BAT ASSEMBLAGES AT A HIGH-ALTITUDE AREA IN THE ATLANTIC FOREST OF SOUTHEASTERN BRAZIL

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ABSTRACT. Most Brazilian landscapes lie below 600 m above sea level and studies on the rich Brazilian bat fauna at higher altitudes are scarce. In this study, we investigated bat assemblages associated with different habitats in Chapada do Abanador, Minas Gerais, an area with altitudes ranging from 1000 to 1580 m. Forty-five nights of sampling (153 000 m² h) were performed in semideciduous montane forest, cloud forest and campo de altitude. A total of 137 individuals were captured, belonging to 12 species of the families Phyllostomidae and Vespertilionidae, with a large dominance of the former. Species-accumulation curves reached values close to the asymptote for the campo de altitude and cloud forest habitats, but not for montane forest, suggesting that more species may be added by extending the sampling effort in this habitat. A non-metric multidimensional scaling analysis indicated no strong separation between sampled habitats. Higher abundances of Desmodus rotundus and Histiotus velatus in the campo de altitude were observed, with the latter being exclusively recorded in this habitat. Moreover, a higher abundance of frugivores was observed in forested habitats, while hematophagous, insectivores and nectarivores were more abundant in the campo de altitude. Although presenting lower species richness when compared with environments below 1000 m, the campos de altitude and cloud forests are ecologically important and poorly protected portions of the Atlantic Forest in Minas Gerais, whose biodiversity must be preserved. Our data contributes with a better description of the local fauna and fills gaps on the species distribution for high altitude sites in Brazil.

RESUMO. Assembléia de morcegos em uma área de elevada altitude na Floresta Atlântica do sudeste do Brasil. Grande parte das paisagens brasileiras se encontra abaixo dos 600 m de altitude e os estudos sobre a rica fauna de morcegos brasileiros em elevadas altitudes são escassos. Nesse estudo, investigamos a assembleia de morcegos associada a diferentes habitats na Chapada do Abanador, Minas Gerais, cuja altitude varia de 1000 a 1580 m. Foram conduzidas 45 noites de amostragem (153 000 m² h) na floresta semidecidual montana, floresta nebular e campo de altitude. Foram capturados 137 indivíduos pertencentes a 12 espécies das famílias Phyllostomidae e Vespertilionidae, com grande predominância da primeira. Curvas de acumulação de espécies alcançaram valores próximos à assíntota para o campo de altitude e floresta nebular, mas não para a floresta montana, sugerindo que mais espécies seriam adicionadas com o aumento do esforço amostral nesse habitat. A análise de escalonamento multidimensional não-métrico não indicou forte separação entre os habitats. Entretanto, foi observada uma maior abundância de Desmodus rotundus e Histiotus velatus no campo de altitude, sendo a última exclusiva desse habitat. Além disso, foi observada uma maior abundância de frugívoros nos habitats florestados, enquanto hematofágos e insetívoros foram mais abundantes no campo de altitude. Embora apresentem menor riqueza de espécies quando comparados com ambientes abaixo de 1000 m, os campos de altitude e as florestas nebulares constituem porções ecologicamente importantes e pouco protegidas da Floresta Atlântica em...
INTRODUCTION

Although most of Brazilian landscapes lie below 600 m above sea level (Ab'Saber, 1977), the Atlantic Forest, one of the most threatened biomes in the country, extends from the sea level up to 1600 m, mainly in Southern and southeastern Brazil (Tabarelli et al., 2010). This biome has one of the richest mammal faunas in the world, estimated in 298 species, with bats responding for about 40% of the species (Paglia et al., 2012). Despite such species richness, knowledge about the bat fauna distribution in Brazil is heterogeneous; there are species records for only 40% of the Brazilian territory and less than 10% of the country can be considered satisfactorily sampled (Bernard et al., 2011). The Atlantic Forest is the best sampled biome, with records in almost 80% of its extension. Nevertheless, bat species distribution there is uneven, and only few studies were done above 1000 m (Dias and Peracchi, 2008; Modesto et al., 2008; Nobre et al., 2009).

Minas Gerais holds the largest remaining area of Atlantic Forest in Brazil (SOS Mata Atlântica/INPE, 2010) and presents a high bat-species richness (80 species; Tavares et al., 2010; Gregorin et al., 2011; Gregorin and Loureiro, 2011). However, despite the fact that 10% of the original Atlantic Forest coverage in Minas Gerais lies above 1000 m (SOS Mata Atlântica/INPE, 2010), bat fauna at these elevations has been poorly sampled (Glass and Encarnação, 1982; Falcao et al., 2003; Nobre et al., 2009). Studies in such elevated areas, thus, can help us to fulfill distributional gaps, and support a better understanding on how bats use higher elevation environments (such as campo rupestre, campos de altitude and cloud forests). In addition, it may be useful to better identify and characterize key areas for the conservation of this biome, which is highly fragmented and under strong anthropic pressure (e.g. Riberio et al., 2009; Tabarelli et al., 2010).

Some key areas for biodiversity conservation in Minas Gerais have already been identified and few of them overlap exactly with areas of Atlantic Forest above 1000 m (Heringer and Montenegro, 2000). One of those areas is the Chapada do Abanador, in southern Minas Gerais, a rich mosaic of semideciduous montane forest, cloud forest and campos de altitude (Rodrigues and Carvalho, 2001; Oliveira-Filho et al., 2004). Chapada do Abanador has a very irregular landscape with altitudes between 1000 and 1580 m, with high plant diversity along the springs of Rio Capivari, a tributary of Rio Grande (Oliveira-Filho et al., 2004; Drummond et al., 2005).

With the aim to characterize and compare the bat fauna associated with highland areas of the Atlantic Forest of southern Minas Gerais, we document species richness and species composition, as well as structure of bat assemblages in cloud forest, montane forest and campo de altitude at Chapada do Abanador, a priority area for biodiversity conservation in the state.

MATERIALS AND METHODS

Study area

Chapada do Abanador (21º35’S; 46º33’W) is located between the municipalities of Minduri and Carancas, southern Minas Gerais, Brazil (Fig. 1). The annual average precipitation and temperature vary between 1536-1605 mm and 14.8-18.6°C, respectively (Pereira et al., 2007). The vegetation in Chapada do Abanador consists, mainly, of campos de altitude and campos rupestres (Safford, 1999; Vasconcelos, 2011) with large extensions of grasslands and eventually some shrubby species, intersected by rock outcrops.
Cloud forests are present on humid areas in the campo de altitude. The montane forest covers a very steeply landscape, from 1000 to 1500 m, and cloud forests are above that height, imbibed in a matrix of campos de altitude.

**Bat sampling**

Bats were sampled in the montane forest, cloud forest and campo de altitude (Fig. 1; Table 1). At each environment, two sites were sampled, and all of them were between 1345 and 1549 m. The total sampled area was about 760 ha and distances between sites ranged from 0.11 to 2.26 km. The shortest distance was between montane forest sites due to the steep inclination of the terrain and little availability of places for sampling with mist nets. Forty-two nights of sampling were carried out between July 2009 and April 2010, with all the 6 sites visited 7 times. Three

**Table 1**

Sites sampled for bats between July 2009 and April 2010 in three different habitats at Chapada do Abanador, state of Minas Gerais, Brazil. Abbreviations: CA, campo de altitude; CF, cloud forest; MF, montane forest.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Site</th>
<th>Area (ha)</th>
<th>Altitude (m)</th>
<th>Coordinates</th>
</tr>
</thead>
<tbody>
<tr>
<td>CF</td>
<td>1</td>
<td>37</td>
<td>1501</td>
<td>21°35'36&quot;S/44°35'06&quot;W</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>34</td>
<td>1530</td>
<td>21°35'36&quot;S/44°34'14&quot;W</td>
</tr>
<tr>
<td>CA</td>
<td>3</td>
<td>387</td>
<td>1540</td>
<td>21°35'22&quot;S/44°33'50&quot;W</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>387</td>
<td>1549</td>
<td>21°35'39&quot;S/44°34'04&quot;W</td>
</tr>
<tr>
<td>MF</td>
<td>5</td>
<td>300</td>
<td>1345</td>
<td>21°35'48&quot;S/44°33'44&quot;W</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>300</td>
<td>1425</td>
<td>21°35'46&quot;S/44°33'47&quot;W</td>
</tr>
</tbody>
</table>
other additional sites were sampled only once due to logistics. Ten mist nets (12 x 2.5 m, or 30 m²) were open from dusk to dawn (~12 hours/night) and checked every 30 minutes. Sampling effort was calculated in m²h (Straube and Bianconi, 2002) and capture success was obtained by dividing captures per total sampling effort. Individuals were marked with a metallic ball-chain necklace numbered with colored plastic rings (Esberard and Daemon, 1999). Three individuals of each species were collected, and vouchers deposited at the Mammal Collection of the Universidade Federal de Lavras (CMUFLA). Taxonomy used herein is in accordance to Simmons (2005).

Data analysis
Species accumulation curves for each habitat and for the entire area were plotted (Gotelli and Colwell, 2001). These curves, together with parametric and non-parametric models, may be used to estimate the number of species in an area (Colwell, 2004). Species estimator Jackknife 1 was employed to estimate species richness, based on 1000 randomizations, without replacing the sample sequences (EstimateS, version 8.0; Colwell, 2004). A Nonmetric Multidimensional Scaling (NMDS) analysis based on species abundance was used to verify differences in structure and composition of bat assemblages among habitats, applying Bray-Curtis index as a measure of similarity. An analysis of similarity (ANOSIM; Clarke, 1993) was used to compare the groups created by the NDMS. The analyses were performed using the software PRIMER, version 5.0 (Clarke and Gorley, 2001).

To characterize bat assemblages, species were categorized based on their major diet item, i.e., carnivores, frugivores, hematophagous, insectivores and nectarivores (Gardner, 1977; Kalko et al., 1996). Structuring and trophic composition of bats were used to compare the distribution of feeding habits in the studied habitats.

RESULTS
Richness and abundance patterns
Sampling effort for each habitat was 51 000 m²h, totaling 153 000 m²h for the study area. Capture success was 0.001 ind./m²h, with 137 individuals from 12 species of Phyllostomidae and Vespertilionidae. The former family was dominant with 87% of the captures and 83% of the recorded species (Table 2).

The most abundant species was Desmodus rotundus (35 individuals; 25.5% of captures), followed by Carolia perspicillata (26; 19%) and Anoura geoffroyi (22; 16.1%). Pygoderma bilabiatum, Vampyressa pusilla and Myotis nigricans were rare and contributed with 2.9% of the captures (Table 2).

Species accumulation curves reached values close to the asymptote for campo de altitude and cloud forest, suggesting that their bat fauna was almost entirely captured and few species would be added with an increase in the mist-netting sampling effort. The accumulation curve for montane forest did not reach the asymptote (Fig. 2). The species richness estimator suggested a total of 14 bat species in Chapada do Abanador, indicating that samplings recorded approximately 86% of the local bat fauna: 77% of the species expected for the montane forest (estimated total species: 13), 82% for the cloud forests (estimated total species: 11), and 80% for the campo de altitude (estimated total species: 10).

Similarities among habitats
Out of the 12 recorded species, 10 were found in the montane forest, nine in the cloud forests and eight in the campo de altitude, with four species occurring in only one of the habitats (Table 2): Chrotopterus auritus and V. pusilla exclusively in the montane forest, P. bilabiatum in the cloud forests, and H. velatus in the campo de altitude.

The NDMS analysis did not indicate a clear separation among habitats (Fig. 3), although bat assemblages showed significant differences between the montane forest (MF) and the campo de altitude (CA), and between the cloud forest (CF) and the campo de altitude. However, the bat abundance explained only 14% and 19% of the observed differences (ANOSIM RMF-CF = -0.039, P = 0.74; RMF-CA = 0.14, P = 0.01; RCF-CA = 0.19, P = 0.01). The same occurred in the analysis of composition among assemblages, with bat incidence explaining only 13% and 19% of the observed differences (ANOSIM RMF-CF = -0.045, P = 0.79; RMF-CA = 0.13, P = 0.01; RCF-CA = 0.19, P = 0.01).
Table 2
Bat species composition, abundance, relative frequency (%), habitat and diet at Chapada do Abanador, state of Minas Gerais, Brazil, sampled between July 2009 and April 2010. Abbreviations: Habitats = MF, montane forest; CF, cloud forest; CA, campo de altitude. Guilds = C, carnivores; F, frugivores; H, hematophagous; I, insectivores; N, nectarivores.

<table>
<thead>
<tr>
<th>Family</th>
<th>Abundance per habitat</th>
<th>Relative frequency (%)</th>
<th>Guild</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MF</td>
<td>CF</td>
<td>CA</td>
</tr>
<tr>
<td>Phyllostomidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anoura caudifer</td>
<td>2</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Anoura geoffroyi</td>
<td>2</td>
<td>9</td>
<td>11</td>
</tr>
<tr>
<td>Artibeus fimbriatus</td>
<td>4</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Artibeus lituratus</td>
<td>3</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Carollia persicillata</td>
<td>10</td>
<td>11</td>
<td>5</td>
</tr>
<tr>
<td>Chrotopterus auritus</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Desmodus rotundus</td>
<td>5</td>
<td>9</td>
<td>21</td>
</tr>
<tr>
<td>Pygoderma bilabiatum</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Sturnira lilium</td>
<td>1</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Vampyressa pusilla</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Vespertilionidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Histiotus velatus</td>
<td>0</td>
<td>0</td>
<td>15</td>
</tr>
<tr>
<td>Myotis nigricans</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>34</td>
<td>45</td>
<td>58</td>
</tr>
</tbody>
</table>

Fig. 2. Species accumulation curves based on numbers of bats captured in three habitats (montane forest, cloud forests and campo de altitude) at Chapada do Abanador, state of Minas Gerais, Brazil. ‘Total’ represents all habitats pooled.
Comparisons of feeding habits indicated higher abundance of frugivores (> 50%) in the forest dominated habitats (Fig. 4, top). In the campo de altitude, there was a higher abundance of hematophagous bats (36%), followed by insectivores (26%) and nectarivores (22%). Considering species richness (Fig. 4, bottom), guilds were similarly distributed among the different habitats, except for carnivores, which were only found in the montane forest.

**DISCUSSION**

With 12 bat species recorded, Chapada do Abanador presented an impoverished, simply-structured bat assemblage, including both widespread generalist consumers (e.g., *C. perspicillata* and *Artibeus lituratus*) and specialized nectarivores (*Anoura caudifer* and *A. geoffroyi*) and insectivores (*H. velatus*). Such reduced number of species and simplified community structure were expected, considering that samplings took place between 1345 and 1549 m. In fact, our results regarding species richness are similar to those found in other studies at high altitudes in southern Minas Gerais and Rio de Janeiro states (Glass and Encarnação, 1982; Falcão et al., 2003; Modesto et al., 2008; Nobre et al., 2009), in which a lower richness is reported in comparison with other Atlantic Forest sites collecting below 1000 m in the mountainous portions of Southeastern Brazil. At those lower altitudes, samplings recorded between 16 and 40 bat species (Dias et al., 2002; Esbérard, 2003; Moratelli and Peracchi, 2007). The capture success in Chapada do Abanador (0.001 ind./m²h) was also reduced when compared to studies in lower altitudes in the Atlantic Forest (generally 0.02 ind./m²h; e.g. Faria, 2006; Moratelli and Peracchi, 2007), but it is closer to values obtained at Atlantic Forest sites in southern Brazil (0.004 ind./m²h; Bianconi et al., 2004), and in other high-altitude sites in the region, such as in Serra do Desengano, in Rio de Janeiro (0.006 ind./m²h; Modesto et al., 2008), and in other high-altitude sites in South America, such as in Tolina, Colombia (0.001 ind./m²h; Bejarano-Bonilla et al., 2007), and in the Andean portions of Venezuela (Soriano et al., 1999; Soriano et al., 2002). Therefore, bat assemblage in Chapada do Abanador fits a pattern in which the higher the elevations is, the lower the bat species richness and capture success. The observed pattern may be explained by direct thermoregulation...
and indirect factors (e.g., food resources; Soriano et al., 2002; McCain, 2007). In fact, those regions are colder when compared to lower tropical regions, suggesting that temperature is likely to be a limiting factor for many Phyllostomidae, which is a mostly tropical group regarding thermoregulation needs (MacNab, 1969; Graham, 1983; Patterson et al., 1996; Soriano et al., 2002). Furthermore, lower temperatures may influence food availability, since insect abundance, nectar and fruit productions, and small vertebrate abundance, are predictably lower in colder regions (Janzen et al., 1976; Fauth et al., 1989; Loiselle and Blake, 1991). Such hypothesis remains to be tested at Chapada do Abanador.

Considering that species richness estimation were based solely on mist netting, the addition of complementary techniques, such as roost search (Simmons and Voss, 1998) and, especially, the recording of echolocation calls, may contribute to add more species, mostly aerial insectivores that forage far from net range and, therefore, are underestimated in inventories that are based solely on mist-net capture (Kalko et al., 1996; Bernard et al., 2011). Unpublished studies conducted in the same region at a lower elevation (ca. 900 m), with a lower capture effort (16 888 m²h) and which roost searching was implemented besides mist netting, recorded 14 bat species, five of them complementary to the current study: Eptesicus furinalis (d’Orbigny, 1847), Eptesicus brasiliensis (Desmarest, 1819), Eumops auripendulus (Shaw, 1800), Platyrhinus lineatus (E. Geoffroy, 1810) and Micronycteris megalotis (Gray, 1842). Thus, at least 17 bat species are known to occur in Chapada do Abanador.

Richness and number of recorded individuals were similar among the three habitats in Chapada do Abanador, and most species were captured in all habitats. However, species composition and assemblage structure differed between the campo de altitude and the forested areas, indicating that some bats might recognize them as distinct foraging habitats. The high mobility displayed by the majority of bats (Clarke et al., 1993; Robinson and Stebbings, 1997; Bernard and Fenton, 2003), associated to the matrix composed by campos de altitude in Chapada do Abanador, with shrubs and sparse trees, as well as the fairly short distances between the forested areas, may favor the use of
the various habitats by bats. Among the shrubs and grasses present in campo de altitude, there are some species whose fruits may be consumed by bats, including *Byrsonima* spp., *Myrcia* spp., and other species in the Cactaceae and Orchidaceae families present in rocky outcrops. Moreover, the low spatial complexity of the campo de altitude may favor the search for food by the aerial insectivore *H. velatus*. This and other species of aerial insectivores tend to avoid areas with high spatial complexity, where flight can be difficult due to the abundance of obstacles (Brigham et al., 1997; Grindal and Brigham, 1998).

This study contributes to the characterization of the bat fauna in campos de altitude and cloud forests of southern Minas Gerais, two of the rarest and poorest sampled environments of the Atlantic Forest. Moreover, our inventory included systematic samplings above 1300 m, which are rare in Brazil. Although a simplified bat community was documented at Chapada do Abanador, the three studied habitats showed an apparently well adapted fauna, including frugivorous, nectarivorous and insectivorous bats within forested habitats surrounded by a grassland matrix. Bats play a fundamental role in the reestablishment and maintenance of natural landscapes due to the ecosystem services they provide (Fleming and Sosa, 1994; Patterson et al., 2003; Kunz et al., 2011). The ecological role that the species we recorded play in those high elevation landscapes remains unknown and should be addressed by proper ecological studies. Chapada do Abanador, a priority area for biodiversity conservation in Minas Gerais (Drummond et al., 2005) is an ideal site for such studies.

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