

Bat diversity in three roosts in the Coast region of Oaxaca, México

Diversidade de morcegos em três abrigos na região costeira de Oaxaca, México

Itandehui Hernández-Aguilar¹, Antonio Santos-Moreno¹

¹ *Laboratorio de Ecología Animal. Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Oaxaca. Instituto Politécnico Nacional. Calle Hornos No. 1003, Col. La Noche Buena, Santa Cruz Xoxocotlán, Código Postal 71230, Oaxaca, México*

Corresponding author: Antonio Santos-Moreno (asantosm90@hotmail.com)

Academic editor: A. M. Leal-Zanchet | Received 15 January 2020 | Accepted 31 March 2020 | Published 29 May 2020

Citation: Hernández-Aguilar I, Santos-Moreno A (2020) Bat diversity in three roosts in the Coast region of Oaxaca, México. *Neotropical Biology and Conservation* 15(2): 135–152. <https://doi.org/10.3897/neotropical.15.e50136>

Abstract

In this paper, we analyze the richness, abundance, diversity and trophic guilds in a mine (La Mina) and two caves (El Apanguito and Cerro Huatulco) in the municipalities of Pluma Hidalgo and Santa María Huatulco, in the state of Oaxaca, México, a state with high species richness of bats nationwide. Fieldwork was conducted from July 2016 to June 2017. Using a harp trap, we captured 5,836 bats belonging to 14 species, 10 genera and five families. The greatest species richness was found in Cerro Huatulco (12 species), followed by La Mina (nine species) and El Apanguito (four species). Overall, the most abundant species were *Pteronotus fulvus* (40.59% of captures) and *Pteronotus mesoamericanus* (32.01%). Half of the species captured corresponded to the insectivore trophic guild. Results show that the three roosts, but particularly Cerro Huatulco and El Apanguito, maintain high species richness and abundances of individuals due to processes that favor colonies of thousands of individuals. We therefore argue that they represent priority roosts for the conservation of bats in the State of Oaxaca.

Resumo

Neste artigo, analisamos a riqueza, abundância, diversidade e associações tróficas em uma mina (La Mina) e duas cavernas (El Apanguito e Cerro Huatulco) nos municípios de Pluma Hidalgo e Santa María Huatulco, no estado de Oaxaca, México, um estado com alta riqueza de espécies de morcegos

em todo o país. O trabalho de campo foi realizado de julho de 2016 a junho de 2017. Utilizando uma armadilha de harpa, capturamos 5,836 morcegos pertencentes a 14 espécies, 10 gêneros e 5 famílias. A maior riqueza de espécies foi encontrada em Cerro Huatulco (12 espécies), seguida por La Mina (nove espécies) e El Apanguito (quatro espécies). No geral, as espécies mais abundantes foram *Pteronotus fulvus* (40,59% das capturas) e *Pteronotus mesoamericanus* (32,01%). Metade das espécies capturadas correspondia à guilda trófica de insetívoros. Os resultados mostram que os três abrigos, principalmente Cerro Huatulco e El Apanguito, mantêm alta riqueza de espécies e abundância de indivíduos devido a processos que favorecem colônias de milhares de indivíduos. Argumentamos, portanto, que eles representam focos prioritários para a conservação de morcegos no Estado de Oaxaca.

Keywords

Cave, Chiroptera, species richness, true diversity

Palavras-chave

Caverna, Chiroptera, verdadeira diversidade, riqueza de espécies

Introduction

Bats constitute one of the most important and crucial groups for tropical ecosystems (Arita 1993; Sánchez-Cordero 2001) due to the wide diversity of functions they perform, including seed dispersal, regulation of insect populations and pollination (Patterson et al. 2003; MacSwiney 2010). Estimates indicate that bats disperse 2–8 times more seeds than birds in tropical regions and, in lowland forests, bats disperse between 80% and 100% of the seeds that reach the ground during the dry season (MacSwiney 2010). Regarding regulation of insect populations, some bats consume between 50% to 150% of their body weight every night, whereas estimates suggest that at least 500 plant species of 96 genera are pollinated by bats (Patterson et al. 2003; MacSwiney 2010).

Roosts are important in the ecology and evolution of bat populations, since these organisms spend over half their lives in them (Kunz 1982; De Paz et al. 1990). Bats roost in a wide variety of natural sites like caves, crevasses, rocks, stalks, roots, tree cavities, and foliage which they use to build tents (Aguirre et al. 2003; Kunz and Lumsden 2003). They also use artificial structures like abandoned mines and houses, bridges and sewers (Kunz 1982; Nowak 1999; Ávila-Flores and Medellín 2004). Of all these, caves are among the most important for bats because they offer them advantageous characteristics such as low light conditions, humidity, relatively constant temperatures, a relatively stable flow of air, and often a complex structure that provides bats with a diversity of microhabitats and abundant perching sites. This is particularly relevant during their reproductive stage, which explains why caves can host a considerable diversity of species with colonies of up to thousands of individuals (Arita 1993; Watson et al. 1997; Trajano and Giménez 1998). The importance of caves is evidenced by the fact that ca. 50% of the species distributed in México use this type of environment throughout the year or seasonally, that is, the size of the colonies, the composition of species, the sex ratio, the reproductive con-

dition, age structure and perching sites may vary over time (Glover and Altringham 2008; Humphrey and Oli 2015). By sharing many of the characteristics of caves, inactive mines can also serve as roosting sites and, in the face of increasing habitat loss, they represent potential and alternative roosts for many bat species (Altenbach 1998; López-González 2005).

México is one of the countries with the highest biodiversity of bats in the world (136 species) (Ceballos and Arroyo-Cabrales 2012), and Oaxaca with 93 species, is a hotspot of species richness in the country (Santos-Moreno 2014). The hypothesis of the present study was that the richness, abundance and diversity in the sites studied varies throughout the year. Therefore, this study presents the results of species richness, abundance and diversity in three refuges that allows identifying and declaring Priority Sites for the Protection and Conservation of Bats in the state of Oaxaca and that will help in the conservation of bat roosts. Although there has been significant progress in our knowledge of the bat diversity of Oaxaca (Sánchez-Cordero 2001; Briones-Salas et al. 2004; Lira-Torres et al. 2008; Barragán et al. 2010; Santos-Moreno et al. 2010; Buenrostro-Silva et al. 2013; Calderón-Patrón et al. 2013; Kraker-Castañeda et al. 2013; García-García and Santos-Moreno 2014), there are still many areas which need to be studied before having a reasonable overview of the distribution of bat species in the State (García-García et al. 2006). But only two mammal inventories were conducted, one in the bay and basin of the Cacaluta river in Santa María Huatulco (Lira-Torres et al. 2008), and other in shaded coffee plantations associated to the Copalita River basin, in the municipalities of Candelaria Loxicha, Pluma Hidalgo, San Mateo Piñas and Santa María Huatulco (Palacios-Romo et al. 2012). So far, there are no studies of bats in caves in the municipalities of Pluma Hidalgo and Santa María Huatulco. In this study we describe the species richness, abundance, diversity and trophic guilds present in three roosts used by bats in these municipalities in Oaxaca, México.

Methods

Study site

The study was conducted in three roosts found in the coastal region of the state of Oaxaca, México. The first corresponds to the tunnel of a mine (henceforth La Mina, located at 15°54'52"N, 96°24'59"W and an altitude of 1,110 masl) in the municipality of Pluma Hidalgo, and the other two are caves in Santa María Huatulco (Fig. 1): El Apanguito (15°51'58"N, 96°21'13.2"W and 695 masl) and Cerro Huatulco (15°50'59"N, 96°21'04.3"W and 475 masl). The climate in the study area is warm and subhumid with rain in the summer (Aw_1 according to the Köppen's system modified by García (1988)) and temperature in the roosts fluctuates from 20 to 26 °C. The dominant vegetation-type is tropical deciduous forest which forms three vertical stratum with a notable presence of bejuco-vines and epiphytes. The highest stratum is composed by trees 20–30 m high like *Manilkara chicle* and *Brosium alicastrum*;

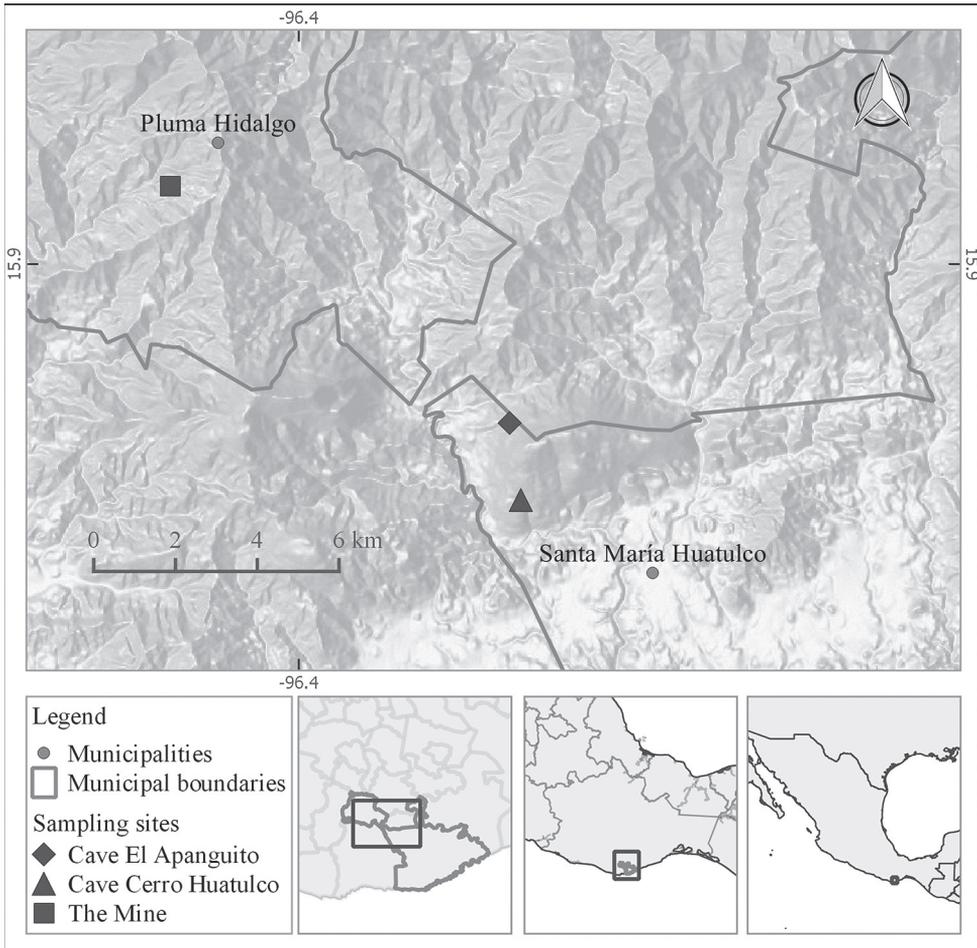


Figure 1. Location of the municipalities of Pluma Hidalgo and Santa María Huatulco, Oaxaca, México.

the mid-stratum has trees 10–15 m high with species like *Cupania dentata*, *Heliocarpus appendiculatus*, *Pseudobombax ellipticum*, *Cordia allidora*; and the lower stratum goes from ground level to 4 to 8 meters, and is represented by *Crataeva tapia*, *Exostema mexicanum*, *Louteridium donnell-smithii*, *Pouteria durlandii* and *Ficus maxima* (Rzedowski 1994; Torres-Colín 2004). The region is widely used to produce shaded coffee using a rustic management system where the canopy of the forest is used as shade for the coffee plants (Trejo 2004; OEIDRUS 2005).

Field work. – We conducted monthly sampling throughout 12 months from July 2016 to June 2017 including a dry (October–April) and rainy (May–September) season. Each month, we sampled each roost for two nights, bats were captured with a harp trap model G5 (Bat Conservation and Management, Inc., Carlisle, PA, EE. UU.) 1.5 m wide by 2 m high, which was positioned at the only entrance of the roosts from 18:00 pm to 00:00 am and was inspected every 20 minutes. Bats were

identified based on morphological criteria (e.g. length of forearm, pelage coloration patterns, etc) according to identification keys Medellín et al. (1997, 2007) and Álvarez-Castañeda et al. (2015) and the recent bibliography of Pavan (2019), Solari et al (2019), Tejedor (2019) and Moratelli and Burgin (2019) was consulted for the taxonomic changes that have occurred after the publication of these works. Sex and age class (young or adult) were determined by the degree of phalanx ossification observed against the light (Anthony 1988). Once the mentioned information was recorded, each bat was released in the capture site.

Data analysis. – Sampling effort was calculated by multiplying the area of the trap by the number of nights and the number of hours it was open per night. The result was expressed in $m^2 \text{net} \cdot \text{hour}$. Sampling sufficiency in each site was evaluated from accumulation curves using the first order Jackknife non-parametric estimator, which performs well in terms of precision and accuracy and is recommended for mobile taxa such as bats (Brose et al. 2003). Data were randomized 1000 times using the EstimateS software, version 9.1.0 (Colwell 2013) to eliminate the effect of order. Alpha diversity was measured with respect to the effective number of species, i.e. the diversity of a community with a number of species with the same abundances (Jost 2006). We calculated the true diversity (qD) of orders 0, 1 and 2 (values of q) for each one of the roosts (Jost 2006). When q is equal to 0 (0D), it corresponds to the diversity expressed as the observed richness; when its value is 1 (1D) it represents the diversity expressed as the exponential of the classic Shannon index in which species are valued depending on their abundance; if $q = 2$ (2D), the most abundant species have a greater influence on the diversity value. We also calculated a true diversity unevenness index which indicates if abundances are homogeneous. Similarity between roosts was estimated with the Morisita-Horn index and was assessed visually on a dendrogram generated from a conglomerate analysis with the Unweighted Pair Group Method with Arithmetic Means (UPGMA). Data were analyzed in the PAST software version 3.16 (Hammer et al. 2001).

The community structure can also be analyzed through trophic guilds, size ranges and flight sites since it allows detection of overlapping sites of similar or closely related species that use a resource in a similar way, and subdivision by size-interval assume that the species that make up an interval allow coexistence and avoid competition (Schoener 1984; Medellín 1993). For the analysis, each species was classified in one of the categories recognized by McNab (1971), but dividing frugivores as *Piper* or *Ficus* specialists, following Medellín (1993). The trophic guilds considered were insectivorous, nectarivorous, hematofagous, frugivorous specialists in *Piper*, and frugivorous specialists in *Ficus*. These groups were subdivided in size-intervals based on forearm length following Medellín (1993). Intervals maintain a relationship of approximately 1.25 between each other, according to Hutchinson's quotient between 1.2 and 1.3. This indicates that the mean of each interval is 1.25 times larger than the mean of the previous one (Hutchinson 1959). To assign each species in an interval, we used the average length of the forearm. Overall, a species could be assigned to one of three size intervals: 35.5–44.4 mm (interval I), 44.5–55.5 mm

(interval II) and 55.6–69.5 (interval III). Information on forearm length and body mass was recorded from the individuals captured in the field and was used to calculate averages and standard deviations for each species. We constructed four contingency tables of trophic guild by size interval (based on forearm length): one for each roost and a fourth one combining the results from all sites. To know if the frequency distribution was uniform along the different combinations of guild and size-intervals, we used a Chi-squared test (χ^2) on the contingency tables. Total biomass was calculated from the average body-mass for each species multiplied by the number of individuals of each species recorded per roost throughout the sampling period and was expressed as a percentage (%).

Results

Sampling effort total was 1,242 m²net*hour throughout 69 effective sampling nights. At La Mina, sampling effort was 393 m²net*hour and in El Apanguito and Cerro Huatulco was 432 m²net*hour and 414 m²net*hour, respectively. We captured a total of 5,836 bats from 14 species, 10 genera and 5 families (Table 1). Overall, 50% of the species belonged to the family Phyllostomidae, 28.57% to Mormoopidae, and the Natalidae and Emballonuridae families were represented by a single species each

Table 1. Taxonomic listing, trophic guild, forearm length, abundance and biomass (%) for each of the species present in three roosts. TG: Trophic guild, INS: Insectivore, HEM: Sanguivore, NEC: Nectarivore, FFE: Frugivore, *Ficus* specialist, FPE: Frugivore, *Piper* specialist, AFL \pm SD: Average forearm length \pm Standard Deviation, Na: Abbreviated name of the species, TM: The Mine, CEA: Cave El Apanguito, CCH: Cave Cerro Huatulco. Biomass percentage is shown in parenthesis followed by the abundance.

Order Chiroptera	TG	AFL \pm SD	Na	TM	CEA	CCH	Total
Family Emballonuridae							
<i>Balantiopteryx plicata</i> Peters, 1867	INS	40.3 \pm 1.53	<i>Bp</i>	0	0	1 (0.08)	1
Family Mormoopidae							
<i>Mormoops megalophylla</i> (Peters, 1864)	INS	54.1 \pm 2.36	<i>Mm</i>	0	816 (22.42)	29 (5.01)	845
<i>Pteronotus fulvus</i> (Thomas, 1892)	INS	44.3 \pm 1.46	<i>Pf</i>	2 (0.16)	1,609 (19.50)	758 (57.77)	2,369
<i>Pteronotus mesoamericanus</i> J.D. Smith, 1972	INS	57.8 \pm 2.10	<i>Pm</i>	112 (25.48)	1,682 (56.75)	74 (15.70)	1,868
<i>Pteronotus psilotis</i> (Dobson, 1878)	INS	42.3 \pm 0.58	<i>Pp</i>	0	0	2 (0.18)	2
Family Phyllostomidae							
<i>Desmodus rotundus</i> (É. Geoffroy, 1810)	HEM	57.5 \pm 1.95	<i>Dr</i>	0	0	19 (6.30)	19
<i>Glossophaga soricina</i> (Pallas, 1766)	NEC	36.6 \pm 2.58	<i>Gs</i>	130 (18.30)	0	52 (6.73)	182
<i>Carollia perspicillata</i> (Linnaeus, 1758)	FPE	40.0 \pm 1.11	<i>Cp</i>	227 (41.83)	0	1 (0.17)	228
<i>Artibeus jamaicensis</i> Leach, 1821	FFE	56.6 \pm 1.72	<i>Aj</i>	0	0	17 (7.53)	17
<i>Artibeus toltecus</i> (Saussure, 1860)	FFE	39.9 \pm 1.59	<i>At</i>	75 (11.60)	0	1 (0.14)	76
<i>Artibeus watsoni</i> Thomas, 1901	FFE	38.5 \pm 0.71	<i>Aw</i>	7 (0.95)	0	0	7
<i>Sturnira hondurensis</i> Goodwin, 1924	FPE	41.8 \pm 3.20	<i>Sh</i>	7 (1.34)	0	1 (0.18)	8
Family Natalidae							
<i>Natalus mexicanus</i> Miller, 1902	INS	39.9 \pm 2.19	<i>Nm</i>	4 (0.18)	199 (1.33)	5 (0.21)	208
Family Vespertilionidae							
<i>Myotis pilosatibialis</i> LaVal, 1973	INS	35.5 \pm 0.71	<i>Mp</i>	6 (0.42)	0	0	6
Species				9	4	12	
Captured individuals				570	4,306	960	5,836

(7.14%). Of the total, 73.78% individuals (4,306) were captured in El Apanguito, 16.45% (960) in Cerro Huatulco and 9.77% (570) in La Mina (Table 2). Only in El Apanguito did the species accumulation curve reach an asymptote (Fig. 2a). At La Mina, the number of observed species was nine, which represents 90% of the estimated value, and in Cerro Huatulco we found 70.58% of the estimated value. Results for Cerro Huatulco indicate that, in order to record 95% of the estimated species (14), we would need 63.18 additional sampling visits (Fig. 2b, c).

The most abundant species were *Pteronotus fulvus* (40.59%), *P. mesoamericanus* (32.01%) and *Mormoops megalophylla* (14.48%), while *P. psilotis* and *Balantiopteryx plicata* were the least abundant with 0.03% and 0.02%, respectively. *Pteronotus mesoamericanus* remained as one of the three most abundant species in all three roosts, while *Natalus mexicanus* was one of the least abundant. *Pteronotus fulvus* was among the most abundant in both caves but in La Mina its presence was rare (Table 2). Order zero diversity indicated that Cerro Huatulco had the highest species richness (12), followed by La Mina (9) and lastly, El Apanguito (4). The highest order one diversity was observed in La Mina (4.48), which was 1.88 times more diverse than

Table 2. Monthly abundance of 14 bat species in three roosts in Pluma Hidalgo and Santa María Huatulco, Oaxaca, México.

Species	2016						2017						Total
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	
La Mina													
<i>Pteronotus fulvus</i>	0	0	0	0	0	0	1	0	2	0	0	0	2
<i>Pteronotus mesoamericanus</i>	2	10	41	14	16	8	15	1	0	5	0	0	112
<i>Glossophaga soricina</i>	0	0	11	10	27	6	7	11	19	39	0	0	130
<i>Carollia perspicillata</i>	23	17	32	11	25	8	10	20	5	69	0	7	227
<i>Artibeus toltecus</i>	15	4	8	3	14	2	2	3	15	4	0	5	75
<i>Artibeus watsoni</i>	0	2	0	0	3	0	0	1	1	0	0	0	7
<i>Sturnira hondurensis</i>	2	1	2	0	1	0	0	0	0	0	0	1	7
<i>Natalus mexicanus</i>	1	1	0	1	0	0	1	0	0	0	0	0	4
<i>Myotis pilosatibialis</i>	0	0	0	1	3	0	0	0	1	0	0	1	6
El Apanguito													
<i>Mormoops megalophylla</i>	0	14	12	66	143	99	133	155	159	35	0	0	816
<i>Pteronotus fulvus</i>	0	2	151	65	138	190	177	499	311	38	27	11	1,609
<i>Pteronotus mesoamericanus</i>	58	108	136	216	117	88	74	114	74	186	202	309	1,682
<i>Natalus mexicanus</i>	0	12	28	17	61	17	18	11	15	13	3	4	199
Cerro Huatulco													
<i>Balantiopteryx plicata</i>	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Mormoops megalophylla</i>	6	0	2	0	1	0	1	0	0	0	6	13	29
<i>Pteronotus fulvus</i>	6	81	70	37	167	78	23	110	100	68	8	10	758
<i>Pteronotus mesoamericanus</i>	12	6	9	12	1	1	0	3	4	1	17	8	74
<i>Pteronotus psilotis</i>	2	0	0	0	0	0	0	0	0	0	0	0	2
<i>Desmodus rotundus</i>	15	0	0	0	2	0	0	0	0	0	2	0	19
<i>Glossophaga soricina</i>	2	4	0	2	33	0	0	0	0	0	11	0	52
<i>Carollia perspicillata</i>	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Artibeus jamaicensis</i>	12	0	0	0	0	0	0	0	0	0	3	2	17
<i>Artibeus toltecus</i>	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Sturnira hondurensis</i>	0	0	0	0	0	0	0	0	0	0	1	0	1
<i>Natalus mexicanus</i>	0	0	0	1	0	0	0	1	3	0	0	0	5
Total	158	263	502	456	752	497	462	929	707	458	280	371	5,836

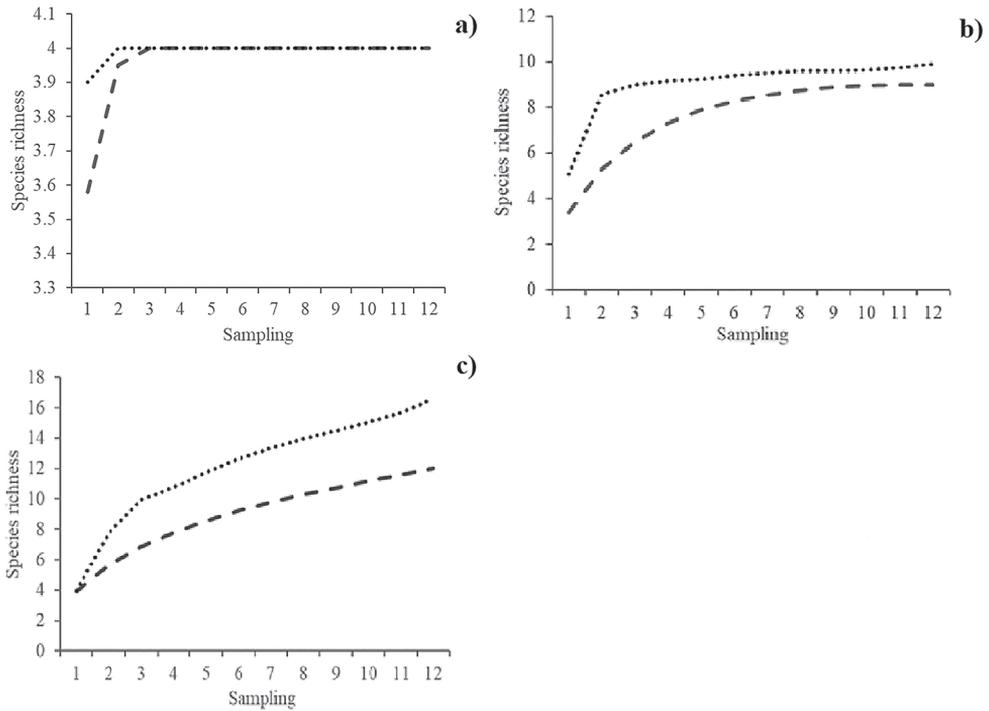


Figure 2. Species accumulation curves based on the Jackknife first-order non-parametric estimator for El Apanguito (a), La Mina (b) and Cerro Huatulco (c). Dashed lines indicate the accumulated average number of species (from randomizations) and the dotted lines show the number of species estimated by Jackknife 1.

Cerro Huatulco (2.37) and 1.36 times more diverse than El Apanguito (3.29). Order two diversity was also highest in La Mina (3.74) followed by El Apanguito (3.02), and the lowest value was for Cerro Huatulco (1.57). The highest unevenness value corresponded to Cerro Huatulco (7.61), indicating it is the roost with the highest dominance of certain species, mostly due to *P. fulvus* which was the most abundant (78.95% of the captured individuals). The second highest dominance value corresponded to La Mina (2.40), and the roost with the lowest value was El Apanguito (1.32). According to the Morisita-Horn index, the highest similarity was found between El Apanguito and Cerro Huatulco (0.68) (Fig. 3).

The 14 species recorded are grouped in five trophic guilds, insectivores represented by the highest number of species (7 species; 50%), followed by frugivores specialized in *Ficus* (3 species; 21.4%) and frugivores specialized in *Piper* (2 species; 14.2%). We only recorded one hematofagous and one nectarivorous species. The contingency table generated for the combination of trophic guild and size-interval was composed of 15 cells (5 trophic groups by three size intervals). The χ^2 test indicated that statistically, the distribution is uniform ($\chi^2 = 5.95$, $p = 0.652$) (Table 3). For La Mina, 88.9% of the species were of size I and the χ^2 test indicated there were

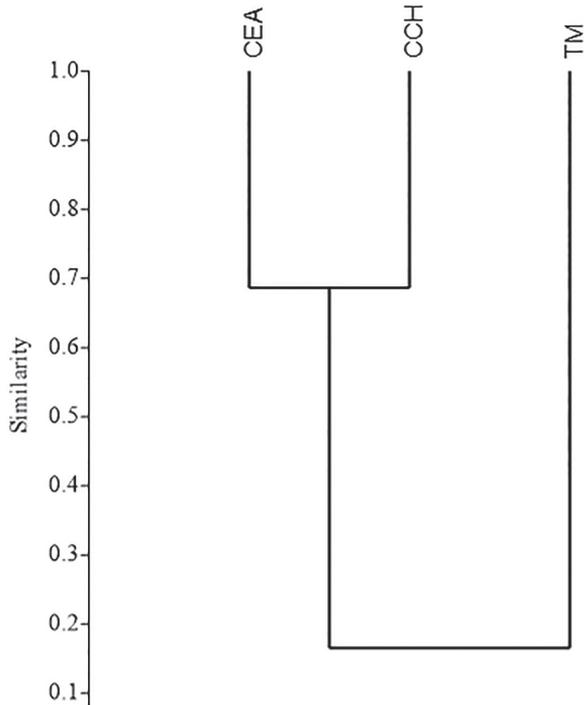


Figure 3. Similarity dendrogram (UPGMA method) based on the Morisita-Horn index for the species present in three roosts in Pluma Hidalgo and Santa María Huatulco, Oaxaca. Abbreviations: CEA = El Apanguito Cave, CCH = Cerro Huatulco Cave, TM = La Mina Mine

Table 3. Contingency table for trophic guild by size-interval for the species recorded in this study. Interval I: 33.5–44.4 mm, interval II: 44.5–55.5, interval III: 55.6–69.5 mm. Letters correspond to the initial letter of each species listed in Table 1.

Trophic guilds	I	II	III	Total
Frugivore <i>Ficus</i> specialist	At, Aw	0	Aj	3
Frugivore <i>Piper</i> specialist	Cp, Sh	0	0	2
Hematofagous	0	0	Dr	1
Insectivorous	Bp, Mp, Nm, Pf, Pp	Mm	Pm	7
Nectarivorous	Gs	0	0	1
Total	10	1	3	14

no significant differences ($\chi^2 = 1.40$, $p = 0.704$) between guild-size interval combinations. At Cerro Huatulco, 66.7% of the species corresponded to the size I interval and the χ^2 test again showed that the distribution is uniform across cells ($\chi^2 = 5.91$, $p = 0.656$). At El Apanguito, 50% of the species were size I insectivores (*N. mexicanus* and *P. fulvus*). The contingency test could not be done for this roost because only the insectivorous guild was present.

From the total biomass estimated, 89.07% corresponded to insectivores, followed by *Piper* specialists with 4.95% and hematofagous contributed the least to the

total biomass with 0.77%. At La Mina, 41.83% of the biomass was represented by *C. perspicillata*, a *Piper* specialist. At El Apanguito, most biomass corresponded to *P. mesoamericanus* and *M. megalophylla* with 56.75% and 22.42% respectively, while at Cerro Huatulco the highest values were for *P. fulvus* and *P. mesoamericanus* with 57.77% and 15.70%, respectively (Table 1).

Discussion

The 14 species of bats recorded in this study represent 15.05% of the known bat species for Oaxaca (Santos-Moreno 2014). With respect to the richness of species reported in some caves and mines-between 4–13 – of México (Arita 1993; Escalona-Segura et al. 2002; López-González 2005; Vásquez-Pérez et al. 2010; Torres-Flores et al. 2012), Central and South America (Honduras with 5 species, Cuba and Venezuela with 6 species, Bolivia with 7, Guatemala with 8, Colombia with 10 and Brazil with 21 species) (Muñoz-Saba et al. 2007; Siles et al. 2007; Divoll and Buck 2013; Cajas-Castillo et al. 2015; García et al. 2015; Pérez-Torres et al. 2015; Felix et al. 2016), the number of species found in La Mina (9) and Cerro Huatulco (12) can be considered high. These results agree with Arita (1993) who included caves with 8 (La Trinitaria, La Murcielaguera), 9 (Juxtlahuaca Cave, del Cerro Cave, Mina del tigre, Don Luis cave, Quintero Cave, Laguna Encantada Cave and Spukil Cave), 11 (Gruta de Lol-Tún), 12 (Cueva del Salitre) and 13 species (Cueva de Las Vegas) in a high-richness category. The abundance observed in Cerro Huatulco (970 individuals) and El Apanguito (4,306 individuals) can be considered moderate according to Torres-Flores and Santos-Moreno (2017) and high according to Arita (1993), who classified sites with populations between 1000 and 10,000 individuals in each of those classes. Taking into account that caves are the main underground roosts for bats in México (62.2% of the species distributed in the country use caves as their main, alternative or occasional roost) (Torres-Flores and Santos-Moreno 2017), that only 10% of the caves in the country have high species richness, that sites with high abundance are rare (Arita 1993), and that we are facing an urgent need for the protection of roosts (only one cave from Oaxaca is included in the 53 priority sites for conservation in México proposed by Torres-Flores and Santos-Moreno (2017)), the results of this study give scientific support for declaring the three roosts as Priority Sites for the Protection and Conservation of Bats in Oaxaca.

Regarding our sampling effort, it is possible that the asymptote observed in the species accumulation curve for El Apanguito is a consequence of its structure, because it has only one small entrance (1.20 m high by 1.15 m wide) which was covered completely by the harp trap (1.5 m wide by 2 m high), minimizing the number of individuals that could escape or evade it. On the other hand, the low representativeness in Cerro Huatulco (only 70.58% of the species predicted by the first order Jackknife non-parametric estimator were recorded) could be caused by two factors: first, as opposed to El Apanguito, the wide entrance of the cave (10 m high by 15 m wide) could have allowed a considerable number of bats to avoid the trap. The second reason could be that its species were rare. In this cave, 41.66% of the spe-

cies were rare, i.e., they were captured only in one or two sampling periods or their abundance amounted only to one or two individuals in most samples (Colwell and Coddington 1994; Moreno 2001). Therefore, we could expect that any species yet to be found, will also be of this type, because it has been reported that the proportion of rare species present in a sample influences the shape of the accumulation curve. The likelihood to reach the asymptote decreases with an increasing number of rare species (Gimaret-Carpentier et al. 1998).

The high abundance of *P. fulvus* and *P. mesoamericanus* at El Apanguito and Cerro Huatulco is expected if we consider they are strict cave-dwellers which, in other sites, form colonies of thousands of individuals (Villa 1967; Medellín and López-Forment 1986; Adams 1989). Both at El Apanguito and in Cerro Huatulco, mormoopids represented over 90% of captures, forming relatively large colonies (larger than 1000 individuals). This association between mormoopids has been observed in other caves and mines of México (Bateman and Vaughan 1974; Arita 1993; Arita and Vargas 1995). Therefore, it is unusual that *P. mesoamericanus* and *P. fulvus* are not the most abundant species at La Mina. This could be due to factors like temperature and precipitation. Several studies have concluded that mormoopids show preference for roosts with temperatures over 30 °C and small horizontal entrances at ground level which limit the flow of air (Arita and Vargas 1995). These characteristics do not occur at La Mina, which has maximum temperatures of 23.5 °C and, although it does have a small entrance at ground level, it has abundant water flow throughout most of the year and unlimited flow of air. At La Mina, the most abundant species was *C. perspicillata* (39.82%). The high number of individuals of *C. perspicillata* captured could be related to high food availability, as fruits of *Piper* and *Solanum* genera were observed throughout the whole study period and are known to fruit constantly all-year round (Fleming 1991; Estrada et al. 1993). This could allow bats of this species to use La Mina as their main roost without having to move to other sites.

Difference in order one diversity or species richness between the three sites can be explained by several factors, mostly related to their physical characteristics. Cerro Huatulco, which was the site with the highest richness (12 effective species), has a more complex structural configuration (in terms of variety of formations, cavities and crevasses) than the others. A complex structural configuration and a higher number of chambers gives place to a larger number of available microhabitats (due to the microclimatic differences which arise inside), besides having a larger area available, which altogether allow the coexistence of several species (Tuttle and Stevenson 1982; Hill and Smith 1984; Brunet and Medellín 2001). The high order one and order two diversities at La Mina, suggests higher unevenness in abundances with respect to Cerro Huatulco and El Apanguito. On the other hand, the low diversity observed at Cerro Huatulco is due to the high abundance (dominance) of *P. fulvus*, which represented 78.95% of the total captures in the roost throughout the sampling period; a result also observed in the high degree of unevenness (7.61). The Morisita-Horn index accounts for the abundance of each species, making it sensitive to the abundance of the most numerous species (Magurran 1988; Wilson and

Schmida 1984). This could explain the higher similarity between El Apanguito and Cerro Huatulco (0.68), since *P. fulvus* and *P. mesoamericanus* were the most abundant species in both sites. On the other hand, the matrix of trophic guild by size-interval showed that the most abundant species corresponded to interval I (35.5–44.9 mm forearm length) insectivores in the three roosts (Table 3). At La Mina, this group was formed by *M. pilosatibialis*, *N. mexicanus* and *P. fulvus*; in Cerro Huatulco by *B. plicata*, *N. mexicanus*, *P. fulvus* and *P. psilotis*; and at El Apanguito, by *N. mexicanus* and *P. fulvus*. The coexistence of species from the same trophic guild could suggest high resource competition between them (McNab 1971), although there may not always be a high specialization with low dietary overlap. However, there are differences which may minimize or prevent competition. First, the difference in abundances and the only occasional presence of some of the species (*B. plicata*, *M. pilosatibialis*, *N. mexicanus*, *P. fulvus* and *P. psilotis*) in the roosts, notably minimizes feeding competition. For example, at La Mina, the three species had abundances between 2–6 individuals and their presence only overlapped in October (*M. pilosatibialis* and *N. mexicanus*) and January (*N. mexicanus* and *P. fulvus*). In Cerro Huatulco the difference in abundances is notable (758 individuals of *P. fulvus* and fewer than five individuals of *B. plicata*, *N. mexicanus* and *P. psilotis*) and *P. fulvus* was present all year round, while the other three species used the cave only occasionally. At El Apanguito, even though *N. mexicanus* and *P. fulvus* shared the cave in all sampling periods, their abundances were also notably different (199 individuals of *N. mexicanus* and 1609 of *P. fulvus*). And even though both species are ecomorphologically similar (i.e., they can capture prey of similar size), differences in prey preferences could further minimize competition for resources. For example, the smaller size of *N. mexicanus*, with a body mass under five grams, could indicate that this species feeds on smaller prey than *P. fulvus* (which can weigh up to 10 grams). Besides, both species forage in different areas. For example, *P. fulvus* uses open areas, corridors, areas under the canopy, trails, vegetation margins and areas near bodies of water, and hunts flying insects in flight, while *N. mexicanus*, has a slower flying speed, forages between vegetation and probably feeds mostly on insects captured while sitting on rocks, leaves and other substrates, or flying insects with limited mobility (Bateman and Vaughan 1974). Due to the number of species (50%), the high abundance of individuals (90.78%) and the biomass that insectivores represented overall (89.07%) and in each roost (100% in El Apanguito, 78.95% in Cerro Huatulco and 26.24% in La Mina), it is necessary to highlight the importance of this trophic guild for the ecosystem functions they perform by controlling insect populations that could potentially become pests; mostly lepidoptera, coleopterans, homopterans and hemipterans (McNab 1982; Palmeirim and Rodrigues 1991).

Conclusions and conservation considerations

The three roosts studied had high species richness and abundance of individuals, particularly Cerro Huatulco (12 species) and El Apanguito (4,306 individuals), in-

dicating they should be catalogued as Priority Sites for the Protection and Conservation of Bats in Oaxaca. During fieldwork, we observed different factors which represent threats for the roosts, such as guano extraction at El Apanguito and Cerro Huatulco, and the celebration of ceremonies involving candle-lighting and burning of tires and wood, which drive the bats away from the caves. Additionally, access to the roosts is completely unregulated (excepting at La Mina, where the mining company controls the entrance); and clandestine logging in the surroundings of the two caves can have an important negative impact on the bat populations by reducing food availability. Therefore, it is necessary to implement effective conservation measures in these sites, which help eliminate these risk factors and ensure the long-term persistence of the bats. In addition, it would be pertinent to promote environmental education programs which emphasize the importance of the roosts and raise the interest of the local communities in the protection of both bats and their roosts.

Acknowledgements

To the authorities of Pluma Hidalgo and Santa María Huatulco for their support while conducting the study. To Mr. Armando Ramírez and Mr. Carlos from El Apanguito and San Francisco coffee plantations. To Mr. Rutilo for inviting us into his home and for his help during field activities. To M. Soriano, A. García, A. Matus, D. Peña, E. Ruiz, E. Caballero, J. Arellanes, J. López, L. Jiménez, L. Pacheco, M. Sánchez and R. Prado for their valuable assistance during field work. Special thanks to M. C. M. Calixto Rojas for his valuable help in the field, for his revision of the text and for the map of the study site. G. Ramos Fernández, M. U. García Guerrero, M. Röss and J. N. Williams for valuable comments to previous versions of the manuscript. This work was supported by the Instituto Politécnico Nacional de México (SIP-20161645 and SIP-20171154 a AS-M) and the México National Council for Science and Technology awarded a master's degree postgraduate studies scholarship to first author.

References

- Adams JK (1989) *Pteronotus davyi*. Mammalian Species 346(346): 1–5. <https://doi.org/10.2307/3504116>
- Aguirre LF, Lens L, Matthysen E (2003) Patterns of roost use by bats in a Neotropical savanna: Implications for conservation. *Biological Conservation* 111(3): 435–443. [https://doi.org/10.1016/S0006-3207\(02\)00313-0](https://doi.org/10.1016/S0006-3207(02)00313-0)
- Altenbach JS (1998) Abandoned Mines as Bat Habitat. National Park Service, Cultural Resource Management Magazine, No. 7, USA.
- Álvarez-Castañeda ST, Álvarez T, González-Ruiz N (2015) Guía para la identificación de los mamíferos de México en campo y en laboratorio. Centro de investigaciones Biológicas del Noroeste, S. C. Asociación Mexicana de Mastozoología A. C., México.
- Anthony ELP (1988) Age determination in bats. In: Kunz TH (Ed.) *Ecological and Behavioral Methods for the Study of Bats*. Smithsonian Institution Press, Washington, 44–72.

- Arita H (1993) Conservation biology of the caves bats of México. *Journal of Mammalogy* 7(3): 693–702. <https://doi.org/10.2307/1382291>
- Arita H, Vargas JA (1995) Natural history, interspecific association, and incidence of cave bats of Yucatan, México. *The Southwestern Naturalist* 40: 29–37. <https://www.jstor.org/stable/30054390>
- Ávila-Flores R, Medellín R (2004) Ecological, taxonomic, and physiological correlates of cave use by Mexican Bats. *Journal of Mammalogy* 85(4): 675–687. <https://doi.org/10.1644/BOS-127>
- Barragán F, Lorenzo C, Morón A, Briones-Salas MA, López S (2010) Bat and rodent diversity in a fragmented landscape on the Isthmus of Tehuantepec, Oaxaca, México. *Tropical Conservation Science* 3(1): 1–16. <https://doi.org/10.1177/194008291000300101>
- Bateman GC, Vaughan TA (1974) Nightly activities of mormoopid bats. *Journal of Mammalogy* 55(1): 45–65. <https://doi.org/10.2307/1379256>
- Briones-Salas M, Sánchez-Cordero V, Santos-Moreno A (2004) Diversidad de murciélagos en el gradiente altitudinal de la Sierra Mazateca, Oaxaca, México. In: Sánchez-Cordero V, Medellín RA (Eds) *Contribuciones Mastozoológicas en Homenaje a Bernardo Villa*. Instituto de Biología e Instituto de Ecología, UNAM, México, 65–74.
- Brose U, Martínez ND, Williams RJ (2003) Estimating species richness: Sensitivity to sample coverage and insensitivity to spatial patterns. *Ecology* 84(9): 2364–2377. <https://doi.org/10.1890/02-0558>
- Brunet AK, Medellín R (2001) The species-area relationships in bat assemblages of tropical caves. *Journal of Mammalogy* 82(4): 1114–1122. [https://doi.org/10.1644/1545-1542\(2001\)082<1114:TSARIB>2.0.CO;2](https://doi.org/10.1644/1545-1542(2001)082<1114:TSARIB>2.0.CO;2)
- Buenrostro-Silva A, Antonio-Gutiérrez M, García-Grajales J (2013) Diversidad de murciélagos de la cuenca baja del Río Verde, Oaxaca. *Therya* 4(2): 361–376. <https://doi.org/10.12933/therya-13-115>
- Cajas-Castillo JO, Echeverría JL, Trujillo L (2015) Murciélagos del Parque Nacional Cuevas del Silvino, Izabal, Guatemala. *Boletín de la Red Latinoamericana para la Conservación de los Murciélagos* 6: 4–8.
- Calderón-Patrón JM, Briones-Salas M, Moreno CE (2013) Diversidad de murciélagos en cuatro tipos de bosque de la Sierra Norte de Oaxaca, México. *Therya* 4(1): 121–137. <https://doi.org/10.12933/therya-13-90>
- Ceballos G, Arroyo-Cabrales J (2012) Lista actualizada de los mamíferos de México. *Revista Mexicana de Mastozología* 2: 27–80. [nueva época] <https://doi.org/10.22201/ie.20074484e.2012.2.1.20>
- Colwell RK (2013) *Estimates: Statistical Estimation of Species Richness and Shared Species from Samples*, version 9.1.0. University of Connecticut, USA.
- Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transaction of the Royal Society* 345(1311): 101–118. <https://doi.org/10.1098/rstb.1994.0091>
- De Paz O, Benzal J, Fernández R (1990) Criterios de valoración de refugios para murciélagos: Aplicación al inventario nacional. *Ecología (Madrid)* 4: 191–206.
- Divoll TJ, Buck DG (2013) Noteworthy field observations of cave roosting bats in Honduras. *Mastozología Neotropical* 20: 149–151. http://www.sarem.org.ar/wp-content/uploads/2013/07/SAREM_MastNeotrop_20-1_12_Divoll.pdf

- Escalona-Segura G, Vargas-Contreras JA, Sosa L (2002) Registros importantes de mamíferos para Campeche, México. *Revista Mexicana de Mastozoología* 6(1): 99–103. <https://doi.org/10.22201/ie.20074484e.2002.6.1.109>
- Estrada A, Coates-Estrada R, Meritt D (1993) Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, México. *Ecography* 16(4): 309–318. <https://doi.org/10.1111/j.1600-0587.1993.tb00220.x>
- Felix S, Novaes R, Souza R, Avilla L (2016) Bat assemblage in a karstic area from northern Brazil: Seven new occurrences for Tocantins state, including the first record of *Glyphoncteris sylvestris* Thomas, 1896 for the Cerrado. *Check List* 12(6): 1–1999. <https://doi.org/10.15560/12.6.1999>
- Fleming TH (1991) The relationship between body size, diet and habitat use in frugivorous bats, genus *Carollia* (Phyllostomidae). *Journal of Mammalogy* 72(3): 493–501. <https://doi.org/10.2307/1382132>
- García E (1988) Modificaciones al Sistema de Clasificación Climática de Köppen. (Para adaptarlo a las condiciones de la República Mexicana). Offset Larios, México.
- García FJ, Araujo-Reyes D, Vásquez-Parra O, Brito H, Machado M (2015) Murciélagos (Mammalia: Chiroptera) asociados con una cueva en el Parque Nacional Yurubí, Sierra de Aroa, Estado Yaracuy, Venezuela. *Caldasia* 37(2): 381–391. <https://doi.org/10.15446/caldasia.v37n2.53986>
- García-García JL, Santos-Moreno A (2014) Efectos de la estructura del paisaje y de la vegetación en la diversidad de murciélagos filostómidos (Chiroptera: Phyllostomidae) de Oaxaca, México. *Revista de Biología Tropical* 62(1): 217–240. <https://doi.org/10.15517/rbt.v62i1.12094>
- García-García JL, Alfaro AM, Santos-Moreno A (2006) Registros notables de murciélagos en el estado de Oaxaca, México. *Revista Mexicana de Mastozoología* 10(1): 88–91. <https://doi.org/10.22201/ie.20074484e.2006.10.1.146>
- Gimaret-Carpentier C, Pélissier R, Pascal JP, Houllier F (1998) Sampling strategies for the assessment of tree species diversity. *Journal of Vegetation Science* 9(2): 161–172. <https://doi.org/10.2307/3237115>
- Glover AM, Altringham JD (2008) Cave selection and use by swarming bat species. *Biological Conservation* 141(6): 1493–1504. <https://doi.org/10.1016/j.biocon.2008.03.012>
- Hammer Ø, Harper DA, Ryan DP (2001) PAST: Paleontological Statistics, version 3.16.
- Hill JE, Smith JD (1984) *Bats: a Natural History*. University of Texas Press, Austin.
- Humphrey SR, Oli MK (2015) Population dynamics and site fidelity of the cave bat, *Myotis velifer*, in Oklahoma. *Journal of Mammalogy* 96(5): 946–956. <https://doi.org/10.1093/jmammal/gyv095>
- Hutchinson GE (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist* 93(870): 145–159. <https://doi.org/10.1086/282070>
- Jost L (2006) Entropy and diversity. *Oikos* 113(2): 363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- Kraker-Castañeda C, Santos-Moreno A, García-García JL (2013) Riqueza de especies y actividad relativa de murciélagos insectívoros aéreos en una selva tropical y pastizales en Oaxaca, México. *Mastozoología Neotropical* 20: 255–267. <http://www.redalyc.org/pdf/457/45729294004.pdf>

- Kunz TH (1982) Roosting ecology of bats. In: Kunz TH (Ed.) *Ecology of Bats*. Plenum Press, New York, 55 pp. https://doi.org/10.1007/978-1-4613-3421-7_1
- Kunz TH, Lumsden LF (2003) Ecology of cavity and foliage roosting bats. In: Kunz TH, Fenton MB (Eds) *Bat Ecology*. University of Chicago Press, Chicago, 3–89.
- Lira-Torres I, Camacho-Escobar EMA, Hernández-Sánchez C (2008) Mamíferos de la bahía y microcuenca del río Cacaluta, municipio de Santa María Huatulco, Oaxaca. In: Domínguez-Licona JM (Ed.) *Diagnostico de los Recursos Naturales de la Bahía y Microcuenca del río Cacaluta, municipio de Santa María Huatulco, Oaxaca*. Universidad del Mar, SEMARNAT, CONACYT, México, 267–280.
- López-González C (2005) Use of abandoned mines by a community of temperate bats in Durango, México. *Acta Chiropterologica* 7(2): 285–292. [https://doi.org/10.3161/1733-5329\(2005\)7\[285:UOAMBA\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2005)7[285:UOAMBA]2.0.CO;2)
- MacSwiney GMC (2010) Murciélagos. In: Durán R, Méndez M (Eds) *Biodiversidad y Desarrollo Humano en Yucatán*. CICY, PPD-FMAM, CONABIO, SEDUMA, México, 496–523.
- Magurran AE (1988) *Ecological diversity and its measurement*. Princeton Univ. Press. <https://doi.org/10.1007/978-94-015-7358-0>
- McNab B (1971) The structure of tropical bat faunas. *Ecology* 52(2): 353–358. <https://doi.org/10.2307/1934596>
- McNab B (1982) Evolutionary alternatives in the psychological ecology of bats. In: Kunz TH (Ed.) *Ecology of Bats*. Plenum Publishing Co., New York, 151–196. https://doi.org/10.1007/978-1-4613-3421-7_4
- Medellín R (1993) Estructura y diversidad de una comunidad de murciélagos en el trópico húmedo mexicano. In: Medellín RA, Ceballos G (Eds) *Avances en el Estudio de los Mamíferos de México*. Asociación Mexicana de Mastozoología, A. C., México, 353–354.
- Medellín R, López-Forment W (1986) Las cuevas: un recurso compartido. *Anales del Instituto de Biología, UNAM. Serie Zoología* 56: 1027–1034. <http://web.ecologia.unam.mx/medellin/images/Medellin-y-Lopez-Forment.1985.pdf>
- Medellín R, Arita H, Sánchez O (1997) *Identificación de los Murciélagos de México: Clave de Campo*. Talleres Offset, México.
- Medellín R, Arita H, Sánchez O (2007) *Identificación de los Murciélagos de México, Clave de Campo*. Segunda edición. Instituto de Ecología, UNAM, México.
- Moratelli R, Burgin CJ (2019) Family Vespertilionidae. In: Wilson DE, Mittermeier RA (Eds) *Handbook of the Mammals of the World*, 716–981.
- Moreno CE (2001) *Métodos Para Medir la Biodiversidad*. MyT-Manuales y Tesis SEA, Zaragoza, España.
- Muñoz-Saba Y, Hoyos-Rodríguez MA, Guillermo-Baptiste L (2007) ¿Conservación de murciélagos asociados con las cavernas o conservación de las cavernas a través de los murciélagos? *Focus VI* 2: 57–63. <https://www.academia.edu/22032347>
- Nowak RM (1999) *Walker's Mammals of the World*. Johns Hopkins University Press, Baltimore.
- OEIDRUS (2005) *Oficina Estatal de Información para el Desarrollo Rural Sustentable. Tarjeta municipal de información estadística básica*.

- Palacios-Romo TM, Sánchez-Vázquez A, Contreras-Díaz RG, Pérez-Lustre M (2012) Inventario de mamíferos en sistemas cafetaleros de sombra en la cuenca baja del río Copalita en el estado de Oaxaca, México. *Therya* 3: 303–310. <https://doi.org/10.12933/therya-12-86>
- Palmeirim J, Rodrigues L (1991) Estatus y conservación de los murciélagos en Portugal. In: Benzal J, Paz O (Eds) *Monografías del ICONA, Colección Técnica*, 163–179.
- Patterson BD, Willig MR, Stevens RD (2003) Trophic strategies, niche partitioning, and patterns of ecological organization. In: Kunz TH, Fenton MB (Eds) *Bat Ecology*. University of Chicago Press, Chicago, 536–579.
- Pavan AC (2019) Family Mormoopidae. In: Wilson DE, Mittermeier RA (Eds) *Handbook of the Mammals of the World*, 424–443.
- Pérez-Torres J, Martínez-Medina D, Peñuela-Sangado M, Ríos-Blanco MC, Estrada-Villegas S, Martínez-Luque L (2015) Macaregua: The cave with the highest bat richness in Colombia. *Check List* 11(2): 1–1616. <https://doi.org/10.15560/11.2.1616>
- Rzedowski J (1994) *Vegetación de México*. Limusa y Noriega Eds, México.
- Sánchez-Cordero V (2001) Elevational gradients for bats and rodents. *Global Ecology and Biogeography* 10: 63–76. <https://doi.org/10.1046/j.1466-822x.2001.00235.x>
- Santos-Moreno A (2014) Los mamíferos del estado de Oaxaca. *Revista Mexicana de Mastozoología* 4(2): 18–32. <https://doi.org/10.22201/ie.20074484e.2014.4.2.194> [nueva época]
- Santos-Moreno A, Ruiz-Velásquez E, Sánchez-Martínez A (2010) Efecto de la intensidad de la luz lunar y de la velocidad del viento en la actividad de murciélagos filostómidos de Mena Nizanda, Oaxaca, México. *Revista Mexicana de Biodiversidad* 81(003): 839–845. <https://doi.org/10.22201/ib.20078706e.2010.003.653>
- Schoener TW (1984) Size differences among sympatric, bird-eating hawks: a worldwide survey. In: Strong DR, Simberloff D, Abele LG, Thistle AB (Eds) *Ecological Communities, Conceptual Issues and the Evidence*. Princeton University Press, 254–281. <https://doi.org/10.1515/9781400857081.254>
- Siles L, Muñoz A, Aguirre LF (2007) Bat diversity in three caves in a montane forest of Bolivia. *Ecotropica* (Bonn) 13: 67–74. https://www.socetropecol.eu/PDF/Ecotropica_2007_01/Siles%20&%20Aguirre%202007,%20Ecotropica%2013-1.pdf
- Solari S, Medellín RA, Rodríguez-Herrera B, Dumont ER, Burneo SF (2019) Family Phyllostomidae. In: Wilson DE, Mittermeier RA (Eds) *Handbook of the Mammals of the World*, 444–583.
- Tejedor A (2019) Family Natalidae. In: Wilson DE, Mittermeier RA (Eds) *Handbook of the Mammals of the World*, 584–596.
- Torres-Colín R (2004) Tipos de vegetación. In: García-Mendoza AJ, Ordoñez MJ, Briones-Salas M (Eds) *Biodiversidad de Oaxaca*. Instituto de Biología, UNAM-Fondo Oaxaqueño para la conservación de la naturaleza-World Wildlife Fund, México, 105–117.
- Torres-Flores JW, Santos-Moreno A (2017) Inventory, features, and protection of underground roots used by bats in México. *Acta Chiropterologica* 19(2): 439–454. <https://doi.org/10.3161/15081109ACC2017.19.2.019>
- Torres-Flores JW, López-Wilchis R, Soto-Castruita A (2012) Dinámica poblacional, selección de sitios de percha y patrones reproductivos de algunos murciélagos caverníco-

- las en el oeste de México. *Revista de Biología Tropical* 60(3): 1369–1389. <https://doi.org/10.15517/rbt.v60i3.1814>
- Trajano E, Giménez EA (1998) Bat community in a cave from eastern Brazil, including a new record of *Lionycteris* (Phyllostomidae, Glossophaginae). *Studies on Neotropical Fauna and Environment* 33(2): 69–75. <https://doi.org/10.1076/snfe.33.2.69.2156>
- Trejo I (2004) Clima. In: García-Mendoza AJ, Ordóñez MJ, Briones-Salas M (Eds) *Biodiversidad de Oaxaca*. Instituto de Biología, UNAM-Fondo Oaxaqueño para la Conservación de la Naturaleza-World Wildlife Fund, México, 67–85.
- Tuttle MD, Stevenson D (1982) Growth and survival of bats. In: Kunz TH (Ed.) *Ecology of Bats*. Plenum Press, New York, 105–150. https://doi.org/10.1007/978-1-4613-3421-7_3
- Vásquez-Pérez EU, Roque-Velázquez JA, Velázquez-Velázquez E (2010) Diversidad alfa y beta en murciélagos cavernícolas de la Depresión Central, Chiapas, México. *Lacandonia* 4: 47–54.
- Villa RB (1967) *Los Murciélagos de México. Su Importancia en la Economía y la Salubridad. Su Clasificación Sistemática*. Instituto de Biología, UNAM, México.
- Watson J, Hamilton-Smith E, Gillieson D, Kiernan K (1997) *Guidelines for Cave and Karst Protection*. IUCN, Gland y Cambridge.
- Wilson MV, Schmida A (1984) Measuring beta diversity with presence-absence data. *Journal of Ecology* 72(3): 1055–1064. <https://doi.org/10.2307/2259551>