ZOOLOGIA 34: e13732
ISSN 1984-4689 (online)
zoologia.pensoft.net

RESEARCH ARTICLE

# Differences between caves with and without bats in a Brazilian karst habitat

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*http://zoobank.org/1ADB499A-1195-4B60-BE87-DDA5C1E4D623*

ABSTRACT. Since bats shelter in roosts during their period of diurnal inactivity, the quality and availability of roosts are important aspects of their ecology. Karst areas have great potential for the availability of day roosts, since they form caves, which serve as bat shelters. Here we characterize the caves used by bats in a preserved karst area of Southeastern Brazil. Using logistic regression analysis we identified the cave characteristics that influence bat occupation. Sixty-six caves were characterized based on measurements of internal height and width, height and width of the entrance(s) of the cave, number of entrances, maximum horizontal development of cave, and internal temperature and humidity. In nineteen months we found 14 species in 32 caves. Most species were eventually recorded in multiple caves, with the exception of *D. rotundus*, *G. soricina* and *A. planirostris*, which were always found in the same caves. *Desmodus rotundus* showed maternity roost fidelity. We found no differences in microclimate between the caves that are occupied and those that are not. In other words, the microclimate of the caves studied herein can be characterized as stable over the years. The only predictor affecting the presence of bats in the study area was the cave's maximum horizontal development: the caves that are occupied have greater horizontal development. Based on our results, we conclude that bats occupy many of the caves and that some species are more frequent in certain caves than in others, including some roosts that are used as maternity roosts. These findings indicate that these caves are important resources for the bats in the karst environment studied, and should be preserved.

KEY WORDS. Day roost, *Desmodus*, *Glossophaga*, Lagoa Santa Karst, maternity roost.

## INTRODUCTION

Diurnal roosts are vitally important to bats because they serve as sites for mating, shelter and rest, care of offspring, as well as for social interactions (Twente 1955, Kunz and Lumsden 2003, Otto et al. 2016). The conditions and events associated with roosting have played a major role in the ecology and evolution of bats (Kunz 1982). The type of diurnal roosts used by bats is dependent upon their availability in the environment, the distribution and abundance of food surrounding the roost, predation risk and the species' social system, as well as the structural and microclimatic characteristics of the roost site (Vonhof and Barclay 1996, Sedgeley 2001, Kunz and Lumsden 2003, Ávila-Flores and Medellín 2004, Lopez-Gonzales and Torres Morales 2004, Chaverri et al. 2007, Boland et al. 2009, O'Keefe et al. 2009).

In temperate regions, studies on the use of roosts are not rare (Sedgeley and O'Donnell 1999, Ruczynski and Bogdanowicz 2005, O'Keefe et al. 2009, Otto et al. 2016). These studies have shown that roost use is primarily influenced by climate (Kunz and Pierson 1994). Therefore, the type of diurnal roost has profound implications for energy economy and the reproductive success of bats (Arlettaz et al. 2001, Papadotou et al. 2008, Sedgeley 2001, Pretzlaff et al. 2010, Otto et al. 2016).

Caves are a special type of diurnal roost used by many species of bats. They provide a stable microclimate and protection from predators and adverse weather (Kunz 1982, Arita 1993, Lewis 1995, Trajano 1995). The occurrence of potential cave roosts in karst areas is high, since the geological formations typical of the karst topography are numerous and varied (Trajano 2000, Furey et al. 2010). Despite the potential interest of these areas for the study of bat diurnal roosts in caves, few studies have been undertaken in the karst areas of Brazil (Trajano 1984, Campanhã and Fowler 1993, Trajano 2000, Bredt et al. 1999, Esbérard et al. 2005, Sbragia and Cardoso 2008).

The abundance and distribution of caves may influence their use as roost sites by bats (Trajano 1984, Lewis 1995, Struebig et al. 2009). In a given region, the number of existing caves may not match the number of suitable roosts needed by the bat assemblage, since the demand for roosts varies depending on the species, sex, and reproductive condition of individuals (Kerth et al. 2001, Sedgeley 2001, Ávila-Flores and Medellín 2004, Otto et al. 2016). Bats are essential components of ecosystems. Therefore, understanding the appropriate conditions for their roosts is essential for their proper management and conservation (Arita 1993, 1996, Sedgeley 2001). Considering that little is known about the roost ecology of bats in Brazil (Trajano 1984, Bredt et al. 1999, Gomes and Uieda 2004, Esbérard et al. 2005, Sbragia and Cardoso 2008), we undertook this study to determine the microclimatic and structural differences between caves that are occupied by bats and those that are not, in a karst region of Southeastern Brazil. Ultimately we aimed to characterize caves used by bats, and identify the species that use them.

## MATERIAL AND METHODS

The study was conducted in the karst area of Lagoa Santa, state of Minas Gerais, Brazil. The karst area of Lagoa Santa has over 500 registered caves (CECAV 2012), and is of great anthropological, speleological and paleontological importance because many of the caves are repositories of Pleistocene fossils and have produced evidence of prehistoric human occupation (Neves et al. 2007). The vegetation in the region is transitional between the Atlantic Forest and Cerrado biomes, with patches of deciduous and semideciduous forest associated with rock outcrops. The climate of the region is seasonal, with a rainy season from October to March, and a dry season from April to September (Sá-Jr et al. 2012). Annual rainfall there ranges from 1,400 mm to 1,600 mm and the mean annual temperature is about 21 °C. The warmest month corresponds to February (~23 °C), and the coolest month corresponds to July (~19 °C). Sampling was performed within the Lagoa Santa Karst Environmental Protection Area (APA) at several preserved rock outcrop sites of the Cauaia farm (19°28'57"S, 44°00'50"W, 1,760 ha) in the municipality of Matozinhos.

Searches for caves were undertaken monthly from November 2009 to May 2011 in a preserved area of approximately 83.5 ha of limestone outcrops. A total of 66 caves were randomly selected and monitored. The caves are located in five different rocky outcrops (Cuvier, Lapa, Lapa vermelha, Britador, Escorpião), which were located and documented during the first six months of the study. After this initial period, the caves were systematically inspected. We decided that a cave was occupied after either observing bats, or any amount of guano in it.

To characterize the physical structure of the caves, we measured their internal height and width at several locations along the horizontal development of each cave. The means of those measurements were calculated and used in the analyses. We also measured the maximum height and width of the entrance of each cave and the maximum horizontal development of each cave. The number of entrances to each cave was also recorded. An entrance was considered any opening that would allow the entrance and exit of bats. All measurements were made in meters, using a measuring tape. The microclimate of each cave was characterized using the means of the temperature and relative humidity, measured at each measuring point with a calibrated thermo-hygrometer (accuracy ± 0.8 °C, ± 10%). Measurements of the internal temperature and humidity of the caves were made systematically during each monthly inspection, while measurements of the physical structure were taken just once. Searches inside all caves (occupied and unoccupied) were performed in the morning, whereas measurements of their physical structure and internal temperature and humidity were taken in the afternoon (12:00 p.m. to 6:00 p.m.).

Bats were captured using mist-nets, set inside the caves. Prior to installation of the mist-nets, only a few people (usually two) were allowed to enter the caves for bat detection during the monthly sampling, to avoid disturbing the colony. When encountered, bats were located and the number of individuals was recorded. Subsequently, mist-nets were placed aiming to capture the individuals to be identified, as well as to confirm the number of individuals. When numerous colonies were present, the number of animals was estimated visually. On some occasions, when the researchers entered the caves, some individuals flew inside the cave. Therefore, it is possible that some animals were not properly registered. Consequently, we consider that the number of individuals presented in this study represents an approximation of real number.

Species identification followed Gardner (2007), plus assistance from experts (see Acknowledgements). Voucher specimens were deposited in the bat reference collection of the Pontifícia Universidade Católica de Minas Gerais (PUC Minas). This study was carried out under a license granted by the Brazilian Chico Mendes Institute for Biodiversity Conservation (ICMBio).

Generalized Linear Models (GLM) using binomial distribution and logit link function, and with backward stepwise elimination of predictors, were used to determine which variables influenced the occupation of caves by bats. Logistic regression models were used because the dependent variable was dichotomous (presence vs. absence of bats) and the independent variables were categorical and continuous (McCullagh and Nelder 1989, Sokal and Rohlf 1995). The initial model included the average values of each predictor variable: internal height and width, height and width of entrance, number of entrances, and maximum horizontal development of the cave, internal temperature and relative humidity. We used Spearman rank correlation coefficient to assess collinearity between the predictor variables and considered correlations between pairs of variables with magnitudes greater than ± 40% as having high

Table 1. Descriptive statistics and comparisons of means of structural and microclimatic characteristics among caves occupied by *Desmodus rotundus* (n = 13), *Glossophaga soricina* (n = 8), and *Artibeus planirostris* (n = 4) at the APA Karst area of Lagoa Santa, Minas Gerais, Brazil. The mean number of individuals found in caves for all inspections is provided.

| | *D. rotundus* (A) | | *G. soricina* (B) | | *A. planirostris* (C) | |
|---|---|---|---|---|---|---|
| | Mean ± SD | Range, N | Mean ± SD | Range, N | Mean ± SD | Range, N |
| Internal temperature (°C) | 22.4 ± 1.8 | 18.3–25.4, 47 | 22.7 ± 2.3 | 17.1–26.3, 25 | 21.70 ± 2.3 | 16.0–25.9, 28 |
| Relative humidity (%) | 78.5 ± 8.8 | 56.0–90.0, 47 | 73.8 ± 10.7 | 48.0–90.0, 25 | 78.80 ± 8.2 | 62.0–90.0, 28 |
| Internal Height (m)* | $3.6 \pm 0.7^{C}$ | 2.2–6.0, 13 | $2.9 \pm 1.0^{C}$ | 1.1–4.3, 8 | $4.40 \pm 0.7^{A, B}$ | 3.0–6.0, 4 |
| Internal Width (m)** | 2.2 ± 1.2 | 1.1–5.2, 13 | $1.7 \pm 0.7^{C}$ | 1.0–3.2, 8 | $3.00 \pm 2.0^{B}$ | 1.4–8.7, 4 |
| Horizontal development (m)** | $31.2 \pm 15.6^{B}$ | 8.3–59.8, 13 | $11.8 \pm 8.0^{A}$ | 2.8–26.5, 8 | 31.60 ± 20.0 | 3.1–50.0, 4 |
| Entrance height (m)** | $2.9 \pm 1.4^{C}$ | 1.4–6.0, 13 | 2.9 ± 0.9 | 1.0–4.0, 8 | $5.25 \pm 1.3^{A}$ | 3.7–6.7, 4 |
| Entrance width (m)** | $4.9 \pm 4.5^{B}$ | 1.2–16.0, 13 | $2.0 \pm 1.2^{A}$ | 0.7–4.1, 8 | 3.40 ± 1.0 | 2.8–5.4, 4 |
| Number of entrances | 1.3 ± 0.6 | 1.0–3.0, 13 | 1.1 ± 0.7 | 1.0–2.0, 8 | 1.50 ± 0.5 | 1.0–2.0, 4 |
| Individuals number | 8.0 ± 1.2 | 1.0–53.0, 47 | $3.3\ 1.6^{C}$ | 1.0–7.0, 20 | $6.30 \pm 4.0^{B}$ | 1.0–20.0, 28 |

Different column superscripts show statistically significant differences between species, represented by letters in brackets: *one way ANOVA followed by Tukey test ($p < 0.05$); ** Kruskal-Wallis test followed by Dunn test ($p < 0.05$). The sample size (N) represents the number of times that the measure was taken during the monthly inspections.

collinearity (Hair et al. 2010), and removed them from further analysis. The model was built using data for all bat species recorded in the caves. Therefore, in the final models, only the variables that contributed significantly ($P < 0.05$) were retained. The adherence of the final model was assessed by the ratio of the statistic deviance and its degrees of freedom, with the closer to 1.0 being the better fit (McCullagh and Nelder 1989).

The Student's t-test, with two-tailed t-values ($\alpha = 0.05$) were used to compare the means of the different structural and microclimatic parameters of occupied and unoccupied caves. Considering the microclimate variables, comparisons of means were performed using the measurements obtained for each cave in each weather station. The statistical analyses were performed using Statistica 8.0 (StatSoft Inc. 2007).

## RESULTS

Bats were found in 32 caves during 117 inspections (55 inspections in the dry season and 62 inspections in the rainy season), while another 34 caves had no bats (48 inspections in the dry season and 46 inspections in the rainy season). The mean number of inspections by cave was 3.2 ± 4.0 inspections (range = 1-14 monthly inspections).

We identified 14 species of bats in the study caves, including: one vespertilionid – *Myotis nigricans* (Schinz, 1821), Black Myotis; one emballonurid – *Peropteryx macrotis* (Wagner, 1843), Lesser dog-like bat; and 12 phyllostomids – *Anoura caudifer* (E. Geoffroy, 1818), Lesser tailless bat, *Artibeus planirostris* (Spix, 1823), Spix's Artibeus, *Carollia perspicillata* (Linnaeus, 1758), Seba's short-tailed bat, *Chrotopterus auritus* (Peters, 1856), Great woolly bat, *Desmodus rotundus* (E. Geoffroy, 1810), Common vampire bat, *Diaemus youngi* (Jentink, 1893), White-winged vampire bat, *Diphylla ecaudata* Spix, 1823, Hairy-legged vampire bat, *Glossophaga soricina* (Pallas, 1766), Long-tongued bat, *Micronycteris megalotis* (Gray, 1842), Brazilian big-eared bat, *Mimon bennettii* (Gray, 1838), Bennett's spear-nosed bat, *Phyllostomus hastatus* (Pallas, 1767), Great spear-nosed bat, and *Platyrrhinus lineatus* (E. Geoffroy, 1810), White-lined broad-nosed bat.

We found a mean of 1.2 species/cave. Considering all inspections of the 32 occupied caves, an average of 7.1 ± 9.6 (1-53) individuals was found. The largest colonies were those of *D. rotundus* (53 individuals in November, 2010), *P. lineatus* (20 individuals in January, 2010), *A. planirostris* (20 individuals in March, 2010), *A. caudifer* (20 individuals in May, 2010) and *D. ecaudata* (50 individuals in June, 2010). *Desmodus rotundus* was the species with the highest number of co-occurrences, involving six other species (*D. youngi*, *C. auritus*, *A. planirostris*, *P. hastatus*, *P. macrotis*, *M. megalotis*).

During the inspections, most species were eventually recorded from multiple caves, but *D. rotundus*, *A. planirostris* and *G. soricina* were always found in the same caves and therefore, the caves occupied by these species were inspected more often. The mean (± SD) number of individuals found at these roosts is provided and the structural and microclimate characteristics of these roosts are compared (Table 1). The most significant structural difference among caves occupied by these species was cave height (Table 1). *Glossophaga soricina* occupied smaller caves (Table 1). Most of the caves occupied by *D. rotundus* (69%) and *G. soricina* (75%) had only one entrance.

Considering all the sampled caves, the maximum horizontal development was significantly higher ($p < 0.05$) in occupied caves (Table 2). There was no statistically significant variation ($p > 0.05$) related the mean values of the microclimatic variables (Table 3), except in relation to the mean temperature of unoccupied roost, which differed seasonally (Table 3).

Correlation analysis of the explanatory variables showed that cave width was positively correlated with the width of the entrance ($r_s = 0.45$). To eliminate the collinearity of these pairwise correlated explanatory variables, we removed the first variable (cave width) from the analysis. The only predictor affecting the presence of bats in the study area was maximum

Table 2. Descriptive statistics (mean, standard deviation, range) and comparisons of means (Student's t-test, $p < 0.05$) of structural characteristics (in meters) among 32 caves occupied by bats and 34 unoccupied caves at the APA karst area of Lagoa Santa, Minas Gerais, Brazil.

| Season/Cave | Occupied | | Unoccupied | | p |
|---|---|---|---|---|---|
| | Mean ± SD | Range | Mean ± SD | Range | |
| Internal temperature (°C) | 22.3 ± 1.3 | 18.6–25.9 | 22.6 ± 1.8 | 16.5–27.8 | 0.43 |
| Relative humidity (%) | 79.5 ± 6.6 | 67.6–90.0 | 81.8 ± 8.4 | 64.0–90.0 | 0.23 |
| Internal height (m) | 3.0 ± 1.1 | 1.1–6.0 | 3.2 ± 1.0 | 1.0–5.4 | 0.65 |
| Internal width (m) | 2.6 ± 1.6 | 1.1–8.2 | 2.4 ± 1.3 | 0.9–7.4 | 0.62 |
| Horizontal development (m) | 20.1 ± 13.8 | 2.8–59.8 | 12.6 ± 9.5 | 2.9–49.3 | 0.01 |
| Entrance height (m) | 3.1 ± 1.6 | 1.0–7.9 | 3.3 ± 2.6 | 0.9–16.3 | 0.53 |
| Entrance width (m) | 4.0 ± 4.1 | 0.7–17.9 | 2.8 ± 1.9 | 0.8–8.9 | 0.12 |
| Number of entrances | 1.3 ± 0.5 | 1.0–3.0 | 1.4 ± 0.7 | 1.0–3.0 | 0.77 |

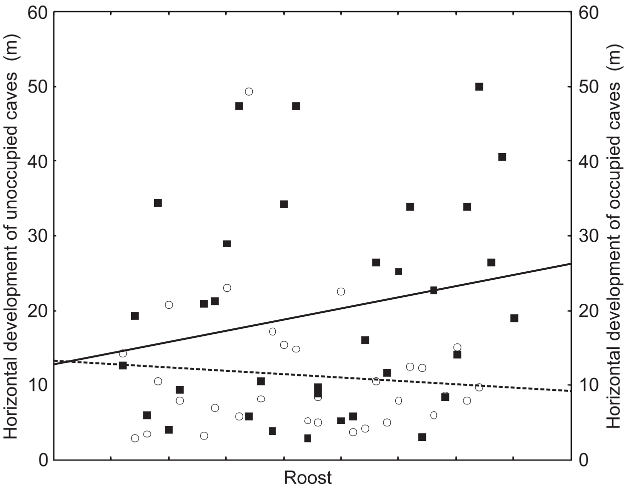


Figure 1. Maximum horizontal development of caves occupied (square filled) and unoccupied (open circles) as diurnal roosts by bats at the APA karst area of Lagoa Santa, Minas Gerais, Brazil, during 2009–2011.

horizontal development (Fig. 1), with occupied caves showing greater horizontal development (GLM: Wald Stat. = 4.648716, p = 0.03; Deviance = 81.4811, DF = 61, Stat/DF = 1.335755).

## DISCUSSION

Our data show that almost half of the studied caves are used by bats and that most species recorded eventually occupy these caves. The exceptions to this were *D. rotundus*, *G. soricina* and *A. planirostris*, which occupied the same caves almost continuously throughout the study period, indicating that individuals of these species roost in more permanent sites. We found no differences in microclimate between occupied and unoccupied caves. The microclimate among the caves studied can be characterized as consistent, and it is stable over the year. These results are not surprising, given that variation in climate and weather are not pronounced in the study area (Sá-Jr et al. 2012), and are likely insufficient to lead to selective pressure for the occupancy of a particular type of cave. It is also possible that this similarity in temperature between caves, measured in different rocky outcrops, results from the similar geomorphological nature of these outcrops at the Lagoa Santa's karst (Auler and Farrant 1996), which are subject to the same variations in climate, both within and between seasons. However, since there are no geomorphological assessments of the study area, this hypothesis needs to be tested in further studies.

Given that the mean temperatures of the caves used by *D. rotundus*, *G. soricina*, and *A. planirostris* are similar to the overall mean of all occupied caves, we conclude that, in the study area, temperature does not play an important role in the choice of cave by these species. Similar results were obtained in Mexico, where Ávila-Flores and Medellín (2004) found that microclimate had little influence on the use of caves by 23 species of bats. These findings contrast with those from temperate regions, where many studies have found microclimate to be the principal factor in the selection of roosts by bats. This makes sense since microclimate is directly related to thermoregulation of bats in those areas (Kurta et al. 1990, Baudinette et al. 2000, Kerth et al. 2001, Sedgeley 2001, Rodríguez-Durán and Soto-Centeno 2003).

Table 3. Comparisons of means (Student t-test, $p < 0.05$) of microclimatic characteristics among 32 caves occupied by bats and 34 unoccupied caves at the APA karst area of Lagoa Santa, Minas Gerais, Brazil. The sample size (N) represents the number of times that the measure was taken during the monthly inspections.

| Season/Cave | Internal temperature (°C) | | | | | Relative humidity (%) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Occupied | | Unoccupied | | | Occupied | | Unoccupied | | |
| | Mean ± SD | Range, N | Mean ± SD | Range, N | p | Mean ± SD | Range, N | Mean ± SD | Range, N | p |
| Dry season | 20.5 ± 1.1 | 19.3–21.7, 3 | 20.4 ± 2.0 | 16.5–24.0, 21 | 0.93 | 74.1 ± 7.6 | 68.3–82.9, 3 | 79.2 ± 7.4 | 69.0–90.0, 21 | 0.28 |
| Rainy season | 22.9 ± 1.9 | 18.6–26.6, 40 | 23.4 ± 1.2 | 21.7–27.8, 30 | 0.10 | 79.3 ± 7.0 | 64.0–90.0, 40 | 82.2 ± 9.5 | 59.0–90.0, 30 | 0.14 |
| p | 0.09 | | 0.00 | | | 0.22 | | 0.22 | | |

Logistic regression analysis showed that maximum horizontal development influenced the presence or absence of individuals of different species in caves. It is known that more extensive caves offer more hiding places, such as cavities, cracks and tunnels, and such characteristics reflect greater structural heterogeneity, which provides more options for occupation as roosts (McNab 1974, Arita 1996, Brunet and Medellín 2001). Although no measure of the structural heterogeneity of caves was obtained in this study, it is safe to assume that there are more possibilities for finding appropriate roosting places in caves that have greater horizontal development, and that this increases the likelihood of their occupation by bats.

The dimensions of caves are related to the maintenance of the microclimate and the protection from adverse weather and predation (Vonhof and Barclay 1996, Sedgeley and O'Donnell 1999). As the microclimates of the caves sampled in this study are very similar, it is possible that protection from predators is an important factor in the occupation of these caves. Predation on bats inside caves has been insufficiently investigated (Martínez-Coronel et al. 2009, Rodríguez-Durán et al. 2010), and only studies designed with the specific objective to test this hypothesis could show conclusively the influence of predation in study area. However, the two most frequent species during this study always occupied the same roosts, which had only one opening, such as those used by *D. rotundus* and *G. soricina*. Thus, it is possible that caves with only one entrance offer a certain level of protection compared to those with multiple entries, since it is supposedly easier to monitor the approach of potential predators from only one entrance, thus promoting the continued use of these caves (Kunz and Lumsden 2003).

In conclusion, caves seem to vary in their adequacy for certain species or under certain conditions (Kerth et al. 2001, Sedgeley 2001, Ávila-Flores and Medellín 2004). For the vampire bat, for example, it became clear that some caves are used as maternity roosts. We observed great variation in the number of individuals of *D. rotundus* in four caves, since their colonies become more numerous from October to January (rainy season), when we observed a greater number of females and juveniles (20-53 individuals); in non-reproductive periods, few individuals (1-4) remained in these roosts. This variation in the number of individuals and the dwelling of some animals for a long time in the maternity roost is referred to as maternity roost fidelity (Lewis 1995, Kunz and Lumsden 2003). In areas with high availability of roosts, males tend to have higher roost fidelity than females, since this resource is important for attracting females during the mating season (Chaverri et al. 2007); unfortunately we did not check the sex of individuals when the colonies became reduced.

We did not find any evidence of breeding activity in *G. soricina* and *A. planirostris*. Evidence of reproductive activity such as the presence of pups was observed in two other species, which only had single roost records – nine individuals of *Mimon bennettii* were recorded in November, 2010 (rainy season) and 20 individuals of *Anoura caudifer* were recorded in May, 2010 (dry season).

The average species richness found in this study is relatively low (1.2 species/roost) when compared with other karst areas; Trajano (1984), Arita (1996) and Bredt et al. (1999) reported four, three and four species/roost, respectively. Species richness is often related to the extent and area of a cave, since larger caves provide more and different microhabitats, which can facilitate the coexistence of species with different preferences (McNab 1974, Arita 1996, Brunet and Medellín 2001). However, the number of bat species in a particular cave may also be related to the availability of roosts in the vicinity, so a more isolated cave is prone to harbour more species and larger numbers of individuals (Trajano 1984, Bredt et al. 1999). Thus, it is possible that the low species richness found in this study is related to the large supply of caves in the region. However, differences in richness could also be due to differences in cave characteristics, or even to differences in regional bat faunas.

Bats seek shelter in a wide variety of roost types, which can be characterized in a continuum that ranges from ephemeral to permanent, with the selection of a particular type of roost dependent on its availability (Kunz and Lumsden 2003). Therefore, based on our results, we conclude that many caves are occupied by bats, and some caves are more frequently occupied by some species than others, including some roosts that are used as maternity roosts. These findings indicate that since caves are important resources for the bats in the studied karst environment, they should be preserved. While the limestone outcrops that provide the roosts for bats in the studied area are protected, other karst habitats in the region are under great pressure from human activities, mainly the calcining industry, so that bat populations in the region are certainly very susceptible and in need of protective measures.

## ACKNOWLEDGEMENTS

We are grateful to the anonymous reviewers for all the suggestions, which improved this manuscript, to Fundação de Amparo à Pesquisa do estado de Minas Gerais (FAPEMIG) and Fundo de Incentivo à Pesquisa (FIP PUC Minas) for funding the project, and FAPEMIG and National Counsel of Technological and Scientific Development (CNPq) for scholarships granted to Camila G. Torquetti and Sabrina Silva Alves do Carmo, respectively, who aided in the fieldwork. We also thank Mr. José Hein and Fazenda Cauaia for providing logistical support for the fieldwork, Valéria da Cunha Tavares for identification of some of the bat species, and the Chico Mendes Institute for Biodiversity Conservation (ICMBio) for the license (#22231-1) to capture bats.

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Submitted: 16 May 2016
Received in revised form: 26 September 2016
Accepted: 29 November 2016
Editorial responsibility: Darren Norris

**Author Contributions:** CGT and SAT designed the experiments; CGT conducted the experiments; CGT, SAT and MXS analyzed the data; CGT and SAT wrote the paper.
**Competing Interests:** The authors have declared that no competing interests exist.