urban rainy	**0.031**	**0.036**	**0.037**	0.925	**0.014**	**0.018**	ns	ns	ns
	Peri-urban rainy x Urban dry	0.633	0.856	0.618	0.355	0.768	0.743	ns	ns	ns
	Peri-urban rainy x Urban rainy	0.802	0.849	0.824	0.923	0.916	0.917	ns	ns	ns
	Urban dry x Urban rainy	1.000	1.000	1.000	0.892	1.000	0.999	ns	ns	ns

Table 2. 3. Pulse parameters measurements and duty-cycle (mean ± SD) for *Molossus currentium* across the urbanization gradient and between seasons.

			FME (Hz)	F$_{MAX}$ (Hz)	F$_{MIN}$ (Hz)	BW (Hz)	F$_{INITIAL}$ (Hz)	F$_{END}$ (Hz)
Habitat	Non-urban	Annual	31298.72 ± 2322.74	33356.24 ± 2239.19	29509.90 ± 2405.94	3846.33 ± 1119.51	32683.22 ± 2292.99	30229.08 ± 2527.93
		Dry	30645.68 ± 1905.17	32944.99 ± 1641.14	28724.80 ± 1764.07	4220.19 ± 955.31	32276.48 ± 1523.36	29423.07 ± 2013.37
		Rainy	32202.93 ± 2611.58	33925.66 ± 2848.59	30596.97 ± 2803.22	3328.69 ± 1157.78	33246.40 ± 3043.89	31345.10 ± 2812.40
	Peri-urban	Annual	34333.61 ± 2097.24	35397.27 ± 2014.47	32740.16 ± 2259.67	2657.11 ± 618.65	34077.85 ± 2178.57	33462.03 ± 2294.12
		Dry	35446.12 ± 1162.88	36413.90 ± 1037.43	33913.99 ± 1052.22	2499.91 ± 536.53	35185.51 ± 1044.17	34659.65 ± 1080.62
		Rainy	33785.91 ± 2240.34	34896.78 ± 2189.66	32162.27 ± 2468.76	2734.51 ± 645.15	33532.54 ± 2382.37	32872.44 ± 2501.73
	Urban	Annual	34352.69 ± 1771.21	35341.72 ± 1759.06	32752.29 ± 1884.15	2589.43 ± 615.39	34006.89 ± 1845.30	33491.84 ± 1906.16
		Dry	34356.37 ± 1828.54	35333.34 ± 1791.61	32769.32 ± 1915.67	2564.02 ± 623.71	34039.10 ± 1856.11	33513.92 ± 1920.29
		Rainy	34347.09 ± 1689.22	35354.45 ± 1717.10	32726.41 ± 1844.28	2628.05 ± 603.51	33957.93 ± 1836.78	33458.27 ± 1893.43
Season	Dry		34200.66 ± 2099.73	35292.31 ± 1869.73	32592.88 ± 2194.43	2699.43 ± 798.56	34063.28 ± 1854.60	33333.57 ± 2224.59
	Rainy		33989.59 ± 2044.89	35085.99 ± 2018.35	32368.90 ± 2222.95	2717.09 ± 689.92	33752.93 ± 2148.09	33094.10 ± 2259.74

Table 2.3 (cont.)

D (ms)	IPI (ms)	DC
3.30 ± 1.62	267.17 ± 112.48	1.38% ± 0.72%
2.78 ± 1.14	260.83 ± 96.96	1.19% ± 0.55%
4.01 ± 1.94	275.95 ± 134.79	1.64% ± 0.85%
5.06 ± 1.69	262.57 ± 134.41	2.83% ± 4.47%
5.01 ± 1.31	276.18 ± 135.61	2.16% ± 1.07%
5.08 ± 1.86	255.86 ± 134.37	3.16% ± 5.40%
5.10 ± 1.59	281.35 ± 142.56	2.38% ± 1.65%
5.06 ± 1.55	271.20 ± 139.71	2.47% ± 1.73%
5.17 ± 1.64	296.78 ± 146.13	2.26% ± 1.52%
4.85 ± 1.61	271.07 ± 135.37	2.31% ± 1.61%
5.05 ± 1.76	280.50 ± 141.76	2.54% ± 3.47%

Table 2.4. 2-Way ANOVA performed on ranks for *Molossus molossus* echolocation pulses.

Parameter	Response	Df	Sum Sq	Mean Sq	F value	Pr(>F)
FME	habitat	2	38638	19319	1.62	0.1990
	season	1	58806	58806	4.93	**0.0270**
	habitat:season	2	13983	6992	0.586	0.5570
	Residuals	374	4461207	11928		
F_{MAX}	habitat	2	21137	10569	0.881	0.4153
	season	1	64037	64037	5.338	**0.0214**
	habitat:season	2	524	262	0.022	0.9784
	Residuals	374	4486936	11997		
F_{MIN}	habitat	2	33884	16942	1.416	0.2440
	season	1	44316	44316	3.705	0.0550
	habitat:season	2	20346	10173	0.85	0.4280
	Residuals	374	4474088	11963		
BW	habitat	2	1043	522	0.043	0.9575
	season	1	20838	20838	1.735	0.1886
	habitat:season	2	57904	28952	2.41	0.0912
	Residuals	374	4492851	12013		
$F_{INITIAL}$	habitat	2	30300	15150	1.264	0.2838
	season	1	55381	55381	4.619	**0.0323**
	habitat:season	2	2784	1392	0.116	0.8904
	Residuals	374	4484170	11990		
F_{END}	habitat	2	25871	12936	1.082	0.3399
	season	1	62106	62106	5.197	**0.0232**
	habitat:season	2	14808	7404	0.62	0.5388
	Residuals	374	4469850	11951		
D	habitat	2	2.3	1.15	0.655	0.5200
	season	1	1.6	1.576	0.897	0.3440
	habitat:season	2	3.7	1.864	1.061	0.3470
	Residuals	374	657.1	1.757		
IPI	habitat	2	24753	12377	1.045	0.3528
	season	1	94329	94329	7.963	**0.0050**
	habitat:season	2	23072	11536	0.974	0.3786
	Residuals	374	4430480	11846		
DC	habitat	2	43642	21821	1.84	0.1603
	season	1	90844	90844	7.66	**0.0059**
	habitat:season	2	2490	1245	0.105	0.9004
	Residuals	374	4435659	11860		

Table 2.5. Pulse parameters measurements and duty-cycle (mean ± SD) for *Molossus currentium* across the urbanization gradient and between seasons.

			FME (Hz)	F_{MAX} (Hz)	F_{MIN} (Hz)	BW (Hz)	$F_{INITIAL}$ (Hz)	F_{END} (Hz)
Habitat	Non-urban	Annual	36327.92 ± 950.95	37540.21 ± 1234.89	34690.62 ± 1174.48	2849.59 ± 994.89	35739.08 ± 1921.65	35717.69 ± 1210.34
		Dry	35813.02 ± 329.74	37738.64 ± 1719.89	33864.62 ± 795.49	3874.02 ± 924.40	36076.01 ± 3632.48	35065.13 ± 277.96
		Rainy	36585.36 ± 1098.09	37440.99 ± 1231.34	35103.61 ± 1185.67	2337.38 ± 561.61	35570.61 ± 1281.70	36043.97 ± 1410.65
	Peri-urban	Annual	37185.86 ± 1150.64	38298.27 ± 1113.21	35627.53 ± 1100.48	2670.74 ± 770.96	36815.96 ± 989.35	36308.72 ± 1296.93
		Dry	37231.59 ± 1305.13	38384.18 ± 1130.34	35845.93 ± 1026.65	2538.25 ± 512.67	37028.04 ± 937.65	36512.32 ± 1061.31
		Rainy	37172.41 ± 1145.00	38273.00 ± 1141.97	35563.29 ± 1143.11	2709.71 ± 841.02	36753.58 ± 1023.08	36248.83 ± 1381.78
	Urban	Annual	37257.04 ± 1303.78	38324.72 ± 1455.78	35704.06 ± 1396.57	2620.65 ± 602.67	36924.03 ± 1662.70	36434.89 ± 1352.98
		Dry	37390.01 ± 1343.97	38469.96 ± 1501.86	35831.48 ± 1430.53	2638.48 ± 582.96	37070.94 ± 1710.07	36572.15 ± 1392.92
		Rainy	37038.09 ± 1208.04	38085.55 ± 1348.21	35494.25 ± 1317.32	2591.30 ± 634.95	36682.12 ± 1557.85	36208.88 ± 1257.22
Season	Dry		37372.55 ± 1342.83	35814.40 ± 1427.73	35814.40 ± 1427.73	2647.20 ± 592.84	37061.19 ± 1707.74	36557.49 ± 1385.74
	Rainy		37041.16 ± 1194.64	35491.73 ± 1290.69	35491.73 ± 2597.78	2717.09 ± 656.64	36661.14 ± 1505.95	36209.01 ± 1266.18

Table 2.5. (cont).

D (ms)	IPI (ms)	DC
4.34 ± 2.40	292.65 ± 150.86	1.78% ± 1.30%
3.47 ± 2.08	154.60 ± 4.63	2.17% ± 1.23%
4.77 ± 2.72	361.68 ± 137.35	1.59% ± 1.47%
4.89 ± 1.42	226.98 ± 174.01	3.23% ± 2.23%
5.39 ± 1.66	161.81 ± 89.22	4.60% ± 3.38%
4.75 ± 1.37	246.14 ± 189.83	2.83% ± 1.71%
4.96 ± 1.30	223.58 ± 130.94	3.03% ± 2.07%
5.01 ± 1.22	211.80 ± 128.02	3.27% ± 2.24%
4.87 ± 1.42	242.98 ± 133.85	2.64% ± 1.71%
5.00 ± 1.24	210.19 ± 126.89	3.29% ± 2.26%
4.86 ± 1.44	246.41 ± 141.25	2.63% ± 1.70%

Table 2.6. 2-Way ANOVA performed on ranks for *Nyctinomops laticaudatus* echolocation

pulses.

Parameter	Response	Df	Sum Sq	Mean Sq	F value	Pr(>F)
FME	habitat	2	6164	3082	1.728	0.181
	season	1	2819	2819	1.58	0.211
	habitat:season	2	15400	7700	4.317	**0.015**
	Residuals	144	256855	1784		
F_{MAX}	habitat	2	7888	3944	2.386	0.096
	season	1	15208	15208	9.202	**0.003**
	habitat:season	2	20154	10077	6.097	**0.003**
	Residuals	144	237988	1653		
F_{MIN}	habitat	2	5595	2797	1.534	0.219
	season	1	592	592	0.324	0.570
	habitat:season	2	12474	6237	3.42	**0.035**
	Residuals	144	262577	1823		
BW	habitat	2	4111	2056	1.216	0.300
	season	1	20434	20434	12.083	**0.001**
	habitat:season	2	13172	6586	3.895	**0.023**
	Residuals	144	243519	1691		
$F_{INITIAL}$	habitat	2	10464	5232	3.231	**0.042**
	season	1	21046	21046	12.995	**0.000**
	habitat:season	2	16523	8261	5.101	**0.007**
	Residuals	144	233205	1619		
F_{END}	habitat	2	12600	6300	3.466	**0.034**
	season	1	3373	3373	1.855	0.175
	habitat:season	2	3504	1752	0.964	0.384
	Residuals	144	261761	1818		
D	habitat	2	42.2	21.096	5.704	**0.004**
	season	1	0	0	0	0.993
	habitat:season	2	4.4	2.177	0.588	0.556
	Residuals	144	532.6	3.699		
IPI	habitat	2	12382	6191	3.494	**0.033**
	season	1	8286	8286	4.676	**0.032**
	habitat:season	2	5428	2714	1.532	0.220
	Residuals	144	255141	1772		
DC	habitat	2	18761	9380	5.386	**0.006**
	season	1	3298	3298	1.893	0.171
	habitat:season	2	8386	4193	2.407	0.094
	Residuals	144	250793	1742		

Table 2.7. *Post-hoc* Tukey comparisons for habitat and interaction habitat x season for *Nyctinomops laticaudatus* echolocation pulses performed on ranks. (ns = not significant in ANOVA).

		FME	F_{MAX}	F_{MIN}	BW	$F_{INITIAL}$	F_{END}	D	IPI	DC
Habitat	Non-urban x Peri-urban	ns	ns	ns	ns	0.561	**0.043**	**0.016**	0.976	0.433
	Non-urban x Urban	ns	ns	ns	ns	**0.035**	ns	0.496	**0.028**	**0.026**
	Peri-urban x Urban	ns	ns	ns	ns	0.416	ns	**0.005**	0.116	**0.005**
Interação	Non-urban dry x Non-urban rainy	0.081	**0.002**	0.907	**0.008**	**0.001**	ns	ns	ns	ns
	Non-urban dry x Peri-urban dry	0.247	1.000	0.165	0.544	1.000	ns	ns	ns	ns
	Non-urban dry x Urban dry	0.140	**0.006**	0.224	0.209	**0.009**	ns	ns	ns	ns
	Non-urban dry x Peri-urban rainy	0.317	**0.045**	0.823	0.539	0.026	ns	ns	ns	ns
	Non-urban dry x Urban rainy	0.708	0.163	1.000	0.474	**0.033**	ns	ns	ns	ns
	Non-urban rainy x Peri-urban dry	0.976	0.480	0.464	**0.009**	0.261	ns	ns	ns	ns
	Non-urban rainy x Urban dry	0.913	0.688	0.559	0.998	0.839	ns	ns	ns	ns
	Non-urban rainy x Peri-urban rainy	1.000	0.995	1.000	0.783	0.992	ns	ns	ns	ns
	Non-urban rainy x Urban rainy	0.967	0.950	0.994	0.885	0.996	ns	ns	ns	ns
	Peri-urban dry x Peri-urban rainy	0.947	0.728	0.629	0.116	0.512	ns	ns	ns	ns
	Peri-urban dry x Urban dry	1.000	0.131	1.000	0.038	0.108	ns	ns	ns	ns
	Peri-urban dry x Urban rainy	0.838	0.862	0.315	0.099	0.512	ns	ns	ns	ns
	Peri-urban rainy x Urban dry	0.857	0.518	0.718	0.845	0.668	ns	ns	ns	ns
	Peri-urban rainy x Urban rainy	0.997	0.999	0.971	1.000	1.000	ns	ns	ns	ns
	Urban dry x Urban rainy	0.694	0.386	0.395	0.895	0.698	ns	ns	ns	ns

Table 2.8. Pulse parameters measurements and duty-cycle (mean ± SD) for *Nyctinomops laticaudatus* across the urbanization gradient and between seasons.

			FME (Hz)	F_{MAX} (Hz)	F_{MIN} (Hz)	BW (Hz)	$F_{INITIAL}$ (Hz)	F_{END} (Hz)
Habitat	Non-urban	Annual	24169.20 ± 1291.91	25907.68 ± 1193.38	22555.79 ± 1038.56	3351.89 ± 837.01	25029.38 ± 1259.43	23149.40 ± 1158.85
		Dry	24440.22 ± 1276.13	26232.16 ± 1086.86	22641.49 ± 1034.37	3590.66 ± 863.86	25435.18 ± 1136.99	23158.10 ± 1229.81
		Rainy	23805.47 ± 1237.64	25472.21 ± 1204.58	22440.77 ± 1046.79	3031.44 ± 688.31	24484.77 ± 1222.27	23137.74 ± 1072.36
	Peri-urban	Annual	23592.78 ± 1202.75	25505.67 ± 1253.23	22040.16 ± 982.04	3465.51 ± 888.86	24688.91 ± 1337.45	22571.88 ± 1008.93
		Dry	23184.31 ± 1073.11	25795.01 ± 1557.81	21603.89 ± 903.80	4191.12 ± 822.73	25221.31 ± 1471.63	22078.00 ± 869.89
		Rainy	23707.15 ± 1232.21	25424.66 ± 1179.29	22162.31 ± 985.10	3262.35 ± 809.15	24539.84 ± 1289.67	22710.17 ± 1017.15
	Urban	Annual	23647.29 ± 1413.09	25303.94 ± 1530.22	22173.55 ± 1356.12	3130.39 ± 672.57	24274.51 ± 1607.78	22778.66 ± 1514.55
		Dry	22907.68 ± 1627.37	24433.79 ± 2016.48	21560.19 ± 1595.05	2873.60 ± 728.21	23566.83 ± 2102.93	22015.20 ± 1586.97
		Rainy	23882.63 ± 1290.51	25580.81 ± 1275.79	22368.71 ± 1248.95	3212.09 ± 650.11	24499.68 ± 1401.08	23021.58 ± 1443.19
Season	Dry		24139.92 ± 1402.26	25991.41 ± 1359.17	22413.31 ± 1159.20	3578.10 ± 889.77	25210.94 ± 1401.19	22918.70 ± 1304.18
	Rainy		23796.52 ± 1236.62	25486.33 ± 1202.89	22340.22 ± 1078.93	3146.11 ± 715.90	24504.83 ± 1274.59	22981.92 ± 1164.56

Table 2.8. (cont.).

D (ms)	IPI (ms)	DC
4.97 ± 2.00	448.55 ± 192.98	1.35% ± 0.90%
5.03 ± 1.67	412.09 ± 188.67	1.49% ± 0.93%
4.87 ± 2.39	497.48 ± 190.22	1.17% ± 0.83%
3.86 ± 1.60	427.89 ± 193.82	1.78% ± 3.94%
3.22 ± 1.12	477.91 ± 188.69	0.77% ± 0.40%
4.04 ± 1.68	413.88 ± 196.69	2.06% ± 4.43%
5.43 ± 1.94	345.15 ± 109.47	1.70% ± 0.75%
5.56 ± 2.40	303.30 ± 118.34	1.94% ± 0.89%
5.39 ± 1.84	358.46 ± 105.86	1.62% ± 0.70%
4.90 ± 1.79	407.46 ± 184.95	1.46% ± 0.91%
4.76 ± 2.11	436.91 ± 182.27	1.55% ± 2.48%

CAPÍTULO 3

ADAPTAÇÃO ÀS CIDADES? ATIVIDADE DE MOLOSSIDAE EM UM

GRADIENTE DE URBANIZAÇÃO

Adapting to cities? Molossidae activity across an urbanization gradient

ABSTRACT

Bats adjust their activity period to the night/day cycle. During the day, they remain in shelters, and at the end of the day, they emerge from these shelters. During the night, species-specific responses are observed, and intrinsic and extrinsic factors influence their activity patterns. In urban habitats, anthropic factors can affect the activity pattern of insectivorous bats. The availability of shelters and their flexibility, artificial lighting, and noise pollution can exclude species from urban habitats or fragment the habitat and change their activity pattern. On the other hand, some species are considered synurbic or synanthropic, this is the case with some Molossidae. In this article, we aimed to describe and investigate differences in the nightly temporal activity pattern of *Molossus currentium*, *Molossus molossus*, and *Nyctinomops laticaudatus* in an urbanization gradient and seasonal differences in these patterns. Therefore, we tested the hypothesis that the activity is concentrated in urbanized habitats in the early evening. In contrast, in non-urban habitats, we hypothesized the activity is continuous throughout the night and that the pattern change according to the season. The bat activity is measured as the number of passes/hour. The selection of GLMM models through the AIC indicated that for the Molossus species, the model considering the habitat, the season, and the interaction between them is the one that best explained the activity patterns, while for *N. laticaudatus* the null model is the most suitable. We found unimodal, bimodal, and continuous patterns throughout the night for the species in the different habitats, which does not support our hypothesis for the habitat. At the same time, the GLMM coefficients were not significant for the season, refuting our seasonality hypothesis. Similar activity patterns have been described for the same species in Central America, in southeastern Brazil's Atlantic Forest and Brazilian islands. Species of Molossidae, such as *Tadarida brasiliensis*, have a variation in the activity pattern and their distribution throughout the night can respond to season, temperature, moon phase, artificial lighting, noise pollution or the presence of bodies of water. The fast transformation in Cerrado predicted for the coming years and the effects of climate change on insectivorous bats present in the biome creates a demand on more studies to evaluate more species and ways to mitigate these impacts.

Key words: behavior, Brazil, Chiroptera, Cities, insectivores, savanna.

INTRODUCTION

Bats synchronize their activity period with the day-night cycle, starting just before sunset and ending shortly after sunrise (Esbérard and Bergallo, 2004; Holland et al. 2011; Costa et al. 2011; Divoll et al. 2015). During the day, they remain inactive in shelters such as exposed parts of vegetation (trunk and branches), hidden parts of vegetation (cavities in the trunk, tents built with leaves and under leaf litter), caves and crevices in rocks and cliffs (Santana et al. 2011). At dusk, emergency period is influenced by each individual or bat species' energy requirements, predation risk and diet (Duvergé et al. 2000; Jones and Rydell, 1994). For example, mothers emerge before the young and pregnant females emerge after the lactating ones (Duvergé et al. 2000). Gleaning insectivorous bats emerge after the aerial insectivorous bats, as they fly slower, leaving them susceptible to crepuscular predators; additionally, they feed on insects whose abundance peak occurs later (Jones and Rydell, 1994).

While active at night, bats exhibit species-specific activity patterns that may vary due to several factors. Consequently, different patterns of activity can be found accordingly by the habitat (Threlfall et al. 2011; Jung et al. 2012; Frey-Ehrenbold et al. 2013), the lunar phase (Meyer et al. 2004), precipitation (Erickson and West, 2002), temperature (Erickson and West, 2002) feeding guild (Frey-Ehrenbold et al. 2013), insect availability (Taylor and Oneill, 1998; Meyer et al. 2004), water availability to meet physiological needs (Razgour et al. 2010; Korine et al. 2016; López-Gonzalez et al. 2015), morphological characters (Erickson and West, 2002; Threlfall et al. 2012; Emrich et al. 2014), and echolocation type (Meyer et al. 2004, Emrich et al. 2014). For example, in northern South Africa, insectivorous bats have a peak of activity between 20:00 and 22:00, and another between 23:00 and 00:00 and the total activity varies in response to seasonality (Taylor et al. 2013). In the temperate zone, insectivorous bats have a peak of activity after dusk, another just before dawn, and is correlated with insect biomass and minimum night temperature (Hayes, 1997). In Brasília National Park, in Brazil, insectivorous bats have two activity peaks, one after sunset and another at two in the morning, the smallest species forage in the first part of the night and the largest in the second part of the night; moreover, the activity is positively correlated with temperature and habitat biomass (Militão, 2017).

In urban habitats, in addition to natural variables, bats need to deal with variables of anthropic origin. The ability to adapt and use human structures and exotic plants as new sources of shelter, for example, can lead to the exclusion of species (Russo and Ancilloto,

2015). Artificial lighting can negatively impact the emergence period of bats (Stone et al. 2009; Haddock et al. 2019) and act as a source of habitat fragmentation for species that avoid moving and foraging in illuminated environments (Stone et al. 2015; Haddock et al. 2019). Similarly, bats delay the emergence period in places with noise pollution (Russo and Ancilloto, 2015) and avoid or decrease activity in these habitats (Finch et al. 2020; Li et al. 2020; Domer et al. 2021). Morphological characteristics such as lower body weight, low wing load, and low aspect ratio are also limiting factors for bat mobility and are directly correlated with the absence of these animals in the urban environment (Bader et al. 2015; Jung and Kalko. 2011). Therefore, the ability to flex foraging behavior and movement in fragmented and poorly connected landscapes are ecological limitations for bats in urban habitats (Russo and Ancilloto, 2015).

On the other hand, open space foragers such as the Molossidae species are more tolerant to urbanization (Jung and Threlfall, 2018), and some species are synurbic or synanthropic (Russo and Ancilloto, 2015). In Brazil, 22 species of Molossidae are present in urban areas, and many use different human structures as shelters, mainly roofs and expansion joints (Nunes et al. 2017). Some species feed above posts lights in fast and straight flights (Jung and Kalko, 2010). Artificial posts lights are associated with a 50% increase in the abundance of insects of the orders Hymenoptera, Diptera, Coleoptera, Hemiptera, Homoptera, and Trichoptera in relation to adjacent natural habitats and the concentration of insectivorous bat activity in the early hours of the night (Jung and Kalko, 2010). Reis, 2009 found that fast-flying species benefit from artificial lighting in the Federal District urban parks. Fast and straight flights are characteristic of Molossidae due to their narrow and long wings adapted for fast flights with low maneuverability (Voight and Holderied, 2012). These morphological characteristics are associated with the high mobility of Molossidae in urban habitats and the species' ability to move in those fragmented and poorly connected landscapes (Bader et al. 2015). Another factor that can increase Molossidae activity in urban areas is the proximity to water bodies (Krauel and LeBuhn, 2016). This increase in activity is due to a higher abundance of insects in these bodies of water (Straka et al. 2020). In urban habitats in the Cerrado, the highest concentration of insects of the Lepidoptera orders, for example, occurs in the early hours of the night (Scherrer et al. 2013), and Molossidae were observed active in the early hours of the night, and subsequently, reducing the level of activity by up to tenfold in forested and urbanized habitats in Panama (Jung and Kalko, 2010). In the Cerrado, an increased abundance of insects of the orders Coleoptera, Diptera, Hemiptera, Hymenoptera,

Isoptera, Lepidoptera and Trichoptera and insectivorous bat activity in natural and urbanized habitats are associated with the rainy season (Silva et al. 2011; Barros et al. 2014; Aranda et al. 2021).

This study aims to describe the daily temporal activity pattern of the Molossidae species *Molossus currentium*, *Molossus molossus,* and *Nyctinomops laticaudatus* in an urbanization gradient in the Brazilian Cerrado and to test whether these species change the activity pattern as a function of habitat and seasonality. Therefore, our hypotheses are (a) Species will concentrate activity in the early evening hours in urbanized habitats and non-urban habitat activity is continuous throughout the night, and (b) Species activity will be different between the dry and rainy seasons.

MATERIALS AND METHODS

Study area

Urban habitats are central areas in cities and peri-urban areas are areas at the interface of urban, rural, and natural vegetation (Clergeau et al. 2001). For this study, we selected seven parks within the Cerrado biome and previously classified them into non-urban (<10% urban habitat), peri-urban (11 – 50% urban habitat), and urban (>50% urban habitat) habitats based on land use in a 3 km buffer around the parks. We used the Cerrado land use map (30x30 m resolution) from the NGO Mapbiomas (Souza et al. 2020) to create the buffers and shapefiles of the parks obtained from the Ministry of the Environment and the Instituto Brasília Ambiental. We performed the reclassification of the map in Cerrado, agriculture, urban, and water was in R software (v. 4.0.5; R. Core Team, 2021) with the help of 'sf' (Pebesma, 2018), 'raster' (Hijmans, 2021), 'tmap' (Tennekes, 2018), 'dplyr' (Wickham et al., 2021a), and 'stars' (Pesbema, 2021) packages.

Non-urban habitat. – We classified two parks in the state of Goiás: Chapada dos Veadeiros National Park (CVNP; 14° 10' S, 47° 30' W) and Terra Ronca State Park (TRSP; 13°29' S, 46°23' W). These parks have 255,137.9 hectares (ha) and 40,615.15 ha and the buffers have 143,834 ha and 32,343.1 ha, respectively. In both, 0% were classified as urban habitat. The local climate is Aw (tropical with a dry season in winter) in Köppen classification, CVNP has a maximum altitude of 1670 m, average annual temperature between 19ºC and 22ºC, and average annual precipitation between 1600 mm and 1800 mm, TRSP has an average annual temperature between 24 – 25ºC and average annual rainfall between 1000 – 1200 mm (Cardoso et al. 2014). We selected one more park, but this one in the Federal

District (FD): Águas Emendadas Ecological Station (ESAE; 15° 33' S, 47° 36' W), this park has 9,203.74 ha and a buffer of 17,401.50 ha, of which 8% of the area is classified as urban area. The FD has an average annual temperature between 1400 – 1600 mm and an average annual temperature between 20 – 21 ºC (Cardoso et al. 2014). In these parks, it is possible to find Cerrado phytophysiognomies of forest, savanna, and grassland types (Felfili et al. 2007; MMA/ICMBio, 2009).

Peri-urban and urban parks were all selected in FD and are under the same climate conditions as ESAE.

Peri-urban habitat. – Brasilia National Park (BNP; 15° 38' S 48° 1' W) has 42,697.74 ha and a buffer of 42,327.72 ha, of which 13% is classified as urban habitat, and the Brasilia Botanical Garden Ecological Station (BBGES; 15º 88' S, 47º 85' W) has 4,581.45 ha, and a buffer of 12,038 ha, of which 25% is classified as urban habitat. Inside BNP, the predominant Cerrado phytophysiognomy is Cerrado *stricto sensu*, not excluding other forest, savanna, and grassland formations, as well as in the BBGES (Moreira, 2000; Nobrega et al. 2001; Farias et al. 2008; Arruda, 2018).

Urban habitat. –Águas Claras Ecological Park (ACEP; 15º 83' S, 48º 02' W) has 115.29 ha and a buffer of 4559.13 ha, of which 72% of the area is classified as urban habitat, and the Ezachias Heringer Ecological Park (EHEP; 15º 83' S, 47º 95' W) has 350 ha and a buffer of 5,895.45 ha, of which 72% of the area is classified as an urban habitat. In the parks, it is possible to find typical Cerrado formations, such as gallery forest, Cerrado *stricto sensu*, and grassland formations (Nogueira et al. 2002; Munhoz and Amaral, 2007).

Data collection

We obtained the data from the Laboratory of Biology and Conservation of Bats, Department of Zoology, Institute of Biological Sciences, University of Brasília. In each park, we selected seven or eight recorders, totaling 15 recorders per habitat/season, in exception the non-urban habitat in dry season where we selected 14 recorders. All records obtained were done in non-urban habitats with Songmeter (Wildlife Acoustics) recorders and in urbanized habitats with Audiomoth (LABmaker) recorders, and all of them were positioned 3m above the ground in an open area, set to record between 18:00 and 6:00 of the following day, with a sampling rate of 384 kHz and remained active for three minutes in 15-minute cycles overnight. In contrasting Neotropical habitats, one night of sampling is enough to detect differences in habitat selection differences in insectivorous bats (López-Baucells et al.

2021). The recordings in the CVNP took place in dry season (September/2014), in the TRSP in rainy season (February/2014), in ESAE, BBGES, BNP, EHEP and ACEP parks the recordings took place in dry season (August/2017 and September/2018) and in rainy season (February/2018 and 2019. The total sampling effort for non-urban habitat in dry season was 2.016 min and in all other habitat/season was 2,160 min.

Species

Molossus currentium, *M. molossus* and *N. laticaudatus* are species of the Molossidae family. The three species emit echolocation pulses of the QCFd type (quasi-constant frequency down) with alternation in the frequency of maximum energy (FME) of the pulses. *M. currentium* emits pulses with FME of 30 kHz, 33 kHz and 36 kHz, *M. molossus* emits pulses with FME of 34 kHz, 39 kHz and 42 kHz and *Nyctinomops laticaudatus* emits pulses with FME of 24 kHz and 28 kHz (Arias-Aguilar et al. 2018). Pulses frequencies from *N. laticaudatus* can overlap with other Molossidae species from Cynomops, Nyctinomops and Molossus genus (Jung et al. 2014, Arias-Aguilar et al. 2018). There are no studies on the diet of *M. currentium* nor on differences with *M. molossus*. However, the diet of insectivorous bats in Cerrado can be driven by the availability and abundance of insects throughout the year, resulting in significant overlap in the diet of congener species (Sallinas-Ramos et al. 2015). In relation to *M. molossus*, *N. laticaudatus* has a diet with greater variability of insects and preys on insects of the orders Isoptera, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Mantodea, Neuroptera and Orthoptera. *M. molossus* preys on insects of the orders Coleoptera, Diptera, Hemiptera and Lepidoptera (Aguiar et al. 2021).

Data treatment

We extracted pulses in R software (v. 4.0.5; R Core Team, 2021) with 'bioacoustics' package (Marchal et al. 2021). We separated pulses and exported to an Excel table for later identification with 'dplyr' (v. 1.0.6; Whickham et al. 2021a), 'tools' (v. 4.0.5; R Core Team, 2020) and 'tidyr' packages (v. 1.3.3; Wickham et al. 2021b. In this work, we define a bat pass as a sequence of three or more pulses with an interval of less than 1 second between pulses. When the pass consisted of more than three pulses, we used only three sequential pulses for species identification based on qualitative parameters (FM, CF or qCF; modulation upwards or downwards) and eight quantitative parameters, six tonal and two temporals, following Marchal et al. (2021) and Arias-Aguilar et al. (2018) definitions: FME is the frequency of maximum energy in pulse, F_{MAX} is the highest pulse frequency, F_{MIN} is the lowest pulse

frequency, BW is the difference between F_{MAX} and F_{MIN}, $F_{INITIAL}$ is the frequency at the beginning of the pulse, F_{END} is the final pulse frequency, D is the pulse duration, IPI is the interval between the end of the current pulse and the beginning of the next pulse. Finally, species identification was performed following Arias-Aguilar et al (2018). The duty cycle was defined as D/(D+IPI), which means the pulse duration divided by the period (Fenton et al. 2012), based on the mean of the D and the first two IPIs of each pass.

Statistical analyzes

To test the temporal activity pattern of each of the selected species, we made Generalized Mixed Effects Models (GLMM) using the lme function of the 'nlme' package (Pinheiro et al. 2021). We used habitat and season as fixed effects, and the area and the recorder as random effects, as these cover the variation between areas and between recorders inside areas. GLMM allows a more flexible approach to non-normal data, because, in addition to the fixed effects that quantify the variation of each predicted, there are random factors that quantify the variation between units (Bolker et al. 2008). We created five models: null (random effect of parks), nested null (random effect of recorders within parks), habitat effect (random effect of recorders within parks and fixed habitat effect), additive of habitat and season (random effect of recorders within parks and fixed effects of habitat and season) and interactive of habitat and season (random effect of recorders within parks and fixed effect of habitat, season and the interaction between fixed effects). The models considered more parsimonious were those that presented ΔAIC ≤ 2 in relation to the null model, and the best model presented the lowest AIC value.

RESULTS

M. currentium

During the dry season, the activity period in non-urban habitat occurred between 19:00 - 22:00. In the peri-urban habitat, from the beginning of the recordings until 21:00. In the urban habitat, there were two periods of activity: First, from the beginning of the recordings until 21:00, with a large peak at 18:00, and another more discreet 20:00, second starting at 04:00 that continued until the end of the recordings with a peak at 05:00. During the rainy season, in non-urban habitat there was an initial activity period from the beginning of the recordings until 22:00 which was interrupted at 20:00 and there was a later register at 02:00. In the peri-urban habitat, activity occurred from the beginning of the recordings until 20:00, then a record at 23:00 and a second period of activity from 03:00 until the end of the

recordings. In the urban habitat, individuals remained active all night, except for 03:00, and there was a peak of activity at 19:00 and another at 05:00 (Fig. 2.1). The model that best explains the activity pattern of *M. currentium* was the interactive model (AIC=495, Table 2.1). However, the coefficients showed significant differences only in the periurban:dry and urban:rainy interactions, where there was a reduction in activity (-6.12. Std.Error = 2.76, df = 31, t-value = -2, 22, p = 0.03) (Table 2.2).

M. molossus

During the dry season, *M. molossus* had almost no records in non-urban habitat, we found activity only at 20:00, 21:00 and 23:00. In the peri-urban habitat, activity remained low and constant throughout the night, with passes only at 01:00, 02:00 and 05:00 not being recorded. In the urban habitat, *M. molossus* remained active from the beginning of the recordings until 02:00, with a major peak of activity at 18:00 and a smaller one at 00:00, no activity at 03:00 and then the activity rose again until the end of recordings. During the rainy season, in the non-urban habitat, activity period was from the beginning of the recordings until 04:00, there were at least two similar peaks of activity: 20:00 and 02:00. In the peri-urban habitat, there were only no records at 02:00 and 04:00, there was an initial peak of activity at 18:00 and then activity fluctuated for the rest of the night at lower levels. In the urban habitat, there was no activity only at 02:00, and there were two activity peaks, one at 19:00 and the other at 05:00 (Fig. 2.2). The model that best explained the activity pattern of *M. molossus* was the interactive model (AIC = 653, Table 2.11). Among the coefficients, significant differences were found only in urban versus peri-urban habitats (25.05, std. Error = 7.33, df=4, t-value=3.41, p = 0.027 (Table 2.2).

N. laticaudatus

During the dry season, *N. laticaudatus* remained active in non-urban habitat from the beginning of the recordings until 23:00, with some registers later at 01:00 and 03:00. In peri-urban habitat, activity fluctuated between few and no records throughout the night with no evident peak. In the urban habitat, activity period was concentrated in the first three hours of monitoring. During the rainy season, *N. laticaudatus* remained active in the non-urban habitat until 04:00, there was an activity peak at 18:00, a second and intermediate 21:00 and a third and smaller 23:00. In the peri-urban habitat, there was no activity in the early evening at 19:00 and then in the middle of the night at 23:00 and 00:00, in the first half of the night there

was a peak at 21:00 and in the second half of the night the activity was constant . In the urban habitat, until 00:00 the activity oscillated between few records and no activity, then there was a peak of activity at 02:00 and a second peak at 05:00 (Fig. 2.3). The model that best explained the activity pattern of *N. laticaudatus* was the null model (AIC = 439, Table 2.1).

Discussion

Unlike our hypothesis, the activity was not unimodal in urbanized habitats (i. e., with a peak at dusk and ceased after the first hours of the night) while the activity was not constant throughout the night in the non-urbanized habitat, neither differed among seasons. We observed species-specific responses with variations in the models that best explain such patterns.

The temporal activity pattern of *M. currentium* is better explained by the interactive model. In both non-urban and peri-urban habitats, we observed a peak in the early hours of the night and reduced or no activity during the rest of the night in both seasons. This pattern is similar to that found in the illuminated streets of a village of 500 inhabitants in Panama throughout the year, where the species is most active between 18:00 and 20:30 (1.2 passes/min), after that time activity is reduced by 10-fold (Jung and Kalko, 2010). Apparently, in places of lower urbanization and human density, *M. currentium* behaves similar. In the urban habitat, *M. currentium* has two activity peaks, one at the dusk and the other at dawn, and low or zero activity between the peaks. In Brasília's urban parks, a likewise pattern has been previously described (Reis, 2019). The periods of activity concentrated at the beginning and end of the night coincides with the periods of greatest abundance of Lepidoptera in Brasilia Botanical Garden Ecological Station and in Emas National Park found by Scherrer et al. 2013 and Moreno et al. 2021. These are also the times with the highest abundance of Coleoptera, Diptera, Hemiptera and Hymenoptera in urban areas of the DF (Reis, 2019). The first three orders are part of the diet of the congener *M. molossus* (Aguiar et al. 2021) and possibly part of the diet of *M. currentium* as well.

The activity pattern of *M. molossus* is best explained by habitat and season and the interaction between them. In the peri-urban habitat, the species remain with low activity while in the urban habitat the highest amounts of passes are recorded during almost the entire night, with three activity peaks in decreasing order of magnitude. This difference in activity between the more peripheral and central areas of cities is explained by the adaptability and mobility of bats in urban areas (Li et al. 2020). Furthermore, the foraging behavior of the species is the

result of a trade-off between exploiting available prey and avoiding predation (Holland et al. 2011). Jung and Kalko (2010) also recorded the activity of *M. molossus* in the village of Panama and observed the concentration of activity in the early hours of the night (16.9 passes/min in the dark streets and 11.0 in the illuminated streets between 18:00 - 20:30) and the reduction in the following hours (2.9 passes/min on dark streets). Unlike the dry season, during the rainy season activity fluctuated throughout the night with a peak at dusk and a peak at dawn in the urban habitat. The unimodal activity pattern with a peak at dusk is similar to that found in Marambaia Island, south coast of Rio de Janeiro, with typical Atlantic Forest vegetation. 71.1% of net captures occurr in the first 120 minutes after sunset and some individuals are captured before sunset and after sunrise the following day (Costa et al. 2011). The pattern described in the urban habitat is the most commonly recorded for the species. In the Rio de Janeiro city, the first records of the species occur before sunset and last until 88 minutes after sunrise. The two peaks of activity occur in the first hour after sunset and approximately 10 hours later (Esbérard and Bergallo, 2010). A similar pattern is found on an island in Panama, where the first peak occurs at dusk between 18:00 – 21:00, with the first animals emerging from shelters between ten minutes before sunset and 37 minutes after sunset, and the second peak at dawn at approximately 06:00 with individuals returning 6 ± 29 min before sunrise (Holland et al. 2011). In urban parks in Brasília, the species is active throughout the night and with two activity peaks: one at the beginning of the night and another at the end (Reis, 2019). Variations in the activity pattern may indicate the species' flexibility and adaptability to optimize opportunities in different habitats. In urban habitats, for example, the species may alter the foraging microhabitat in response to the phase of the moon (Jung and Kalko, 2010).

The best model that explains the activity of *N. laticaudatus* is the null model. To date, there are two records of the temporal activity patter of this specie in natural habitats and they do not resemble those found in the non-urbanized habitat in both seasons. On Marambaia Island, the species is captured in nets continuously throughout the night without an evident peak (Costa et al. 2011). The continuous temporal activity pattern can also be found in the forests of Panama and in the urbanized habitats the species is only recorded in light streets until 20:30 (1.7 passes/min) and after that time the passes occurred in a reduced way in the streets dark (0.03 passes/min) (Jung and Kalko, 2010).

The Molossidae family has a wide distribution. It can be found in Africa, southern Eurasia, Oceania and from southern North America to southern South America (Koopman,

2020). Some species of this family are considered synurbic or synanthropic (Russo and Ancillotto, 2015). Species of the Molossus and Cynomops genera, for example, benefit from human-altered habitats (Bader et al. 2015). This seems to be the case with *M. currentium* and *M. molossus* from Cerrado, both species presents higher activity peaks at dusk in urban habitats and a second peak at dawn, different from non-urban habitat. The habitat type can influence the activity pattern of African and Brazilian molossids' species (Taylor et al. 2013, Barros et al. 2014), and the presence of artificial lighting may increase Molossidae activity in Mexico and South Africa (Schoeman, 2015; Rodriguez-Aguilar et al. 2017). Molossidae activity is also influenced by amount of rainfall and temperature, although, responses are species-specific in the Americas (Appel et al. 2019). Cerrado's seasons are a combination of temperature and amount of rainfall, but it did not influence *M. currentium*, *M. molossus* and *N. laticaudatus* activity. At last, the vertical stratification of insects in Asia (Nguyen et al. 2019), the pattern of invertebrate activity in Australia (Westerhuis et al. 2020), and the availability of insects in Panama (Jung and Kalko et al. 2010) also are correlated with Molossidae activity. Even tough insects diversity and abundance peak occurs in rainy season in Cerrado (Silva et al. 2011; Barros et al. 2014; Aranda et al. 2021), it did not lead to different activities patterns among seasons for *M. currentium*, *M. molossus* and *N. laticaudatus.*

One of the most studied species of Molossidae and the most widely distributed mammal in the Americas is *Tadarida brasiliensis*, occurring from central the United States to Patagonia (Simmons, 2005; Nabte et al. 2011). This species exemplifies molossids' adaptability and flexibility. For example, in Chile's agricultural habitats it increases activity on full moon nights and at intermediate levels of lighting the activity is homogeneous throughout the night (Vásquez et al. 2020), the increase also occurs in response to local variables, such as tree density, and landscape variables, such as the amount of native vegetation, and in landscapes dominated by natural vegetation activity increases with increasing fragmentation (Rodriguez-San Pedro and Simonetti, 2015). Naturally, Cerrado has a fragmented vegetation (Eiten, 1972), and in recent years it lost 55% of its natural vegetation due to intense occupation and agriculture expansion over the biome (Klink and Machado, 2005). *N. laticaudatus* analyzed here live in both naturally and anthropogenic fragmented habitats and habitat type did not cause significant differences in activity. In Mexico, the size of the urban vegetation patch and the presence of artificial lighting are associated with *T. brasiliensis* increased activity and feeding buzzes in relation to natural patches and residential

areas (Ávila-Flores and Fenton, 2005). Park areas was not evaluated here, but peri-urban parks monitored in this study have a bigger area than urban parks and could be associated with the differences in Molossus activity. In Texas, *T. brasiliensis* activity and number of feeding buzzes increase in urban habitat in relation to pastures and plantations (Lee and McCracken, 2002) and in California this increase occurs at high altitudes due to the vertical displacement of individuals to feed on migratory moths (Krauel et al. 2018). In California, the activity can also respond to the amount of edge of natural fragments, the size of urban parks and the proximity to water bodies (Krauel and LeBuhn, 2016) and is greater in urban habitats and in higher temperature than in non-urban and lower temperature (Schimpp et al. 2018). Thus, differences in buffer composition and in the Cerrado, agriculture, urban and water proportion could be linked to Molossus species differences between peri-urban and urban habitat.

Not only environmental variables, but also institutional, social and economic variables guide the urban habitat (Alberti, 2005). To our knowledge, this was the first study to evaluate insectivorous bats activity along an urbanization gradient in Cerrado at species level and to demonstrate bats different activities patterns here, this puts in evidence the lack of understanding over urbanization effects in bats in Brazil. Taking into account the possible effects of climate change on Cerrado bats expected by 2050 (Aguiar et al. 2016), its urgent more investments so a wider diversity of species can be monitored, the effects of urbanization explored, and the negative impacts might be minimized.

ACKNOWLEDGMENTS

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Table 3.1. Selection of GLMM models of the activity pattern for *M. currentium* (Mcur), *M. molossus* (Mmol) and *N. laticaudatus* (N. lat) in the urbanization gradient. Best model in bold.

Model	Formula	Specie					
		Mcur		Mmol		Nlat	
		AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC
Null	Passes ~ 1, random= ~ 1|Recorder	534	0	656	0	**439**	0
Nested null	Passes ~ 1, random= ~ 1|Recorder/Park	509	-25	680	24	447	8
Habitat	Passes ~ Habitat, random= ~ 1| Recorder/Park	500	-34	668	12	443	4
Addictive	Passes ~ Habitat + Season, random= ~ 1| Recorder/Park	503	-31	665	9	443	4
Interactive	Passes ~ Habitat * Season, random= ~ 1| Recorder/Park	**495**	-39	**653**	-3	442	3

Table 3.2. Coefficient from the selected GLMM models that best explained the activity pattern from *M. currentium* (Mcur), *M. molossus* (Mmol) and *N. laticaudatus* (N. lat) in the urbanization gradient.

| Specie	Coefficient	Value	Std. Error	df	t value	p
Mcur	(Intercept)	2.12	2.56	48	0.83	0.4120
	habitatpreserved	-0.71	3.26	4	-0.22	0.8392
	habitaturban	8.54	3.97	4	2.15	0.0981
	seasonrain	2	1.07	31	1.87	0.0707
	habitatpreserved:seasonrain	-2.14	1.1	31	-1.95	0.0600
	habitaturban:seasonrain	-6.12	2.76	31	-2.22	**0.0338**
Mmol	(Intercept)	1.4	2.72	48	0.51	0.6091
	habitatpreserved	0.69	4.84	4	0.14	0.8935
	habitaturban	25.05	7.33	4	3.42	**0.0269**
	seasonrain	2.2	1.11	31	1.98	0.0570
	habitatpreserved:seasonrain	4.11	5.04	31	0.82	0.4209
	habitaturban:seasonrain	-17.96	8.97	31	-2	0.0541
Nlat	(Intercept)	1.1	0.22	50	5	0.0000
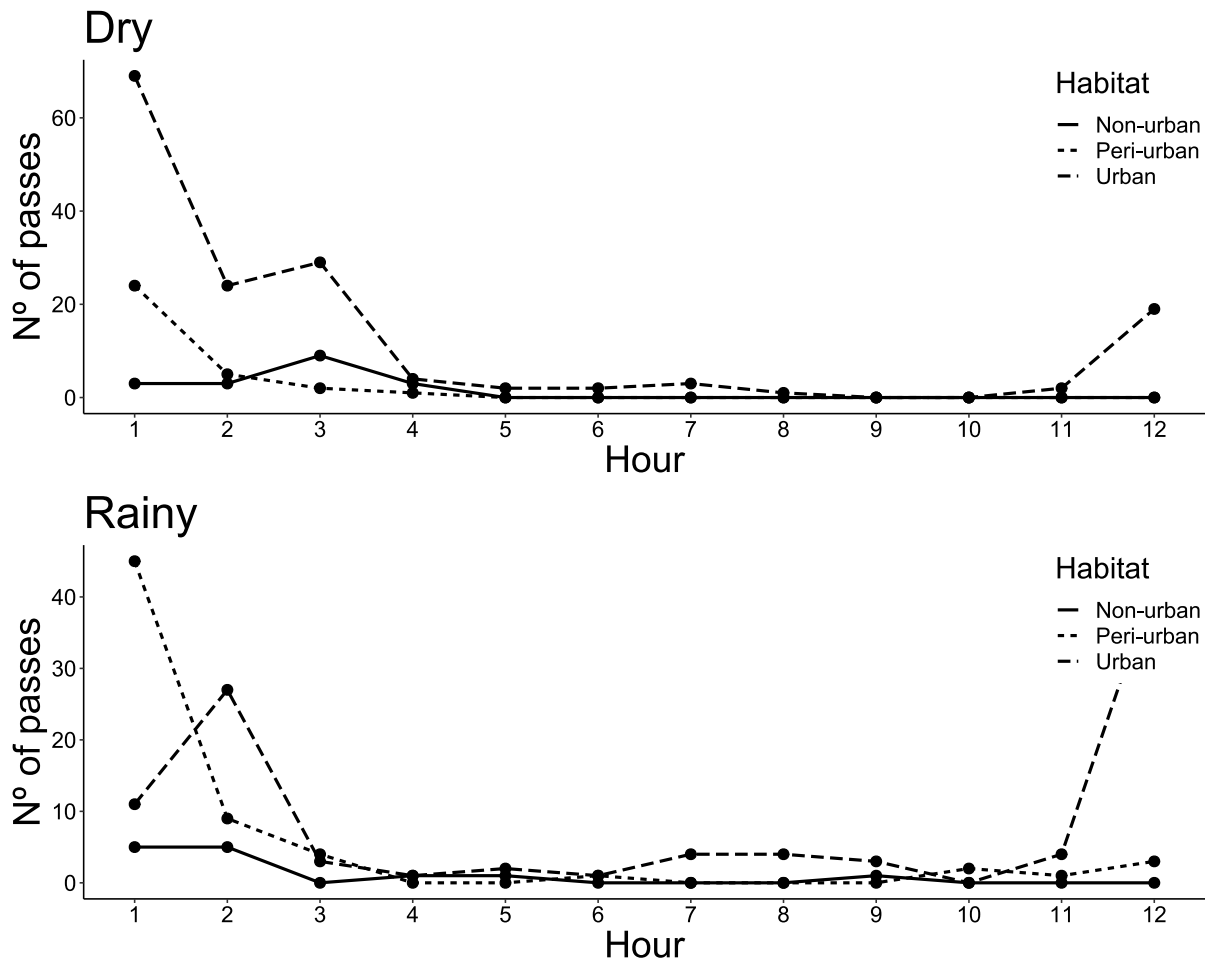
Figure 3.1. *Molossus currentium* nightly activity pattern of acoustical monitoring, starting 18:00 (1) and following the next 12 hours, from non-urban, peri-urban and urban habitats in dry and rainy seasons in Cerrado.
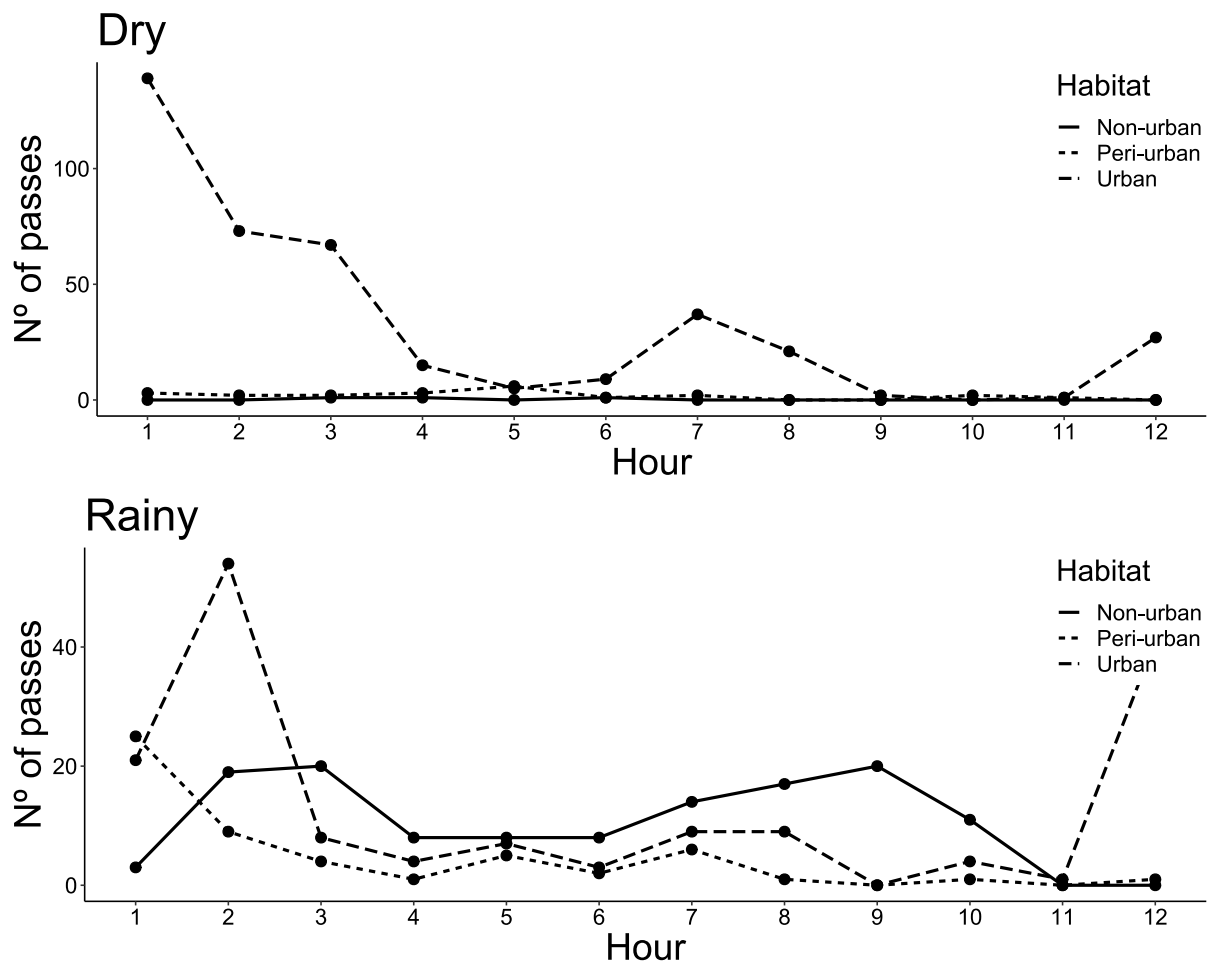
Figure 3.2. *Molossus molossus* nightly activity pattern of acoustical monitoring, starting 18:00 (1) and following the next 12 hours, from non-urban, peri-urban and urban habitats in dry and rainy seasons in Cerrado.
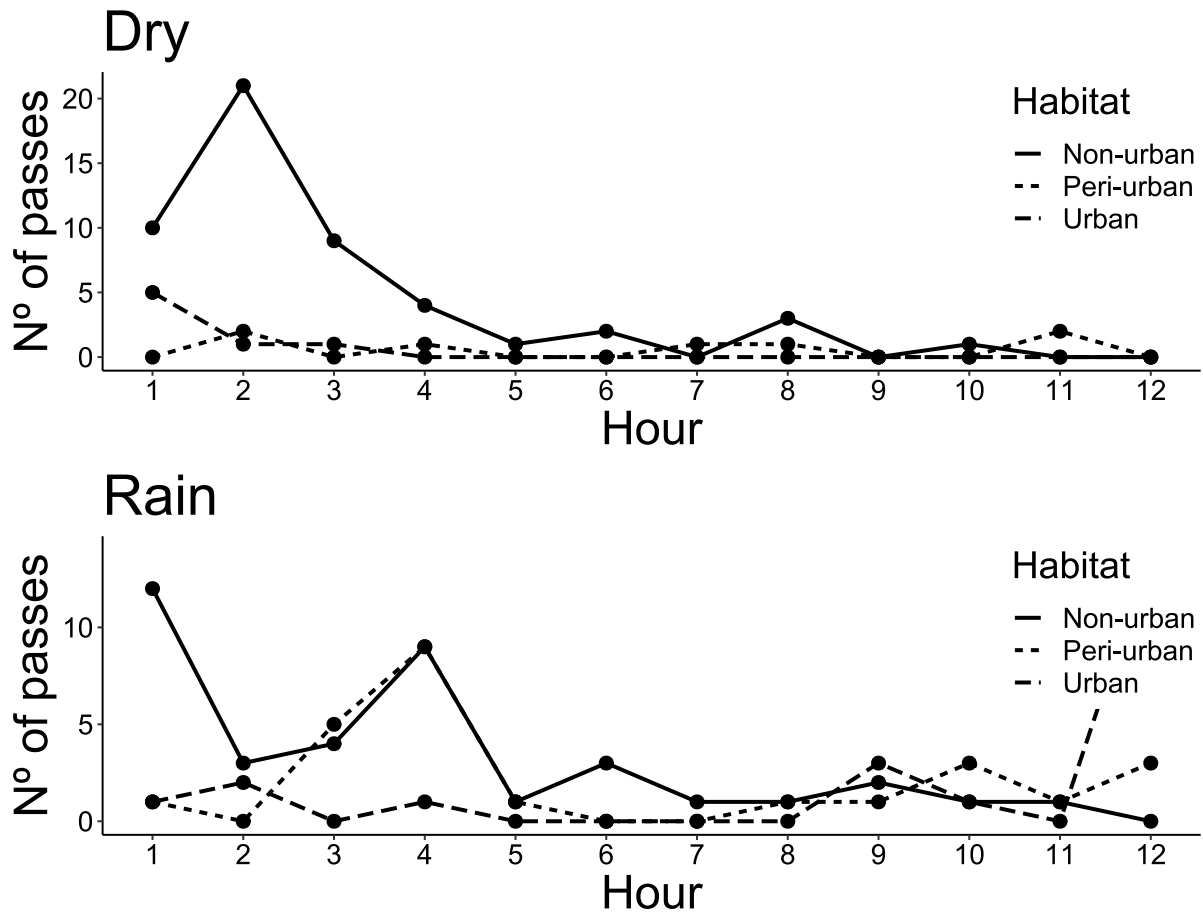
Figure 3.3. *Nyctinomops laticaudatus* nightly activity pattern of acoustical monitoring, starting 18:00 (1) and following the next 12 hours, from non-urban, peri-urban and urban habitats in dry and rainy seasons in Cerrado.

O Cerrado possui uma rica fauna de morcegos insetívoros. Em habitats naturais, é possível encontrar mais de 20 espécies de cinco famílias. Muitas são capazes de habitar os centros urbanos do bioma. Os parques periurbanos, ou seja, os parques localizados em regiões com menor nível de urbanização e imersos em uma matriz mista de habitat urbano, vegetação nativa e agropecuária, se destacam ao sustentar riqueza e composição de morcegos insetívoros semelhantes aos parques naturais, portanto os habitats periurbanos são fundamentais para manutenção da diversidade de morcegos insetívoros no Cerrado. A redução efetiva da riqueza de espécies ocorre apenas nos parques imersos em uma matriz predominantemente urbana e morcegos das famílias Vespertilionidae e Emballonuridae são menos comuns nesses habitats, ao contrário dos Molossidae, por exemplo. A sazonalidade do Cerrado também pode influenciar a comunidade de morcegos insetívoros, limitando o número de espécies nesses habitats durante a estação seca.

Os morcegos da família Molossidae que habitam os habitats urbano do Cerrado apresentam alterações comportamentais. *Molossus currentium, M. molossus* e *N. laticaudatus*, por exemplo, apresentam diferentes padrões de atividade temporal quando comparadas populações não urbanas e urbanas. Os diferentes padrões também podem estar associados a sazonalidade.

Outras alterações associadas ao gradiente de urbanização estão relacionadas aos pulsos de ecolocalização. As espécies *Molossus currentium e N. laticaudatus,* por exemplo, apresentam diferenças em aspectos tonais, temporais e no *duty cycle*. No Cerrado, a sazonalidade também está associadas a diferenças nos pulsos emitidos dessas espécies e de *M. molossus*. A riqueza de Molossidae constante ao longo do gradiente e as adaptações do padrão de atividade temporal e dos pulsos de ecolocalização indicam que esta família é tolerante aos habitats urbanos no Cerrado.