



Original investigation

## Feeding and social activity of insectivorous bats in a complex landscape: The importance of gallery forests and karst areas

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### ABSTRACT

Worldwide, increasing human activity, such as agriculture and mining, and decreased landscape complexity, are negatively affecting numerous mammal species. For example, bat communities are becoming threatened in many locations mostly due to the loss of their preferred roosting and foraging habitats. Brazilian landscapes and their associated bat communities are no exception, with the situation being further exacerbated by recently adopted permissive environmental laws that have resulted in reduced biodiversity protection and conservation. Therefore, there is an urgent need to understand how landscape and environmental variables relate to bat activities in Brazil in order to support efforts for their conservation. We used acoustic monitoring data to investigate differences in foraging and social activity of insectivorous bats among four habitat types in a heterogeneous landscape in the Cerrado-Atlantic forest ecotone in southeastern Brazil. We also sampled insect availability and measured temperature at the same sites. Our results showed increased social activity and a greater number of species emitting social calls in karst, and increased feeding activity with a greater number of species emitting feeding buzzes in gallery forest. We also found a positive influence of both temperature and insect abundance on foraging and social activity. Our study provides new insights regarding habitat use by bats in a heterogeneous landscape, and demonstrates the importance of preserving different habitats in heterogeneous landscapes for the conservation of bat species and the ecological functions they perform.

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### Introduction

Globally, numerous mammal species are negatively affected by increased human activity, such as agriculture and mining (Duarte et al., 2015; Wickramasinghe et al., 2004). These activities result in land cover changes that create inhospitable habitats for native species (Dorresteijn et al., 2015; Foley et al., 2005). Furthermore, the structural complexity of landscapes is decreasing worldwide, with profound negative effects on resource availability (e.g., food, shelter) for mammal species (Bazzaz, 1975; Tews et al., 2004). For example, although bats generally have a high capacity for displacement, bat communities are becoming threatened in many locations

mostly due to the loss of their preferred roosting and foraging habitats (Furey and Racey, 2016; Muylaert et al., 2016).

Although the scientific community is already aware of the ongoing massive loss of biodiversity (Ceballos et al., 2015), some countries are facing legislative changes that will actually reduce the protection and conservation of biodiversity, as is the case for Brazil (Sparovek et al., 2012). In 2012, the promulgation of Brazil's new Forest Code (Law 12.651, 2012) severely modified the conservation requirements for private properties, reducing the amount of area to be protected or restored and providing amnesty for past illegal deforestation (Soares-Filho et al., 2014). Moreover, a new Brazilian federal law recently reduced the range of legal protection of caves and karst areas, eliminating the previous mandatory protection of all cave sites and replacing it with minor protection of only those considered as most relevant (Brasil, 2009). As a result, these areas have become more susceptible to degradation from economic activities such as mining (Ferreira et al., 2014). Both of these

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legal changes, together with several others at the state level, as well as the continuous reduction of human and financial support of the environmental conservation authorities, have the potential to negatively affect Brazilian bat communities in important ways because many species rely on natural areas outside of conservation units (Bernard et al., 2011). Therefore, there is an urgent need to understand how landscape and environmental variables relate to bat activities in Brazil in order to support efforts for their conservation.

Habitat selection by bats for foraging, roosting and swarming, among other uses, is typically related to microclimatic conditions, vegetation structure, and resource availability, including distance to water and roosting sites (Ford et al., 2006; Rainho et al., 2010; Rainho and Palmeirim, 2011; Schnitzler and Kalko, 2001; Torquetti et al., 2017). For example, in general, sites with rivers and lakes with good water quality are expected to have greater activity of insectivorous bats from different ecomorphological guilds (Barros et al., 2014; Ramos-Pereira et al., 2010). Temperature in particular influences bats in a variety of ways, including their selection of shelter (Torquetti et al., 2017) and when and where to forage (e.g. the use of open habitats during periods of high temperatures (O'Donnell, 2000)).

Griffin (1944) introduced a novel method for studying spatial distribution and habitat use by bats through the interpretation of echolocation calls. This technique allows the characterization of bat activities using their different echolocation calls (Gillam and Fenton, 2016). Among the types of calls that have been related to specific bat activities are two well-defined behavioral signatures that are associated with feeding and social activities (Budenz et al., 2009; Schnitzler and Kalko, 2001): feeding buzzes and social calls. Feeding buzzes are terminal phases of calls emitted only when pursuing prey and are characterized by a sudden decrease in interpulse interval and call frequency modulation (FM), followed by a pause (Schnitzler and Kalko, 2001). Social calls are usually composed of isolated or irregularly emitted pulses, and are often multi-harmonic and low in frequency. As the name suggests, social calls are associated with social interactions, including courtship, learning, aggregation, group coordination and agonistic interactions (Budenz et al., 2009; Downs and Racey, 2007).

Studies using feeding buzzes and social calls are still rare (Estrada-Villegas et al., 2010; Fenton, 2003; Hintze et al., 2016a; Knörnschild et al., 2012), although the knowledge of bat preferences for foraging and social interactions are key to the conservation of these mammals and the ecosystem services they provide (Kunz et al., 2011). Some studies, especially in temperate areas, have begun to show how habitat type and heterogeneity (Mendes et al., 2017), climatic conditions (Meyer et al., 2016), and food availability (Coleman and Barclay, 2013) influence insectivorous bat activity and feeding. However, there remains a need to evaluate the influence of these factors in complex Neotropical landscapes. In fact, few studies have evaluated feeding and social activity of insectivorous bats within the same landscape, and these are restricted to a few species in temperate regions (Downs and Racey, 2007).

In this work, we used acoustic monitoring to investigate the spatial distribution of two behavioral signatures of insectivorous bats in a heterogeneous landscape of a Cerrado Atlantic Forest transition zone in southeastern Brazil. Specifically, we tested the hypothesis that insectivorous bats use different habitats for distinct purposes. We predicted that there would be: (i) more feeding activity and a higher number of species foraging in areas of gallery forest, since this habitat type has waterbodies that potentiate foraging activity (Hintze et al., 2016a; Marques et al., 2016); and (ii) more social calls and a higher number of species socializing in karst outcrops, since these areas are usually used as swarming sites and for underground roosts (Avila-Flores and Medellín, 2004). We also tested the

hypothesis that temperature affects foraging and social activities, and that foraging behavior can be explained by food availability. We predicted there would be: (i) a positive relationship between feeding activity and temperature; and (ii) a positive relationship between bat feeding activity and richness and abundance of flying insects.

## Methods

### Study area

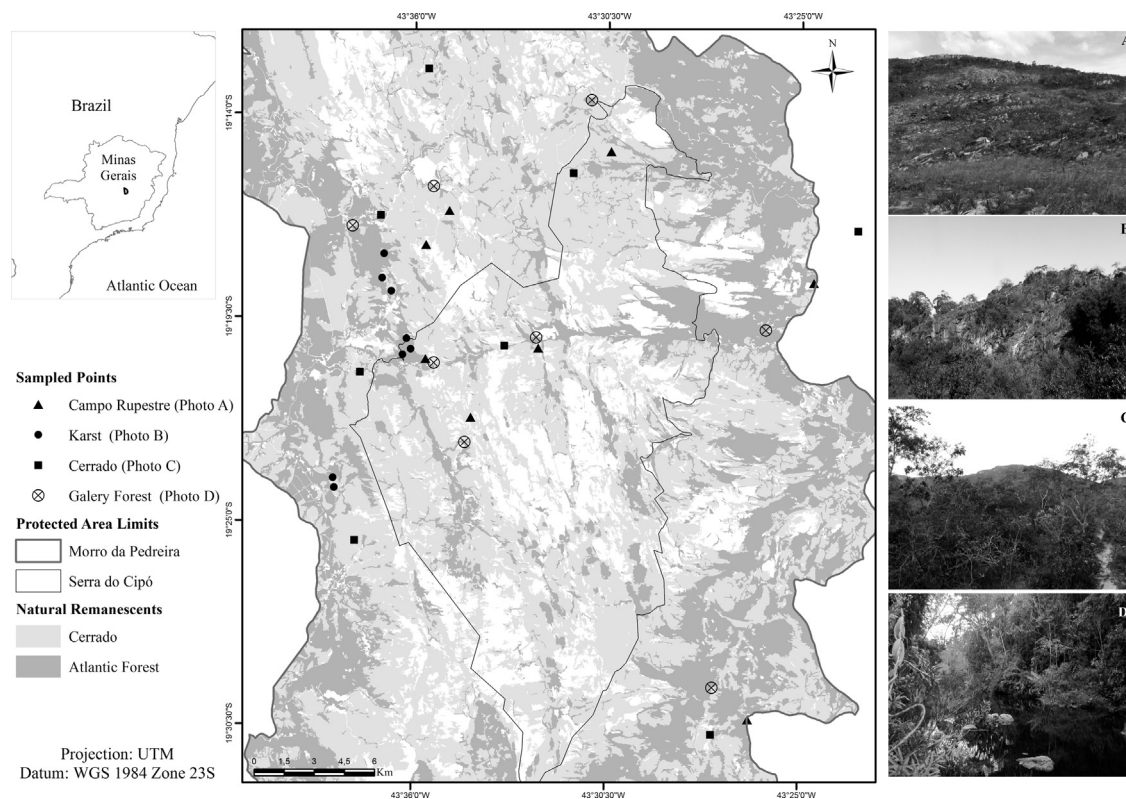
We conducted the study in the Serra do Cipó National Park and in the Morro da Pedreira Environmental Protection Area, two of the largest protected areas in southeastern Brazil, together comprising 131,769 ha with elevations varying between 750 and 1200 m. These areas are part of the transition zone between the largest karst system in Latin America, known as the Sistema Bambuí (Auler, 2002), and the Serra do Espinhaço Complex, a mountain range very rich in iron, manganese, bauxite and gold (Fig. 1). Both protected areas possess a predominance of campos rupestres (rocky grasslands) (Fig. 1, Photo A; Silveira et al., 2016), but also have areas of cerrado *sensu stricto* (Fig. 1, Photo C) and gallery forest (Fig. 1, Photo D). We also studied a site located 1 km outside the Morro da Pedreira boundary.

There are limestone outcrops in the western portion of Morro da Pedreira, at the border of the Bambuí karst complex (Auler, 2002), which usually form karst areas (Fig. 1, Photo B). This type of habitat is important for bats mainly because it provides daytime refugia (Kunz et al., 2011) in the form of caves and crevices (Furey and Racey, 2016). We sampled three distinct karst outcrops, which together contain more than 100 natural cavities. Campos rupestres are easily recognizable habitats, consisting of shrubs and sparse small trees located among rocky terrain and quartzitic outcrops. Small bodies of water are commonly found in these habitats (Benites et al., 2007). Gallery forests have a closer resemblance to the Atlantic Forest biome than the other habitat types of the study and occur as narrow well-defined strips (no more than 100 m wide) along streams with tall tree cover with canopies reaching up to 20 m to 30 m. The trees in this region are mostly evergreen, with water available throughout the year. Finally, cerrado *sensu stricto* (hereafter referred to as cerrado) is a typical Brazilian savanna and is defined as a habitat that includes a large proportion of grassland with abundant medium-sized trees and shrubby and herbaceous plant species (Eiten, 1982).

The climatic regime of the region is Tropical Altitudinal (Alvares et al., 2013) with markedly dry and cold winters, and hot and wet summers. The mean annual temperature is around 22° C and the mean annual rainfall is 1500 mm (Rocha et al., 2016). The rainy season typically occurs between November and April, but during 2014 and 2015, the period of the present study, the Brazilian southeast experienced a severe drought, with the first rains not occurring until January 2015, and lasting until the middle of June of the same year (Coelho et al., 2016; Nobre et al., 2016).

### Acoustic data collection

In each of the four habitat types (campos rupestres, cerrado, gallery forest, and karst), we defined eight sampling sites located at least 1 km apart, with the exception of two sites in the karst area, which were only 450 m apart (due to the small size of the karst outcrop), and a campos rupestres site and a gallery forest site 650 m apart. We acoustically sampled each of the 32 sites on different nights. In each site we established three 100-m linear transects separated by 50–100 meters. We established three sampling stations spaced 50 m apart along each transect (start, middle and



**Fig. 1.** Map of the study area with the locations of the sampling sites in each habitat type. The line indicates the limits of the Serra do Cipó National Park and the Morro da Pedreira Environmental Protection Area in Minas Gerais State, Brazil. Photos: (A) campos rupestres, (B) karst, (C) cerrado *sensu stricto*, and (D) gallery forest.

end; Fig A1). We sampled each station for 3 min and then moved to the next station while continuously scanning for bat activity while walking at a speed of approximately 0.5 m/s. Thus, we used a combination of mobile (between stations) and static (at stations) recordings, following methods similar to that of Jung et al. (2014).

Recordings began at twilight and each transect was sampled three times per night, except when sampling ended early due to rainfall. In the case of rainfall, if monitoring was possible for 90 min prior the rain then the night was considered sampled; if sampling lasted for less than 90 min, the site was re-sampled. Total sampling time considered for analysis was 160 min. To avoid a lunar effect (Appel et al., 2017), we only collected data when the moon was in dark phase. We performed acoustic sampling between January and May 2015, corresponding to the rainy season that year.

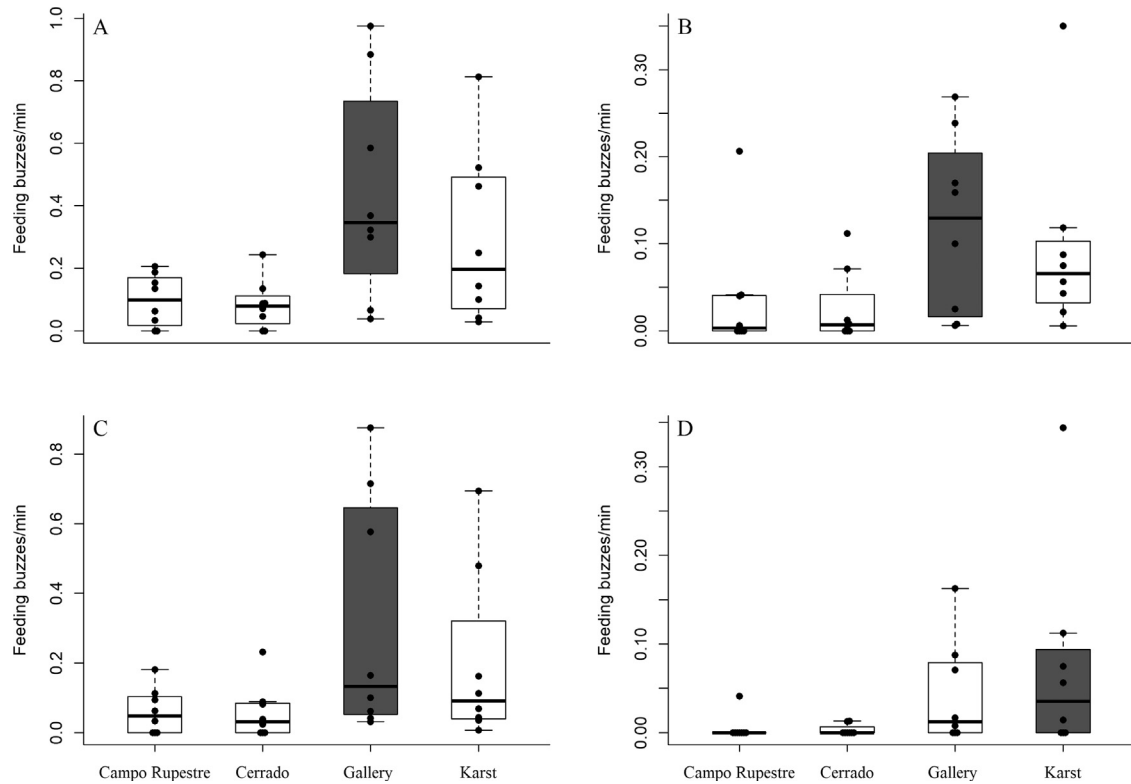
Bat activity was monitored using a Pettersson D1000x ultrasonic detector. Recordings were made in real time and activated with a manual trigger system using the following configuration: 400 kHz sampling rate, 3 s pre-trigger, and 20 s post trigger. We fired the trigger whenever a bat was heard in the heterodyne and frequency division modes. We identified feeding buzzes and social calls through analysis of their characteristic patterns in spectrograms following the work of Schnitzler & Kalko (Schnitzler and Kalko, 2001). A bat pass was considered as a sequence of two or more echolocation calls, delimited by the trigger time or a feeding buzz (Estrada-Villegas et al., 2010; Fenton, 2004).

#### Acoustic data analysis

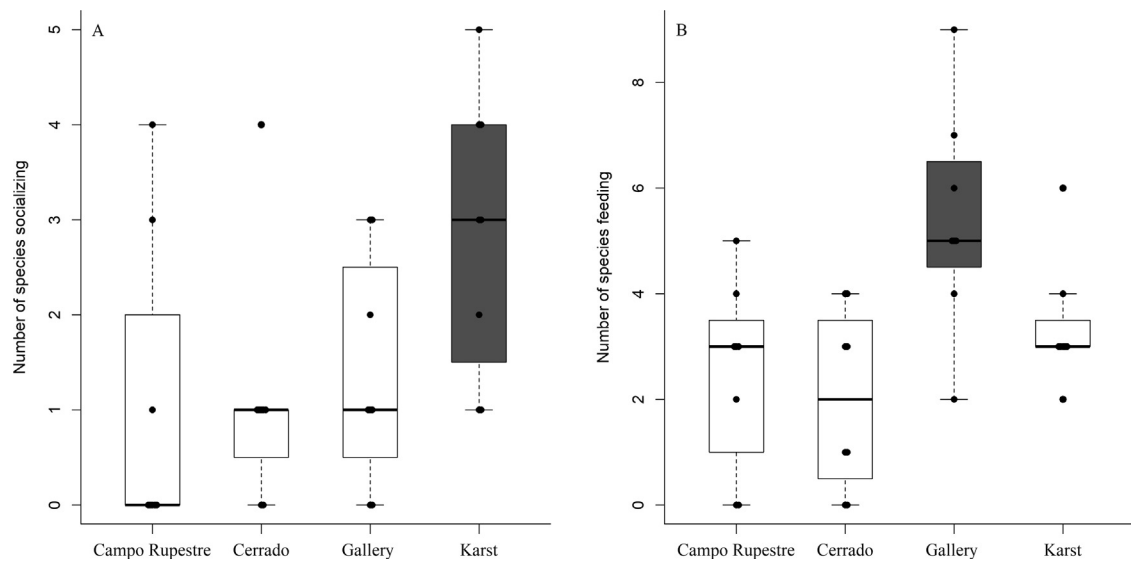
We identified echolocation calls manually using the software Avisoft – SASlab pro 5.1. We excluded attenuated calls following the quality standard of Jung et al. (2014). To relate taxonomic

groups to their respective echolocation calls and, therefore, classify each call as a species or sonotype, we only identified feeding buzzes and social calls when these were emitted after search calls in the same sound file (*i.e.*, calls emitted during bat flight to scan the landscape and avoid obstacles; Fenton and Bell, 1981). For this, we used reference libraries from Mexico (Zamora-Gutierrez et al., 2016), Panama (Jung et al., 2014, 2007), the Amazon (Appel et al., 2016), and the recently published Field Guide to Amazon Bats (López-Baucells et al., 2016). We only used high quality recordings to extract duration, pulse interval, peak frequency, terminal frequency, and harmonics with higher energy. This was accomplished using a spectrogram with a 540 fast Fourier transformation with 100% frame size and an overlap of 93.75%. These measures were used as explanatory variables in a discriminant analysis done in Past (Hammer et al., 2017).

Feeding buzzes and social calls without precise taxonomic identification were used only for guild group analysis (see below). Ecomorphological guilds were established following Schnitzler and Kalko (2001), Denzinger and Schnitzler (2013), and supplementary materials provided by Heer et al. (2015) and Marques et al. (2016). We only recorded insectivorous bats of two guilds. The first guild comprised open-space foragers who emit long-range, low frequency narrowband calls (CF-QCF). Species of this guild are characterized by fast and energetically low-cost flight, and includes representatives of Molossidae and most of the species of Emballonuridae. The second guild comprised edge-space foragers, which emit frequency-modulated broadband ultrasonic calls of short duration. Species of this guild typically possess energy-efficient flight, and includes, in the Neotropics, mainly representatives of Vespertilionidae (Table A1). In the Neotropics, cluttered-space bats belong mostly to the Phyllostomidae, which include bats from



**Fig. 2.** Feeding activity of insectivorous bats (feeding buzzes/min). Feeding buzzes per minute for all insectivorous bats (A); edge-space foragers (B); open-space foragers (C); and *Myotis nigricans* (D). Boxes represent quartiles, lines represent the median, and the whiskers indicate the maximum and minimum. Black dots represent sampling sites. Points outside the whiskers are outliers. Dark boxes indicate significant differences by contrast test.

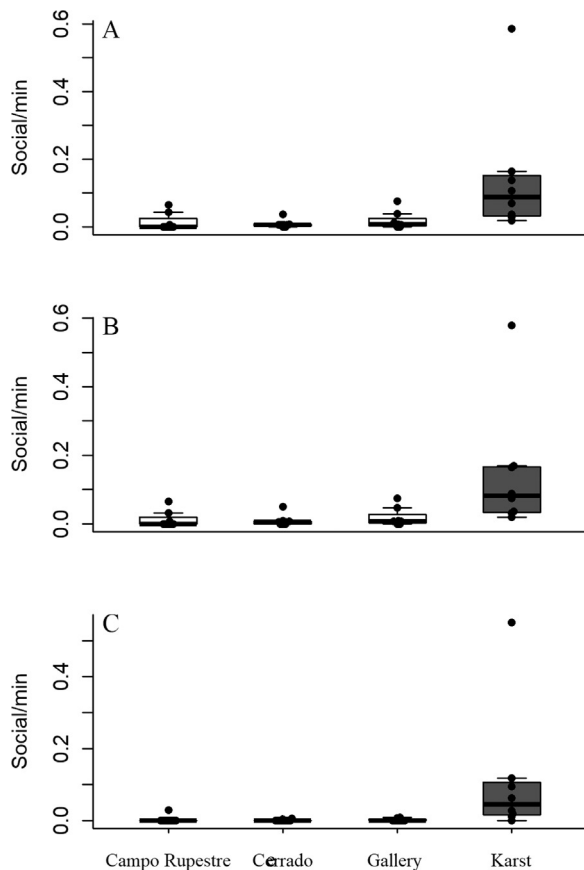


**Fig. 3.** Number of species of insectivorous bats that emitted social calls (A) and feeding buzzes (B) per habitat type. Dark boxes indicate significant differences between habitat types and significant differences by contrast test. The boxes represent quartiles, the lines represent the median, and the whiskers indicate the maximum and minimum. Black dots represent the sample sites. Points outside the whiskers are considered outliers.

several foraging guilds (carnivores, frugivores, nectarivores, insectivores and sanguinivores) (Barataud and Giosa, 2013; Kalko et al., 1996); these species emit high-frequency calls that are highly directional and very homogeneous, and which are quite difficult to detect by acoustic monitoring. However, these bats are easily captured in mist-nets. For this reason these bats do not appear in our sampling. Another Neotropical species, *Pteronotus parnelli* (Mormoopidae) is also a cluttered-space forager, but was not detected in our study area.

#### Temperature and insect abundance

During acoustic monitoring we collected insects using two light traps (Pugedo et al., 2005) installed 100 m apart and 50 m from the bat monitoring transects at 1.5 m above the ground. To ensure that the light traps did not interfere with bat activity and did not attract insects from other habitats, we used an incandescent yellow low-voltage light (1.5V). The collected insects were stored in 70% alcohol and screened in the laboratory. For the analysis we considered only winged insects with body sizes between 0.5 and



**Fig. 4.** Social activity (social calls/min) in insectivorous bats. Social calls per minute for all bats (A), open space foragers (B), and Molossid group 3 (C) per habitat type (campos rupestres, cerrado, karst, and gallery forest). The boxes represent quartiles, the lines represent the median, and the whiskers indicate the maximum and minimum. Black dots represent the sample sites. Points outside of the whiskers are considered outliers. Dark boxes represent significant differences from the contrast analyses.

1.5 cm of the orders Coleoptera, Diptera, Lepidoptera, Neuroptera, Hymenoptera, Heteroptera, Psocoptera, Thysanoptera, Odonata, and Trichoptera, since these are all considered common prey of aerial insectivorous bats (Aguiar and Antonini, 2008; Bernard, 2002). For estimates of food availability, we used total insect abundance (number of individuals captured each night), insect biomass dry weight (insects dried for 72 h at a temperature of 70 °C and weighed on a precision scale), and richness of orders per site sampled. There was a significant correlation between insect abundance and order richness (Pearson,  $r=0.6485$ ;  $p=0.0008$ ), and insect abundance and insect biomass dry weight (Pearson,  $r=0.9001$ ;  $p=0.00002$ ), so we used only insect abundance in subsequent analyses.

During acoustic sampling, we measured the temperature at each sampling site every 30 min using a Skymaster SM 28 (Weather-Hawk Inc.) handheld meteorological mini-station. We performed six measurements per night per site and used the mean temperature at each site for subsequent analyses. We used data from 23 sites for insect abundance and from 22 sites for temperature due to logistical constraints.

#### Data analysis

The distance between the sampling points did not influence species occurrence (Mantel test  $R=0.02851$ ;  $p=0.2528$ ) or bat activity (Mantel test  $R=0.0798$ ;  $p=0.0643$ ). Thus, the 32 sample sites were treated as independent units. Because bat activity

was strongly correlated with feeding activity (Pearson,  $r=0.8565$ ;  $P=0.000031$ ) we used only feeding activity in subsequent analyses.

We quantified feeding activity and social activity as the ratio between the number of feeding buzzes or social calls and time sampled, respectively (Jung et al., 2014). As bat species have specific vocal signatures (O'Farrell and Miller, 1999), we used sonotype richness as a proxy for species richness. Sonotype richness is the number of distinct sonotypes, including those that were identified to the species level and others that, while not allowing the identification of the call to the species level, undoubtedly belonged to different species than those previously identified. Therefore, we did our analysis using four distinct types of response variables: (i) each activity type without taxonomic distinction, (ii) each activity type per species or sonotype group, (iii) each activity type per ecomorphological guild, and (iv) species/sonotype richness.

For the first three types of response variables we used linear models (LMs) to test if habitat type, temperature, and insect abundance affected feeding activity (feeding buzzes/min) and social activity (social calls/min). To linearize and stabilize the variance for a better distribution of residuals, data for feeding buzzes/min and social calls/min were square root transformed (Crawley, 2012). For the fourth type of response variable we used Poisson-distributed generalized linear models (GLM) to test whether the richness of species feeding and socializing was affected by habitat type, temperature, or insect abundance. We considered as richness the number of species (or sonotypes) per night in each habitat type emitting feeding or social calls. We also tested whether temperature and insect abundance varied among habitat types using linear models (LMs). All models and spatial correlation tests were carried out in R (R Core Team, 2017) using the vegan package (Oksanen et al., 2017). Post hoc tests by contrast analysis were made using the 'coms' function of the RT4Bio package (Reis et al., 2013).

## Results

In 4920 min of recordings we recorded and analyzed 4560 bat passes, 1144 of which were characterized as feeding buzzes and 248 characterized as social calls (Table 1). Most of the feeding buzzes (98%) and social calls (84%) were high quality recordings, allowing identification to species or sonotype level.

We identified three families of insectivorous bats, and after discriminant analysis it was possible to identify seven species and eight sonotype groups. The groups were as follows: for the Molossidae: i) Molossid group 1, including *Molossus currentium* and *Molossus rufus*; ii) Molossid group 2 included *Cynomops greenhalli*, *Eumops auripendulus* and *Nyctinomops macrotis*; iii) Molossid group 3 included *Cynomops planirostris*, *Nyctinomops laticaudatus*, *Tadarida brasiliensis* and *Eumops glaucinus*; and iv) Molossid group 4 included *Eumops perotis* and *Eumops* sp. For the Vespertilionidae: i) Vespertilionid group 1 included *Eptesicus brasiliensis* and *E. furinalis*; ii) Vespertilionid group 2 included *Lasiurus blossevillei*, *Rhogessa* sp. and *Myotis levis*; iii) Vespertilionid group 3 included *Lasiurus ega* and *Eptesicus chiriquinus*; and iv) Vespertilionid group 4 included *Myotis ruber* and *Myotis riparius*. For more details on sonotype grouping see the appendices (Table A1). We captured 4290 insects belonging to 15 orders. Habitat types showed no significant differences in temperature or insect abundance (Table A2).

Gallery forests possessed greater feeding activity than the other habitats ( $R^2 = 0.33$ ,  $p = 0.009$ ,  $F = 4.7137$ , Fig. 2a), and there were no significant differences in the number of feeding buzzes between campos rupestres, cerrado, and karst. This pattern was consistent for both open-space foragers ( $R^2 = 0.26$ ,  $p = 0.03$ ,  $F = 3.2616$ , Fig. 2b) and edge-space foragers ( $R^2 = 0.27$ ,  $p = 0.0296$ ,  $F = 3.4573$ , Fig. 2c). At the level of species or species groups, only *Myotis nigricans* showed higher feeding activity in karst areas ( $R^2 = 0.24$ ,  $p = 0.04$ ,  $F = 3.0991$ , Fig. 2d). The number of bat species exhibiting feeding

**Table 1**  
Feeding buzzes and social calls for insectivorous bats.

Species	Feeding buzzes (N = 32)				Social/min (N = 32)			
	Campo Rupestre	Cerrado	Gallery Forest	Karst	Campo Rupestre	Cerrado	Gallery Forest	Karst
<b>Edge space</b>	<b>47b</b>	<b>34b</b>	<b>150a</b>	<b>120b</b>	2	5	3	15
Vespertilionid 1	41	7	29	15	0	3	0	0
Vespertilionid 2	3	33	31	1	0	1	0	0
Vespertilionid 3	0	0	2	2	0	0	1	0
<i>Myotis nigricans</i>	<b>19b</b>	<b>11b</b>	<b>69b</b>	<b>96a</b>	0	0	0	0
Vespertilionid 4	8	0	1	0	0	0	0	0
<b>Sub-total (edge space)</b>	351				25			
<b>Open space</b>	<b>77b</b>	<b>74b</b>	<b>395a</b>	<b>247b</b>	<b>17b</b>	<b>12b</b>	<b>19b</b>	<b>175a</b>
Molossid 1	6	0	8	1	1	0	0	2
<i>Molossus molossus</i>	0	2	22	1	0	0	7	0
<i>Molossops temminckii</i>	0	1	5	0	0	0	0	0
<i>Peropteryx</i> sp1	0	38	30	4	0	0	0	1
<i>Peropteryx macrotis</i>	0	19	23	13	0	1	0	5
<i>Peropteryx trinitatis</i>	2	22	91	103	0	0	0	0
<i>Peropteryx</i> sp2	0	0	116	0	0	0	0	0
<i>Promops centralis</i>	0	0	2	1	0	0	0	2
Molossid 2	9	19	11	10	2	3	3	9
Molossid 3	55	56	86	108	<b>9b</b>	<b>2b</b>	<b>2b</b>	<b>131a</b>
Molossid 4	13	2	0	0	5	1	0	0
General	<b>124b</b>	<b>108b</b>	<b>545a</b>	<b>367b</b>	<b>19b</b>	<b>16b</b>	<b>16b</b>	<b>165a</b>
<b>Sub-total (open space)</b>		793				223		
Total		1144				248		

Number of feeding buzzes and social calls per species, sonotype group and ecomorphological guild in gallery forest, karst, campos rupestres and cerrado habitat types. Significant results of the LMs ( $p < 0.05$ ) are in bold, and different letters indicate significant differences among habitat types from the contrast analyses ( $p < 0.05$ ).

**Table 2**  
Number of bats species that emitted feeding buzzes or social calls per habitat type.

Number of species	Campo Rupestre			Cerrado			Gallery			Karst		
	mean	SE	DP	mean	SE	DP	mean	SE	DP	mean	SE	DP
Feeding buzzes	2.500b	0.166	1.773	2.000b	0.162	1.690	<b>5.370a</b>	0.179	2.065	3.375 b	0.136	1.188
Social call	1.000b	0.158	1.604	1.125b	0.139	1.246	1.370b	0.136	1.187	<b>2.875a</b>	0.151	1.458

Results are reported as the mean number of species, standard error (SE), and standard deviation (SD) per habitat type. Significant results of the GLM ( $p < 0.05$ ) are in bold; letters associated to mean values represent significant differences between habitat types from the contrast analyses ( $p < 0.05$ ).

activity was higher in gallery forest (Fig. 3A,  $R^2 = 0.30$ ,  $p < 0.0016$ ,  $F = 5.0786$ ), with no significant differences among the other habitat types (Table 2). Only foraging activity for Molossid group 2 showed a positive correlation with insect abundance ( $R^2 = 0.27$ ,  $p = 0.0103$ ,  $F = 7.9429$ , Table A3). The number of species emitting feeding buzzes was positively correlated with insect abundance ( $R^2 = 0.15$ ,  $p = 0.02515$ ,  $F = 5.8132$ ; Table 2).

Social activity was higher in karst ( $R^2 = 0.45$ ,  $p = 0.0007$ ;  $F = 7.7479$ , Fig. 4A) with no differences among the other habitat types (Table A3). This pattern was the same for open-space foragers ( $R^2 = 0.46$ ,  $p = 0.0005$ ,  $F = 8.0195$ , Fig. 4b), but there were no significant differences in social activity among habitats for edge-space foragers (Table A3). Molossid group 3 also exhibited higher social activity in karst areas ( $R^2 = 0.46$ ,  $p = 0.0004$ ,  $F = 8.1253$ , Fig. 4c). The number of species emitting social calls was also higher in karst areas ( $R^2 = 0.20$ ,  $p = 0.0173$ ,  $F = 3.3878$ ; Fig. 3B).

Foraging activity was positively related to temperature both for bats as a whole ( $R^2 = 0.23$ ,  $p = 0.0087$ ;  $F = 4.7137$ , Fig. 5A) and for open-space foragers ( $R^2 = 0.18$ ,  $p = 0.0361$ ,  $F = 4.9449$ , Fig. 5B). Social activity was positively related to temperature for open-space foragers ( $R^2 = 0.19$ ,  $p = 0.0354$ ,  $F = 5.024$ , Fig. 5C) and the Molossid group 3 ( $R^2 = 0.19$ ,  $p = 0.0297$ ,  $F = 5.4053$ , Fig. 5D).

## Discussion

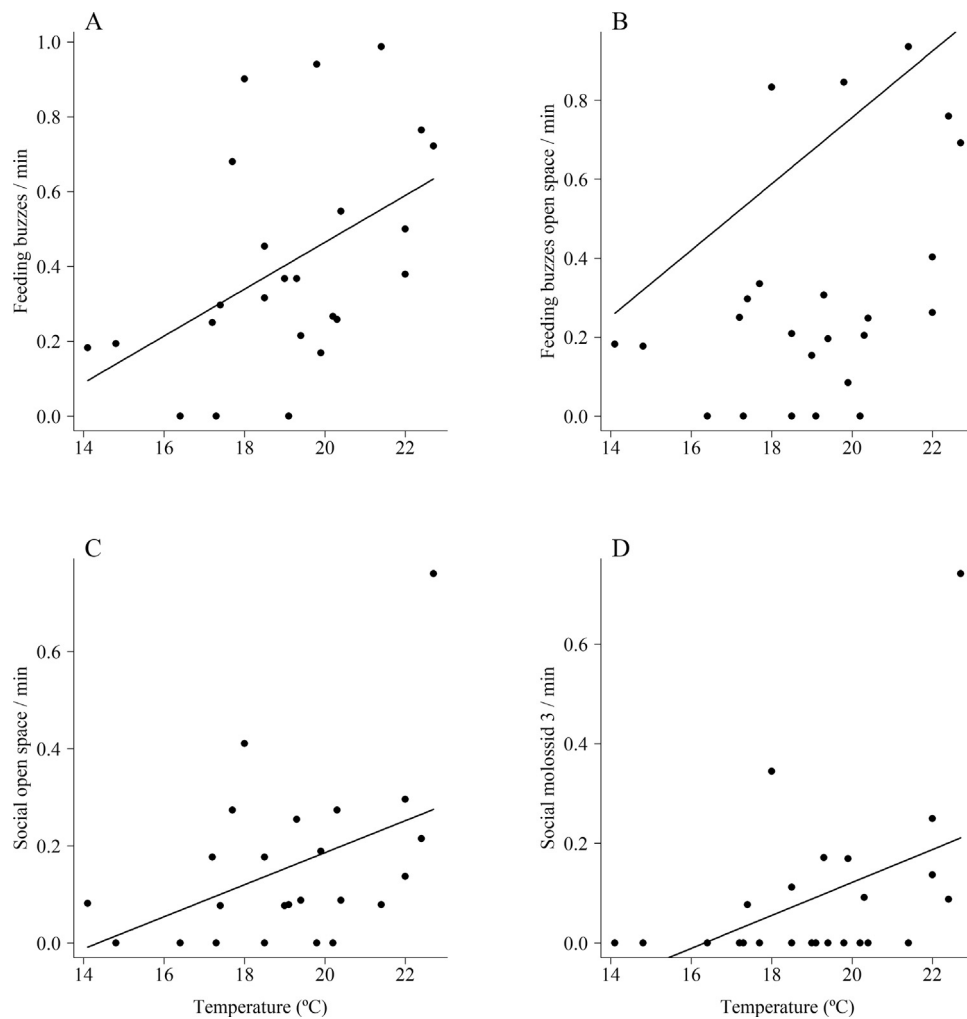
Our results indicate that aerial insectivorous bats, especially open-space foragers, exhibit higher levels of foraging activity in gallery forests, while the level of social activity is higher in karst environments. Previous studies have also highlighted the importance of proximity to waterbodies for bat foraging (Hintze et al.,

2016a) and complex habitats containing underground roost for finding shelter (Medellin et al., 2017). However, to our knowledge, this is the first attempt to assess how social activity in karst areas is related to habitat and climate. Our results demonstrate the importance of preserving different types of natural environments within the same landscape for the conservation of bat species and the ecological functions they perform.

Gallery forests appear to be an important environment for bats, both in terms of number of species and activity. Higher feeding activity near waterbodies is a pattern that has been demonstrated in both temperate (Heim et al., 2015; Hintze et al., 2016a) and tropical (Barros et al., 2014; Marques et al., 2016) regions, and is attributed to the greater availability of food resources in these areas (de Oliveira et al., 2015). Bats invest more time and energy foraging near water due to the greater probability of predation success, thus maximizing the benefits derived from the energy expended (Macarthur and Pianka, 1966). Additionally, the trees of gallery forests provide shaded environments that prolong the foraging activity of bats (Downs and Racey, 2006).

In our work, we observed a positive relationship between insect abundance and feeding activity for Molossid group 2 and all species together. Therefore, contrary to our expectations, there were no significant relationships between insect abundance and feeding activity for most of the levels investigated (all species, species/groups and guilds), as was also previously observed by Jung and Kalko (2011) in tropical forests.

One possible reason for this finding is that insectivorous bats have distinct food preferences for certain insect species or sub-groups (Bernard, 2002). A more refined taxonomic analysis of



**Fig. 5.** Linear regression of feeding and social activities as a function of temperature. Feeding activity is compared between A) all bats; and B) open space foragers. Social activity is compared between: C) open space foragers; and D) Molossid group 3. All responses were temperature-dependent.

insects would likely lead to a better understanding of this relationship between bat activity and the availability of certain prey.

The rate of feeding buzzes did not differ among karst, cerrado and campos rupestres for the all species of bats considered together, nor for open-space and edge-space foraging species considered separately. However, *Myotis nigricans* did not fit this pattern because it exhibited greater feeding activity in karst. *Myotis nigricans* has been reported to roost in human structures (Esbérard et al., 2014) as well as caves in natural environments (Wilson, 2010). Our results indicate that *M. nigricans* is strongly associated with karst areas in the study region, which is supported by other studies that have reported this species in cave environments (Arita, 1996; Brunet and Medellín, 2001; Talamoni et al., 2013; Torquetti et al., 2017).

We found higher levels of social activity by a greater number of species in karst areas. Social calls are used for individual identification and territorial defense in daytime shelters, such as caves and hollows (Schöner et al., 2010), and are also linked to the time of emergence from roosts and swarming, when they are most frequently used for purposes of directional and joint flight (Chaverri et al., 2010; Glover and Altringham, 2008). In both cases, our sampling time period (twilight and the first three hours thereafter) favored the recording of these types of activities (Jones and Siemers, 2011). The greater number of species emitting social calls in karst areas was expected, as this habitat provides several roost for many bat species in the Neotropical region (Arita, 1996; Medellín et al.,

2017; Trajano, 1984), though gallery forests are certainly known to provide foraging and roosting sites as well (Barros et al., 2014; Willis and Brigham, 2004). Although not all bats roost in underground caves (Kunz, 1982), these environments are potentially more important for the social activities of a greater number of species than are gallery forests, campos rupestres, and cerrado. We highlight that Molossid group 3 accounted for almost 53% of all social calls, which suggests that these animals are strongly associated with karst areas. This finding was not a surprise since all of the species that comprise Molossid group 3 (*Cynomops planirostris*, *Eumops glaucinus*, *Nyctinomops laticaudatus*, and *Tadarida brasiliensis*) have previously been documented in caves or cracks in rocks in karst areas (Arita, 1996; Brunet and Medellín, 2001; Talamoni et al., 2013; Trajano, 1984).

Temperature is an important factor in the selection of roosting sites (Rodríguez-Duran, 2003) and foraging habitats by bats (McCain, 2006). Indeed, temperature is one of the most important factors for explaining insectivorous bat activity (Barros et al., 2014; Wolbert et al., 2014). As expected, temperature was found positively related to feeding and social activity. Thus, the relationship between feeding activity and the number of species foraging can be explained by higher temperatures, which potentially favor insect abundance and activity and, consequently, an increase in foraging bats (Meyer et al., 2004; Savopoulou-Soultani et al., 2012). Regarding social activity, the present study is the first, to our knowledge, to demonstrate a positive effect of temperature on social behavior of

insectivorous bats, although there are other studies that have evaluated both parameters (e.g. Downs and Racey, 2007). We argue that higher temperatures favor the emergence of bats from their roosts, as reported in the temperate region where temperature is the factor responsible for the timing of bat emergence from roosts after winter (Meyer et al., 2016). Consequently, temperature also influences the social interactions involved in colony aggregation and territorial defense.

There was a certain degree of imprecision in identifying some echolocation calls to the species level since libraries for the distinction of species of some taxonomic groups are still lacking. Therefore, the estimation of the number of species foraging and socializing may have been underestimated; in fact, species with similar calls were grouped, particularly in the Molossid group 2, which was the most represented group among social calls. Therefore, the creation and continued updating of public bat call libraries, such as Appel et al. (2016) and Zamora-Gutierrez et al. (2016), is of extreme importance. With improved acoustic identification, our understanding of the patterns of habitat use by aerial insectivores will grow, especially in the Neotropics where this kind of work is still scarce.

Our results suggest that the conservation of insectivorous bats in southeastern Brazil will depend on the maintenance of karst areas, and that the recent changes in federal environmental laws that reduced the range of legal protection of caves and karst areas could threaten the conservation of these bat species and the benefits they provide to humans (Brasil, 2009; Kunz et al., 2011). These areas are critical for various stages of the life cycle of these animals and probably function not only in provisioning roosts sites (Torquetti et al., 2017), but also sites for swarming for reproduction, and so they need to be strictly protected (Medellin et al., 2017). In addition, because waterbodies and gallery forests are important foraging sites for bats, the minimum area of protection along waterbodies needs to be reinstated to that defined prior to the new Forest Code of 2012, which relaxed regulations that aimed to preserve natural areas in rural properties (Soares-Filho et al., 2014).

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## Appendix A

**Table A1**  
Classification of acoustic activity by sonotype, based on the structure of echolocation calls.

Sonotype	Species	Family	Guild	Call structure	Harmonic with main intensity	Frequency type	Range of frequency (Khz)	Alternance	Reference
Vespertilionid 1	<i>Eptesicus brasiliensis</i> , <i>Eptesicus furiinalis</i>	VES	Edge	Dfm	First	Taerminal	32 – 38	irregular	López-Baucells et al. (2016), Ochoa et al. (1999), Rydell et al. (2002)
Vespertilionid 2	<i>Lasurus blossevilli</i> ; <i>Rhogeessa sp.</i> , <i>Myotis levis</i>	VES	Edge	Dfm	First	Terminal	42 – 46	irregular	López-Baucells et al. (2016), Ochoa et al. (1999), Rydell et al. (2002)
Vespertilionid 3	<i>Lasurus ega</i> ; <i>Eptesicus chiroquinus</i>	VES	Edge	Dfm	First	Terminal	24 – 32	irregular	López-Baucells et al. (2016), Ochoa et al. (1999), Rydell et al. (2002)
<i>Myotis nigricans</i>	<i>Myotis nigricans</i>	VES	Edge	Dfm	First	Terminal	52 – 56	irregular	López-Baucells et al. (2016), Ochoa et al. (1999), Rydell et al. (2002)
Vespertilionid 4	<i>Myotis ruber</i> ; <i>Myotis riparius</i>	VES	Edge	Dfm	First	Terminal	58 – 64	irregular	López-Baucells et al. (2016), Ochoa et al. (1999), Rydell et al. (2002)



Table A1 (Continued)

Sonotype	Species	Family	Guild	Call structure	Harmonic with main intensity	Frequency type	Range of frequency (Khz)	Alternance	Reference
Molossid 1	<i>Cynomops greenhalli</i> ; <i>Eumops auripendulus</i> ; <i>Nyctinomops macrotis</i>	MOS	Open	qcf down	First	Peak	12.5- 16	irregular	Jung et al. (2014)
Molossid 2	<i>Cynomops planirostris</i> ; <i>Nyctinomops laticaudatus</i> ; <i>Tadarida brasiliensis</i> ; <i>Eumops glaucinus</i>	MOS	Open	qcf down	First	Peak	17 – 27	irregular	Jung et al. (2014)
Molossid 3	<i>Eumops perotis</i> ; <i>Eumops</i> sp.	MOS	Open	qcf down	First	Peak	9 – 11	irregular	Jung et al. (2014), Marques et al. (2016)
Molossid 4	<i>Molossus currentium</i> ; <i>Molossus rufus</i>	MOS	Open	qcf down	First	Peak	24–28	regular	Jung et al. (2014)
<i>Molossus molossus</i>	<i>Molossus molossus</i>	MOS	Open	qcf down	First	Peak	32 – 34	regular	Jung et al. (2014)
<i>Molossops temminckii</i>	<i>Molossops temminckii</i>	MOS	Open	ufm qcf	First	Peak	48 – 55	irregular	Jung et al. (2014)
<i>Promops centralis</i>	<i>Promops centralis</i>	MOS	Open	ufm qcf	First	Peak	28 – 32	irregular	Jung et al. (2014)
<i>Peropteryx</i> sp1	<i>Peropteryx</i> sp1	EMBA	Open	qcf down	Second	Peak	45 – 46	regular	Hintze et al. (2016b)
<i>Peropteryx Macrotis</i>	<i>Peropteryx Macrotis</i>	EMBA	Open	qcf down	Second	Peak	39 – 40	regular	López-Baucells et al. (2016), Jung et al. (2007)
<i>Peropteryx trinitatis</i>	<i>Peropteryx trinitatis</i>	EMBA	Open	qcf down	Second	Peak	42 – 44	regular	López-Baucells et al. (2016), Jung et al. (2007)
<i>Peropteryx</i> sp2	<i>Peropteryx</i> sp2	EMBA	Open	qcf down	Second	Peak	32 – 34	regular	López-Baucells et al. (2016), Jung et al. (2007)

Legend: (qcf = quasi constant frequency; dfm = down frequency modulated; ufm = up frequency modulated), and the harmonic with the highest intensity and frequency (Terminal = final frequency of echolocation; Peak = frequency with greatest energy; only for those with characteristic frequency). The classification is divided by species, families, and guilds (EMBA = Emballonuridae, MOL = Molossidae, VES = Vespertilionidae).

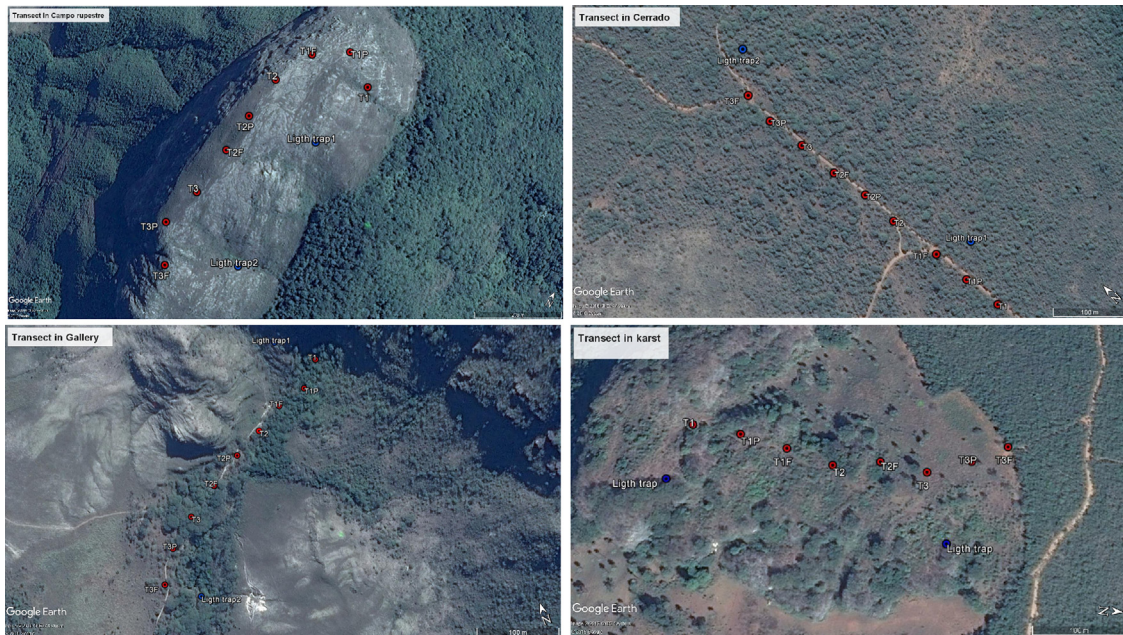


Fig. A1. Example of transects sampled in each habitat type. Numbers indicate transect ID. T=beginning of transect; TP=pause in transect; and TF=end of transect.

Table A2  
Temperature and insect abundance of each habitat type.

	temperature				Insect abundance				Insect dry mass				insect ordem richness			
	mean (c °)	n	dp (±)	p value	mean	n	dp (±)	p value	mean (g)	n	dp (±)	p value	mean	n	dp (±)	p value
Campo Rupestre	17.13	6	1.8	–	188	5	216.746	–	0.071	5	0.079	–	3.6	5	2.88	–
Karst	20.11	7	2.11	–	241.28	7	578.948	–	0.065	7	0.128	–	5.14	7	2.672	–
Cerrado	19.02	5	1.02	–	103.2	5	86.384	–	0.033	5	0.045	–	5.2	5	1.483	–
Gallery Forest	19.85	6	2.64	–	191.66	6	210.455	–	0.029	7	0.026	–	4.66	6	1.751	–
~habitat type	–	–	–	0.07016g	–	–	–	0.9021qp	–	–	–	0.7575g	–	–	–	0.6551g

Legend: Mean temperature, mean insect abundance, number of observations (n) standard deviation (dp ±) and the results (P-values) of the Poisson-generalized linear models (GLM) for the relationships between the response variables (temperature and insect abundance, order and dry weight) and the predictor variable of habitat type. Letters indicate the distribution adopted in GLM: qp = quasipoisson, g = gaussian.

Table A3  
Results of the linear models.

Species	Feeding buzzes/min ~ habitat			Feeding buzzes/min ~ temperaturẽnsect			Feeding buzzes/min ~			Social/min ~ habitat			Social/min ~ temperature		
	R <sup>2</sup>	F	p	R <sup>2</sup>	F	p	R <sup>2</sup>	F	p	R <sup>2</sup>	F	p	R <sup>2</sup>	F	p
<b>Edge space</b>	<b>0.27</b>	<b>3.457</b>	<b>0.029</b>	0.12	3.01	0.096	0.02	0.517	0.479	0.1303	1.3987	0.2639	0.02	0.5213	0.4779
Vespertilionid 1	0.07	0.782	0.513	0.08	2.15	0.156	0.02	0.507	0.483	–	–	–	–	–	–
Vespertilionid 2	0.12	1.34	0.278	0.02	0.55	0.464	0.001	0.024	0.876	–	–	–	–	–	–
Vespertilionid 3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Myotis nigricans</i>	<b>0.24</b>	<b>3.1</b>	<b>0.042</b>	0.03	0.56	0.46	0.02	0.514	0.48	–	–	–	–	–	–
Vespertilionid 4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<b>Sub-total</b>	<b>0.26</b>	<b>3.26</b>	<b>0.036</b>	<b>0.18</b>	<b>4.94</b>	<b>0.036</b>	0.05	1.234	0.279	<b>0.4621</b>	<b>8.0195</b>	<b>0.0005</b>	<b>0.19</b>	<b>5.024</b>	<b>0.0354</b>
<b>Open space</b>	<b>0.12</b>	1.39	0.265	0.1	2.65	0.117	0.001	0.024	0.876	–	–	–	–	–	–
Molossid 1	0.12	1.37	0.269	0.09	2.18	0.153	0.09	2.121	0.16	–	–	–	–	–	–
<i>Molossus molossus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Molossops temminckii</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Peropteryx sp1	0.21	2.49	0.08	0.12	3.11	0.091	0.004	0	0.976	–	–	–	–	–	–
<i>Peropteryx macrotis</i>	0.09	0.95	0.427	0.03	0.84	0.367	0.003	0.071	0.791	–	–	–	–	–	–
<i>Peropteryx trinitatis</i>	0.14	1.64	0.202	0.05	1.32	0.261	0.001	0.026	0.873	–	–	–	–	–	–
<i>Peropteryx sp2</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Promops centralis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Molossid 2	0.01	0.1	0.961	0.06	1.51	0.231	<b>0.27</b>	<b>7.942</b>	<b>0.01</b>	0.03876	0.3764	0.77	0.05	1.1629	0.2926
Molossid 3	0.07	0.67	0.575	0.23	<b>6.92</b>	<b>0.015</b>	0.058	1.304	0.266	<b>0.4654</b>	<b>8.1253</b>	<b>0.0004</b>	<b>0.19</b>	<b>5.4053</b>	<b>0.0297</b>
Molossid 4	0.01	0.1	0.961	0.19	–	–	0.009	0.191	0.666	–	–	–	–	–	–
General	<b>0.33</b>	<b>4.71</b>	<b>0.008</b>	<b>0.23</b>	<b>6.58</b>	<b>0.017</b>	0.05	1.28	0.27	<b>0.4536</b>	<b>7.7479</b>	<b>0.0006</b>	0.13	3.2735	0.0841

Legend: Results (F-fisher and P-values) of the linear models (LM) for the relationships between the response variables – number of feeding buzzes and social calls per guilds, species, and groups – and the predictor variables – habitat type, temperature and insect abundance.

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