ECOLOGICAL, TAXONOMIC, AND PHYSIOLOGICAL CORRELATES OF CAVE USE BY MEXICAN BATS

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Roost use by bats is likely affected by their water balance and thermoregulatory abilities. To test this hypothesis, we explored the relationship between 4 traits of different species of bats (body size, general food habits, taxonomic group, and thermoregulatory pattern) and microclimates at roosts (temperature and humidity). We recorded roost variables and presence of bats in 18 caves from 5 contrasting biomes in central Mexico. There was little evidence of microclimatic specificity among the 23 species studied, but maternity colonies used warmer roosts and hibernating bats used cooler roosts. Heterothermic species (Vespertilionidae) used colder caves with the widest temperature range (1.6–29.8°C), whereas homeothermic species (Emballonuridae, Mormoopidae, Phyllostomidae, and Natalidae) occupied warmer roosts (14.5–37.5°C). Within these caves, precise (narrow body temperature range) homeotherms occupied slightly cooler roosts than more labile homeotherms. Body size alone was not associated with cave use patterns. However, when homeotherms and heterotherms were examined separately, body size and temperature were negatively correlated. The smallest homeothermic insectivorous species (<10 g) consistently occupied roosts with temperatures >20°C (more often >25°C), whereas only the largest homeothermic insectivores were found as low as 16°C. Frugivorous, nectarivorous, and sanguivorous bats were found in a wide range of temperatures (14.5–37°C), but often at <20°C. Humidity in roosts was highly variable for most species and we did not detect any trend regarding this factor. Our data suggest that the thermoregulatory ability resulting from the complex interaction of body size, type of food, and taxonomic affiliation constrains species with respect to types of roosts that they can successfully exploit. Our results support the hypothesis that temperature is the most important physical factor influencing roost selection in bats.

Key words: bats, caves, Mexico, microclimate, thermoregulation, use of roosts

Roosts are key resources for bats because bats spend over half their lives subjected to selective pressures of roost environments (Kunz 1982; Vaughan and O’Shea 1976). Bats occupy a variety of roosts, but many species use caves as roosting sites (Hill and Smith 1984; Kunz 1982). In Mexico, almost half of the 138 species use caves as primary or alternative roosts (Arita 1993).

Roost selection by bats depends on many factors, including temperature, humidity, air flow, light intensity, safety from predators, proximity to foraging areas, and takeoff height (Gaur 1980; Hill and Smith 1984; Kunz 1982; McCracken 1989; Morrison 1980; Tuttle and Stevenson 1981). Within a given species, individual roost requirements vary according to season, sex, reproductive status, and age (Humphrey 1975; Stebbings 1995). Roost selection can be important for optimizing several physiological processes. For example, temperature, humidity, and airflow could be the most important physical factors influencing roost selection (Hill and Smith 1984; Tuttle and Stevenson 1981). Occupation of roost sites with appropriate microclimate can minimize energetic costs related to thermoregulation, food digestion and assimilation, maintenance of a permanent state of alertness (which allow bats to avoid predation and to interact socially), gestation, embryonic development, parental care, lactation, and spermatogenesis (Bonaccorso et al. 1992; Hamilton and Barclay 1994; Hill and Smith 1984; Humphrey 1975; Kunz 1973; McNab 1982; Tuttle and Stevenson 1981; Twente 1955).

Given the benefits obtained from selecting optimal roosting sites, a high specificity in roost use can be expected among species of bats. Although several bat species have highly specific roost requirements (Baudinette et al. 2000; Humphrey 1975; McCracken 1989; McNab 1974), the opposite trend can be expected for wide ranging, common species considering that optimal roosts are limited in number (e.g., Tuttle and Stevenson 1981). Most bats are opportunistic with respect to roosting habits, using a variety of roosts, including man-made structures.
Anecdotal observations suggest that many species can tolerate a wide range of roost conditions. If optimal roost conditions are not frequently available and high specificity is not common among bats, what factors ultimately limit the type of roosts that bats can use? Diversity of roost use by bats may largely reflect different physiological responses to microenvironmental conditions (Silva 1979). Thermoregulatory and water-balance abilities seem to influence the ability of species to use different kinds of roosts (Baudinette et al. 2000). If this is true, factors that determine such physiological traits should also influence the degree of plasticity shown by bats regarding use of roosts.

Thermoregulatory abilities of mammals (including bats) depend on factors such as body size, basal metabolic rate, thermal conductance, food habits (Degen 1997; Elgar and Harvey 1987; Hayssen and Lacy 1985; Lyman 1970; McNab 1982, 1989, 1992), and probably phylogeny (Elgar and Harvey 1987; Hayssen and Lacy 1985; McNab 1997). The problem of water balance is more complex because it is linked to osmoregulation and excretory systems. For example, although food habits are known to affect water intake, some mammals have adapted to eat dry foods by modifying kidney structure (Degen 1997). However, body size is a primary factor influencing water balance in small mammals (Degen 1997; Studier 1970).

In this study we explore the hypothesis that variation in roost use exhibited by bats strongly reflects their thermoregulatory and water-balance abilities. We evaluated the relationship between some features associated with physiological performance and the microclimate of sites used as roosts. Particularly, we related body mass, food habits, taxonomic affinity, and thermoregulatory pattern of 23 species of bats to levels of temperature recorded in natural roosts of central Mexico. Because of the complexity of factors affecting balance of water in mammals, we restricted correlates of roost humidity exclusively to body size.

Materials and Methods

Study sites.—We studied 18 caves and mines in the states of Puebla and Mexico, in central Mexico. This area is complex and heterogeneous in topography, vegetation, and climate (Ortega and Arita 1998; Rzedowski 1978). We studied caves in 3 physiographic regions (Balsas River Basin, Gulf Coastal Plain, Sierra Madre Oriental, Tehuacan Valley, and Trans-volcanic Belt—Rzedowski 1978) and 5 habitats (tropical evergreen forest, tropical deciduous forest, subtropical cloud forest, temperate coniferous forest, and xerophytic scrub; Appendix I).

Roost characteristics.—From December 1997 to October 1998, we conducted 4-day-long seasonal (winter, spring, summer, and autumn) visits to each cave. At each visit we measured air temperature and relative humidity using a digital thermohygrometer (precision ± 2% relative humidity and ± 0.4°C; Hanna Instruments, Inc., Ann Arbor, Michigan) as close as possible to the roosting surfaces. Microclimatic variables were measured at 0400, 1000, 1600, and 2200 h each day. Microclimatic stations were established exclusively at sites occupied by bat colonies, regardless of colony size. We started each visit by mapping the specific roosting sites of each species. The number of stations in each cave ranged from 2 to 13.

We determined the type of rock by direct observation and made a topographic map of each cave following methods of Nuñez-Jiménez et al. (1988). We also noted if bats roosted inside or outside cavities (crevices, cracks, fissures) with a diameter or width < 50 cm.

Biological data.—We captured bats nightly and daily at entrances or inside caves using mist nets and hand nets, and identified species following Medellín et al. (1997). We obtained information on size, sex, age (juvenile, adult), reproductive status (only for females: inactive, pregnant, lactating), and apparent thermoregulatory state (normothermic, hypothermic, torpid), partly to determine roost use—hibernacula, maternity roost, or nonbreeding male and/or female roosts. Normothermic bats were individuals observed visibly awake when encountered and/or found warm at touch (normothermia refers to optimal body temperature, i.e., a temperature that allows common physiological processes to occur); torpid bats (including hibernating) were those individuals exhibiting no apparent movement and found cold at touch; hypothermic bats were identified as above, but were arbitrarily placed in this category when corresponding to typical homeothermic species (e.g., McNab 1969, 1982) that can decrease body temperature under unusual conditions (Audet and Thomas 1997). Because roost use can reflect different individual physiological requirements, we compared the observed physiological state of bats to roost temperature and humidity, regardless of species. We compared roosts used by basal state bats (not pregnant or lactating, normothermic bats) to those used by reproductive (pregnant or lactating) females, torpid bats, and hypothermic bats.

We calculated mean body size of species based on body mass of captured specimens; we obtained additional measurements from museum specimens (Colección Nacional de Mamíferos, Instituto de Biología, UNAM) when < 10 individuals were measured in the field. We combined masses for males and females in calculating means. Information about diet, taxonomy, and physiological responses to changes in environmental humidity and temperature (both free living and captive) was obtained from the literature.

Main food type, taxonomic affiliation and thermoregulatory pattern were separated into categories, and each species was assigned to 1 of these categories. Food categories were insects, nectar and pollen, fruit, and blood. Taxonomic groups included families Emballonuridae, Mormoopidae, Natalidae, and Vespertilionidae, and subfamilies Phyllostominae, Glossophaginae, Carollininae, Stenodermatinae, and Desmodontinae (Phyllostomidae). We classified thermoregulatory patterns as follows (modified from Dwyer 1971 and McNab 1982). Type 0, species that can maintain body temperature (Tb) a few degrees above ambient temperature (Ta), capable of entering deep torpor and arousing from it at very low Tb; basal metabolic rate lower than that expected from Kleiber function. Type 1, species that behave like Type 0 but do not enter deep torpor nor arouse from low Tb; basal metabolic rate lower than or equal to that expected from Kleiber function. Type 2, labile homeotherms, or species that maintain Tb within a moderately wide range when exposed to a variety of T; Tb; basal metabolic rate less than or equal to that expected. Type 3, precise homeotherms, species that maintain Tb within a narrow range under a wide range of Tb, although some species can relax Tb at moderate Tb (Audet and Thomas 1997; McNab 1969; Studier and Wilson 1970); basal metabolic rate is equal or higher to that expected from the Kleiber function.

Species were classified into types 0, 2, and 3. We classified no species as type 1. Although individuals of N. stramineus can become lethargic in nature under unusual environmental conditions (McNab 1982; Nowak 1994), we always observed this species alert at Ta ranging between 17°C and 25°C, and never forming compact groups or entering a state resembling hypothermia or torpor. Although vampire bats (Desmodus rotundus and Diphylla ecaudata) can tolerate Ta as
low as 10°C (McNab 1969, 1982; Villa-R. 1966), and could be placed in category 3, we assigned these species to category 2 because of their very low basal metabolic rates (McNab 1989), and because some individuals maintain body temperatures lower than 33°C at ambient temperatures of 10°C (McNab 1969).

Statistical analysis.—We calculated mean and range of temperature and humidity for each species using the measurements taken when at least some individuals were present at the roost site. In order to group species that use microclimatically similar roosts, we performed a cluster analysis using Ward’s hierarchical method (SAS Institute Inc. 1995) and obtained corresponding dendrograms. We computed 2-cluster analyses, 1 for temperature and 1 for humidity, comparing species that use microclimatically similar roosts, we performed

Further statistical analyses were performed using a database containing all temperature and humidity site-specific averages. We calculated these averages using both nightly and daily measurements of temperature and humidity taken at a given site during each 2-day visit, each average representing 1 data point. Differences in roost use according to observed physiological state of bats were evaluated by 2-cluster analyses, 1 for temperature and 1 for humidity, comparing categories or groups of species separately for each of the other 3 variables. Our data did not follow a normal distribution and variances were not homogeneous, thus we used nonparametric, 1-way analysis of variance (Kruskall–Wallis test) to look for differences among groups. Paired differences between groups were evaluated by means of Mann–Whitney tests. For relative humidity, we only explored correlations with body size. In all cases we used a critical alpha value of 0.05. We used computational software from SAS Institute Inc. to conduct the cluster analysis and SPSS software for other analyses.

RESULTS

We found 23 species of bats of 5 families (number of species in parentheses): Emballonuridae (1), Mormoopidae (4), Phyllostomidae (11), Natalidae (1), and Vespertilionidae (6). Five subfamilies were represented among phyllostomids: Phyllostominae (2), Glossophaginae (4), Carolliiinae (2), Stenodermatinae (1), and Desmodontinae (2). Information about each species is summarized in Tables 1–3.

### Table 1. Body size and thermoregulatory traits of 23 species of bats that use caves in central Mexico. Patterns of thermoregulation: 0, heterotherms which can enter in deep torpor; 2, labile homeotherms (moderate range of Tb); 3, precise homeotherms (narrow range of Tb).

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean body mass (g)</th>
<th>Mean basal metabolic rate (ml O₂ g/h)</th>
<th>Mean Tb in thermoneutrality (°C)</th>
<th>Mean Tb at Ta = 10°C (°C)</th>
<th>Thermoregulatory pattern</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balantiopteryx picta</td>
<td>5.3</td>
<td>1.86–2.65a</td>
<td>36.9</td>
<td>37.0</td>
<td>2</td>
<td>Genoud and Bonaccorso 1986</td>
</tr>
<tr>
<td>Mormoops megalophylla</td>
<td>15.1</td>
<td>1.48</td>
<td>36.9</td>
<td>37.0</td>
<td>3</td>
<td>Bonaccorso et al. 1992</td>
</tr>
<tr>
<td>Pteronotus davii</td>
<td>7.3</td>
<td>1.63</td>
<td>38.8</td>
<td>33.0</td>
<td>2</td>
<td>Bonaccorso et al. 1992</td>
</tr>
<tr>
<td>P. parnellii</td>
<td>16.0</td>
<td>1.60</td>
<td>36.4</td>
<td>34.5–35.3</td>
<td>3</td>
<td>Bonaccorso et al. 1992</td>
</tr>
<tr>
<td>P. personatus</td>
<td>5.5</td>
<td>1.64</td>
<td>37.5</td>
<td>32.5</td>
<td>2</td>
<td>Bonaccorso et al. 1992</td>
</tr>
<tr>
<td>Macrocterus waterhousii</td>
<td>15.1</td>
<td>1.25b</td>
<td>33.5–37.5</td>
<td>32.0</td>
<td>2</td>
<td>Bell et al. 1986; Riedesel and Williams 1976</td>
</tr>
<tr>
<td>Micronycteris megalotis</td>
<td>6.7</td>
<td></td>
<td>38.6</td>
<td>17.5</td>
<td>2</td>
<td>McManus 1977; Studier and Wilson 1970</td>
</tr>
<tr>
<td>Choeronycteris mexicana</td>
<td>15.2</td>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>McManus 1977; McNab 1969, 1989; Studier and Wilson 1970</td>
</tr>
<tr>
<td>Glossophaga soricina</td>
<td>9.8</td>
<td>2.25</td>
<td>35.5</td>
<td>11.5–36.5</td>
<td>3</td>
<td>Arends et al. 1995; Carpenter and Graham 1967; McNab 1969, 1989</td>
</tr>
<tr>
<td>Leptonycteris curasoae</td>
<td>22.5</td>
<td>1.42, 1.66, 2.00</td>
<td>35.3–35.7</td>
<td>35.0–37.0</td>
<td>3</td>
<td>McManus 1977; McNab 1969, 1989; Studier and Wilson 1970</td>
</tr>
<tr>
<td>L. nivalis</td>
<td>30.2</td>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>McNab 1969; Studier and Wilson 1970</td>
</tr>
<tr>
<td>Carollia brevicauda</td>
<td>15.9</td>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>McNab 1969; Studier and Wilson 1970</td>
</tr>
<tr>
<td>C. perspicillata</td>
<td>18.3</td>
<td>2.11</td>
<td>36.4</td>
<td>12.0–37.0</td>
<td>3</td>
<td>McNab 1977; McNab 1969, 1989, Studier and Wilson 1970</td>
</tr>
<tr>
<td>Artibeus jamaicensis</td>
<td>41.5</td>
<td>1.25</td>
<td>36.4</td>
<td>14.0–38.0</td>
<td>3</td>
<td>McNab 1977; McNab 1969, 1989, Studier and Wilson 1970</td>
</tr>
<tr>
<td>Desmodus rotundus</td>
<td>34.9</td>
<td>0.91</td>
<td>35.0</td>
<td>32.0–36.0</td>
<td>2</td>
<td>McNab 1977; McNab 1969, 1989, Studier and Wilson 1970</td>
</tr>
<tr>
<td>Diphylla ecaudata</td>
<td>31.1</td>
<td>1.22</td>
<td>32.4</td>
<td>31.0–32.5</td>
<td>2</td>
<td>McNab 1977; McNab 1969, 1989, Studier and Wilson 1970</td>
</tr>
<tr>
<td>Natalus stramineus</td>
<td>5.9</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>McNab 1977; McNab 1969, 1989, Studier and Wilson 1970</td>
</tr>
<tr>
<td>C. townsendi</td>
<td>8.8</td>
<td></td>
<td></td>
<td></td>
<td>0</td>
<td>Herreid and Schmidt–Nielsen 1966</td>
</tr>
<tr>
<td>Eptesicus juscus</td>
<td>16.2</td>
<td>0.80–1.20</td>
<td></td>
<td></td>
<td>0</td>
<td>McNab 1989</td>
</tr>
<tr>
<td>Myotis keayi</td>
<td>3.8</td>
<td>1.30d</td>
<td></td>
<td></td>
<td>0</td>
<td>Riedesel and Williams 1976</td>
</tr>
<tr>
<td>M. velifer</td>
<td>9.7</td>
<td>0.65–1.55</td>
<td>36.0–36.2</td>
<td>11.8–12.1</td>
<td>0</td>
<td>Riedesel and Williams 1976</td>
</tr>
<tr>
<td>M. volans</td>
<td>5.8</td>
<td></td>
<td></td>
<td></td>
<td>0</td>
<td>Riedesel and Williams 1976</td>
</tr>
</tbody>
</table>

a Calculated for other emballonurids (Saccopteryx leptura, S. bilineata, and Peropteryx macrotis).
b Calculated for Macrocterus californicus.
c McNab (1982) places this species in thermoregulatory pattern 1.
d Calculated for Myotis nigricans.
nonreproductive, normothermic bats. No significant differences were observed between roosts of hypothermic bats and those of nonreproductive bats ($U = 273, P = 0.542$) and reproductive females ($U = 20, P = 0.250$), probably because of the few records (2) from hypothermic bats.

Cluster analysis using temperature data (Fig. 2) yielded 2 main groups: species that were observed in a wide roost temperature range ($>10^\circ C$), and species that were found in a narrower range of roost temperatures ($<10^\circ C$). Within the 1st group, 5 homeothermic insectivores belonging to 3 taxa (Balantiopteryx plicata, Pteronotus parnellii, Mormoops megalophylla, Macrotox waterhousii, and Micronycteris megalotis) and Leptonycteris curasoae, a pollen-nectarivore (species feeding primarily on nectar and secondarily on pollen), formed a unique subgroup distinguished by the use of hot roosts ($X$ temperatures between 26 and 32°C). Frugivores (Carollia perspicillata and Artibeus jamaicensis), other pollen-nectarivores (Choeronycteris mexicana and Glossophaga soricina), 1 sanguivore (Desmodus rotundus), and 2 heterothermic insectivores (Myotis keaysi and P. personatus) formed another subgroup at the highest roost temperatures ($X \sim 35^\circ C$); another subgroup was formed by a large nectarivore (Leptonycteris nivalis), a frugivore (Carollia brevicauda), a vampire (Diphylla ecaudata), and an insectivore (Natalus stramineus), all of which roosted at intermediate temperatures ($X \sim 20^\circ C$). The 3rd subgroup was formed by 3 Nearctic heterothermic insectivores (Corynorhinus mexicanus, Eptesicus fuscus, and Myotis volans) observed at the coolest roost temperatures ($X: 7–13^\circ C$).

Log body mass and log roost temperature were positively correlated ($r = 0.132, P = 0.009$; Fig. 3). Correlation between these variables was significant and negative as expected when homeotherms and heterotherms were evaluated separately ($r = -0.344, P < 0.001$ for homeotherms; $r = -0.426, P < 0.001$ for heterotherms; Fig. 3). Within the homeothermic group, type 2 species, hypothesized to be the most sensitive to roost temperature, showed a significant correlation between roost temperature and body size ($r = -0.559, P < 0.001$; type 3 species, hypothesized to be less sensitive to changes in ambient temperature, showed no correlation ($r = -0.132, P = 0.125$; Fig. 3). This indicates that body mass is not strongly related to roost temperature for all species of bats, but is an important factor for labile homeotherms. Roost temperature trends were also evaluated within trophic, thermoregulatory, and taxonomic groups of species (Fig. 4). Kruskall–Wallis tests on each variable yielded significant differences at least between 1 of the pairs of groups (for general food habit categories: $\chi^2 = 13.2,$...
E. fuscus  
D, Na
D, N  
Barbour and Davis 1969; Kurta and Baker 1990; Reid 1997

C. townsendii
D, N
D, N  
Barbour and Davis 1969; Kunz and Martin 1982

M. velifer
D, Na
D, N  
Barbour and Davis 1969; Reid 1997

D. rotundus
D, Na
D, N  
Greenhall et al. 1983; Reid 1997

G. soricina
D, Na
(D)
(D)  
Reid 1997

M. keaysi
D, Na
Tumlison 1992

C. mexicanus
D, Na
D, N  
Alvarez et al. 1991; Reid 1997

C. perspicillata
D, Na
(D), N  
Cloutier and Thomas 1992

L. nivalis
D, Na
D, N  
Cockrum 1991; Reid 1997

C. breviceps
D, Na
D, N  
Arroyo-Cabrales et al. 1987; Davis and Russell 1952

M. megalotis
D, Na
D
Anderson 1969; Barbour and Davis 1969; Reid 1997

M. waterhousii
D, Na
D
Bateman and Vaughan 1974; Reid 1997

P. personatus
D, Na
D
Herd 1983; Reid 1997

P. parnellii
D, Na
D  
Adams 1989; Bateman and Vaughan 1974

P. davyi
D, Na
D
Reid 1997; Rezsutek and Cameron 1993

M. megalophylla
D, Na
D, Na
Barbour and Davis 1969; Bateman and Vaughan 1974; Reid 1997

L. curasoae
D, Na
D, N  
Alvarez et al. 1991; Reid 1997

M. megalophylla
D, Na
D, Na
Arroyo-Cabrales et al. 1987; Davis and Russell 1952

C. mexicana
D, Na
D  
McNab 1969.

### DISCUSSION

**Specificity in roost requirements.**—Our results support the hypothesis that most species of bats in caves of Mexico have little specificity (i.e., they are not obligated to exploit a narrow range of environmental conditions) in roost requirements. However, we did not measure preference (i.e., optimal conditions sought by individuals regardless of degree of tolerance). Only 8 of the 23 species studied used roosts showing temperature variations less than 10°C, whereas only 5 species were observed within ranges of relative humidity less than 20%. These relatively narrow ranges of roost temperature and humidity were found in species from which we obtained few data, such as *Leptonycteris curasoae* and *Eptesicus fuscus*. Only *Pteronotus davyi* and *P. personatus* showed some degree of thermal specificity. The small *Pteronotus* (*P. davyi, P. personatus, and P. quadridens*) usually are reported from very hot caves (33.0–36.0°C—Aguilar and Ruiz 1995; Bonaccorso et al. 1992; Rodriguez–Durán 1995; this study), with 27°C being the lowest recorded temperature (Arita and Vargas 1995; McNab 1969).

Torpid and reproductive bats tend to have a relatively narrow microclimatic specificity. The significant association observed between roost temperature and physiological state of individuals, regardless of species, suggests that this specificity is a reflection of individual energetic demands rather than species-specific requirements. *Pteronotus parnellii, M. megalophylla,* and *L. curasoae* seem to depend on hot caves during lactation; they were observed in wide ranges of temperature (>15°C) and humidity (>50%), but only used the hottest cave as maternity roost. In all 3 cases, maternity

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**Table 3.**—Types of roosts reported for species of bats using caves in central Mexico, with additional data on night roosts from this study (see Table 1 for generic names). Letters in parentheses refer to occasional roosts. D, day roosts; N, night roosts.

<table>
<thead>
<tr>
<th>Species</th>
<th>Caves</th>
<th>Mines</th>
<th>Man-made structures</th>
<th>Trees</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>B. pilica</em></td>
<td>D, N</td>
<td>D</td>
<td>D</td>
<td>D</td>
<td>Arroyo-Cabales and Jones 1988</td>
</tr>
<tr>
<td><em>M. megalophylla</em></td>
<td>D, N</td>
<td>D</td>
<td>(D)</td>
<td></td>
<td>Reid 1997; Rezsutek and Cameron 1993</td>
</tr>
<tr>
<td><em>P. davyi</em></td>
<td>D, N</td>
<td>D,N</td>
<td></td>
<td></td>
<td>Adams 1989; Bateman and Vaughan 1974</td>
</tr>
<tr>
<td><em>P. pteronyx</em></td>
<td>D, N</td>
<td>D</td>
<td></td>
<td></td>
<td>Herd 1983; Reid 1997</td>
</tr>
<tr>
<td><em>P. personatus</em></td>
<td>D, N</td>
<td>D,N</td>
<td></td>
<td></td>
<td>Bateman and Vaughan 1974; Reid 1997</td>
</tr>
<tr>
<td><em>M. townsendii</em></td>
<td>D, N</td>
<td>D,N</td>
<td></td>
<td></td>
<td>Anderson 1969; Barbour and Davis 1969; Reid 1997</td>
</tr>
<tr>
<td><em>M. velifer</em></td>
<td>D, Na</td>
<td>D</td>
<td></td>
<td></td>
<td>Greenhall et al. 1983; Reid 1997</td>
</tr>
<tr>
<td><em>M. megalophylla</em></td>
<td>D, N</td>
<td>D</td>
<td></td>
<td></td>
<td>Greenhall et al. 1984; Reid 1997; Villa–R. 1966</td>
</tr>
<tr>
<td><em>A. jamaicensis</em></td>
<td>D, N</td>
<td>D,N</td>
<td></td>
<td></td>
<td>Moreno 1996</td>
</tr>
<tr>
<td><em>D. rotundus</em></td>
<td>D, N</td>
<td>D,N</td>
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<td>Greenhall et al. 1983; Reid 1997</td>
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<td><em>D. ecaudata</em></td>
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<td>Greenhall et al. 1984; Reid 1997; Villa–R. 1966</td>
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<td><em>N. stramineus</em></td>
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<td>Moreno 1996</td>
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<td><em>C. mexicanus</em></td>
<td>D</td>
<td>D</td>
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<td></td>
<td>Tumlison 1992</td>
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<tr>
<td><em>C. townsendii</em></td>
<td>D, N</td>
<td>D</td>
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<td></td>
<td>Barbour and Davis 1969; Kunz and Martin 1982</td>
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<tr>
<td><em>E. fuscus</em></td>
<td>D, N</td>
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<td>Barbour and Davis 1969; Barbour and Davis 1969; Reid 1997</td>
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<tr>
<td><em>M. keaysi</em></td>
<td>D, N</td>
<td>D</td>
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<td></td>
<td>Reid 1997</td>
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<tr>
<td><em>M. velifer</em></td>
<td>D, N</td>
<td>D,N</td>
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<td></td>
<td>Barbour and Davis 1969; Barbour and Davis 1969; Reid 1997</td>
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<tr>
<td><em>M. volans</em></td>
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<td>D,N</td>
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<td>Warner and Czaplewski 1984</td>
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* Information from this study.
roost temperature was 33.5–37.0°C and humidity ranged between 45% and 90%, consistent with data from other studies (Aguilar and Ruiz 1995; Arends et al. 1995; Bonaccorso et al. 1992; Fleming et al. 1998; Riechers et al. 1998; C. Chávez-Tovar and G. Ceballos pers. comm.; Program for Conservation of Mexican Bats [PCMM], in litt.).

Temporal specificity in roost use has been reported for many Holarctic species, mainly vespertilionids, which typically show 2 well defined stages: the winter phase, when both males and females roost in cold sites to hibernate, and summer phase, when females use warm roosts to rear young, while most males roost in cooler places (Kunz 1982). In this study, only M. velifer differentially used both kinds of roost, similar to reports from more temperate regions (Fitch et al. 1981; Kunz 1973; Twente 1955). However, we found a nonhibernating, year-round resident colony using the same cave as a maternity roost, suggesting that the 2-phase pattern is not typical of the species.

Rock type, perch surfaces, cave size, and degree of lighting seem to have minimal direct effects on roost site selection (Table 2), as has been described elsewhere (see Table 3). However, these parameters can become very important as they affect microclimate (Tuttle and Stevenson 1981). Microstructural heterogeneity probably favors the establishment of multispecific assemblages in single caves, as has been recently documented in dissolved sandstone caves from northern Puebla, Mexico (Brunet and Medellín 2001).

Most cases of roost specificity are related to optimization of several physiological processes for which temperature plays a fundamental role. Parturition, lactation, and hibernation are critical phases for bats (Gittleman 1988; Kunz 1973; Kurta et al. 1990; McNab 1974; Richter et al. 1993; Speakman and Racey 1987; Studier et al. 1973; Tuttle 1975). Because high-latitude species face both the coldest temperatures and most pronounced food shortage during winter, and because warm roosts necessary for successful reproduction are not common during summer in many of these regions (Tuttle and Stevenson 1981), Holarctic species should display some degree of seasonal specificity. This might be why temperature has been identified as the single most important physical factor governing roost selection by bats in temperate and cold regions (e.g., Betts 1997; Callahan et al. 1997; Hamilton and Barclay 1994; Kalcounis and Brigham 1998; Kunz 1973; McNab 1974; Ormsbee and McComb 1998; Rabe et al. 1998; Richter et al. 1993; Rydell 1990; Vonhof and Barclay 1996). Roost temperature also might be critical for subtropical and tropical species (Arita and Vargas 1995; Bonaccorso et al. 1992; Fleming et al. 1998; McCracken and Gustin 1991; Rodríguez-Durán 1995; this study).

Correlates to body size, diet, taxonomic affiliation, and thermoregulatory pattern.—Strict specificity in use of cave roosts seems to be uncommon among bats, and only some species show some degree of seasonal specificity, particularly in relation to roost temperature. Within an annual cycle, the ranges of temperature and humidity tolerated by each species in roosts are usually quite broad. Although bat microclimatic
plasticity must have limits, factors determining natural limits of roost temperature for any given species are unclear. Our data show that body size, diet, taxonomic affinity, and thermoregulatory pattern (traits associated with thermoregulatory ability) are related in some degree to roost temperature. Although each of these traits shows statistically significant differences among categories, no single factor determined strongly the temperature range that any species tolerates within roosts. Considering that such characters are not independent from one another (McNab 1992), we combined characteristics of each species to explain the observed patterns. Three of these characteristics (size, feeding habits, and taxonomic group) interact through metabolic rate to set the thermoregulatory capability of a species (Elgar and Harvey 1987; Hayssen and Lacy 1985; McNab 1992).

**Fig. 3.**—Correlation between mean body mass and roost temperature for 23 bat species from central Mexico. Points represent average seasonal temperatures for sites occupied by bat colonies. Three fitted lines were obtained for roost temperature according to thermoregulatory patterns of species: a) type 0 species (heterotherms), b) type 2 species (labile homeotherms), and c) type 3 species (more precise homeotherms).

**Fig. 4.**—Box plots of roost temperatures at colonies of 23 cave-dwelling bat species from central Mexico, grouped according to general food habits, pattern of thermoregulation, and taxonomic group. Box plots as in Fig. 1. Sample size indicated above each box. Categories for thermoregulatory patterns: 0, heterotherms capable of entering torpor; 2, homeotherms that maintain relatively wide ranges of body temperature under a variety of air temperatures (labile homeotherms); 3, homeotherms that maintain their body temperature in a narrow range under a variety of air temperatures (precise homeotherms). Categories for main source of food: insects, pollen–nectar, fruit, and blood. Taxonomic groups: *Emb*, Emballonuridae; *Mor*, Mormoopidae; *Phy*, Phyllostominae; *Glo*, Glossophaginae; *Car*, Carollini; *Ste*, Stenodermatinae; *Des*, Desmodontinae; *Nat*, Natalidae, *Ves*, Vespertilionidae.
Species able to enter torpor (pattern type 0) occupied the widest temperature range and the coldest roosts, from near 0°C to almost 30°C. Adding some extreme temperature data for type 0 species from the literature (e.g., Gaisler 1970; Harmata 1973; Henshaw and Folk 1966; Licht and Leitner 1967; Vaughan and O’Shea 1976), that range would increase at least by 20°C (from under −5°C to at least 45°C), which comprises the entire range of temperatures observed among bat species. Within homeotherms, those species with precise thermoregulatory capabilities (pattern type 3) were observed in the lowest temperatures and in a wider temperature range (14.5°C–37°C). Species with a more labile thermoregulatory capacity (pattern type 2) occupied a slightly narrower range of temperatures (15.9–37.5°C). The difference between these 2 groups was statistically significant, perhaps because type 3 species tend to use colder roosts (below 20°C) than type 2 species. If vampires (that indeed seem to be precise thermoregulators) were excluded from group 2, the difference between these groups would be even greater. Thus, the general pattern exhibited by each group would be much clearer, possibly as follows: species in group 0 use the more diverse roosts, from extreme temperatures below 0°C to near 40°C; group 1 species only use warm sites (between 30°C and 40°C, comprising the thermoneutral zone of many species); group 2 occupies sites between 20° and 40°C; and group 3 uses roosts with temperatures ranging from 10°C to 40°C. The lower limit of 10°C for homeothermic species is suggested by many studies in captivity (see data compiled by Lyman 1970; McManus 1977; McNab 1969) and by the scarce empirical data collected in the field (López-Wilchis 1999; McNab 1969; Vargas 1998; Villa-R. 1966).

Because thermoregulatory patterns at the species level are an outcome of the interaction of characteristics such as body size, type of diet, and taxonomic affinity (which are known or can be inferred for virtually all species), the combination of these variables could have practical predictive value. Such variables yielded more diffuse and complex patterns when they were treated separately. Body size alone, the primary factor determining basal metabolic rate (McNab 1969, 1992), was not correlated with roost temperature, but when diet, taxonomic affinity, and thermoregulatory performance are incorporated into this relationship, the pattern changes. The almost null correlation between body size and roost temperature is accentuated by the high dispersion of points along the y axis, which results from the great variation of roost temperatures for each species (Fig. 3). Assuming that maximum roost temperatures tolerated are similar for all species (slightly above the thermoneutral zone, i.e., around 40°C), it would be more appropriate to fit a line employing only the minimum roost temperatures used by species. This approach is more useful for homeothermic species, because heterotherms could theoretically occupy very similar minimum roost temperatures irrespective of size (but see McNab 1974 for preferred minimum roost temperatures as a function of size in vesperilionids).

The slope of this line could approximate a line that sets the lower limit of temperature, as a function of size, that any homeothermic bat can tolerate while roosting; similar to the relationship between body size and basal metabolic rate (McNab 1969, 1982), the residual variation could be explained mainly by feeding habits and taxonomic affiliation. Although our 1st approach to this relationship showed a negative relationship, where in general large species were found at lower minimum temperatures, more data are needed.

Relationships between feeding habits per se with roost temperature point out that frugivores, pollen–nectarivores, and sanguivores frequently can occupy minimum temperatures close to 15°C (lowest records: 15.0°C, 14.5°C and 15.9°C, respectively). Our records of medium-sized homeothermic insectivorous *P. parrelli* and *M. megalophylla* at temperatures near 16°C are noteworthy. In the literature, roost temperatures for these and other mormoopids generally have been reported as above 25°C (Arita and Vargas 1995; Bateman and Vaughan 1974; Bonaccorso et al. 1992; Rodríguez-Durán 1995), and a minimum of 22°C has been reported for *P. parrelli* (Vargas 1998). These 2 species and *Macrotus waterhousii* were the largest insectivorous bats evaluated in our study. Data from other sources for neotropical species confirm the trends observed here for each trophic group. Minimum roost temperatures reported for each group are: homeothermic insectivores, 18.5–27°C (Arita and Vargas 1995; McNab 1969; Vargas 1998); frugivores, 11.5–19°C (López-Wilchis 1999; McNab 1969; Vargas 1998); nectarivores, 12–19°C (McNab 1969; Vargas 1998; PCMM, in litt.); sanguivores, 13–16.5°C (McNab 1969; Vargas 1998); and carnivores, 14°C (McNab 1969).

Diets of fruit, pollen–nectar, vertebrates, and perhaps to a lesser degree blood allow their consumers to use colder roosts, sometimes dipping to 10°C for short periods. Our data on minimum roost temperature for homeothermic insectivores...
(B. plicata, M. megalophylla, P. parnelli and N. stramineus) are lower than previous records, probably because the study area is close to the northernmost limit for many tropical species. In stable environments, a diet of insects probably allows only medium and large species (such as M. megalophylla and P. parnelli) to use roosts where temperature sometimes drops to 15°C. The smallest insectivores can use roosts with temperatures as low as 20°C (there are only a few records slightly below this for B. plicata and N. stramineus), although most species prefer temperatures above 25°C (Table 2). Strict microclimatic specialization occurs among the small homeothermic insectivores, the least efficient thermoregulators, which select roosts with temperatures within their thermoneutral zone (30–40°C); the 2 smallest Mormoopids are restricted to very hot roosts (Table 2; Fig. 4).

In general, species that can acquire large quantities of energy during feeding can employ a larger proportion of available energy to face a great variety of thermal environments, including those that are energetically expensive (roost temperature below thermoneutral zone). Thus, fruit, nectar–pollen, and vertebrates, available throughout the year in many tropical regions, provide an abundant and constant energy supply (McManus 1977; McNab 1969). High caloric value of fruits (Dinerstein 1986) and nectar (Howell 1974) facilitate the acquisition of a surplus of energy. Moreover, large sizes associated with carnivory and frugivory can increase thermoregulatory ability by reducing surface-to-volume ratio (hence reducing heat loss) and by making the turnover of energy stores more efficient (Dwyer 1971; McNab 1982). Thus, species of the latter trophic guilds show high rates of metabolic heat production, which permit them to exploit otherwise unfavorable roosts. Insectivores face at least 2 major problems: their size is generally small, which makes them more vulnerable to low temperatures; and their food source exhibits a strong seasonality even in tropical environments, which reduces energy acquisition (McManus 1977; McNab 1969). Torpor-capable insectivores can exploit the coldest roosts, whereas other species must use almost exclusively hot roosts. The case of sanguivores is more complex. Their prey can be locally abundant, but their inability to transport large quantities of food limits their daily energy intake (McNab 1973); also, the usable caloric value of blood is very low (Wimsatt 1969). Both factors explain the low metabolic rates of vampires (McNab 1989), but they do not explain the observed ability of vampires to tolerate ambient temperatures in roosts close to 10°C (McNab 1969; PCMM, in litt.).

Microchiroptera exhibit strong relationships between taxonomic affiliation and several morphological, physiological and ecological traits of species (Cruz-Neto and Jones in press; Freeman 2000; McNab 1986, 1992). Although phylogeny might have a strong influence on basal metabolic rate of bats (Cruz-Neto and Jones in press), it is difficult to separate its individual effects upon other traits such as thermoregulatory pattern or roost use. However, vespertilionids showed the only pattern clearly determined by phylogenetic inertia. In the Americas, there are many small insectivorous species, but vespertilionids are the only group that can enter deep torpor (Hill and Smith 1984; McNab 1982), including at least some of its tropical members (e.g., Studier and Wilson 1970); our observations on Myotis keaysi in the field and laboratory support this view (it is capable of entering and arousing from deep torpor at 3°C). The use of torpor allows vespertilionids to use a variety of roosting conditions, and to range around the world, exploiting nearly all terrestrial biomes and environments.

No clear pattern regarding roost humidity was found. The observed trend in roost humidity can reflect the aridity of the external environment. Species observed in zones of xerophytic scrub and/or tropical deciduous forest were also those observed in the driest roosts and in the widest ranges of relative humidity, whereas species found in humid roosts inhabit tropical evergreen forests, subtropical cloud forests, and coniferous forests. Alternatively, bats roosting in hot caves could select sites with low to moderate levels of humidity to facilitate pulmocutaneous water loss (Baudinette et al. 2000; Bonaccorso et al. 1992). Variation in roost humidity is positively correlated with species richness within some tropical caves, which suggests that water balance might be a significant factor for bats in warm environments and could partially determine species richness of cave bats (Arita 1993; Brunet and Medellín 2001). Our results, however, suggest that roost use is limited more by temperature than by relative humidity. Structural characteristics of roosts might be important because they influence microclimatic parameters. Our findings support the hypothesis that temperature is the most important and restrictive roost parameter for bats.

RESUMEN

El uso de refugios por los murciélagos probablemente refleja las capacidades de termorregulación y de balance hídrico propias de cada especie. Para probar esta hipótesis, exploramos la relación que guardan cuatro atributos de las especies asociados con tales capacidades fisiológicas (tamaño corporal, tipo general de alimentación, grupo taxonómico y patrón de termorregulación) con el microclima (temperatura y humedad relativa) de los sitios utilizados como refugio. Recopilamos datos de microclima y registramos la presencia de especies en 18 cuevas del centro de México situadas en 5 diferentes tipos de ecosistema. Las 23 especies encontradas mostraron poca evidencia de especificidad microclimática, aunque en general utilizaron refugios más calientes durante los períodos de maternidad, y refugios más fríos para hibernar. Los hetero-temnos en su conjunto (Vespertilionidae) ocuparon las cuevas más frías y el más amplio intervalo de temperatura (1.6–29.8°C), mientras que los homeotemnos (Emballonuridae, Mormoopidae, Phyllostomidae, y Natalidae) ocuparon refugios más cálidos (14.5–37.5°C). Dentro de este grupo, los homeotemnos más precisos (temperatura corporal más estable) ocuparon sitios con temperaturas ligeramente más bajas que los homeotemnos menos eficientes (temperatura corporal más variable). El tamaño corporal por sí solo no definió patrones claros de uso de cuevas, pero cuando analizamos por separado homeotemnos y heterotemnos encontramos una relación negativa entre tamaño corporal y temperatura del refugio. Las especies insectívoras más pequeñas (<10 g) ocuparon...
consistentemente refugios >20°C (generalmente >25°C); sólo los insectívoros homeotermos más grandes fueron observados a 16°C. Los frugívoros, nectarívoros, y hematofágos fueron observados en un amplio intervalo de temperatura (14.5–37°C), frecuentemente <20°C. La humedad de los refugios fue altamente variable para la mayoría de las especies, y no se observó ninguna tendencia respecto a este factor. La capacidad termorregulatoria (resultante de la compleja interacción de tamaño corporal, tipo de alimento y afinidad taxonómica) parece limitar el tipo de refugios que cada especie puede explotar. Nuestros resultados apoyan la hipótesis de que la temperatura es el factor físico más importante para los murciélagos en la selección de refugios.

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LITERATURE CITED


Associate Editor was Thomas J. O’Shea.

APPENDIX I

Geographical, physical and ecological values for 18 caves examined in this study. All caves are in central Mexico, in the states of Mexico and Puebla. Data for each cave include (in the following order) name, location (includes township or municipio), coordinates, altitude, physiographic region, surrounding vegetation, type of rock, total length (all tunnels), annual mean temperature, and annual mean humidity. Caves are numbered 1 to 18.

Caves examined: 1), 2), and 3) Cavernas I, Cavernas II, and Cavernas III (entrances located within a radius of 300 m). 1. km NE Presa de Ituribde, townshio of Isidro Fabela, Estado de Mexico; 19°33'02"N, 99°28’11"W, 3,480 m; Transversal Volcanic Belt; coniferous forest; sandstone; 41 m, 44 m, 30 m, respectively; 8.3 ± 1.1°C, 5.9 ± 2.3°C, 8.0 ± 0.9°C, respectively; 87.2 ± 8.5%, 65.6 ± 14.8%, 88.6 ± 7.2%, respectively. 4) El Charro. 0.2 km E Zapotitlán de Méndez, township of Zapotitlán de Méndez, Puebla; 20°00'00"N, 97°42'26"W, 670 m; Sierra Madre Oriental; subtropical cloud forest; limestone; 30 m; 21.0 ± 4.5°C; 93.8 ± 9.7%. 5) El Jardín. Rancho El Jardín, 4 km NW Huehuetlán El Chico, township of Huehuetlán El Chico, Puebla; 18°23'52"N, 98°43’10"W, 850 m; Balsas River Basin; tropical deciduous forest; conglomerate; 14 m; 26.4 ± 3.0°C; 56.1 ± 21.5%. 6) Huitulapan. 7 km W Rio Frio, township of Istapalulca, Estado de Mexico; 19°21’35"N, 98°44’36"W, 3,385 m; Transversal Volcanic Belt; coniferous forests; sandstone; 76 m; 7.7 ± 1.8°C; 91.5 ± 8.3%. 7) Karmida. 0.3 km N Zapotitlán de Méndez, township of Zapotitlán de Méndez, Puebla; 20°00'19"N, 97°42’53"W, 670 m; Sierra Madre Oriental; subtropical cloud forest; sludge stone and limestone; 67 m; 21.9 ± 1.3°C; 95.3 ± 6.0%. 8) La Ahorcada. 1.5 km E Coxcatlán, township of Coxcatlán, Puebla; 18°16’29"N, 97°08’35"W, 1,400 m; Tehuacan Valley; xerophytic scrub; sandstone; 25 m; 26.4 ± 2.3°C; 48.1 ± 13.9%. 9) La Garita. Rancho La Garita, 5 km NW Hueytamalco, township of Hueytamalco, Puebla; 19°57’58"N, 97°19’01"W, 700 m; Sierra Madre Oriental; subtropical cloud forest; sandstone and limestone; 500 m; 19.8 ± 0.8°C; 98.7 ± 3.0%. 10) La Organera. 4 km SE Zapotitlán Salinas, township of Zapotitlán Salinas, Puebla; 18°18’45"N, 97°25’58"W, 1,400 m; Tehuacan Valley; xerophytic scrub; sandstone and metamorphic; 15 m; 21.5 ± 2.4°C; 59.6 ± 13.0%. 11) Las Vegas. 2.5 km S Tenamulco, township of Tenamulco, Puebla; 20’08’54"N, 97°24’39"W, 183 m; Gulf Coastal Plain; tropical evergreen forest; sandstone; 254 m; 21.6 ± 2.5°C; 98.5 ± 3.8%. 12) Lencho Diego I. 1.25 km NW San José Tilapa, township of Coxcatlán, Puebla; 18°10’49"N, 97°07’10"W, 1,200 m; Tehuacan Valley; xerophytic scrub; sandstone and mica; 14 m; 26.3 ± 2.1°C; 48.0 ± 19.9%. 13) Lencho Diego II. 2.7 km NW San José Tilapa, township of Coxcatlán, Puebla; 18°10’42"N, 97°07’04"W, 1,250 m; Tehuacan Valley; xerophytic scrub; sandstone and mica; 35 m; 27.9 ± 1.7°C; 47.5 ± 14.3%. 14) Piedra Encampanada. Rancho El Terrero, 4.5 km NW Huehuetlán El
Chico, township of Huehuetlán El Chico, Puebla; 18°23′31″N, 98°43′38″W, 850 m; Balsas River Basin; tropical deciduous forest; conglomerate; 8 m; 29.9 ± 1.7°C; 69.4 ± 17.4%. 15) San Gabriel. 4.5 km ESE Zapotitlán Salinas, township of Zapotitlán Salinas, Puebla; 18°19′31″N, 97°25′02″W, 1,400 m; Tehuacán Valley; xerophitic scrub; conglomerate; 9.5 m; 25.8 ± 3.7°C; 47.0 ± 20.5%. 16, 17) San Lorenzo I and San Lorenzo II (entrances located within the same large hollow). 1.5 km WNW San Lorenzo, township of Tehuacán, Puebla; 18°27′51″N, 97°26′52″W, 1,740 m; Tehuacán Valley; xerophitic scrub; sandstone; 150 m, 100 m, respectively; 13.2 ± 2.7°C, 17.6 ± 1.6°C, respectively; 79.7 ± 10.8%, 86.0 ± 8.1%, respectively. 18) Tzinacanostoc. 1 km NW Jolalpan, township of Jolalpan, Puebla; 18°19′57″N, 98°53′17″W, 1,037 m; Balsas River Basin; tropical deciduous forest; sandstone; 220 m; 33.2 ± 2.3°C; 60.3 ± 12.8%.