



# City lights, moonlit nights: examining bat responses to urbanization and lunar cycles

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## Abstract

Urbanization is one of the most abrupt mechanisms of land use change. This process can generate significant impacts on biodiversity, and its effects on bat activity patterns need further exploration due to the importance of these animals in controlling insect populations and maintaining ecological balance. This study aims to evaluate and describe the activity patterns of insectivorous bats in the Brazilian Cerrado, using environmental variables such as moon phase (full and new), season (dry and wet), and the level of urbanization. The level of urbanization was defined through an urbanization index and then classified into urban, suburban, and natural habitats to elucidate the impacts of this process on biological communities. We used ultrasonic recorders to sample insectivorous bats and count passes to measure activity in the study areas. A decrease in the activity of aerial insectivorous bat assemblages in the Cerrado was observed with decreasing urbanization. Additionally, bats exhibited higher activity during dry seasons and lower activity during full moon periods, suggesting lunar phobia. We identified significant effects of the time of night and the season of the year on the detectability of these bats, with a higher probability of detection in the first half of the night and during the dry season. Understanding these patterns in urban areas is crucial in the context of expanding cities. This knowledge aids in the maintenance and protection of insectivorous bat species that are fundamental to the balance of ecosystems and the provision of essential ecosystem services in both urban and natural areas of the Cerrado.

**Keywords** Bioacoustics · Bat activity · Insectivorous bats · Lunar phobia · Urban · Suburban · Natural habitats

## Introduction

Urbanization, a primary driver of land-use change, has significantly affected wildlife by transforming habitats, landscapes, and climate (Kalnay and Cai 2003). Unlike other anthropogenic processes, urbanization often leads to permanent ecological changes, resulting in the local extinction of many native species (McKinney 2002; Vale and Vale 1976). Among the affected species, bats play a crucial role as providers of ecosystem services, primarily due to their diverse feeding habits (Kunz et al. 2011). Insectivorous bats, for instance, contribute to agricultural pest control and the regulation of disease vectors in urban settings (Kunz et al. 2011; Aguiar and Antonini 2008; Aguiar et al. 2021; Reiskind and

Wund 2009). Given the importance of bats in maintaining ecological balance, it is essential to investigate how urbanization influences their activity patterns, particularly in biodiversity hotspots like the Cerrado, where these changes may have profound ecological consequences.

To study the effects of urbanization in bats, bioacoustics has emerged as a powerful tool for sampling and monitoring bat populations. This non-invasive method enables that allows rapid access to biodiversity in different environments, providing insights into their activity patterns and habitat use (Machado et al. 2017; Ochoa et al. 2000). By recording bat vocalizations with ultrasonic recorders, researchers can assess the diversity and behavior of these animals (Arias-Aguilar et al. 2018) identifying areas of high activity or frequent foraging through the detection of feeding buzzes, which are distinct components of echolocation sequence (Acharya and Fenton 1992). However, as urbanization leads to habitat fragmentation, the impact on bat activity and habitat use becomes more complex, necessitating the integration of bioacoustic methods with ecological models to fully

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understand these dynamics (Yates and Muzika 2006; Russo and Ancillotto 2015).

Urbanization also introduces a range of environmental factors that can influence bat studies, including habitat fragmentation, seasonal variations, lunar phases, and even the presence of domestic cats (Ancillotto et al. 2013). For instance, the reproductive season and the lunar phase are known to affect bat detection and activity, with increased lunar phobia observed as a mechanism to reduce predation risk under high lunar illumination in tropical environments (Hein et al. 2009; Fenton et al. 1977; Saldaña-Vázquez & Munguía-Rosas 2013). Additionally, the structure of urban environments, including vegetation density and the availability of green spaces, may influence the occupancy patterns of both frugivorous and insectivorous bat species (Silveira et al. 2018; Hein et al. 2009). Understanding these interactions is crucial for using bats as model organisms to study the impacts of urbanization in conjunction with environmental variations and urban landscape structure.

In 2019, the Global Commission on Adaptation recommended adapting cities to environmental changes with nature-based solutions (NBS), a term coined by the IUCN. Among these recommendations is the need to increase understanding of the value of nature and species to improve cities' adaptation to climate change and make them more receptive to biodiversity. The Federal District (DF), home to Brazil's capital, Brasília, features a large urban area with numerous green spaces, including urban parks and Protected Areas, both federal and private. Additionally, the urban areas of the Federal District are surrounded by a rural matrix (Rivero 2019). Due to these unique conditions, Brasília's green areas host threatened species such as the Cerrado bat (*Lonchophylla dekeyseri*) (Aguar et al. 2014). The importance of green spaces in urban centers for preserving insectivorous bats has been demonstrated, for example, in Recife, Pernambuco (de Araújo and Bernard 2016).

Brasília presents an excellent model for creating wildlife-friendly cities with increased investment in nature-based solutions (NBS). Bats are the mammals with the highest number of species in the Cerrado (Aguar et al. 2016), highlighting the urgency of understanding the effects of urbanization on the activity of Cerrado bat species. Urbanization can impair their biological roles, consequently affecting the ecosystem services they provide, such as agricultural pest control, even in urban areas (Aguar et al. 2021). This is particularly important for the agricultural matrix of the Federal District, as bats contribute to pollination and seed dispersal (Kunz et al. 2011). Moreover, bats are known reservoirs of the rabies virus in urban areas (Ribeiro et al. 2018). Understanding their occupancy and activity patterns is essential, as this information can aid species management and potentially influence public health management.

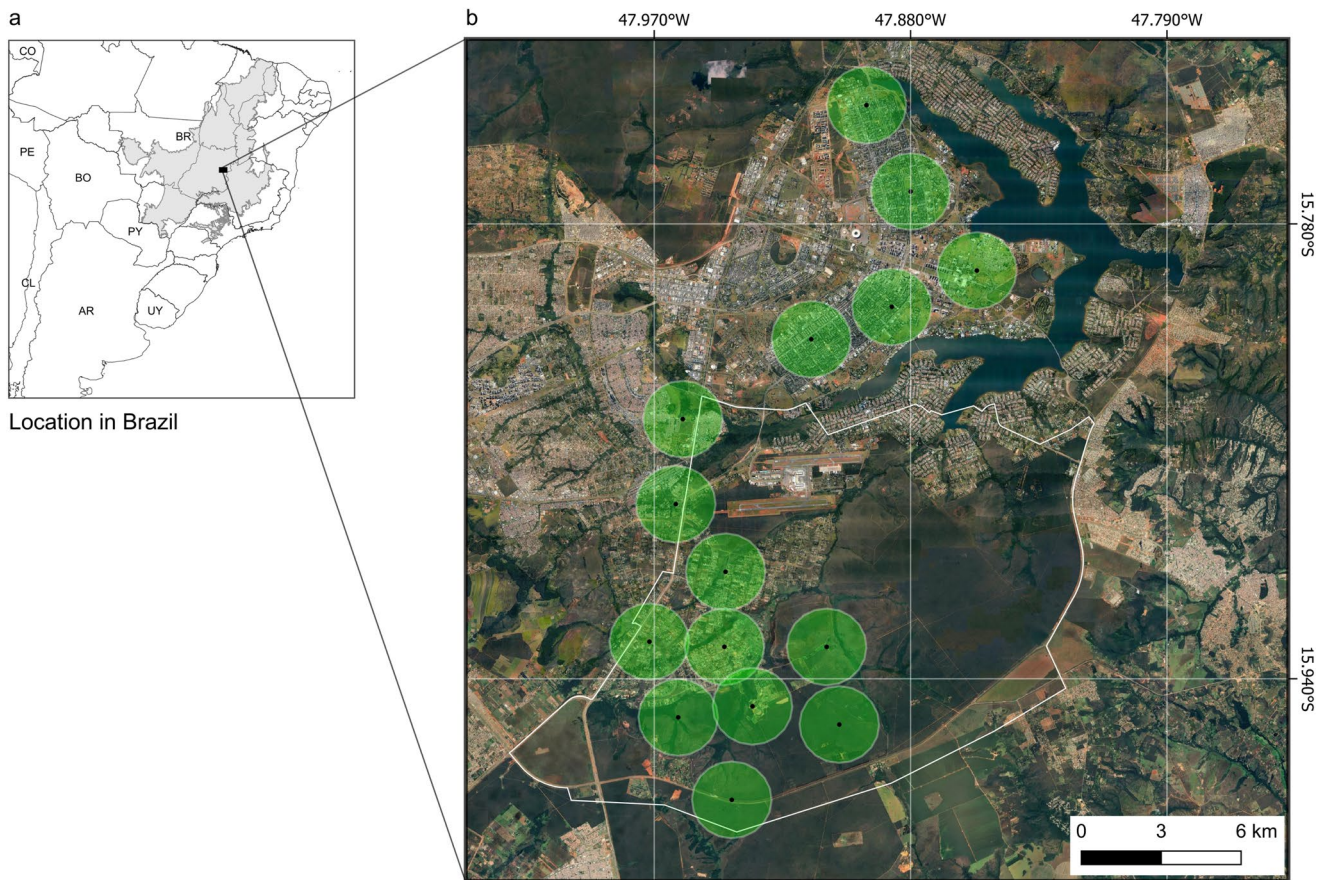
This study aims to understand and define the Cerrado aerial insectivorous bat assemblage activity patterns along an urban-natural gradient. Additionally, it seeks to evaluate whether the seasons affect the activity of these bats and if they exhibit lunar phobia. Finally, we will investigate whether urbanization affects the occupancy of insectivorous bats and how environmental variables (moon phase, season of the year), in addition to the night period (first half and second half), affect the detectability of these bats.

Based on recent studies in Mexico (Rodríguez-Aguilar et al. 2017) and the United States (Gehrt and Chelsvig 2004), we expect to corroborate the following results: (i) Activity patterns will differ along the urban-natural gradient, with higher activity in urban areas, as these are commonly used by open-area foraging bats (Avila-Flores and Fenton 2005; Threlfall et al. 2011), which may benefit from shelters and food sources in these environments. (ii) Higher activity is expected during the rainy season, as this is the period of increased prey availability (Wolda 1980) for these bats. (iii) Higher bat activity is anticipated during the new moon phase, assuming a reduction in predation risk (any predator that can be found in cities such as birds and domestic cats - Ancillotto et al. 2013; Mikula et al. 2013). This effect is expected to be more pronounced in less urbanized areas, where bats can more easily perceive moonlight due to the reduction of artificial light at night (ALAN) (Barré et al. 2022). (iv) Urbanization is expected to positively affect the occupancy of aerial insectivorous bats, as more complex, closed environments such as the natural areas in this study can impose limits on flight and foraging (Bender et al. 2015; Pauli et al. 2017). Lastly, we expect the new moon (Silveira et al. 2018), the wet season (MacSwiney et al. 2009), and the first half of the night (Hayes 1997) to positively affect the detectability of insectivorous bats.

## Materials and methods

### Study area

The study was conducted in Brasília, Federal District, Brazil. Fifteen randomly selected sampling points extended from an urban area (Asa Sul) toward a natural area (Gama and Cabeça de Veado Environmental Protection Area—APA), encompassing regions with varying degrees of urbanization (Fig. 1). The sampling points were spaced approximately 3 km apart to minimize the potential overlap of acoustic recordings. Bat activity was assessed by analyzing vocalization recordings across these locations, which represented different levels of urbanization.



**Fig. 1** (a) Location of the study area, with the limits of the Cerrado biome shown in gray. (b) Sampling points (black dots) and buffers (green circles) for area characterization according to soil cover. The

white line delineates the Environmental Protection Area (APA) of Gama and Cabeça de Veado

### Analysis of urbanization degree

A buffer with a radius of 1.5 km was established for each sampling point. The degree of urbanization was determined based on soil impermeability, verified using satellite images. The coordinates of the sampling points were used to generate .kml files with a function in R version 4.3.3 (R Core Team 2024). These .kml files were then imported into Google Earth to create the corresponding images. Each image was produced with a 1.5 km radius and a camera view altitude of 5.5 km (see Online Resource 1).

Satellite images for each sampling point were processed using the image editing software GIMP (version 2.10.38). The area within the previously defined buffer was selected and color-coded according to five land cover classifications: buildings, pavement, dirt, trees, and grass (see Online Resource 1). After classification, the software counted the pixels and generated a .txt file with the values for each classification.

The pixel counts for each point were then combined into broader categories: “natural” (trees and grass), representing permeable areas, and “roads” (pavement and dirt),

representing both paved and dirt roads. The classification “buildings” was maintained as a separate category due to its importance for bat presence or activity, as these animals often use buildings as roosts (Aguiar et al. 2021). Thus, impermeable areas were defined as pavement and buildings.

A principal component analysis (PCA) was performed using the values for natural, roads, and buildings for each point. The variables were centered (subtracting the mean) and scaled (dividing by the standard deviation) to ensure equal influence in the analysis, regardless of their units or variances. The principal component 1 (PC1) values were used as an urbanization index to classify the areas into three habitat categories: urban, suburban, and natural. The K-means algorithm was applied to cluster the data into three groups. All steps for image creation, processing, and index calculation followed the procedures outlined in the urbanization-index dataset on GitHub (LaZerte 2016).

### Acoustic data collection

Bat recordings were made using AudioMoth recorders (v1.2.0). Recordings were made for 1 min every 15 min,



with a 14-minute interval between recordings. This sampling strategy was chosen to ensure comprehensive coverage of bat activity throughout the night, as bats are known to be most active during the first few hours after sunset and before sunrise. The files were saved in WAV format with 16-bit resolution and a sampling rate of 384 kHz, covering the echolocation frequencies of bats likely to occur in the Cerrado (Aguiar et al. 2016). Recordings began 30 min before sunset and continued for 12 h. Sampling was conducted twice per month at each point (Fig. 1), with simultaneous sampling across all points during both new moon and full moon phases each month (August 2022 and January 2023) to test the effect of moonlight on insectivorous bat activity across different seasons (dry season in August and rainy season in January).

### Acoustic data analysis

Following the recordings, the sound files were analyzed in the laboratory using RavenPro software (version 1.6, 2024). The sound files were used to identify and characterize the bat assemblage composition in the sampled areas. For bat identification, five pulses from the search phase of each pulse sequence produced by the bat were selected from each 1-minute file. Measurements of pulse duration, interval between pulses, peak frequency, maximum frequency, minimum frequency, and bandwidth were obtained for each pulse in the analyzed sequences. Subsequently, the means of the five pulses for each metric were calculated, and bat identification was performed based on these six parameters using published identification keys (Jung et al. 2007, 2014; Barataud et al. 2013; Hintze et al. 2016; Arias-Aguilar et al. 2018).

Species with at most five records were excluded from further analyses. A linear discriminant analysis (LDA) was conducted for the remaining species to check for potential overlaps and ensure correct identification. The LDA tests whether pre-determined bat species can be accurately classified based on selected metrics (in this case, acoustic parameters). Following Russo and Jones (2002), a discrimination threshold of 0.8 was used to consider passes satisfactorily classified as the previously identified species for subsequent analyses. The LDA was performed separately for the three families identified in this study: Molossidae, Vespertilionidae, and Emballonuridae.

Bat activity in the areas was determined by counting the passes of each species at each sampling point. A pass was defined as a sequence of five or more pulses from the typical search phase of bats with at least a 1-second interval between sequences.

### Statistical analysis

To test the influence of urbanization, seasons, and lunar phases on bat activity, generalized linear mixed models (GLMM) with a Poisson family were conducted. The urbanization index, lunar phase, and seasons were the predictor variables, and the number of passes per point was the response variable. Sampling points were treated as random effects in the model. Corrected Akaike Information Criterion (AICc) values for small samples were used to compare the fit of models with and without predictor factor interactions. Spatial autocorrelation in the models was tested by calculating Moran's I index of the model residuals using the 'Moran.I' function from the ape package version 5.5 (Paradis and Schliep 2019).

To better understand bat activity in the areas, recording hours were classified into three activity periods: crepuscular (hours 1 and 12, near sunrise and sunset), early activity (hours 2 to 6), and late activity (hours 7 to 11). The unweighted pair group method with arithmetic mean (UPGMA) was used to assess the similarity in hourly activity among bat species based on the number of recorded passes. A dendrogram was created to present the similarity of activity times among species. Additionally, to understand potential changes in species activity times across different habitats, a dendrogram was created for each previously defined habitat class (urban, suburban, and natural).

### Occupancy and detectability models

To assess the impact of urbanization on bat occupancy, we employed an urbanization index generated through principal component analysis (PCA). We utilized multi-season occupancy models (MacKenzie et al. 2003) to address the challenges of detecting species presence when detectability is less than 1 (MacKenzie et al. 2002). These models require the estimation of four parameters:  $p$  (the probability of detecting a species that occupies the area);  $\psi$  (the occupancy probability in the first season);  $\epsilon$  (the probability of extinction in the subsequent season); and  $\gamma$  (the probability of colonization in the subsequent season).

Detectability was modeled using variables such as recording time (first half of the night vs. second half), moon phase (new moon vs. full moon), and season (dry vs. wet). We used the "colext" function from the unmarked package in R (Fiske and Chandler 2011) to generate concurrent multi-season occupancy models. The goodness of fit was assessed by comparing the chi-squared statistic of the models with the reference distribution generated by 10,000 simulations and evaluating the overdispersion parameter ( $\hat{c}$ ) as suggested by MacKenzie and Bailey (2004).

**Table 1** Urbanization index values per point and classification of points after clustering the values generated in the PCA for the areas defined in the study in Brasília, Brazil. The classification into Urban, Suburban and Natural habitats was determined based on the urbanization index values: where urban areas have an index value between  $-1,865831501$  and  $-0,883109812$ ; suburban areas between  $0,259028800$  and  $1,213864075$ ; and natural habitats between  $2,121712345$  and  $2,584134203$ . These thresholds were set up according to the clustering results from the PCA analysis, as detailed in the methods section

Sampling point	Urbanization index	Classification
1	-1,865831501	Urban
2	-1,890652536	Urban
3	-1,595025902	Urban
4	-1,527650339	Urban
5	-1,380805490	Urban
6	-1,651372854	Urban
7	-0,883109812	Urban
8	0,259028800	Suburban
9	0,110925914	Suburban
10	0,146184297	Suburban
11	1,213864075	Suburban
12	2,121712345	Natural
13	2,096888169	Natural
14	2,261710631	Natural
15	2,584134203	Natural

Models were ranked using the Akaike Information Criterion corrected for small samples (AICc), and we selected only those models that showed no evidence of lack of fit (GOF p-value  $> 0.05$  and  $\hat{c}$  close to 1). The goodness of fit process, along with the AICc and  $\hat{c}$  estimations, were conducted using the AICcmodavg package (Mazerolle 2015). Occupancy and detectability were modeled only for species recorded at a minimum of five sampling points: *Eumops glaucinus*, *Eumops* sp2., *Eumops* sp3., *Molossops temminckii*, *Molossus currentium*, Vesp 1, *Peropteryx macrotis*, Mol 1, and *Molossus molossus*.

## Results

### Urbanization index and sampling points classification

Following the selection and classification of land cover in GIMP, pixel counts were obtained for each category (see Online Resource 1). The first principal component (PC1) of the PCA explained 94.32% of the total variation in the original data, suggesting that the dimensionality of the three variables (natural, roads, and buildings) can be reduced to a single principal component (PC1) without significant loss of information. For more details on the PCA results and PC1 selection, see Online Resource 1. The rotation matrix of PC1 indicates that the natural variable contributes positively to

**Table 2** Species and groupings of bats identified in the study areas in different habitats (urban, suburban and natural) in the Brazilian Cerrado, Brasília

Species or grouping	Habitats
<i>Molossus molossus</i>	all of them
<i>Peropteryx macrotis</i>	Urban and natural
<i>Peropteryx trinitatis</i>	all of them
Mol 1	all of them
Vesp 1	all of them
<i>Nyctinomops laticaudatus</i>	Urban
<i>Lasiurus cinereus</i>	all of them
<i>Eumops</i> sp2.	all of them
<i>Molossus currentium</i>	all of them
<i>Eumops glaucinus</i>	all of them
<i>Molossops temminckii</i>	Suburban and Natural
<i>Eumops</i> sp3.	all of them
<i>Myotis nigricans</i>	Natural
<i>Molossus</i> sp1.	Urban

PC1, whereas the roads and buildings variables contribute negatively. This signifies that PC1 represents a dimension where an increase in the natural variable corresponds to a decrease in the roads and buildings variables. The generated index shows higher values in natural areas compared to urbanized areas. After clustering the PC1 values using the K-means algorithm, seven points were classified as urban habitats, four as suburban, and four as natural (see Online Resource 1). The index values and the classification of each point are presented in Table 1.

### Bat species and activity

From the 2880 one-minute sound files collected, 1440 were recorded during the dry season and 1440 during the rainy season. For each season, 720 files were recorded per night under different lunar phases (full moon and new moon), resulting in 48 files per point per night. Our meticulous data collection methods were designed to capture a comprehensive representation of bat species and activity across various seasons and lunar phases. Throughout the sampling periods, 12 species and two groupings were identified through linear discriminant analysis (LDA) (see Online Resource 1), yielding a total of 14 species or taxa (Table 2). Species identification was based on measurements of pulse duration, interval between pulses, peak frequency, maximum frequency, minimum frequency, and bandwidth for each pulse. This detailed analysis of bat species and activity provides a robust foundation for further ecological research and urban planning decisions.

Bats exhibited a high activity pattern during the early night hours, with a smaller peak in the final hour. Urban areas had the highest number of passes (see Online Resource 1). The best generalized linear mixed model (GLMM), selected

based on its Akaike Information Criterion corrected (AICc) value, indicated a reduction in bat activity along the urban-to-natural gradient ( $z = -3.546$ ,  $p = 0.00143$ ) (Fig. 2).

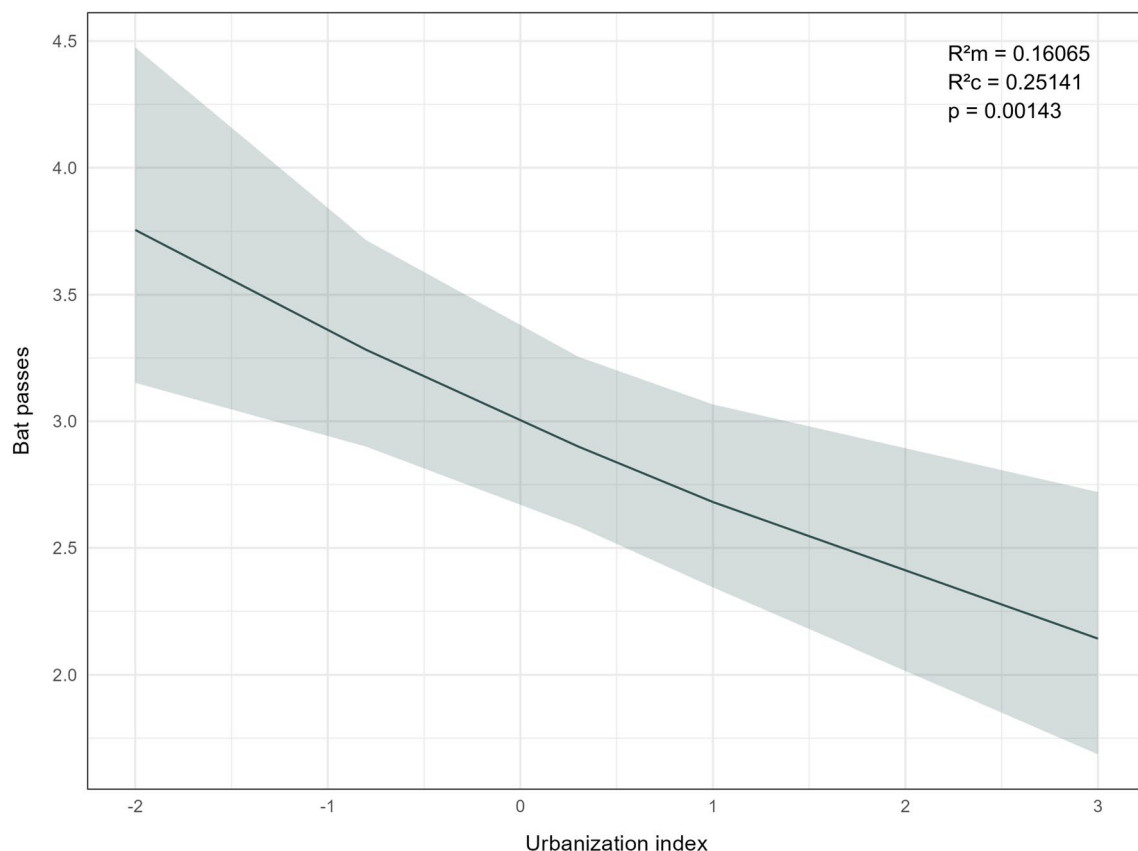
Bat activity was significantly higher on new moon nights compared to full moon nights ( $z = 4.578$ ,  $p < 0.001$ ) and during the dry season compared to the rainy season ( $z = -2.294$ ,  $p = 0.021809$ ) (Fig. 3a and b). Additionally, the model revealed an interaction between moon phase and season, indicating that the difference in activity between moon phases is more pronounced during the dry season ( $z = -2.514$ ,  $p = 0.011933$ ) (Fig. 3c). Importantly, the model did not show significant spatial autocorrelation (Moran's  $I = -0.41989$ ,  $p = 0.6627$ ), further validating the robustness of our findings.

Following UPGMA clustering, a method commonly used in ecology to classify species based on their activity patterns, species were categorized accordingly. *Molossus molossus* (species 1) exhibited crepuscular activity at sunrise and sunset (Fig. 4a). Two species (*Molossus currentium* and the Mol 1 grouping) were active throughout the night. In contrast, 11 species concentrated their activities in the first half of the night, thus classified as early active (Fig. 4a). No species exhibited late activity, defined as activity during the second half of the night.

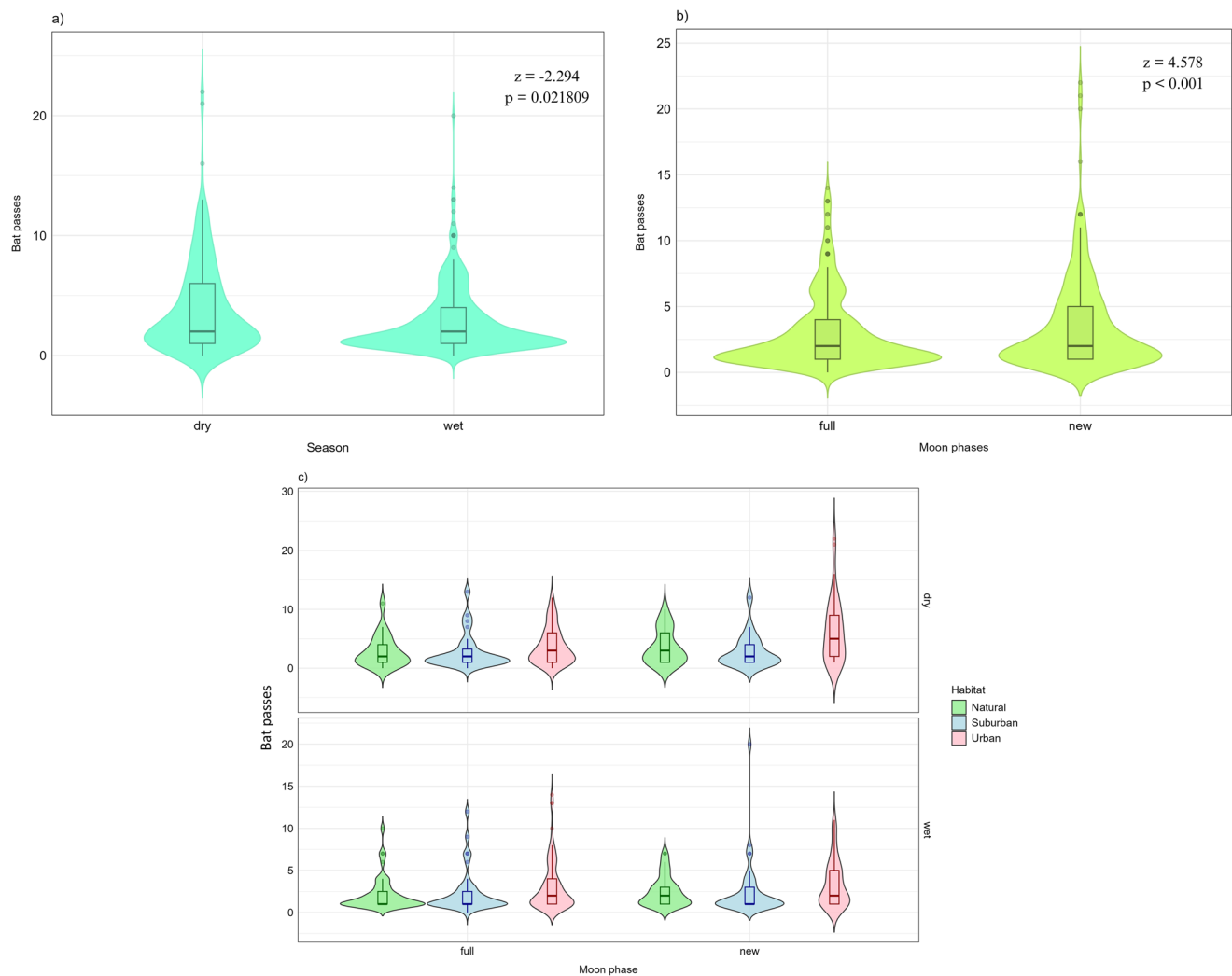
Regarding activity patterns across the three habitat types, species 2 (*Peropteryx macrotis*), species 4 (Mol 1 grouping), and species 9 (*M. currentium*) demonstrated remarkable adaptability by being active throughout the entire night in urban areas (Fig. 4b). In suburban areas, *M. currentium* and the Mol 1 grouping shifted their activity pattern from throughout the night to being concentrated in the early hours, displaying less similarity to other species (Fig. 4c). In natural areas, species 11 (*Molossops temminckii*) and the Vesp 1 grouping (classified as species 5) showed less similarity in activity patterns compared to other species. However, all species, except species 1, exhibited activity concentrated in the first half of the night (Fig. 4d). *M. molossus* maintained a crepuscular activity pattern regardless of habitat type, consistently displaying less similar activity patterns compared to other species.

### Occupancy and detectability models

Two species (*Eumops* sp2. and *Eumops* sp3.) had the null model as the best fit, indicating that none of the variables significantly affect the occupancy and detection patterns of these species. Among the other species, *M. temminckii* was the only one whose occupancy was negatively affected by



**Fig. 2** Plot of the best fitted model considering moon phase, season, and urbanization index as predictors of bat activity in the Brazilian Cerrado, Brasília. The shaded area represents a 95% confidence interval for the trend line.  $R^2m$  = marginal  $R^2$ ,  $R^2c$  = conditional  $R^2$



**Fig. 3** Bat passes in different conditions within the Brazilian Cerrado, Brasília: **(a)** Comparison of bat passes between the dry and wet seasons; **(b)** Comparison of bat passes during full moon and new moon

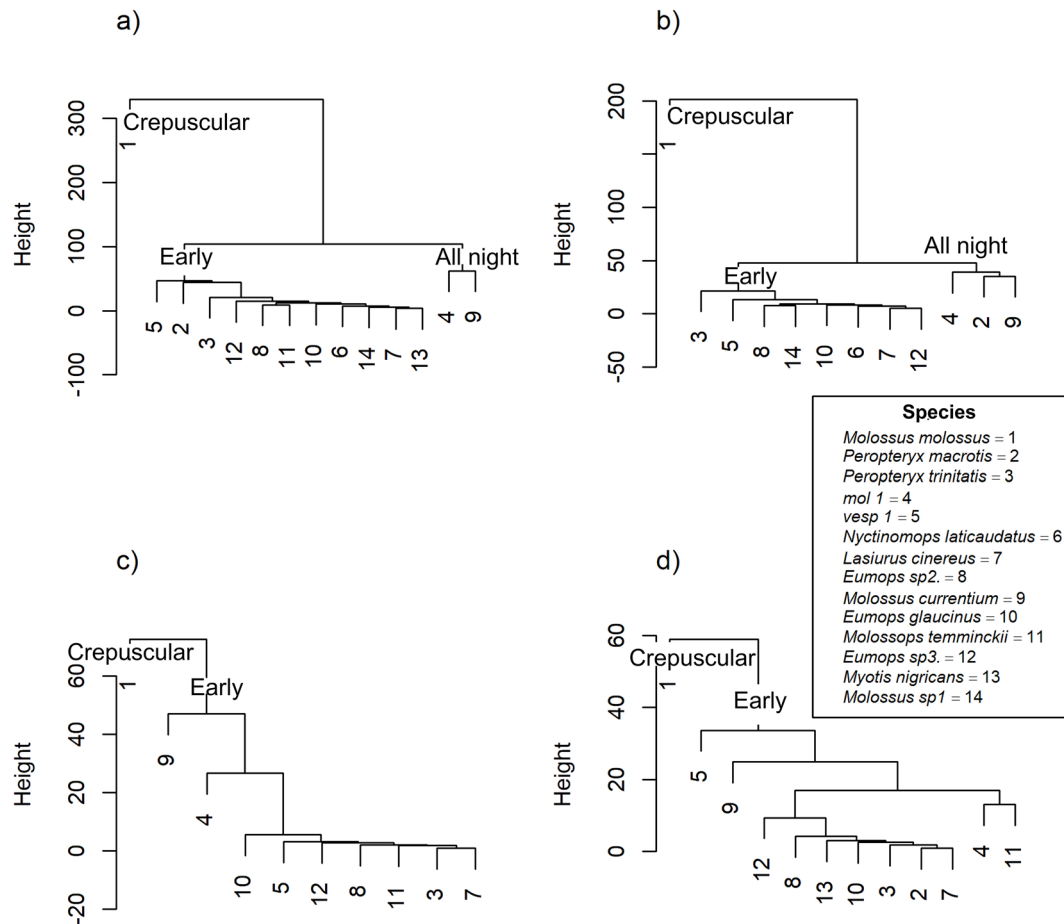
night; **(c)** Interaction of moon phase and season on bat passes across the three sampled habitats

urbanization (as defined by the urbanization index), suggesting a higher probability of occupancy in less urbanized sites. For the remaining species, urbanization was not a significant variable for occupancy; however, the variables season of the year and half of the night can affect detection (Table 3). The detectability models for *Eumops glaucinus* and *Molossus molossus* showed lack-of-fit, with  $p$ -values  $< 0.05$  and  $\hat{c} > 1$ , indicating overdispersion of the data. Therefore, we plotted the detection probabilities only for the remaining species (Fig. 5).

## Discussion

Our hypothesis that activity patterns would differ along the urban-natural gradient, with higher activity in urban areas, was confirmed. The study demonstrated variation in bat

activity based on habitat, with the highest number of passes in urban areas, as modeled by the urbanization index (see Fig. 2). This pattern has been previously observed in vespertilionid species, where bats were more active near major urban centers and less active in rural areas (Gehrt and Chelvig 2004). Stanley et al. (2023) also observed that in urban areas, vespertilionids are more associated with tree-lined streets than non-tree-lined streets, highlighting the importance of plant structures for the group. Similarly, molossid bats have shown more significant activity in urban areas than in non-urban areas (Jung and Kalko 2011; Rodríguez-Aguilar et al. 2017). However, contrary to our findings, Rodríguez-Aguilar et al. (2017) did not observe an apparent change in overall insectivorous bat assemblage activity between urban and non-urban areas. This discrepancy may arise from high vespertilionid activity in non-urban areas balancing the high molossid activity in urban areas.



**Fig. 4** Results of the unweighted pair group method with arithmetic mean (UPGMA) showing similar patterns of bat activity by time of night in the Brazilian Cerrado, Brasília. **(a)** Overall pattern of bat activity across all habitats; **(b)** Bat activity pattern in urban areas; **(c)**

Bat activity pattern in suburban areas; **(d)** Bat activity pattern in natural areas. The numbers represent the different bat species in this study, specified in the legend on the right

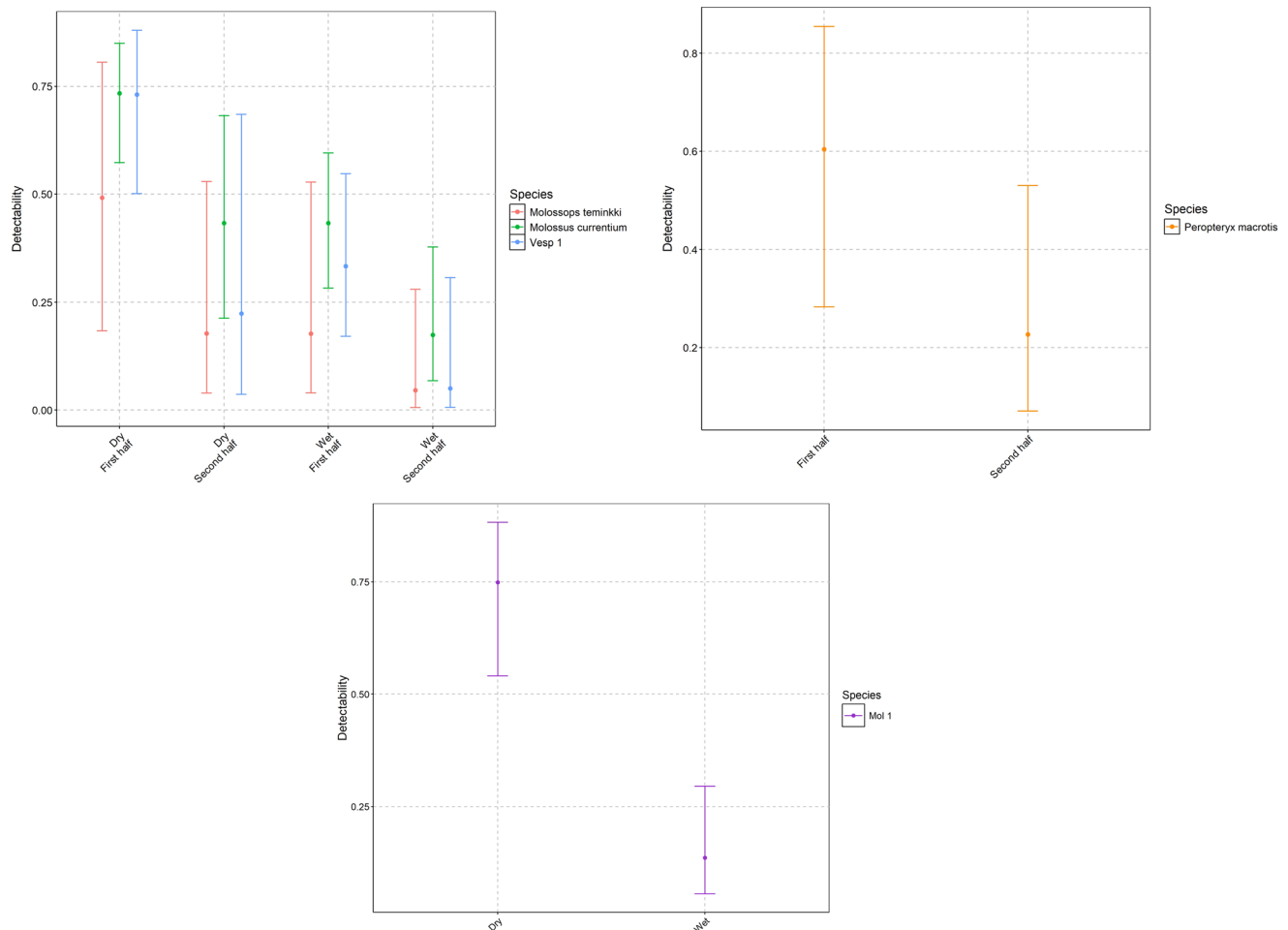
**Table 3** Models of initial occupancy ( $\psi$ ), evasion ( $\epsilon$ ), establishment ( $\gamma$ ), and detection ( $p$ ) for aerial insectivorous bats from the Brazilian Cerrado, Brasília. The models are the best adjusted according to the Akaike Information Criterion for small samples (AICc) and  $\Delta$ AICc for species that had more than one model with  $\Delta$ AICc < 2. The table includes model weight (weight), number of parameters (K), goodness-of-fit probability (p-value) and estimates of the overdispersion parameter ( $\hat{c}$ ). Variables included are urbanization index (urb), half of the night (half), and season (season)

Species	Model	K	AICc	$\Delta$ AICc	Weight	p value	$\hat{c}$
<i>Eumops glaucinus</i>	$\psi(.)\gamma(.)\epsilon(.)p(\text{season} + \text{half})$	6	129.96	0	0.96	0.0022	11.35
<i>Molossops temminckii</i>	$\psi(\text{urb})\gamma(.)\epsilon(.)p(\text{season} + \text{half})$	5	57.77	0	0.9	0.067	1.91
<i>Molossus currentium</i>	$\psi(.)\gamma(.)\epsilon(.)p(\text{season} + \text{half})$	6	159.27	0	0.43	0.1575	1.27
	$\psi(.)\gamma(.)\epsilon(.)p(\text{half})$	5	159.49	0.22	0.39	0.051	1.49
Vesp 1	$\psi(.)\gamma(.)\epsilon(.)p(\text{season} + \text{half})$	6	124.92	0	0.49	0.5819	0.86
	$\psi(.)\gamma(.)\epsilon(.)p(\text{half})$	5	125.47	0.54	0.37	0.1658	1.28
<i>Peropteryx macrotis</i>	$\psi(.)\gamma(.)\epsilon(.)p(.)$	4	73.42	0	0.51	-	-
	$\psi(.)\gamma(.)\epsilon(.)p(\text{half})$	5	74.14	0.72	0.36	0.3428	1.12
Mol 1	$\psi(.)\gamma(.)\epsilon(.)p(.)$	4	144.07	0	0.44	-	-
	$\psi(.)\gamma(.)\epsilon(.)p(\text{season})$	5	144.31	0.24	0.39	0.3157	1.08
<i>Molossus molossus</i>	$\psi(.)\gamma(.)\epsilon(.)p(\text{season} + \text{half})$	6	129.96	0	0.96	0.0016	11.36

Most bats in our study are considered open-area aerial foragers, which could explain their higher use of urbanized areas, as observed by Avila-Flores and Fenton (2005), Jung and Kalko (2011), and Threlfall et al. (2011). However, a

study conducted in green and urban areas of a city located in the Atlantic Forest biome, Brazil, by Almeida et al. (2022) demonstrated an increase in the activity of aerial insectivorous bats in large green areas (> 30 ha), primarily for edge





**Fig. 5** Detectability of aerial insectivorous bats in the Brazilian Cerrado, Brasília. The top figure shows the probability of detection for the species *Molossops temminckii*, *Molossus currentium*, and the Vesp 1 cluster for the first and second half of the night in the dry and wet

seasons. The middle figure shows the detection probability of the species *Pteropteryx macrotis* for the first and second half of the night. The bottom figure shows the detection probability of the Mol 1 cluster for the wet and dry seasons

foraging bats, but also for open area foraging bats, when compared to non-green areas, differing from our observations. This demonstrates how different environments, such as forest and savanna biomes, impose different pressures on aerial insectivorous bats, which behave differently in these environments.

In Germany, aerial insectivorous bats demonstrated an apparent change in behavior across an urban-rural gradient, with greater diversity in non-urbanized areas and changes in activity levels in each class of environment, with most species showing more significant activity in non-urbanized areas (Starik et al. 2024). These different results raise questions about how the growth of urbanization can truly impact bats. In England, a study modeled bats' activity and habitat selection in scenarios of increased urbanization and discontinuous vegetation cover, demonstrating that most species would show a reduction in activity in highly urbanized areas (Gili et al. 2020). This highlights the need to plan more

biodiversity-friendly cities with green areas to preserve bats' diversity and different characteristics. Such planning should be a priority for politicians and managers, as green areas, such as trees, can enable the presence of aerial insectivorous edge-foraging bats in urban landscapes (Parsons et al. 2024), which can also serve as shelter for species with forest habits (Bergeson et al. 2020). Ensuring a healthier assembly of bats enables the whole exercise of their ecosystem services.

Our results show two peaks in insectivorous bat activity (see Online Resource 1), with the central peak occurring in the early hours after sunset, both in general activity and within each habitat type defined in this study. The general activity pattern of these bats, with a peak in the early evening, is well-documented across various locations (Kunz 1973; Scanlon and Petit 2008; Schimpp et al. 2018; Li et al. 2020). The secondary activity peak in the final hour of our study can be attributed to the high activity of *Molossus*

*molossus*, as indicated by its prominence in the dendrogram (Fig. 4a). This species exhibited crepuscular behavior, and it is known that some bat species have more than one activity peak during the night (Li et al. 2020; Rivero-Montagudo and Mena 2023), highlighting the importance of understanding species-specific patterns in landscape use by bats.

In an urban-rural landscape of Peru, aerial insectivorous bats demonstrated changes in species-specific activity patterns depending on the environment, with a more significant overlap of activity patterns in rural areas (Rivero-Montagudo and Mena 2023). In our study, there is no evident change in the activity pattern of the bat assemblage across the urban-natural gradient. However, we also observed species-specific changes in the activity pattern between different habitats, as discussed later. We also emphasize that several other factors may be influencing the activity of insectivorous bats. Temporal partitioning depending on the acoustic niche (low, medium, and high-frequency bats) is already known (Beilke et al. 2021). The phase of the moon can also generate changes in the activity patterns of different species, mainly reducing activity on full moon nights and creating a more significant peak in the first hours of this phase compared to the new moon (Vázquez et al. 2020). Our study also suggests an effect of the moon phase on the activity of insectivorous bats in the Cerrado. Also, altitudinal gradients (Arias-Aguilar et al. 2020) and temperature (Pretorius et al. 2020) influence bat habitat use and behavior. Therefore, it is crucial to investigate and understand how these other factors affect bats in urban areas in future studies.

Contrary to our hypothesis, higher activity was observed in the dry rather than the rainy season (Fig. 3a). Rain can hinder bat flight, reducing overall activity on rainy nights and potentially altering activity peaks (Appel et al. 2019; Perks and Goodenough 2020). Some vespertilionid species exhibit lower activity during rainy seasons (LaVal and Lawton 2021) and may reduce the number of passes per night with increased precipitation (Erickson and West 2002). This decrease in activity during rainy seasons can be attributed to increased metabolic costs during wet flight, which can double the cost compared to dry flight (Voigt et al. 2011). The atmospheric attenuation of echolocation calls with increased humidity makes flight and foraging more challenging (Griffin 1971), and even the sound of rain can alter bat emergence times (Geipel et al. 2019). Additionally, the moon's effect was more pronounced during the dry season, likely because bats cannot increase activity during the new moon in rainy conditions. Flying during rainy periods is more complex and costly, so reducing activity during rainy periods may be advantageous.

Another factor that could increase activity during dry periods is the extended search time for food, which may be less available during the dry season (Wolda 1980). An

increase in the activity of aerial insectivorous bats such as *M. molossus* and *Myotis nigricans* during the dry season over rice fields has been observed in Venezuela (Azofeifa et al. 2019), likely because these fields are a good source of prey during the dry season. However, analyzing species-specific responses during rainy periods and under different rain intensities would be interesting, as some bats, like *Lasiurus cinereus semotus*, maintain activity during light rain (Belwood and Fullard 1984). Furthermore, open-space aerial insectivorous bats demonstrate more significant activity in riparian areas during the dry season (the season in which the study was conducted), showing that the interaction between relative humidity and different habitats affects group activity (da Costa et al. 2021). This raises the question of whether the bats in our study exhibit greater activity in urban areas during the dry season due to possible displacement to regions with more bodies of water. These regions serve as breeding grounds for various insects and can provide water and food for these bats (Zukal and Reháček 2006; Hagen and Sabo 2011; Marteau et al. 2023). Brasília, a city with a large lake and urban areas with water sources such as swimming pools, reflecting pools, and even domestic animal containers, may contribute to this phenomenon.

The breeding season also affects bats' activity patterns. Bats may be more active throughout the night during reproductive periods due to the greater energetic demand imposed by reproduction, as observed in South Africa (Pretorius et al. 2020). Our bats may be more active during the dry season because it is a reproductive period for the group, as observed for *Molossus molossus* in Colombia, which showed peaks of pregnancy in the dry season and births at the beginning of the rainy season (Silva-Duarte et al. 2023).

Our results indicate a possible lunar phobia in aerial insectivorous bats in the Cerrado, evidenced by the higher number of passes during the new moon (Fig. 3b). Analyzing boxplots by season and habitat shows increased average passes and higher pass values, especially in suburban and natural areas, during the new moon. This supports the hypothesis of reduced activity on full moon nights in less urbanized areas. Urban areas likely have higher levels of artificial light at night (ALAN) (Barré et al. 2022), which can overshadow the effect of moonlight on bats. Bats may ignore the predation risk associated with higher illumination (Jones and Rydell 1994) due to potentially lower predator numbers in these areas (Sorace and Gustin 2009), maintaining activity regardless of moonlight (Scanlon and Petit 2008). In the USA, an interaction between the phase of the moon and ALAN was demonstrated, with a decrease in activity on more moonlit nights. For some species, ALAN masked the effect of the moon phase, and in general, ALAN negatively affected bat activity over a decade (Li et al. 2024). However, in our study, bats maintained a very similar

pattern of activity in urban areas regardless of the phase of the moon (see Fig. 3c), suggesting masking of the moon phase by ALAN. In less urbanized areas, where ALAN less influences bats, they may be more aware of increased moonlight. This could be associated with higher predation risk or not (Lima and O’Keefe 2013). Bats exposed to moonlight may change foraging areas, as observed in the insectivorous bat *Nyctalus noctula* (Roeleke et al. 2018), which shifted its activity pattern from forests to more open areas, reducing passes in forested areas. In the Brazilian Amazon, it was seen that the availability of prey in forested areas is more determinant for bat activity than the risk of predation, and only a few species had their activity affected by the moon (Appel et al. 2023). Therefore, a more detailed analysis of the behavior of each species would help to understand the real effects of the moon on bat activity, highlighting the importance of new studies in the Cerrado that investigate the availability of food resources and the risk of predation for aerial insectivorous bats in urban and natural areas.

Lunar phobia has been observed in other aerial insectivorous bats in Costa Rica, with reduced vespertilionid activity on brighter nights (around the full moon) (LaVal and Lawton 2021). However, different species may respond differently to moonlight. In Brazil, *Pteronotus rubiginosus* and *Saccopteryx leptura* have increased activity on brighter nights, while *Myotis riparius* showed higher activity on darker nights (Appel et al. 2019). *Peropteryx kappleri* and *Peropteryx macrotis* showed lower activity on brighter nights, while *Pteronotus gymnonotus*, *Cormura brevirostris*, and *M. molossus* increased activity in French Guiana (Gomes et al. 2020). A meta-analysis suggests that lunar phobia is more likely in tropical bats although the relationship is weak (Saldaña-Vázquez and Munguía-Rosas 2013). In Poland, a temperate region, lunar phobia was rejected for six species of swarming bats (Apoznański et al. 2024), reinforcing the greater likelihood of lunar phobia occurring in tropical regions. However, the study by Saldaña-Vázquez and Munguía-Rosas (2013) does not suggest lunar phobia for open-area foraging insectivores, which face lower predation risk compared to bats with other foraging strategies due to their high flight speed, characteristic of most species we recorded. In Kenya, evidence was found for the effect of season, habitat, and time of day on the activity of aerial insectivorous bats in open spaces. However, no effect of moonlight on activity was observed (Musila et al. 2019), in line with what was proposed by the meta-analysis by Saldaña-Vázquez and Munguía-Rosas (2013).

In our study, there is also the possibility that factors other than predation risk are causing reduced bat activity on brighter nights, such as insect availability. It has been shown that insects are more captured on new moon nights than full moon nights (Williams and Singh 1951). Urban areas

with more ALAN may attract insects to illuminated posts (Owens and Lewis 2018), increasing insect availability and bat activity around these insect aggregations. Investigating species-specific behaviors about moonlight, quantifying prey availability, and describing bat foraging behavior in areas with ALAN would elucidate the effects of these factors on aerial insectivorous bat behavior.

The dendrograms generated by UPGMA (Fig. 4) show crepuscular behavior for *M. molossus*, as observed in other parts of Brazil, where the species shows a peak of activity after sunset (Esbérard and Bergallo 2010; Costa et al. 2011). As observed in this study, the species exhibits crepuscular behavior in Panama, concentrating activity after sunset and before sunrise (Holland et al. 2011) and also in Trinidad and Tobago (Chase et al. 1991). *Molossus molossus* maintained its crepuscular behavior regardless of habitat, with high activity levels, showing a conspicuous activity pattern compared to other species. *Peropteryx macrotis* was recorded in natural and urban habitats, with a behavioral change in urban areas where its activity was well-distributed throughout the night. This behavior has also been recorded in French Guiana but in a forested area (Gomes et al. 2020). In our natural areas, the species showed a pattern more similar to other species, with activity concentrated in the early hours of the night, suggesting possible differences in food availability between natural and urban areas or interspecific competition, altering its activity time to reduce competition with other species.

The Mol 1 grouping and *M. currentium* showed activity throughout the night in urban areas. Molossids are mostly open-area aerial foragers, and all-night activity has been observed in the Brazilian Pantanal, where the group shows a peak of activity in the early evening but maintains activity levels throughout the night in different habitats (da Costa et al. 2021). Like *P. macrotis*, *M. currentium* and Mol 1 changed their behavior in suburban and natural areas, showing activity patterns more similar to other species, concentrated in the early night hours.

Like most species in urban areas but less similar in natural areas, the Vesp 1 grouping showed noticeable changes in activity patterns. The increased activity, represented by greater height in the dendrogram, is closer to *M. molossus*, suggesting a nearly crepuscular pattern for Vespertilionidae in natural areas. Some vespertilionid bat species change their activity patterns between urban and non-urban environments (Schimpp et al. 2018). This change is expected as bats may interpret urban and non-urban landscapes differently due to habitat heterogeneity, varying resource availability, and pressures, leading to behavioral changes in species occupying these different habitats.

Our last hypothesis was partially corroborated. The urbanization index was not a good predictor of the occupancy of

bat species in this study, suggesting that other factors influence habitat selection by Cerrado aerial insectivorous bats. This result contrasts with other studies showing that forest areas or areas with greater vegetation cover are less occupied by aerial insectivorous bats in the USA (Bender et al. 2015; Pauli et al. 2017). Nonetheless, some urbanization-related factors, such as noise, negatively affect bat occupancy in the USA (Lehrer et al. 2021). However, the first half of the night and the dry season were good predictors of the detectability of these bats. Therefore, if there is a need for quick access to the group's biodiversity, such as in studies to define priority areas for conserving the Cerrado, we suggest concentrating sampling efforts in the early hours of the night and during the dry season. According to our results, the probability of detecting species in the area will be greater.

We emphasize the need for additional studies on other groups of bats in urban areas of the Cerrado, given the great diversity of these animals in the biome (Aguilar et al. 2016). Future research should also explore effects not addressed in this study that may impact insectivorous bats in urban areas, such as noise pollution (Schaub et al., 2008; Jiang et al. 2019), the effects of artificial light at night (ALAN) on these groups (Cravens and Boyles 2019; Barré et al. 2022), canopy cover, which positively affects several species in urban environments (Bailey et al. 2019), and roads and green spaces, which can negatively and positively affect the group, respectively (Callas et al. 2024). Additionally, it would be interesting to measure the risk of predation by opportunistic urban predators (Ancillotto et al. 2013; Mikula et al. 2013) and the effects of the heterogeneity of the urban matrix on the movement of these animals (Jung and Kalko 2011) for a more complete and in-depth understanding of the impacts of urbanization.

Knowing that different guilds of aerial insectivorous bats respond differently to urbanization (Jung and Kalko 2011; Flemming et al., 2024), these bats are a resilient model in urban areas to investigate the impacts of urbanization on biodiversity (Gutiérrez-Granados and Rodríguez-Zúñiga 2024). Finally, it is essential and a public health concern to understand the patterns of activity and habitat use by these bats due to the group's potential for disease transmission in urban areas. Bats can use bodies of water close to cities and eventually encounter other mammals, increasing the chances of rabies transmission (Hastings et al. 2024). Aerial insectivorous bats typically show low acceptance of infected individuals with the virus, but interspecific infection is a reality and a reason for attention (Pinero et al. 2012). However, the Neotropical region is known for having low investment in research and pathogen surveillance, in addition to a delay in identifying pathogens transmitted by bats (Rico-Chávez et al. 2024).

We also emphasize the importance of adapting residences, even minimally, to coexist healthily with bats, which is an excellent starting point (Caiza-Villegas et al. 2024). This requires effort and investment from stakeholders, such as local governments, companies, NGOs, and community groups, in educating the public about the importance of bats to humans, reducing prejudices surrounding these animals, and adapting cities to accommodate them (Obudulu et al., 2024). This is particularly important given the potential of these species as agricultural pest controllers in Brasília (Aguilar et al. 2021) and Brazil as a whole. However, more significant investment in technological methods for accessing the group's biodiversity, valuation of ecosystem services, population monitoring, and environmental education is necessary, with incentives and collaboration among different sectors of society (Carvalho et al. 2024).

In conclusion, species from the family Molossidae, which are aerial insectivorous bats, showed increased activity in urban areas in the study region, indicating an adaptation to urban environments. Understanding species-specific habitat use is crucial, as bat activity is influenced by season, with higher activity during the dry season, and by night lighting, with more activity on darker nights. Urban areas are essential for open-area aerial bats, while green spaces and natural areas may be more critical for other aerial foragers. Although Brasília is a city with extensive tree cover and is surrounded by rural and natural landscapes, our results may be influenced by the presence of a lake, which during the dry season could contribute to the presence of bats within the city. It would be interesting additional studies in other urban areas with different characteristics to validate our conclusions. Understanding bat activity patterns is vital for public health, particularly in managing species that can serve as rabies virus reservoirs. This study provides valuable insights for urban planning to create biodiversity-friendly cities, preserving bats' ecological roles as pest controllers and disease vectors amidst increasing urbanization.

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**Data availability** No datasets were generated or analysed during the current study.



## Declarations

**Competing interests** The authors declare no competing interests.

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