THE SPECIES–AREA RELATIONSHIP IN BAT ASSEMBLAGES OF TROPICAL CAVES

ANJA K. BRUNET* AND RODRIGO A. MEDELLÍN

Department of Ecology, Evolution, and Behavior and James Ford Bell Museum of Natural History, University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108 (AKB)
Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, 04510 Mexico City, Mexico (RAM)

We tested for a relationship between number of bat species and surface area of 20 caves in central Mexico and investigated the role of the habitat diversity model as an explanation for this relationship. There was a significant positive correlation between the logarithm of species richness and the logarithm of cave surface area, evidence of a species–area relationship. Our data suggest that roost site diversity, as indicated by spatial variation in relative humidity and presence of avons (conical depressions in cave ceilings) is a cause of the species–area relationship.

Key words: bat assemblages, caves, habitat diversity model, Mexico, species–area relationship

A relationship between the number of species of a particular taxonomic group in a region and the area of the region sampled is a nearly ubiquitous pattern in nature. This pattern, known as the species–area relationship, is commonly observed in species richness of islands (Coleman et al. 1982). While the relationship is unequivocal, causes of the correlation are still debated (Fox and Fox 2000; Kelly et al. 1989; Lomolino 2000). It appears that the pattern likely results from different mechanisms operating on different organism assemblages and at different sites (Anderson 1999; Coleman et al. 1982; Douglas and Lake 1994; Gotelli 1998; Kelly et al. 1989; Ricklefs and Lovette 1999).

Three models are discussed in the literature as possible explanations for the observed species–area relationship. The passive sampling model (Arrhenius 1921; Coleman et al. 1982) describes islands as samples of individuals. If individuals are randomly distributed among islands, then larger islands will contain more species. In this model, species richness depends only on island area and abundance of each species in the species pool. The equilibrium model (MacArthur and Wilson 1963) describes the number of species on an island as the balance between recurrent immigrations of species to the island and the recurrent extinction of resident species. Larger islands have larger populations, which reduces the chance of extinction. Therefore, larger islands are expected to have a greater number of species. As a consequence of the flux of immigrations and extinctions, this model predicts a constant turnover of species. The habitat diversity model (Connor and McCoy 1979; Williams 1943) states that a larger island will contain more habitat niches and consequently be able to sustain more species. This model requires the existence of spatial variation in habitat and predicts a correlation between this variation and both species richness and area of the sampled region.

Caves have been described as islands with their respective assemblages of organisms (Culver 1970). Some cave-dwelling
species might migrate between several caves, but they generally are restricted to these chosen caves. Many bat species use caves as roosting sites. Caves afford bats protection and are sites for hibernation, reproduction, rearing young, and other social events (Kunz 1982). It is not uncommon to find a cave that provides shelter for a number of species, particularly in the neotropics where caves have been reported hosting $\leq 13$ species (Arita 1993). Two studies by Arita (1993, 1996) have surveyed caves in Mexico with the objective of determining associations between species occupying the same caves and assessing the utility of criteria based on these associations for conservation decisions. In one of those studies, Arita (1996) found a positive relationship between length of the cave and number of species roosting in the cave. If we consider caves as islands, it is possible that the number of bat species present in a cave is correlated with surface area of the ceiling and walls available for roosting.

Our objectives were to assess the species–area relationship in bat assemblages in a system of caves in central Mexico and to test the 3rd model discussed, the habitat diversity model, as an explanation for this relationship. We assess the correlation between the species richness of the study caves and 5 cave characteristics quantifying roost site diversity. Under the habitat diversity model, we expected the number of species in a cave to increase with increased roost site diversity and the latter to increase with surface area in a cave. We did not test the equilibrium and passive sampling models because data on abundance, extinction rates, and immigration rates were not available.

**Materials and Methods**

We surveyed caves in Ayotoxco and Tenampulco townships located in the northeastern corner of the Mexican state of Puebla, about 80 km from the state of Veracruz (20°08’N, 97°24’W). Those townships were part of the Sierra Madre Oriental on the slope that drops from the Central Plateau of Mexico to the coast of the Gulf of Mexico. The area was lowland perennial rainforest located about 200 m above mean sea level. Much of the vegetation in the area had been cleared for plantations of coffee, vanilla, banana, and pasturelands. The rainy season extended from May to November with an average annual precipitation of 250 cm (Medellín and López-Forment 1985). The mean annual temperature was $> 18^\circ $C, and daily temperatures can exceed $38^\circ $C during the dry season (de Alba and Reyes 1998).

We located 20 caves with the assistance of local hunters and landowners in July–August 1999 (Global Positioning System locations of the caves can be obtained from the authors). All study caves were sandstone, humid, and warm. Of the approximately 50 different species of bats that occur in northeastern Puebla (Medellín et al. 1997), many have been found to roost in caves, including frugivores, insectivores, nectarivores, and sanguinivores (Medellín and López-Forment 1985). The maximum distance between any 2 caves was about 13 km, a distance easily traveled by bats, and therefore, isolation was not considered in our analysis.

We determined species richness of each cave, defined as the number of species found in a cave, by visually identifying roosting bats. Most species present were identified easily without capture by a combination of visible physical traits, behavior, and guano characteristics.

Immediately after determining species composition, we measured and surveyed the caves using standard survey methods (Ellis 1976). We began all surveys at the cave entrance (survey station 1). From there, we measured the distance to survey station 2, the location of which was determined by a change in height or width of the cave or by the presence of a side shaft or tunnel. From survey station 2, we measured the distance to a 3rd survey station and continued until we measured the entire length of the cave. At each survey station we estimated the height of the cave ceiling, measured width of the tunnel, and recorded the compass bearing to the previous survey station.

The evening after surveying the cave, we captured bats with hand nets and mist nets to confirm identifications. Mist net captures were done with a 6-m-long net placed at the cave entrance from sunset ($\approx 1900$ h) to 2230 h, the period of greatest emergence activity. All bats captured
had been identified during the initial species composition determination.

We calculated an estimate of the surface area of the walls and ceiling of each cave by approximating the surface area with a string of elliptical cylinders. The surface area of an elliptical cylinder was approximated by the formula \( A \approx 2\pi L\left(\frac{a^2 + b^2}{2}\right)^{1/2} \), where \( a \) was the major axis of the ellipse, \( b \) the minor axis, and \( L \) the length of the cylinder. For our calculations, average width and average height of 2 adjacent survey stations were the axes of the ellipse, and the distance between the 2 survey stations was the length of the cylinder. Because caves resemble a half cylinder, we obtained the final estimate of the roosting area available in each cave by adding the surface areas calculated for the cylinders comprising a cave and dividing by 2.

We assessed presence or absence of a species-area relationship by plotting the logarithm of species richness (number of species in each cave) against the logarithm of the estimated surface areas of the caves. The regression line through those data points was equivalent to the logarithm of the power function \( S = cA^z \), where \( S \) was the species richness, \( A \) the sampled area, and \( c \) and \( z \) were fitted constants.

To test the habitat diversity model, we measured 5 cave characteristics quantifying roost site diversity: cave complexity, density of avons, and spatial variation of temperature, relative humidity, and precipitable water. Again, under the habitat diversity model, we expected both species richness and surface area of caves to increase with roost site diversity.

Cave complexity is based on the extent of passages and tunnels in a cave. A measure of complexity is the complexity index calculated as the ratio of total horizontal length of all passages to the maximum horizontal extent between 2 points in a cave (Arita 1996). Single-tunnel caves have a complexity index of 1, and the index increases with the number of passages and side shafts (range = 1–∞). More complex caves might offer a greater number of segregated and distinct roosting sites (increased diversity in roosting sites); thus, we expected species richness to increase with the degree of complexity.

Avons are conical depressions in the ceiling or walls of a cave that trap body heat of bats roosting in them (Churchill et al. 1997). The amount of heat trapped depends on the size and location of the avon and the number of bats roosting in it. Consequently, avons in a cave increase the number of distinct roosting sites with unique microclimatic conditions and allow for species segregation within a chamber. We scored the number of avons directly above each survey station within a cave as either 0 (none), 1 (1–5), or 2 (>5). We calculated an avon index for each cave by averaging scores from all survey stations in a cave. That index reflected the density of avons in a cave, and we expected species richness to be greater in caves with higher avon indices.

Spatial variation of microclimatic conditions within a cave might create greater diversity in roosting sites than homogeneous conditions. Bats have specific temperature and humidity requirements in their choice of roost (McNab 1982). A cave that presents a wide array of conditions might host a larger number of species than one that has constant conditions, as long as these do not exceed the upper and lower boundaries of the microclimatic needs for all potential species. We used data loggers (HOBO Pro, Onset Computer Corporation, Bourne, Massachusetts) to simultaneously record temperature and relative humidity at several sites within a cave and at its entrance. Those data loggers were programmed to measure temperature and relative humidity at certain time intervals. Recordings were stored in the data logger and data could be downloaded onto a computer at any time. Because we had a limited number of data loggers, we restricted microclimate recordings to 7 randomly selected caves. Data loggers were situated at sites with evidence of roosting (presence of bats or fresh guano) and were hoisted on free-standing PVC pipe to the ceiling of the cave. Measurements were taken every 15 min for a 24-h period.

We calculated an index of spatial variation of temperature, relative humidity, and precipitable water (an absolute measure of humidity). That index was the ratio of the number of different average recordings when sequentially comparing data logger sites and the total number of data loggers used multiplied by the total magnitude of the differences. It is a measure of microclimatic variation in space (from site to site within a cave) and increases with both a greater number of differences between data loggers and with larger differences (range = 0–∞). We expected the number of species in a cave to increase with
TABLE 1.—Roosting area, species richness (number of species), and characteristics measured in study caves. The avon category in which the cave was placed (1 = “few or no avons,” 2 = “many avons”) is indicated in parentheses after the avon index.

<table>
<thead>
<tr>
<th>Cave</th>
<th>Area (m²)</th>
<th>Species richness</th>
<th>Avon index</th>
<th>Complexity index</th>
<th>Index of relative humidity variation</th>
<th>Index of temperature variation</th>
<th>Index of precipitable water variation</th>
</tr>
</thead>
<tbody>
<tr>
<td>La Escondida</td>
<td>18</td>
<td>1</td>
<td>0.25 (1)</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>El Escorpion</td>
<td>19</td>
<td>1</td>
<td>0.50 (1)</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>La Herradura</td>
<td>32</td>
<td>1</td>
<td>0.83 (2)</td>
<td>1.74</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Buena Vista</td>
<td>39</td>
<td>0</td>
<td>0.50 (1)</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>El Manantial</td>
<td>47</td>
<td>1</td>
<td>0.50 (1)</td>
<td>1.00</td>
<td>0.05</td>
<td>0.18</td>
<td>0.08</td>
</tr>
<tr>
<td>El Tigre</td>
<td>58</td>
<td>1</td>
<td>0.43 (1)</td>
<td>1.12</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mission Imposible</td>
<td>60</td>
<td>2</td>
<td>0.33 (1)</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>La Salamandra</td>
<td>125</td>
<td>6</td>
<td>0.88 (2)</td>
<td>1.37</td>
<td>1.93</td>
<td>0.26</td>
<td>0.18</td>
</tr>
<tr>
<td>San Martin</td>
<td>128</td>
<td>5</td>
<td>0.20 (1)</td>
<td>1.00</td>
<td>0.00</td>
<td>0.01</td>
<td>0.00</td>
</tr>
<tr>
<td>El Arenal</td>
<td>187</td>
<td>4</td>
<td>0.00 (1)</td>
<td>1.33</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>El Sapo</td>
<td>205</td>
<td>4</td>
<td>0.82 (2)</td>
<td>1.37</td>
<td>0.66</td>
<td>0.18</td>
<td>0.08</td>
</tr>
<tr>
<td>Waterfall</td>
<td>244</td>
<td>1</td>
<td>0.50 (1)</td>
<td>1.00</td>
<td>0.36</td>
<td>0.09</td>
<td>0.00</td>
</tr>
<tr>
<td>Nacho Sosa</td>
<td>293</td>
<td>2</td>
<td>0.00 (1)</td>
<td>1.46</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Los Copales</td>
<td>317</td>
<td>3</td>
<td>1.89 (2)</td>
<td>1.52</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>La Ciudad</td>
<td>344</td>
<td>6</td>
<td>0.38 (1)</td>
<td>1.26</td>
<td>2.99</td>
<td>1.27</td>
<td>0.32</td>
</tr>
<tr>
<td>El Coyote</td>
<td>373</td>
<td>3</td>
<td>0.71 (2)</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>La Piramide</td>
<td>458</td>
<td>3</td>
<td>1.00 (2)</td>
<td>1.37</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Virgen</td>
<td>511</td>
<td>7</td>
<td>1.46 (2)</td>
<td>1.30</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>El Tigre Grande</td>
<td>829</td>
<td>1</td>
<td>0.50 (1)</td>
<td>1.15</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cueva de Las Vegas</td>
<td>3009</td>
<td>11</td>
<td>1.21 (2)</td>
<td>1.06</td>
<td>5.02</td>
<td>0.70</td>
<td>0.32</td>
</tr>
</tbody>
</table>

higher indices of spatial variation in temperature, relative humidity, and precipitable water.

We used regression analysis to assess the correlation of species richness with cave complexity and microclimatic variation, after transforming species richness by taking the square root of each value. That was a standard transformation for stabilizing variance of count data (Box et al. 1978). We used Wilcoxon’s signed-rank sum test to analyze the avon data (JMP, SAS Institute Inc. Cary, North Carolina). We also tested for a correlation between the variation of each cave characteristic and surface area, because the habitat diversity model predicted a positive correlation between those 2 factors. A multivariate analysis incorporating all 5 independent variables was not possible due to a small sample (microclimatic data for only 7 caves).

RESULTS

Species richness varied from no bats in Cueva Buenavista to 11 species in Cueva de Las Vegas (Table 1). There was a positive correlation between logarithm of species richness and logarithm of surface area ($z = 0.31$, $r = 0.44$, $P = 0.002$; Fig. 1).

Cave complexity indices for the 20 study caves exhibited little variation. Eight caves had an index of 1.0 indicating they were single-tunnel caves, and the most complex cave (Cueva La Herradura) had an index of 1.74. We found no significant correlation between cave complexity and species richness ($r = 0.026$, $P = 0.499$), or between complexity and surface area of cave ($r = 0.021$, $P = 0.540$).

Almost all of the study caves had avons, mostly concentrated near the entrance. Artibeus jamaicensis and several species of Myotis were often found roosting in these depressions. Avon index values were 0–1.9 and fell into 2 groups, which we categorized as “few or no avons” with index values ≤0.5 and “many avons” with values
Fig. 1.—Species–area relationship of bat assemblages in study caves in Mexico, as shown by a correlation between log of surface area and log of number of species (species richness). The relationship is described by the equation $S = 0.71A^{0.31}$, where $S$ is species richness and $A$ is surface area ($r = 0.44, P = 0.002$). To allow for the inclusion of Cueva Buenavista, which harbored no bats, we used number of species +1 (logarithm of zero is undefined).

A comparison between those 2 groups revealed that caves with few avons had lower species richness than caves with many avons (Wilcoxon’s signed-rank sum test, rank sums = 112, 98, $P = 0.030$). Surface area did not differ between the 2 groups of caves (rank sums = 107, 103, $P = 0.083$).

All study caves were warm and humid, with temperatures of 23.2–25.7°C and relative humidity values of 95.6–99.1%. The average relative humidity within each cave was higher than outside of the cave (paired $t$-test, $t = -3.43, P = 0.007$), whereas average temperature inside a cave did not differ from that measured outside ($t = 0.769, P = 0.764$). Temperature variation indices were 0.01–1.27, and relative humidity variation indices were 0–5.02, indicating greater variation in relative humidity than temperature (Table 1). There was no correlation between temperature variation and species richness ($r = 0.270, P = 0.231$) or roosting area ($r = 0.137, P = 0.415$). Variation in precipitable water was not correlated with species richness ($r = 0.537, P = 0.061$) or roosting area ($r = 0.376, P = 0.143$). The index of variation in relative humidity was correlated with species richness ($r = 0.673, P = 0.024$; Fig. 2) and roosting area ($r = 0.706, P = 0.018$). Of the 3 microclimatic measurements taken, only variation in relative humidity was correlated with species richness ($r = 0.673, P = 0.024$) and surface area of caves ($r = 0.706, P = 0.018$). Caves with higher variation in relative humidity had a greater number of species.

**Discussion**

Number of species in the study caves was significantly correlated with surface area of caves and spatial variation of relative humidity. Additionally, caves with many avons had greater species richness than those with few avons. We feel confident in asserting that there is a species–area relationship in bat assemblages in the system of caves studied, despite the low correlation coefficient ($r = 0.44$; Fig. 1). A plot of residuals shows Cueva El Tigre Grande as an outlier, which may have biased the analysis. El Tigre Grande was the 2nd largest cave, yet it harbored only 1 species. Anecdotal
evidence suggests that a recent disturbance in the cave likely reduced the population of bats. The correlation coefficient for the species–area relationship increases to 0.60 ($P = 0.001$) when that cave is excluded from our analysis. Our conclusion supports Arista’s (1996) observation of a positive correlation between species richness and the maximum horizontal extent of 36 caves in Yucatán, Mexico.

Microclimatic condition is an important factor in a bat’s choice of roost. It is adaptive for a bat to minimize energy expended while roosting. Minimizing body heat and water loss can be accomplished by roosting in a site with optimal temperature and humidity (McNab 1982). In addition, specific conditions are necessary to maximize growth rate of young ones (McNab 1980). The strong correlation between spatial variation in relative humidity and both species richness and surface area is evidence of a link between these 3 variables. This correlation suggests that the habitat diversity model may be an explanation for the observed species–area relationship. However, no direct cause–effect relationship can be shown with our data. While the correlation suggests that spatial variation in relative humidity is a determinant of species richness and an explanation for the species–area relationship, it also is possible that large caves contain several sites differing in relative humidity and independently host large numbers of species. Distinguishing between these 2 scenarios will require a study that systematically tracks relative humidity preferences of these bats and their choice of roosting site within a cave.

Spatial variation in temperature was not correlated with species richness. Thermal demands placed on bats in tropical environments are modest (McNab 1982), as long as roost temperatures fall within a narrow range favorable to all species. It is possible that spatial variation of temperature in the study caves was not high enough to affect roost choice and consequently species richness. The variation indices calculated for temperature were not as high as those calculated for relative humidity (0.01–1.27 versus 0–5.02), and average temperatures inside the study caves were not significantly different from temperatures outside.

Water balance might be a more significant factor for bats in tropical environments than temperature. Amount of water lost is affected by body size and diet (McNab 1982), so each species in the caves might seek specific humidity levels. The average relative humidity inside each cave was significantly higher than the average relative humidity outside. Again, while we cannot establish a cause–effect relationship between these factors based on our data, it is possible that bats use these caves because of the high humidity levels relative to the outside and then choose a roosting site within the cave based on water-balance needs. In that case, caves with greater spatial variation in humidity would have higher species richness.

Presence of avens in caves appears to be important for some species, especially *Myotis keaysi*, *M. nigricans*, and *M. velifer*, which were observed roosting almost exclusively in avens. Other species, such as *Artibeus jamaicensis* used avens occasionally but also were observed roosting on cave ceilings. The higher number of species in caves with many avens seems to be due to the presence of those species that prefer to roost in avens. *A. jamaicensis*, *M. keaysi*, *M. nigricans*, and *M. velifer* were almost always found roosting in caves that fell into the “many avens” category. It also is likely that a high number of avens increases species diversity in a cave by facilitating species segregation. *Artibeus* and *Myotis* often were found roosting in the same chamber of a cave, each species in separate avens. However, although presence of avens increases the number of species present in a cave, avens alone do not explain the observed species–area relationship because there was no relationship between avon abundance and surface area. The surface area of the caves in the “many avens”
The complexity indices of the study caves were not correlated with species richness ($P = 0.80$). It is known that complexity of a cave influences airflow patterns through passages. Air flowing through a cave with many tunnels is likely to move at varying speeds and become trapped and warmed. This movement affects temperature and relative humidity (Moore and Sullivan 1997). However, our study caves did not have extensive networks of passages and tunnels. Eight caves had complexity indices of 1.0 (Table 1). Instead, spatial gradients of relative humidity in the caves were determined by distance from the entrance, with higher relative humidity in deeper parts of the caves. Note that Cueva de Las Vegas, which had the highest species richness, was the only study cave with 1 entrance.

We present evidence suggesting that the habitat diversity model explains the observed species–area relationship. The habitat diversity we describe is diversity in roosting sites, which may result from spatial variation in relative humidity and is enhanced by the presence of avons. Nonetheless, our data do not exclude the passive sampling or equilibrium models. The passive sampling hypothesis could not be tested because it requires knowledge of the abundances of species in the species pool, which we could not determine during our short field season. Because the passive sampling model predicts increased species richness with increased sample size (larger islands host more individuals), under this model one would expect a positive correlation between species richness and number of individuals present in a cave. Arita (1996) found evidence for this correlation in 36 caves of the Yucatan, but the correlation was absent in a study of 213 caves throughout Mexico (Arita 1993). It remains to be tested whether this correlation is present in caves of northern Puebla. Regarding the equilibrium model, some authors questioned its applicability and assumptions (Brown and Lomolino 2000; Lomolino 2000). Its main prediction is the existence of a species turnover; evidence for this has been difficult to find in other studies (McCoy 1982). Additionally, rates of immigration and extinction necessary to test the hypothesis are difficult to calculate (Coleman et al. 1982).

The data we present warrant further research to explore the relationship between spatial variation in relative humidity with both cave surface area and bat species richness and to test alternative explanations for the observed species–area relationship. Future research also should focus on 2 aspects: characterizing other morphologic features of cave walls and ceilings that might contribute to species segregation or roost choice (such as cracks and crevices) and assessing temporal variation of microclimatic conditions. It is likely that microclimatic conditions in these caves vary annually. Our study was done during summer, but temperatures in the area vary throughout the year, reaching a peak in May. Precipitation, which affects air humidity, is highest during the rainy season. In winter, the area also is often affected by strong winds that quickly change local temperature and humidity for short periods of time (Medellín and López-Forment 1985). If the habitat diversity model holds, we would expect the species richness of bat assemblages in caves to follow the yearly variation in microclimatic conditions.

We have demonstrated that the species–area curve applies to bats living in caves at the regional scale when dealing with a single, shared bat fauna in a relatively small area, and that physical features such as avons might favor a higher species richness. Caves are an interesting model to further test the applicability of the species–area relationship in ecosystems.

**Resumen**

Pusimos a prueba la relación entre el número de especies de murciélagos y el área...
inera de 20 cuevas en el centro de México y estudiamos el papel que juega el modelo de diversidad de hábitat como un factor explicativo de esta relación. Encontramos una correlación positiva significativa entre el logaritmo de la riqueza de especies y el logaritmo del área interna de la cueva, lo que as evidencia de la existencia de una relación especies–área. Nuestros datos sugieren que la diversidad de los sitios de refugio, de acuerdo con la variación espacial en humedad relativa y la presencia de avonis (de presiones cónicas en el techo de las cuevas) es un factor que contribuye a la relación especies–área.

ACKNOWLEDGMENTS

This work is dedicated to the memory of Dr. Elmer C. Birney. R. Timm, K. Kramer, and W. Schmid were instrumental to the writing of this manuscript and comments from M. Lomolino and an anonymous reviewer greatly improved it. We thank the landowners and guides who assisted in finding the study caves, as well as R. Ávila who provided valuable knowledge about the study site. Special recognition goes to our tireless field assistants J. S. Mitre-Morales, M. Cameron, and A. Flis. This study was funded by grants from the Latin American Fellowship of the American Society of Mammalogists, the Dayton–Wilkie Natural History Fund, the Sigefoos Research Fund, and the Explorers Club Exploration Fund. This paper is a publication of the Programa para la Conservación de los Murciélagos Migratorios (PCMM, Program for the Conservation of Migratory Bats).

LITERATURE CITED


APPENDIX I

Bat species found in study caves (abbreviations in parentheses correspond to caves in which the species was found and can be inferred in Table 1): Artibeus jamaicensis (LS, LC, EC, LP, V, CLV); Carollia perspicillata (ET, MI, LS, SM, EA, W, LC, V, CLV); Desmodus rotundus (EE, LH, EM, LS, SM, EA, NS, LCO, EC, LP, V, CLV); Diphylla ecaudata (LS, EA, V, ETG, CLV); Glossophaga soricina (LCH, MI, SM, ES, NS, V, CLV); Leptonycteris curasoae (CLV); Micronycteris megalotis (LS); Myotis keaysi (SM, ES, LCO, LC, CLV); Myotis nigricans (EC, CLV); Myotis thysanodes (SM, LCO, V); Myotis velifer (LS, ES, LC, LP, CLV); Natalus stramineus (ES, CLV, LS, V); Pteronotus parnellii (EA, LC, CLV).