Oecologia Australis
23(3):562-574, 2019
https://doi.org/10.4257/oeco.2019.2303.14

BAT FAUNA (MAMMALIA, CHIROPTERA) FROM GUARAPUAVA HIGHLANDS, SOUTHERN BRAZIL

João Marcelo Deliberador Miranda[1], Luciana Zago da Silva[2], Sidnei Pressinatte-Júnior[1], Luana de Almeida Pereira[3], Sabrina Marchioro[3], Daniela Aparecida Savariz Bôlla[4] & Fernando Carvalho[5]*

[1] Universidade Estadual do Centro Oeste, Departamento de Biologia, campus CEDETEG, Rua Simeão Camargo Varela de Sá, 03, CEP 85040-080, Guarapuava, PR, Brazil.

[2] Faculdade Guairacá, Rua XV de Novembro, 7050, CEP 85010-000, Guarapuava, PR, Brazil.

[3] Universidade Federal do Paraná, Programa de Pós-Graduação em Zoologia, campus Centro Politécnico, Rua Coronel Francisco H. dos Santos, 100, CEP 81531-980, Curitiba, PR, Brazil.

[4] Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo, CEP 69067-375, Manaus, AM, Brazil.

[5] Universidade do Extremo Sul Catarinense, Programa de Pós-Graduação em Ciências Ambientais, Laboratório de Ecologia e Zoologia de Vertebrados, Av. Universitária, 1105, Bairro Universitário, C.P. 3167, CEP 88806-000, Criciúma, SC, Brazil.

E-mails: guaribajoao@yahoo.com.br (*corresponding author); luazagos@gmail.com; spressinatte.jr@gmail.com; luanabio2014@gmail.com; sahmarchioro@gmail.com; danielabolla@hotmail.com; f.carvalho@unesc.net

Abstract: Here, we present an updated list of bats from Guarapuava highlands, center-southern of Paraná state, southern Brazil. This species list is based on four literature records (secondary data) and data from fieldwork (primary data) in three localities. All species recorded (primary and secondary data) were evaluated by the relative frequency and their conservation status were assessed. The species recorded from fieldwork were also evaluated by relative abundance. A beta diversity analysis was done to verify dissimilarities in the bat fauna among the seven localities. We recorded 28 species in the Guarapuava highlands (14 Vespertilionidae, 10 Phyllostomidae and 4 Molossidae), of which, eight are new records for the region. *Sturnira lilium* was the most abundant in three localities (primary data), and the most frequent species in all studies (primary and secondary data). Only four species were classified globally as "Near Threatened" or "Data Deficient", nevertheless they were frequent in this region. The mean regional beta diversity was 0.72, what could be mostly explained by turnover (0.64) rather than by nestedness (0.08). The greatest species richness of the family Vespertilionidae is a common pattern in subtropical and temperate regions as in highlands and mountains. As turnover was the main component of the beta diversity, the communities seemed to be structured mainly by replacement of species among the studied localities. The Guarapuava highlands present a diverse bat fauna, however, this region requires more sampling effort to become well known.

Keywords: Atlantic Forest; Araucaria Pine Forest; beta diversity; community assembly; turnover.

INTRODUCTION

Bats are the only flying mammals (Kunz & Pierson 1994), and they vary widely in both ecology and morphology, providing several ecological services such as pollination, seed dispersal and insect control (Fleming *et al.*1972, Passos *et al.* 2003). The Brazilian bat fauna is still poorly known, despite being among the richest in the world (Bernard *et al.* 2010, Nogueira *et al.* 2014). In Brazil, the Atlantic Forest is the most studied biome in the country, with approximately 98 bat species (Muylaert *et al.* 2017) and one of the most endangered environments (Myers *et al.* 2000). Even in this biome, there are still many gaps in bat species occurrence and distribution (Bernard *et al.* 2010) and consequently, in community assembly, especially in high altitude areas, such as mountains and highlands (Moras *et al.* 2013, Nobre *et al.* 2013).

One of the highlands in southern Brazil is the Guarapuava highlands in Paraná state, whose bat fauna have been poorly studied (Miretzki 2003, Bernard *et al.* 2010). These highlands are mostly characterized by Araucaria Pine Forest and natural grasslands at an altitude above 700 m (Maack 2012). These environments comprise most of Paraná state, with the Guarapuava highlands, alone, being responsible for an area of 6,659 km² (Santos *et al.* 2006). Few studies on bats have been carried out in Brazil above 1000 ma.s.l. (*e.g.*, Moras *et al.* 2013, Nobre *et al.* 2013, Miranda & Zago 2015).

The first bat information from the center-south of Paraná state was from Person & Lorini (1990) in Semidecidual Seasonal Forests close to Iguaçu Valley. After that, Miretzki (2003) recorded some species in the same region in a review of Paraná's bat fauna. More recently, a few mammalian surveys were conducted (Miranda *et al.* 2008, Valle *et al.* 2011), while the first survey focused uniquely on bats was undertaken between 2012 and 2013 (Miranda & Zago 2015). Since 2013, no surveys have been performed in the region to the best of our knowledge. Therefore, we aimed to update the bat fauna list of the Guarapuava highlands region, using primary and secondary data, and assess the conservation status of these species to produce a more informative list for future studies on species conservation. We also aimed to measure the beta diversity in this region and to evaluate nestedness and turnover processes in communities' assembly.

MATERIAL AND METHODS

Study sites

The present study was carried out in the Guarapuava highlands, Paraná state (Center-South region of Paraná State), southern Brazil (Figure 1). The area covers 26,409 km² and comprises 29 municipalities. The original environment was mainly composed of Araucaria Pine Forest and natural grasslands patches. In addition, this region also presents Semideciduous Seasonal Forests under an altitude of 700 m in the Iguaçu valley (Maack 2012). In this study, we focused only on the Araucaria highlands above the altitude of 700 m. The region's climate is *Cfb* according to Koppen's classification, characterized as subtropical humid and mesothermic without dry season, with more than five annual frost events (Maack 2012). The annual average temperature is 17.1°C, with 12.8°C in the coldest month and about 20.8°C in the warmest. The accumulated rainfall ranges between 1,800 and 2,000 mm (Miranda & Zago 2015).

Sources of information for bat species occurrence

Records of bat species for this region were obtained from field works (primary data) and literature (secondary data), totalizing seven localities (Figure 1). Field works were conducted in: (1) Parque Municipal São Francisco da Esperança (PMSFE), Municipality of Guarapuava; (2) Jardim Botânico de Faxinal do Céu (JBFC), Municipality of Pinhão; and (3) Banks of the Jordão River (BJR), Municipality of Candói (Table 1; Figure 1). Bats were captured using ground-level mist nets (6x3 m and 12x3 m; 18-20 mm of mash) in these three localities, and also canopy mist nets in PMSFE and JBFC (see Table 1 for sampling efforts and study period). Each specimen was identified according to identification keys (Barquez *et al.* 1999, Gardner 2008, Miranda *et al.* 2011). The first specimen captured for each species (except juveniles, pregnant or lactating females) was collected and deposited in the mammal collection of the Federal University of Paraná (Appendix I). Animals were captured under authorization of the Brazilian Government's Chico Mendes Institute for Biodiversity and Conservation (SISBIO permits: 44.129-1; 44.193-1).

Secondary data were obtained from four published studies, being two checklists based on museum and literature data compilation and two of original field surveys data: (1) a checklist of bat occurrence on Paraná state, and in Guarapuava highlands, with most of the data from Reserva do Iguaçú and Foz do Jordão municipalities

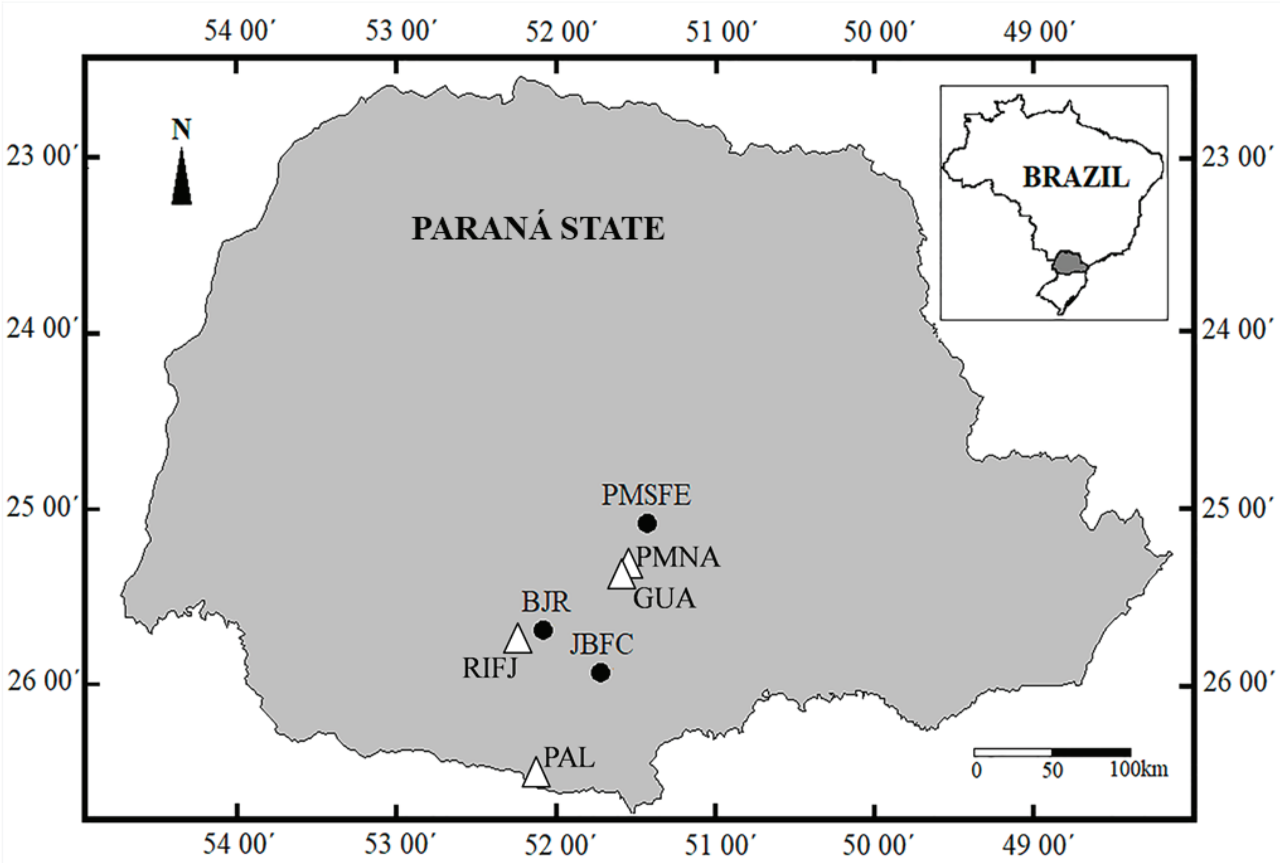

Figure 1. Localities with sampled bat fauna at Guarapuava highlands, Paraná state, southern Brazil. Primary data from 2009 to 2015 mist net samples are marked with black circles: PMSFE=Parque Municipal São Francisco da Esperança (Municipality of Guarapuava); JBFC=JardimBotânico Faxinal do Céu (Municipality of Pinhão); and BJR=Banks of the Jordão River (Municipality of Candói). Localities of secondary data are marked with white triangles: RIFJ=Reserva do Iguaçu and Fóz do Jordão municipalities (Miretzki 2003); PAL=Palmas municipality (Miranda *et al.* 2008), GUA=Guarapuava municipality (Valle *et al.* 2011); and PMNA=Parque Municipal Natural das Araucárias; Guarapuava municipality (Miranda & Zago 2015).

(RIFJ; Miretzki 2003); (2) a checklist of mammal occurrence on Guarapuava municipality (GUA; Valle *et al.* 2011); (3) a mammal survey in grasslands and Araucaria Pine Forest in Palmas municipality (PAL; Miranda *et al.* 2008); and (4) a bat survey on Parque Municipal Natural das Araucárias, on Guarapuava municipality (PMNA; Miranda & Zago 2015) (Figure 1).

Data analyses

We used rarefaction curves to evaluate the adequacy of the sample in relation to species richness. For the primary data, individual rarefaction curves were made using the absolute abundance of each species sampled for each location separately. For the general data (aggregate primary and secondary data), we did a sample-based rarefaction curve (Mao Tau procedure) using the frequency of occurrence of a species as a sampling unit. The frequency of occurrence was calculated by dividing the number of locations in which each species was recorded by the total number of locations used in the study (seven). Species richness was estimated for each of the seven locations using the non-parametric Chao 2 estimator (with 1,000 bootstrapping).

We assessed the conservation status of species at a global level according to the IUCN Red List of Endangered Species (IUCN 2018). At the national level, we used the List of Brazilian Fauna Threatened of Extinction (ICMBio 2016).

To analyze the dissimilarities between the seven localities and evaluate possible nestedness or turnover processes involved in the community assembly, we calculated the beta diversity (BD) and its components: beta diversity nestedness ($BD_{nest)}$ and beta diversity turnover (BD_{turn}). This

Table 1. Localities with primary data about bat fauna sampled with mist nets at Guarapuava highlands, Paraná state, southern Brazil, from 2009 to 2015. BJR = Banks of the Jordão River; PMSFE = Parque Municipal São Francisco da Esperança; JBFC = Jardim Botânico de Faxinal do Céu.

	BJR	PMSFE	JBFC
Coordinates	25º39’21”S, 51º57’49”W	25º03’48”S, 51º17’37”W	25º55’01”S, 51º35’47”W
Altitude (m)	757	1,052	1,162
Year of sampling	2009	2014–2015	2014–2015
Sampling nights	10	25	25
Number of mist nets per night	6 to 12	20	20
Number of canopy mist nets per night	-	5 (54.000 m².h)	5 (54.000 m².h)
Sampling effort	13.736m².h	162.000 m².h	162.000 m².h
Vegetation characteristics	Secondary Forest and disturbed grasslands	Secondary and Primary Forest	Secondary Forest and altered areas (grasslands with exotic tree collection)

analysis was done using the Sorensen dissimilarity index and the Baselga (2010) approach with the R package *betapart* (Baselga *et al.* 2017). To represent the pattern of BD found between the localities, we performed a cluster analysis based on Sorensen dissimilarity index using unweighted pair-group method with arithmetic mean (UPGMA). To confirm this cluster result, we performed a cophenetic distance analysis. These analyses were performed using R 3.3.1 (R Core Team 2016) and the packages *spaa* (Zhang 2016) and *vegan* (Oksanen *et al.* 2017).

RESULTS

Adding all studies together (primary and secondary data), a total of 28 species, 15 genera and three families were recorded for Guarapuava highlands. Vespertilionidae was the richest family (14 species), followed by Phyllostomidae (10 species) and Molossidae (4 species; Table 2). The sample rarefaction curve (Mao Tau) of the general data did not stabilize (Figure 2A). The Chao 2 analyzes estimated 35.8 ± 6.4 (mean ± S.D.) species, suggesting that these studies registered about 78% of the estimated species richness of the region. The primary data included eight new occurrences for the region: *Anoura caudifer*, *Macrophyllum macrophyllum*, *Carollia perspicillata*, *Sturnira tildae*, *Lasiurus cinereus*, *Lasiurus ega*, *Myotis albescens* and *Molossus rufus* (Table 2). Among the recorded species, six were present in most of the localities (> 70% of frequency of occurrence) and can be considered as being common for Guarapuava highlands (Table 2).

In the PMSFE, there were a total of 117 captures of 14 species, while there were 82 captures of 14 species in the JBFC, and 29 captures and six species at BJR. The most abundant species of the three localities was *Sturnira lilium*, and the second most abundant was *C. perspicillata* at PMSFE, *Myotis izecksohni* at JBFC and *Desmodus rotundus* at BJR (Table 2). The rarefaction curves did not stabilize, only the curve for BJR showed a slight tendency to stabilize at the end of the samplings (Figure 2B, C, D).

Regarding the global conservation status, *Myotis ruber* is considered “Near Threatened”, while *Eptesicus taddeii*, *Histiotus velatus* and *M. izecksohni* are “Data Deficient” (IUCN 2018). Based on the Brazilian red list, *E. taddeii* is considered “Vulnerable” and *M. izecksohni* is “Data Deficient” (ICMBio 2016). All other species are classified as “Least Concern” in both lists of species conservation status (ICMBio 2016, IUCN 2018).

In the regional analysis of bat fauna, the localities presented an average BD of 0.72, BD_{turn} of 0.64 and BD_{nest} of 0.08. In the cluster plot, there are two groups with more than 50% of similarity (Figure 3) confirmed by cophenetic distance analysis (0.91). The first group is formed by the areas with larger sampling efforts and with these efforts directed only toward bats: PMNA, JBFC and PMSFE. The

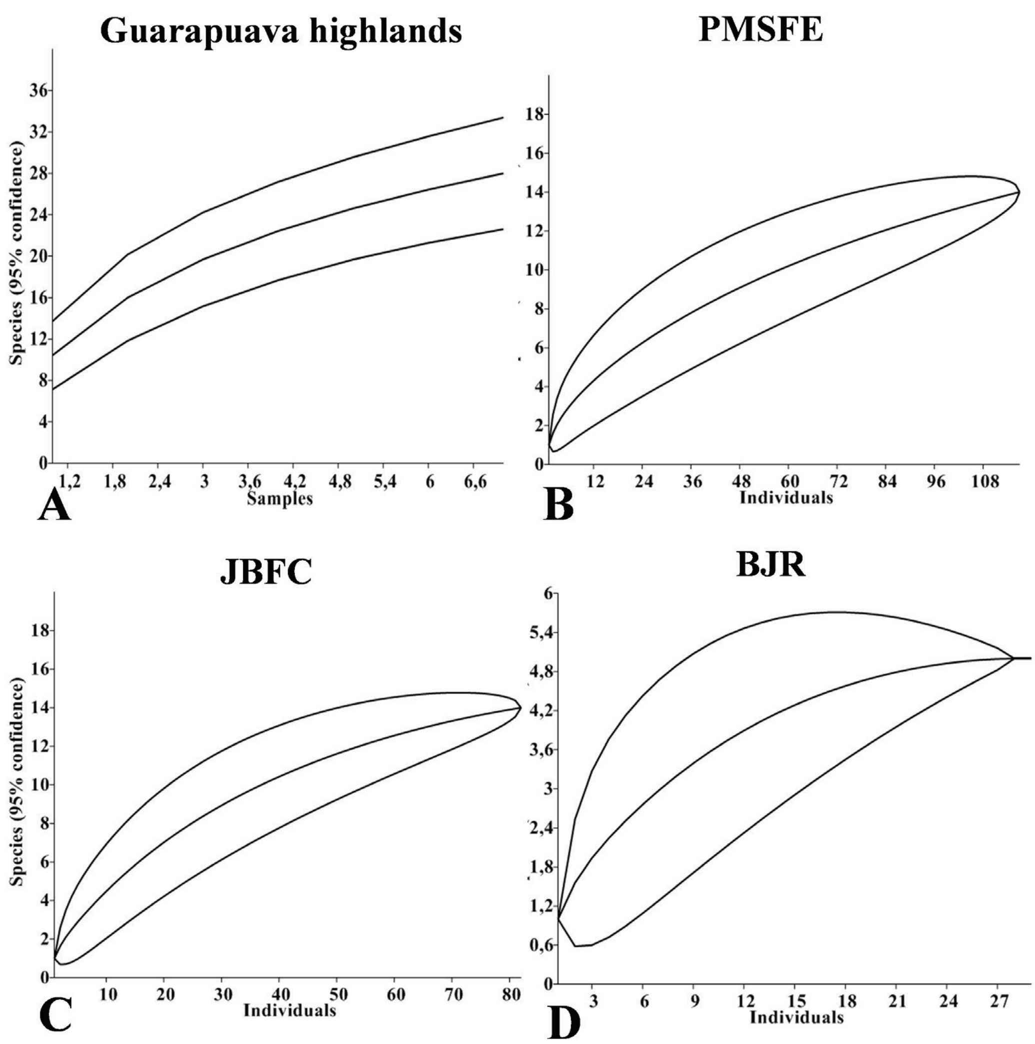

Figure 2. Rarefaction curves of bats species to primary and overall data in Guarapuava highlands region, Paraná, southern Brazil. (A) Sample rarefaction (Mao Tau) of overall studies (primary and secondary data); (B) Individual rarefaction curve from Parque Municipal São Francisco da Esperança (PMSFE); (C) Individual rarefaction curve from Jardim Botânico Faxinal do Céu (JBFC); (D) Individual rarefaction curve from Banks of Jordão River (BJR).

other group clustered the areas with smaller sampling efforts (BJR and PAL) and the areas with only museum and literature data compilation (RIFJ and GUA).

DISCUSSION

The species listed correspond to 71.8% of the already recorded bat fauna from Araucaria Pine Forest (Miretzki 2003, Miranda *et al.*2008, 2009, Marques *et al.* 2011), 28.6% of the Atlantic Forest (Muylaert *et al.* 2017) and 15.7% of Brazilian bat fauna (Nogueira *et al.* 2014). Differing from most studies in the Atlantic Forest, in which the family Phyllostomidae dominates the assemblages (*e.g.*, Bianconi *et al.* 2004, Esbérard *et al.*2006, Reis *et al.* 2006, Tavares *et al.* 2007, Carvalho *et al.* 2013), in our study, Vespertilionidae was the richest family. With increasing of altitude and latitude, there is a decrease in temperature and environmental productivity, leading to less complex ecosystems. Therefore, bat assemblages become simpler (*i.e.*, fewer species, ecological functions and evolutionary lineages) as altitude and latitude increases, until only aerial insectivorous bats persist (Patterson *et al.* 2007, Cisneros *et al.* 2014, Martins *et al.* 2015). In Neotropical biomes, altitudes above 2.000 m for Atlantic Forest (Martins *et al.* 2015) and above 2.500 m for Andean Amazonian (Cisneros *et al.* 20014), only aerial insectivorous bats were recorded. In

Table 2. Updated list of bat fauna from Guarapuava highlands, Paraná state, southern Brazil. Secondary data: RESI = Reserva do Iguaçu and Fóz do Jordão municipalities (Miretzki 2003); PAL = Palmas municipality (Miranda *et al.* 2008); GUA = Guarapuava municipality (Valle *et al.* 2011); PMNA = Parque Municipal Natural das Araucárias (Miranda & Zago 2015). Primary data of bats surveys with mist nets (2009–2015): PMSFE = Parque Municipal São Francisco da Esperança; JBFC = Jardim Botânico de Faxinal do Céu; BRJ = Banks of Jordão River. N = Number of captures. FO = Frequency of occurence.* = Species that represent new records for the region.

Taxa	Secondary Data (presence or absence)				Primary Data (Relative Abundance)			FO (%)
	RIFJ	PAL	GUA	PMNA	PMSFE (N = 123)	JBFC (N = 86)	BJR (N = 36)	
PHYLLOSTOMIDAE								
Anoura caudifer (É. Geoffroy, 1818)	-	-	-	-	1.6*	-	-	14.3
Chrotopterus auritus (Peters, 1856)	●	●	●	-	5.7	-	5.5	71.4
Macrophyllum macrophyllum (Schinz, 1821)	-	-	-	-	-	-	5.5*	14.3
Carollia perspicillata (Linnaeus, 1758)	-	-	-	-	17.9*	-	-	14.3
Artibeus fimbriatus Gray, 1838	-	-	-	●	0.8	-	-	28.6
Artibeus lituratus (Olfers, 1818)	●	-	●	-	2.4	-	-	42.8
Pygoderma bilabiatum (Wagner, 1843)	●	-	-	●	0.8	2.3	-	57.1
Sturnira lilium (É. Geoffroy, 1810)	●	●	●	●	59.3	61.6	63.8	100
Sturnira tildae de La Torre, 1966	-	-	-	-	0.8*	2.3*	-	28.6
Desmodus rotundus (É. Geoffroy, 1810)	●	●	●	-	3.2	1.2	16.7	85.7
VESPERTILIONIDAE								
Eptesicus brasiliensis (Desmarest, 1819)	●	-	●	-	-	-	-	28.6
Eptesicus diminutus Osgood, 1915	-	-	●	-	-	-	-	14.3
Eptesicus furinalis (d'Orbigny & Gervais, 1847)	-	●	-	●	0.8	5.8	2.8	71.4
Eptesicus taddeii Miranda *et al.*, 2006	-	-	-	●	0.8	3.5	-	42.8
Histiotus montanus (Philippi & Landbeck, 1861)	-	●	-	-	-	-	-	14.3
Histiotus velatus (I. Geoffroy, 1824)	●	-	●	●	3.2	4.6	-	71.4
Lasiurus blossevillii ([Lesson, 1826])	-	-	-	●	-	2.3	-	28.6
Lasiurus cinereus (Palisot de Beauvois, 1796)	-	-	-	-	0.8*	-	-	14.3

Table 2. Continued on next page…

Table 2. ...Continued

Taxa	Secondary Data (presence or absence)				Primary Data (Relative Abundance)			FO (%)
	RIFJ	PAL	GUA	PMNA	PMSFE (N = 123)	JBFC (N = 86)	BJR (N = 36)	
Lasiurus ega (Gervais, 1856)	-	-	-	-	-	1.2*	-	14.3
Myotis albescens (É. Geoffroy, 1806)	-	-	-	-	-	1.2*	-	14.3
Myotis levis (I. Geoffroy, 1824)	-	●	-	-	-	-	-	14.3
Myotis izecksohni Moratelli *et al.*, 2011	-	-	-	●	1.6	8.1	-	42.8
Myotis nigricans (Schinz, 1821)	●	●	●	-	-	-	-	42.8
Myotis ruber (É. Geoffroy, 1806)	●	●	-	●	-	1.2	5.5	71.4
MOLOSSIDAE								
Cynomops planirostris (Peters, 1866)	●	-	-	-	-	-	-	14.3
Molossus molossus (Pallas, 1766)	-	-	-	●	-	2.3	-	28.6
Molossus rufus É. Geoffroy, 1805	-	-	-	-	-	2.3*	-	14.3
Tadarida brasiliensis (I. Geoffroy, 1824)	●	●	●	-	-	-	-	42.8
Species richness	**11**	**9**	**9**	**10**	**14**	**14**	**6**	

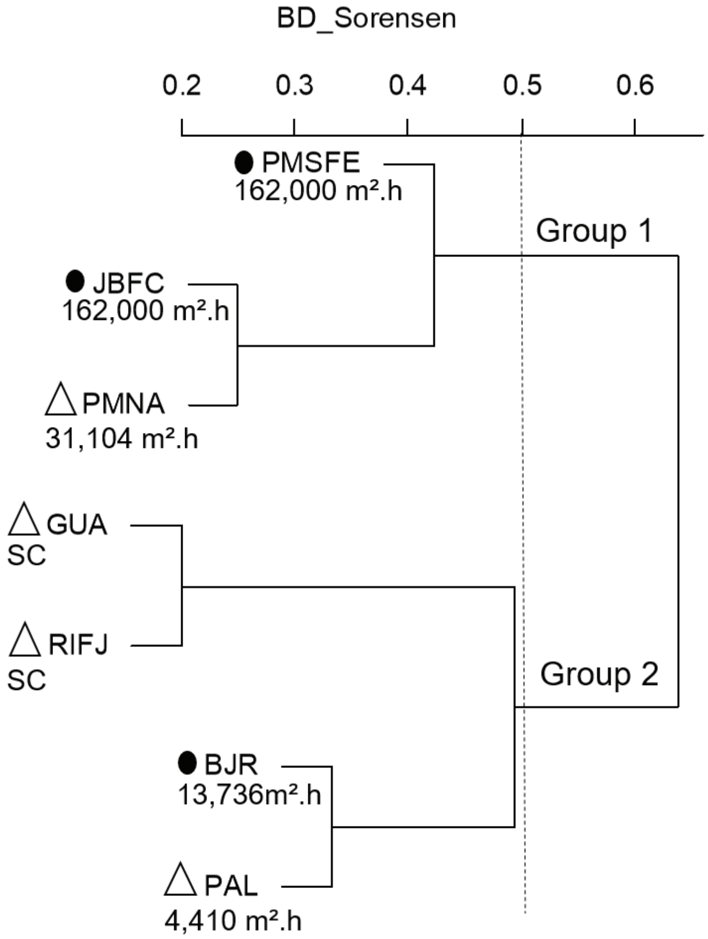

Figure 3. UPGMA (unweighted pair-group method using arithmetic averages) cluster analysis for beta diversity (BD) values among sampled bat fauna. Nodes that are to the left of the dashed line have values under 50% of dissimilarity, showing two groups. The sample effort is below the initials of each area. Primary data from 2009 to 2015 mist net samples are marked with black circles: PMSFE=Parque Municipal São Francisco da Esperança (Municipality of Guarapuava); JBFC=JardimBotânico Faxinal do Céu (Municipality of Pinhão); and BJR=Banks of the Jordão River (Municipality of Candói). Localities of secondary data are marked with white triangles: RIFJ=Reserva do Iguaçu and Fóz do Jordão municipalities (Miretzki 2003); PAL=Palmas municipality (Miranda *et al.* 2008), GUA=Guarapuava municipality (Valle *et al.* 2011); and PMNA=Parque Municipal Natural das Araucárias; Guarapuava municipality (Miranda & Zago 2015). SD = areas with only museum and literature data compilation

the same way, only aerial insectivorous bats are recorded above 30ºN or 35ºS (Patterson *et al.* 2007). The lower temperatures and declines in food supply of higher latitudes seems to be limitations to all New World bats distribution, except to Vespertilionidae, that are aerial insectivorous bats able to do long distance migrations and to hibernate (Zago 2017). The same pattern seems to occur at higher altitudes (Martins *et al.* 2015), thus, the predominance of aerial insectivorous species in the bat assemblages of the Guarapuava highlands may be a consequence of the subtropical and altitude characteristics of the region.

More than half of recorded species were aerial insectivores (Vespertilionidae and Molossidae). These bats tend to be rare in studies that used mist nets (Pedro & Taddei 1997, Kalko & Handley-Jr 2001). Thus, the nature of our records, with several rare species, resulted in the non-stabilization of the rarefaction curves. Therefore, the current list has a tendency to increase with additional bat surveys because, even for well-studied areas, such as the coast of Paraná state (Miretzki 2003), increases in sampling effort have resulted in new species records (*e.g.*, Scultori *et al.*2009, Carvalho *et al.* 2014, Rubio *et al.* 2014, Varzinczak *et al.* 2015).

Most of the species that were highly frequent in the present study were also considered abundant in other Araucaria Pine Forest bat surveys (*e.g.*, Reis *et al.* 2000, 2006, Arnone & Passos 2007, Zanon & Reis 2007, Miranda *et al.* 2009). On the other hand, some species, which were less frequent, have been captured close to their roosts, like *Histiotus montanus* (Miranda *et al.* 2006a, 2008), *Myotis levis* (Miranda *et al.* 2008, 2010), *Molossus molossus* (Miranda & Zago 2015) and *M. macrophyllum* (primary data), or only at canopy nets, like *A. caudifer*, *M. molossus* and *M. rufus* (primary data). These two alternative methods of survey (caught at roost and canopy netting), along with long-term inventories and acoustic monitoring, should be widely used in bat samplings (Simmons & Voss 1999, Sampaio *et al.* 2003, Bernardi *et al.* 2009). In the present study, the two richest areas were those with the greatest sampling effort, and with mist nets installed in the canopy, corroborating several studies that pointed out that this method increases the survey's power (*e.g.*, Bernard 2001, Carvalho *et al.* 2013).

Regarding the species classified as threatened, near threatened or data deficient, the four species presented medium to high frequencies in Guarapuava highlands. The scarce records of *E. taddeii* and *M. izecksohni* in previous studies may be attributed to misidentifications, as both species were recently described and are cryptic (with *Eptesicus brasiliensis* and *Myotis nigricans*, respectively; Miranda *et al.* 2006b, Moratelli *et al.* 2011). Furthermore, all species classified as threatened, near threatened or data deficient are aerial insectivore bats, which are known to be underestimated in studies carried out with mist nets. Therefore, it is possible that these species are underrepresented in the samples instead of being rare in the area (Velazco *et al.* 2011).

The average BD and its components, BD_{turn} and BD_{nest}, found among bat faunas in our regional scale was similar to that found in the overall Atlantic Forest, with the turnover component being lager than the nestedness component (Varzinczak *et al.* 2018). These results indicate that at both scales, the Guarapuava highlands region and the Atlantic forest biome, the bat community assembly is a result of species replacement (*i.e.*, species turnover) among communities instead of species loss. The latter occurs when poor species areas are subsets of richer areas, resulting in nested structure (Baselga 2010). Therefore, other structuring features, rather than environmental filtering, may be acting at both scales. However, the BD observed among the bat faunas analyzed herein may better reflect methodological and sampling biases than ecological gradients. Studies with larger and standardized sampling effort are necessary to confirm these patterns.

This work is the first approach at regional level (beta diversity) about bat diversity in Guarapuava highlands. However, in spite of this regional bat list update, the cluster analysis based on beta diversity approach have highlighted gaps in the surveys carried out in the region. Since species of the family Vespertilionidae are hardly catch using mist nets, multimethod samplings are especially important at the latitudes and altitudes of Guarapuava, where this family is the richest among bats. Taking that into account, we suggest caution when analyzing results from databases with incomplete or subsampled bat assemblages and pointed out that Guarapuava highlands may be a region where the ecology of vespertilionid species, especially those threatened or near threatened, must be investigated.

ACKNOWLEDGEMENTS

We thank Sara Emiliano Bandeira, Fernanda Almeida dos Santos, Bruno Fachin and Katrin Goede for the help in field work, and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the MSc. scholarship awarded to D.A.S.B.

REFERENCES

Arnone, I. S., & Passos, F. C. 2007. Estrutura de comunidade da quiropterofauna (Mammalia, Chiroptera) do Parque Estadual de Campinhos, Paraná, Brasil. Revista Brasileira de Zoologia, 24(3), 73–581. DOI: 10.1590/S0101-81752007000300008

Barquez, R. M., Mares, M. A., & Braun, J. K. 1999. The bats of Argentina. Special Publications of the Museum of Texas Tech University, 42, 1–275.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19, 134–143.

Baselga, A., Orme, D., Villeger, S., Bortoli, J., & Leprieur, F. 2017. betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.4. https://cran.r-project.org/web/packages/betapart/betapart.pdf

Bernard, E. 2001. Vertical stratification of bat communities in primary forests of central Amazon, Brazil. Journal of Tropical Ecology, 17(1), 115–126. DOI: 10.1017/S0266467401001079

Bernard, E., Aguiar, L. M. S., & Machado, R. B. 2010. Discovering the Brazilian bat fauna: a task for two centuries? Mammal Review, 41(1), 23–39. DOI: 10.1111/j.1365-2907.2010.00164.x

Bernardi, I. P., Miranda, J. M. D., Sponchiado, J., Grotto, E., Jacomassa, F. F., Teixeira, E. M., Roani, S. H., & Passos, F. C. 2009. Morcegos de Frederico Westphalen, Rio Grande do Sul, Brasil (Mammalia: Chiroptera): Riqueza e utilização de abrigos. Biota Neotropica, 9(3), 349–354. DOI: 10.1590/S1676 06032009000300029

Bianconi, G. V., Mikich, S. B., & Pedro, W. A. 2004. Diversidade de morcegos (Mammalia, Chiroptera) em remanescentes florestais do município de Fênix, Noroeste do Paraná, Brasil. Revista Brasileira de Zoologia, 21(4), 943–954. DOI: 101590/S0101-81752004000400032

Carvalho, F., Fabián, M. E., & Menegheti, J. O. 2013. Vertical structure of an assemblage of bats (Mammalia: Chiroptera) in a fragment of Atlantic Forest in Southern Brazil. Zoologia, 30(5), 491–498. DOI: 10.1590/S1984–46702013000500004

Carvalho F., Mottin, V., Miranda, J. M. D., & Passos, F. C. 2014. First record of *Vampyrodes caraccioli* (Thomas, 1889) (Chiroptera, Phyllostomidae) for the state of Paraná, and range extension to southern region of Brazil. Check List, 10(5), 1189–1194. DOI: 10.15560/10.5.1189

Cisneros, L. M., Burgio, K. R., Dreiss, L. M., Klingbeil, B. T., Patterson, B. D., Presley, S. J., & Willig, M. R. 2014. Multiple dimensions of bat biodiversity along an extensive tropical elevational gradient. Journal of Animal Ecology, 83, 1124–1136. DOI: 10.1111/1365-2656.12201

Esbérard, C. E. L., Jordão–Nogueira, T., Luz, J. L., Melo, G. G. S., Mangolin, R., Jucá, N., Raíces, D. S. L., Enrici, M. C., & Bergallo, H. 2006. Morcegos da Ilha Grande, Angra dos Reis, RJ, Sudeste do Brasil. Revista Brasileira de Zoociências, 8(2), 147–153.

Fleming, T. H., Hooper, E. T., & Wilson, D. E. 1972. Three Central American bat communities: Structure, reproductive cycles and movement patterns. Ecology, 53(4), 555–569. DOI: 10.2307/1934771

Gardner, A. L. 2008. Mammals of South America, vol. 1,marsupials, xenarthrans, shrews, and bats. Chicago: The University of Chicago Press: p.669.

ICMBio – Intituto Chico Mendes de Conservação da Biodiversidade. 2016. Livro vermelho da fauna brasileira ameaçada de extinção. Brasília: ICMBio: p. 76.

IUCN. 2018. The IUCN Red List of Threatened Species. Version 2014.3. Retrieved on December 1st, 2018, from www.iucnredlist.org

Kalko, E. K. V., & Handley Jr, C. O. 2001. Neotropical bats in the canopy: diversity, community structure, and implications for conservation. Plant Ecology, 153, 319–333.

Kunz, T. H., & Pierson, E. D. 1994. Bats of the world: an introduction. In: R. M. Nowak (Ed.), Walker's bats of the world. pp. 1–46. Baltimore and London: Johns Hopkins University Press.

Maack, R. 2012. Geografia física do estado do Paraná. 4th. Ed. Ponta Grossa: Editora da UEPG: p. 526.

Marques, R. V., Cademartori, C. V., & Pacheco, S. M. 2011. Mastofauna no Planalto das Araucárias, Rio Grande do Sul, Brasil. Revista Brasileira de Biociências, 9(3), 278–288.

Martins, M. A., Carvalho, W. D., Dias, D., França, D. S., Oliveira, M. B., & Peracchi, A. L. 2015. Bat species richness (Mammalia, Chiroptera) along na elevational gradiet in the Atlantic Forest of Southeastern Brazil. Acta Chiropterologica, 17(2), 401–409. DOI: 10.3161/15081109ACC2015.17.2.2016

Miranda, J. M. D., Pulchério-Leite, A., Moro–Rios, R. F., & Passos, F. C. 2006a. Primeiro registro de *Histiotus montanus* (Phillippi & Landbeck) para o Estado do Paraná, Brasil (Chiroptera, Vespertilionidae). Revista Brasileira de

Zoologia, 23(2), 584–587. DOI: 10.1590/S0101-81752006000200035

Miranda, J. M. D., Bernardi, I. P., & Passos, F. C. 2006b. A new species of *Eptesicus* (Mammalia: Chiroptera: Vespertilionidae) from Atlantic Forest of Brazil. Zootaxa, 1383(1), 57–68. DOI: 10.11646/zootaxa.1383.1.4

Miranda, J. M. D., Moro–Rios, R. F., & Passos, F. C. 2008. Contribuição ao conhecimento dos mamíferos dos Campos de Palmas, Paraná, Brasil. Biotemas, 21(2), 97–103.

Miranda, J. M. D., Moro–Rios, R. F., Silva–Pereira, J. E., & Passos, F. C. 2009. Mamíferos da Serra de São Luiz do Purunã. Pelotas: USEB: p. 263.

Miranda, J. M. D., Kaku–Oliveira, N. Y., Munster, L. C., Bernardi, I. P., Moro–Rios, R. F., & Passos, F. C. 2010. Primeiros dados de uma colônia reprodutiva de *Myotis levis* (I. Geoffroy, 1824) nos campos de Palmas, Paraná, Brasil (Vespertilionidae). Chiroptera Neotropical, 16(2), 726–768.

Miranda, J. M. D., Bernardi, I. P., & Passos, F. C. 2011. Chave ilustrada para a determinação de morcegos da região sul do Brasil. Curitiba: João M.D. Miranda: p. 56.

Miranda, J. M. D., & Zago, L. 2015. Assembleia de morcegos em remanescente de Floresta Ombrófila Mista no Planalto de Guarapuava, Paraná, Brasil. Mastozoología Neotropical, 22(1), 55–62.

Miretzki, M. 2003. Morcegos do Estado do Paraná, Brasil (Mammalia, Chiroptera): riqueza de espécies, distribuição e síntese do conhecimento atual. Papéis Avulsos de Zoologia, 43(6), 101–138.

Moras, L. M., Bernard, E., & Gregorin, R. 2013. Bat assemblage at a high–altitude area in the Atlantic Forest of southeastern Brazil. Mastozoología Neotropical, 20(2), 269–278.

Moratelli, R., Peracchi, A. L., Dias, D., & Oliveira, J. A. 2011. Geographic variation in South American populations of *Myotis nigricans* (Schinz, 1821)(Chiroptera, Vespertilionidae), with the description of two new species. Mammalian Biology, 76(1), 592–607. DOI: 10.1016/j.mambio.2011.01.003

Muylaert, R. D. L., Stevens, R. D., Esbérard, C. E., Mello, M. A., Garbino, G. S., Varzinczak, L. H., Faria, D., Weber, M. M., Rogeri, P. K., Regolin, A. L., Oliveira, H. F. M., Costa, L. M., Barros, M. A. S., Sabino-Santos Jr., G., Marais, M. A. C., Kavagutti, V. S., Passos, F. C., Marjakangas, E., Maia, F. G. M., Ribeiro, M. C., & Galetti, M. 2017. Atlantic bats: A data set of bat communities from the Atlantic Forests of South America. Ecology, 98(12), 3227–3227. DOI: 10.1002/ecy.2007

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B., & Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature, 403(1), 853–858. DOI: 10.1038/35002501

Nobre, P. H., Manhães, M. A., Bastos Neto, O. J., Rezende, A. C., & Rodrigues, A. S. 2013. Bat assemblages from mountain forest areas in the Serra Negra region, southeastern Brazil. Mastozoología Neotropical, 20(2), 279–287.

Nogueira, M., Lima, I. P., Moratelli, R., Tavares, V. C., Gregorin, R., & Peracchi, A. L. 2014. Checklist of Brazilian bats, with comments on original records. CheckList, 10(4), 808–821. DOI: 10.15560/10.4.808

Oksanen, F. J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, H., & Wagner, H. 2017. vegan: Community Ecology Package. R package version 2.4-2. Retrieved from: https://CRAN.R-project.org/package=vegan

Passos, F. C., Silva, W. R., Pedro, W. A., & Bonin, M. R. 2003. Frugivoria em morcegos (Mammalia, Chiroptera) no Parque Estadual Intervales, sudeste do Brasil. Revista Brasileira de Zoologia, 20(3), 511–517. DOI: 10.1590/S0101-8175

Patterson, B. D., Ceballos. G., Sechrest, W., Tognelli, M. F., Brooks, T., Luna, L., Ortega, P., Salazar, I., & Young, B. E. 2007. Digital distribution maps of the Mammals of the Western Hemisphere, version 3.0. Arlington: NatureServe.

Pedro, W. A., & Taddei, V. A. 1997. Taxonomic assemblage of bats from Panga Reserve, southeastern Brazil: abundance patterns and trophic relations in the Phyllostomidae (Chiroptera). Boletim do Museu de Biologia Mello Leitão, 6, 3–21.

Person, V. G., & Lorini, M. L. 1990. Contribuição ao conhecimento mastofaunístico da porção centro-sul do Estado do Paraná. Acta Biologica Leopoldensia, 2, 277–282.

R Core Team 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna. Retrieved from https://www.R-project.org/

Reis, N. R., Peracchi, A. L., Sekiama, M. L., & Lima, I. P. 2000. Diversidade de morcegos (Chiroptera; Mammalia) em fragmentos florestais no estado do Paraná, Brasil. Revista Brasileira de Zoologia, 17(3), 697–704. DOI: 10.1590/S0101-81752000000300015

Reis, N. R., Peracchi, A. L., Lima, I. P., & Pedro, W. A. 2006. Riqueza de morcegos (Mammalia; Chiroptera) em diferentes habitats, na região centro–sul do Paraná, sul do Brasil. Revista Brasileira de Zoologia, 23(3), 813–816. DOI: 10.1590/S0101-81752006000300028

Rubio, M. B. G., Varzinczak, L. H., Bernardi, I. P., Passos, F. C., & Miranda, J. M. D. 2014. Bats from two sites of the Paraná State coastal area, southern Brazil. Chiroptera Neotropical, 20(1), 1255–1263.

Sampaio, E. M., Kalko, E. K. V., Bernard, E., Rodríguez–Herrera, B., & Handley, C. O. 2003. A biodiversity assessment of bats (Chiroptera) in a tropical lowland rainforest of Central Amazonia, including methodological and conservation considerations. Studies on Neotropical Fauna and Environment, 38(1), 17–31.

Santos, L. J. C., Oka-Fiori, C., Canali, N. E., Fiori, A. P., Silveira, C. T., Silva, J. M. F., & Ross, J. L. S. 2006. Mapeamento geomorfológico do Estado do Paraná. Revista Brasileira de Geomorfologia, 7(2), 3–12. DOI: 10.20502/rbg.v7i2.74

Scultori, C., Dias, D., & Peracchi, A. L. 2009. Mammalia, Chiroptera, Phyllostomidae, *Lampronycteris brachyotis* (Dobson, 1879): First record in the state of Paraná, southern Brazil. Check List, 5(4), 872–875. DOI: 10.15560/5.4.872

Simmons, N. B., & Voss, R. S. 1999. The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna. Part I: Bats. Bulletin of the American Museum of Natural History, 237(1), 1–219.

Tavares, V. C., Perini, F. A., & Lombardi, J. A. 2007. The bat communities (Chiroptera) of the Parque Estadual do Rio Doce, a large remnant of Atlantic Forest in southeastern Brazil. Revista Lundiana, 8(1), 35–47.

Valle, L. G. E., Vogel, H. F., Sugayama, B. M., Metri, R., Gazarini, J., & Zawadski, C. H. 2011. Mamíferos de Guarapuava, Paraná, Brasil. Revista Brasileira de Zoociências, 13(1,2,3), 151–162.

Varzinczak, L. H., Bernardi, I. P., & Passos, F. C. 2015. Is the knowledge of bat distribution in the Atlantic Rainforest sufficient? Comments about new findings and a case study in the Paraná State coastal area, Brazil. Mammalia, 79(5), 1–7. DOI: 10.1515/mammalia-2014-0130

Varzinczak, L. H., Moura, M. O., Lima, C. S., & Passos, F. C. 2018. How do bat, rodent, and marsupial communities respond to spatial and environmental gradients? Insights from a deconstruction of mammal beta diversity from Atlantic Forest of South America. Oecologia. DOI: 10.1007/s00442-018-4288-y

Velazco, P. M., Pacheco, V., & Meschede, A. 2011. First occurrence of the rare emballonurid bat *Cyttarops alecto* (Thomas, 1913) in Peru - only hard to find or truly rare? Mammalian Biology, 76(1), 373–376.

Zago, L. 2017. Padrões espaciais na biodiversidade de morcegos do Novo Mundo. Doctoral thesis, Setor de Ciências Biológicas da Universidade Federal do Paraná. p. 63.

Zanon, C. M. V., & Reis, N. R. 2007. Bats (Mammalia; Chiroptera) in the Ponta Grossa region, Campos Gerais, Paraná Brazil. Revista Brasileira de Zoologia, 24(2), 327–332. DOI: 10.1590/S0101-81752007000200010

Zhang, J. 2016. spaa: SPecies Association Analysis. R package version 0.2.2. Retrieved from https://CRAN.R-project.org/package=spaa

Submitted: 05 September 2018
Accepted: 03 June 2019
Published online: 06 June 2019
Associate Editor: Rosana Gentile

Appendix I. Collection numbers of specimens of bats from Guarapuava highlands, Paraná state, southern Brazil, from 2009 to 2015, per locality deposited in the mammal collection of the Federal University of Paraná (DZUP – acronym):

Parque Municipal São Francisco da Esperança (Guarapuava municipality, Paraná state, Brazil): *Anoura caudifer:* 2073; *Artibeus fimbriatus*:2083; *Artibeus lituratus*:2058, 2080; *Carollia perspicillata*: 2063, 2066; *Chrotopterus auritus*: 2065, 2067; *Desmodus rotundus*: 2077, 2078; *Eptesicus furinalis*: 2075; *Eptesicus taddeii*: 2076; *Histiotus velatus*: 2057, 2061; *Lasiurus cinereus*: 2079; *Myotis izecksohni*: 2069; *Pygoderma bilabiatum*: 2064; *Sturnira lilium*: 2055, 2056; *Sturnira tildae*: 2086.

Jardim Botânico Faxinal do Céu (Pinhão municipality, Paraná state, Brazil): *Desmodus rotundus*: 2123; *Eptesicus furinalis*: 2110, 2117; *Eptesicus taddeii*: 2108, 2111; *Histiotus velatus*: 2109, 2115; *Lasiurus blossevillii*: 2128, 2129; *Lasiurus ega*: 2130; *Molossus molossus*: 2107; *Molossus rufus*: 2120, 2126; *Myotis albescens*: 2122; *Myotis izecksohni*: 2113, 2114; *Myotis ruber*: 2112; *Pygoderma bilabiatum*: 2121, 2124; *Sturnira lilium*: 2102, 2103; *Sturnira tildae*: 2133, 2134.

Banks of Jordão River (Candói municipality, Paraná state, Brazil): *Chrotopterus auritus*: 1287, 1288; *Desmodus rotundus*: 1340, 1341; *Eptesicus furinalis*: 1291; *Macrophyllum macrophyllum*: 1327, 1328; *Myotis ruber*: 1289, 1290; *Sturnira lilium*: 1292, 1335.